Enrichment in a Producer-Consumer Model with varying rates of Stoichiometric Elimination

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Respectfully submitted by

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Abstract

Producer-consumer (predator-prey) systems have been studied for many years. Stoichiometry has more recently been included in systems to track food quality and quantity. In this work, we assume the food quality is determined by the presence of a nutrient. A certain target (stoichiometric) ratio of nutrient to carbon is necessary for the creation of consumer biomass. Whichever is in excess is eliminated. The model is based on Zimmermann's stoichiometric elimination model[7]. We generalize her model and investigate the dynamics for different parameter values, and bifurcations that arise as parameters are varied. We are especially interested in varying two parameters which can be considered carbon and nutrient enrichment parameters. We also vary the rate of elimination. As this rate approaches infinity, the system can be reduced to a lower dimensional model. We compare the original model to the reduced model Different types of behavior observed include no-life equilibrium, monoculture equilibrium, coexistence equilibrium, periodic coexistence and bistability between periodic equilibrium and periodic coexistence.

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1 Introduction

Mathematical population models follow the size of interacting populations over time. A variety of producer-consumer models has been developed and studied. Recently, stoichiometry, which tracks food quality as well as quantity, has been widely introduced into producer-consumer models (Loladze, Kuang, and Elser 2000 [4], Kuang, Huisman, and Elser 2004 [3], Laura J. Zimmerman 2006[7]).

We start with a producer-consumer model (RM) which is modeled with a variation of the Lotka-Volterra equations (Rosenzweig and MacArthur 1963[6]):

$$\frac{dx}{dt} = rx - bx^2 - f(x)y$$

$$\frac{dy}{dt} = ef(x)y - dy$$

Variables *x* and *y* represent the population of producer and consumer, respectively; *r* is the producer birth rate and *b* is the self limitation coefficient of the producer. Parameter *e* is the consumption efficiency as consumer cannot convert everything from producer to itself, and *d* is the death rate of consumer. Here *f(x)* is the monotonically increasing predation function as the consumer obtains or harvests more food when the population of producer is larger. The RM model has three equilibria: one is in a no life stage, the second is a producer monoculture and the third one is a producer and consumer coexistence.

The RM model also has three bifurcations as the growth rate *r* is increased. The first one is a transcritical bifurcation where the stable equilibrium goes from no-life equilibrium to producer monoculture equilibrium. The second bifurcation is another transcritical bifurcation where the stable equilibrium changes from producer monoculture to producer and consumer coexistence. The last one is a *Hopf* bifurcation where the coexistence equilibrium becomes unstable and a stable limit cycle is born.

In the present model, we keep track of food quantity through carbon and food quality through nutrient, which is typically nitrogen for terrestrial systems and phosphorous for aquatic systems. Following Zimmermann [7] [8], we add a sediment class and nutrient input and exports. This leads to an open model with six variables: P,p,C,c,S,s, which represent densities of carbon of producer, phosphorus of producer, carbon of consumer, phosphorus of consumer, carbon in sediment and phosphorus in sediment. We introduce stoichiometric effect by requiring that the consumer needs a fixed ratio of nutrient to carbon to create biomass. Whichever is in excess is then eliminated. There are many parameters in the model. The model separates into two basic cases: one is high nutrient where the evolution of the producer and consumer are the same as in the RM model, while low nutrient reduces the production rate of consumer biomass. Compared to the Zimmermann study, we have simplified the model by eliminating only excess carbon or nutrient in the consumer rather than eliminating excesses in both the producer and consumer. More generally, we allow different conversion efficiency rates for the carbon and the nutrient. We also perform a more detailed bifurcation analysis, with corresponding time series. The results are significantly different from the RM model because of the introduction of stoichiometric elimination.

Although the same types of bifurcations as for the RM[6] model have been observed (two transcritical bifurcations and a Hopf bifurcation), the stoichiometric model also has a saddle node of limit cycles. When nutrient input levels are low, the stoichiometric elimination model behavior will be significantly different from the nonstoichiometric one.

Through numerical and analytic methods, we compute different equilibrium states for the model: no-life, producer monoculture and coexistence of the producer with the consumer. The result is close to Zimmerman's work but provides more detail by identifying regions of high/low consumer stoichiometry, and high/med/low producer stoichiometry.

The rest of the paper is organized as follows. In section 2, we introduce some terminology of dynamical systems. Section 3 is the development of consumer-producer model. The models with/without stoichiometric elimination are discussed in section 4, and we present our 4D model in section 5. Section 6 is a discussion on the model implications for ecology. Summary, model limitations and future work are in sections 7 and 8

.

2 Dynamical Systems Terminology

The following standard dynamical systems terms will be used throughout this paper [2]. Our dynamical systems model is in the form of an n-dimensional autonomous system of differential equations: $\dot{x} = f(x)$. An *equilibrium point*, p, is a point in state space where all derivative functions in the system simultaneously equal 0; that is $f(x) = 0$. As the rate of change of compartments all equals 0, any solution which starts at an equilibrium point will stay there. Equilibrium points can be classified as stable or unstable. Nearby solution are attracted to stable equilibrium while nearby solutions are mostly repelled from an unstable equilibrium point. The stability of equilibrium point is determined by the signs of the real part of eigenvalues of the linearization of the equations through evaluating Jacobian matrix at each of equilibrium points of the system. When the real parts of all the eigenvalues are negative the equilibrium point is stable and the equilibrium point is unstable if the real part of at least one eigenvalues is positive,

A bifurcation is a qualitative change in the dynamical system when the system parameters are varied, and here we locate and describe 4 different kinds of bifurcations.

A *transcritical bifurcation* occurs when two different equilibrium points come together at a bifurcation point and exchange the stability when they pass through each other. The location of possible transcritical bifurcation can be determined where an eigenvalue of the Jacobian matrix evaluated at equilibrium equals 0.

A *Hopf bifurcation* occurs when a fixed point of a dynamical system loses stability as a pair of complex conjugate eigenvalues of the linearization around the equilibrium point crosses the imaginary axis of the complex plane. *A supercritical Hopf bifurcation* occurs when a stable spiral changes to an unstable spiral surrounded by limit cycle. That means before the Hopf bifurcation solutions spiral into the equilibrium. After Hopf bifurcation, solutions near the equilibrium points spiral out to the limit cycle and solutions starting outside the limit cycle spiral in toward the limit cycle.

A *subcritical 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, solutions inside the unstable limit cycle spiral in toward the equilibrium point. After the subcritical Hopf bifurcation, all local solutions are repelled away from the unstable equilibrium point.

The location of potential Hopf bifurcation points can be found by determining where the real part of a pair of complex eigenvalues of the Jacobian matrix evaluated at the equilibrium point equals zero.

A *saddle-node* bifurcation of equilibrium points occurs when a pair of equilibrium points is destroyed or created. As a parameter is varied, two equilibrium points move toward each other, collide and annihilate each other. At bifurcation, there is a single equilibrium with a zero eigenvalue.

A Saddle node of limit cycles occurs when a pair of limit cycles is destroyed (or created). As a parameter is varied, two limit cycles move toward each other, collide, and annihilate each other.

3 Model Development

We start from a slightly generalized version of Zimmermann's stoichiometric elimination model[8]. That model starts with logistic growth of the producer and a Holling-type-II predation function. It introduces stoichiometric effects by assuming consumer biomass production requires a fixed ratio of nutrient to carbon. Whenever this ratio varies from the target ratio, whichever is in excess is eliminated.

More specifically, following Zimmermann we include the effect of food quality, by making the following stoichiometric assumptions. We intend that consumers tend toward a fixed nutrient to carbon ratio, θ_c, and producers tend toward a range of possible nutrient to carbon ratios, $\theta_3 < p{:}P < \theta_4$.

If consumers have $c{:}C > \theta_c$, they eliminate excess nutrient. If consumers have $c{:}C < \theta_c$, they eliminate excess carbon. The rate of elimination is proportional to the distance from the current ratio to the optimal ratio. The proportionality constant is a parameter we vary in this study.

If producers have $p{:}P > \theta_4$, they eliminate only nutrient at a rate proportional to the distance from the current ratio to θ_4. If producers have $p{:}P < \theta_3$, they eliminate only carbon at a rate proportional to the distance from the current ratio to θ_3. In between θ_3 and θ_4, they neither eliminate carbon nor nutrient. In this study, we keep track of the stoichiometry of the producer, but we simplify the model behavior because producers do not eliminate either excess carbon or nutrient. Equivalently, we set the elimination rates for the producer to zero.

These assumptions give six possible cases:

1. High nutrient consumer, mid nutrient producer $\frac{c}{C} > \theta_c$ and $\theta_3 < \frac{p}{P} < \theta_4$
2. High nutrient consumer, low nutrient producer $\frac{c}{C} > \theta_c$ and $\frac{p}{P} < \theta_3$

3. High nutrient consumer, high nutrient producer $\frac{c}{C} > \theta_c$ and $\frac{p}{P} > \theta_4$
4. Low nutrient consumer, mid nutrient producer $\frac{c}{C} \leq \theta_c$ and $\theta_3 \leq \frac{p}{P} \leq \theta_4$
5. Low nutrient consumer, high nutrient producer $\frac{c}{C} \leq \theta_c$ and $\frac{p}{P} > \theta_3$
6. Low nutrient consumer, high nutrient producer $\frac{c}{C} \leq \theta_c$ and $\frac{p}{P} \geq \theta_4$

For the parameter sets we considered, we only observed cases 1,3,4,6.

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

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

The full 6D model is given here:

$$\frac{dP}{dt} = bP - lP^2 - \frac{mP}{h+P} \cdot C - d_P P - m_1 (P - \frac{p}{\theta_3})^+$$

$$\frac{dp}{dt} = \mu Ps - d_P p - \frac{p}{P} \cdot \frac{mP}{h+P} C - m_3 (p - \theta_4 P)^+$$

$$\frac{dC}{dt} = e_c \cdot \frac{mP}{h+P} \cdot C - d_e C - d_C C - m_2 (C - \frac{c}{\theta_c})^+$$

$$\frac{dc}{dt} = e_n \cdot \frac{mP}{h+P} \cdot C \frac{p}{P} - d_e c - d_C c - m_4 (c - \theta_c C)^+$$

$$\frac{dS}{dt} = d_P P + d_C C - d_s S + (1 - e_c) \cdot \frac{mP}{h+P} \cdot C + m_1 (P - \frac{p}{\theta_3})^+ + m_2 (C - \frac{c}{\theta_c})^+$$

$$\frac{ds}{dt} = d_C c + d_P p + IN - d_s s - \mu Ps + (1 - e_n) C \cdot \frac{p}{P} \cdot \frac{mP}{h+P} + m_3 (p - \theta_4 P)^+ + m_4 (c - \theta_c C)^+$$

where

Phase variables are:

P =density of carbon of producer in environment

p =density of nutrient of producer in environment

C =density of carbon of consumer in environment

c =density of nutrient of producer in environment

S= density of carbon in sediment

s= density of nutrient in sediment

Parameters:

b = growth rate coefficient of the producer without self limitation

l = coefficient of self limitation of the producer

m = the consumer's maximum ingestion rate

$h =$ the consumer's ingestion rate half saturation constant

d_P= coefficient of the producer death rate

e_c= maximum consumer carbon consumption efficiency

e_n= maximum consumer nutrient consumption efficient

d_e= coefficient of consumer export rate

d_C= coefficient of consumer death rate

d_s= coefficient sediment export rate

μ = producer nutrient uptake rate

IN= nutrient input rate

$\theta_c = \text{target c: C in consumer}$

$\theta_3 = \text{minimum target p: P in producer}$

$\theta_4 = \text{maximum target p: P in producer}$

$m_1 = \text{producer carbon elimination rate when p: P is less than } \theta_3$

$m_2 = \text{consumer carbon elemination rate when c: C is less than } \theta_c$

$m_3 = \text{producer carbon elimination rate when p: P is less than } \theta_4$

$m_4 = \text{consumer carbon elemination rate when c: C is greater than } \theta_c$

Terms:

$bp - lp^2$ is the logistic growth rate of the producer on its own

$\frac{mP}{h+P} \cdot C$ is the rate of carbon taken from producer by the consumer

$d_P p$ is the death rate for the producer

$e_c \cdot \frac{mP}{h+P} \cdot C$ is the rate that the consumer ingests food from the producer

$d_e C$ is the export rate of the consumer

$d_C C$ is the death rate for the consumer

$d_s S$ is the export rate of the sediment

μPs is the uptake rate of nutrient from the sediment by the producer

$d_P p$ is the rate of nutrient going into the sediment due to the death of the producer

$\frac{p}{P} \cdot \frac{mP}{h+P} \cdot C$ is the rate of nutrient taken from the producer by the consumer

$e_n \cdot \frac{mP}{h+P} \cdot C \frac{p}{p}$ is the rate of nutrient ingested by the consumer from the producer

$d_e c$ is the export rate of consumer nutrient

$d_C c$ is the rate of nutrient going to the sediment due to consumer death

$d_s s$ is the rate of sediment nutrient leaving the system

$(1 - e_c) \cdot \frac{mP}{h+P} \cdot C$ is the rate at which carbon is taken up by the consumer but not ingested

$(1 - e_n) \cdot \frac{mP}{h+P} \cdot C \frac{p}{P}$ is the rate at which nutrient is taken up by the consumer but not ingested

$\frac{m_1}{\theta_3}(\theta_3 P - p)^+$ is the elimination rate of excess producer carbon when p: P is too low

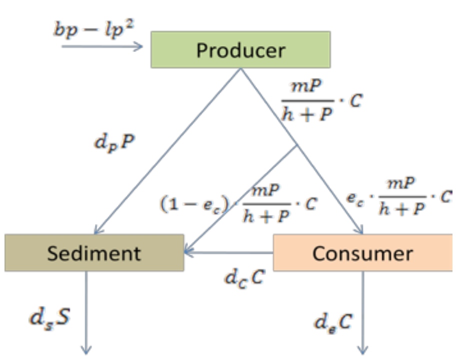
$\frac{m_2}{\theta_c}(\theta_c C - c)^+$ is the elimination rate of excess consumer carbon when c: C is too low

$m_3(p - \theta_4 P)^+$ is the elimination rate of excess producer nutrient when p: P is too high

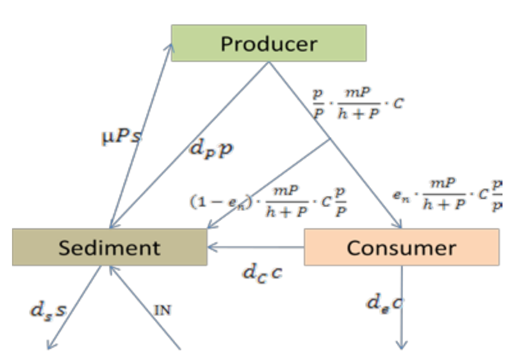
$m_4(c - \theta_c C)^+$ is the elimination rate of excess producer carbon when c: C is too high

Producer and Consumer carbon & nutrient Flow

Carbon flow



Nutrient flow



4 Analysis of Model

4.1 The model without Stoichiometric Elimination

We start our model analysis from Zimmermann's stoichiometric elimination model[7]. The model without stoichiometric elimination is:

$$\frac{dP}{dt} = bP - lP^2 - \frac{mP}{h+P} \cdot C - d_P P$$

$$\frac{dp}{dt} = \mu Ps - d_P p - \frac{p}{P} \cdot \frac{mP}{h+P} \cdot C$$

$$\frac{dC}{dt} = e_c \cdot \frac{mP}{h+P} \cdot C - d_e C - d_C C$$

$$\frac{dc}{dt} = e_n \cdot \frac{mP}{h+P} \cdot C \frac{p}{P} - d_e c - d_C c$$

$$\frac{dS}{dt} = d_P P + d_C C - d_s S + (1 - e_c) \cdot \frac{mP}{h+P} \cdot C$$

$$\frac{ds}{dt} = d_C c + d_P p + IN - d_s s - \mu Ps + (1 - e_n) \cdot \frac{mP}{h+P} \cdot C \cdot \frac{p}{P}$$

Equilibrium Analysis:

Through setting $\frac{dP}{dt} = \frac{dC}{dt} = \frac{dc}{dt} = \frac{dp}{dt} = \frac{ds}{dt} = 0$, we can find the system equilibria. There are three types which we describe below. We used *Mathematica* for some of the computations.

No life equilibrium:

The no-life equilibrium is

$$(P,\ p,\ C,\ c,\ S,\ s) = \left(0,\ 0,\ 0,\ 0,\ 0,\ \frac{IN}{d_s}\right)$$

Monoculture equilibrium:

When C=0, P $\neq$ 0, the solution under monoculture situation is:

$$(P,\ p,\ C,\ c,\ S,\ s) = (\frac{b-d_P}{l},\ \frac{\mu(b-d_P)s}{ld_P},\ 0,\ 0,\ \frac{d_P(b-d_P)}{ld_s},\ \frac{IN}{d_s})$$

Coexistence equilibrium:

When $P \neq 0$ and $C \neq 0$

The coexistence solution with explicit form (with the help of *Mathematica*) of parameters is:

$$P:\ \frac{(d_e+d_C)h}{e_c m - d_C - d_e}$$

$$p:\ \frac{hIN\mu(d_C+d_e)(d_C+d_r-me_c)}{-(b+hl)d_C^2 d_s - bm^2 d_s e_c^2 - d_e^2((b+hl)d_s - h\mu(b+hl-d_p)e_n) + md_e e_c((2b+hl)d_s + h\mu(-b+d_p)e_n) + d_C((2b+hl)md_s e_c + d_r(-2(b+hl)d_s + h\mu(b+hl-d_p)e_n))}$$

$$C: (e_c h)\cdot\frac{(d_P-b)(d_e+d_C-e_c m) - hl(d_e+d_C)}{(d_e+d_C-e_c m)^2}$$

$$c:\ \frac{hIN\mu\left(d_C\left(b+hl-d_p\right) + @\left(b+hl-d_p\right)d_e + m\left(-b+d_p\right)e_c\right)e_n}{-(b+hl)d_C^2 d_s - bm^2 d_s e_c^2 - d_e^2\left((b+hl)d_s - h\mu\left(b+hl-d_p\right)e_n\right) + md_e e_c\left((2b+hl)d_s + h\mu\left(-b+d_p\right)e_n\right) + d_C\left((2b+hl)md_s e_c + d_e\left(-2(b+hl)d_s + h\mu\left(b+hl-d_p\right)e_n\right)\right)}$$

$$S:\ -\frac{h\left((b+hl)d_C^2 + d_e\left(me_c\left(-b+\left(b-d_p\right)e_c\right) + d_e\left(b+hl-\left(b+hl-d_p\right)e_c\right)\right) - d_C\left(bme_c + d_r\left(-2(b+hl) + \left(b+hl-d_p\right)e_c\right)\right)\right)}{d_s(d_C+d_e-me_c)^2}$$

$$s:\ \frac{IN(d_C+d_e-me_c)\left((b+hl)d_C + (b+hl)d_e - bme_c\right)}{(b+hl)d_C^2 d_s + bm^2 d_s e_c^2 + d_e^2\left((b+hl)d_s - h\mu\left(b+hl-d_p\right)e_n\right) - md_e e_c\left((2b+hl)d_s + h\mu\left(-b+d_p\right)e_n\right) + d_C\left(-(2b+hl)md_s e_c + d_e\left(2(b+hl)d_s - h\mu\left(b+hl-d_p\right)e_n\right)\right)}$$

Bifurcation analysis:

Based on above analysis, there is a transcritical bifurcation from the no life to the monoculture equilibrium at b=d_P.

When $0 < b < d_P$, there is no life: $P = C = 0$.

There is a second transcritical bifurcation – at $b = d_P + \frac{hl(d_e+d_C)}{e_c m - d_e - d_C}$ (Determined by setting C equals 0 in the coexistence solution and solving for b.

When $d_P < b < d_P + \frac{hl(d_e+d_C)}{e_c m - d_e - d_C}$, the producer monoculture is stable:

$P = \frac{b-d_P}{l}$ and $C = 0$

When $b > d_P + \frac{hl(d_e+d_C)}{e_c m - d_e - d_C}$, the coexistence equilibrium becomes stable:

$$P = \frac{(d_e+d_C)h}{e_c m - d_C - d_e}$$

$$C = e_c h \cdot \frac{(d_P - b)(d_e + d_C - e_c m) - hl(d_e + d_C)}{(d_e + d_C - e_c m)^2}$$

Coexistence persists until a Hopf bifurcation causes the birth of periodic orbit.

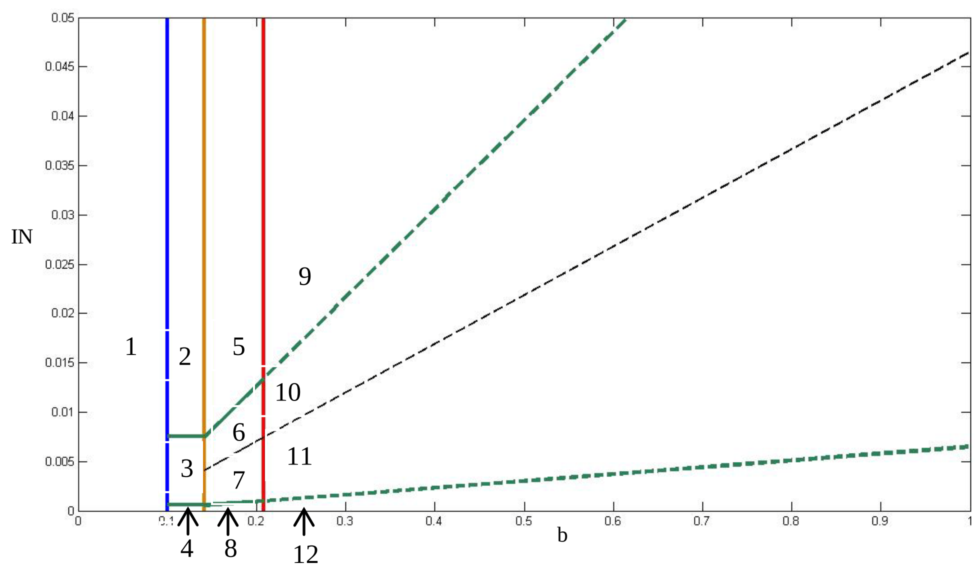
The Hopf bifurcation is located at:

$$b = d_P + \frac{hld_C}{me_c - d_C - d_e} + \frac{hld_s}{me_c - d_C - d_e} + \frac{hlm(d_C + 2d_e - d_s)e_c}{(d_C + d_e)(me_c - d_C - d_e)}$$

Numerical Results

As in the Zimmermann stoichiometric elimination model, the numerical values of parameters we set are $l = 0.05, d_P = 0.1, e_c = 0.8, e_n = 0.9, m = 0.5, h = 0.5, d_e = 0.1, d_C = 0.15, d_s = 0.3, \mu = 0.2, m_1 = m_2 = m_3 = m_4 = 1, \theta_c = 0.031, \theta_3 = 0.0038, \theta_4 = 0.05$

IN vs b Bifurcation Diagrams



Description:

The above picture is the IN vs b plane when $m_2=m_4=10$. There are three vertical lines, the blue one (b=0.1) is the first transcritical bifurcation, the dividing line between no-life and monoculture. It means when crossing this line, some producer starts to exist in this system but not the consumer. The second vertical line (b=0.14167, yellow) is also a transcritical bifurcation and is the dividing line between monoculture and producer-consumer coexistence. It means when crossing that line, consumer and producer can coexist in the system and solutions approach the coexistence equilibrium. The last vertical line (b=0.2083, red) is the Hopf bifurcation. It's the cutoff line between equilibrium coexistence and periodic coexistence. The population of the producer and consumer oscillate in a stable limit cycle instead of converging to an attracting equilibrium after crossing the third vertical line.

In the monoculture area the two horizontal lines separate the regions of high to medium and medium to low levels of producer's stoichiometry. On the upper horizontal line p:P equals 0.05, on the lower horizontal line p:P equals 0.0038. That means the points in the area above the top horizontal line correspond to high nutrient . for producer defined by p:P > 0.05. The points in the area between two lines correspond to medium nutrient levels for the producer defined by 0.05 > p:P > 0.0038. The points of bottom area correspond to low nutrient levels defined by p:P < 0.0038.

In the coexistence regions, there are three upward sloping lines. The upper and lower lines separate high-medium producer stoichiometry and medium-low producer stoichiometry (p:P = 0.05 & p:P = 0.0038), while the middle line represents consumer stoichiometry exactly at its target ratio (c:C=0.031). The points above this line have high nutrient levels for the consumer, below are low consumer nutrient levels. The reason the latter parts of these lines are dashed is because they represent classification of stoichiometry at equilibrium, but in the periodic regions, the orbits are not at equilibrium; the stoichiometry of P and C can cross the stoichiometric classification boundaries. So the corresponding p:P and c:C sometimes crosses dividing lines and sometimes not. More detail will be in the time series analysis.

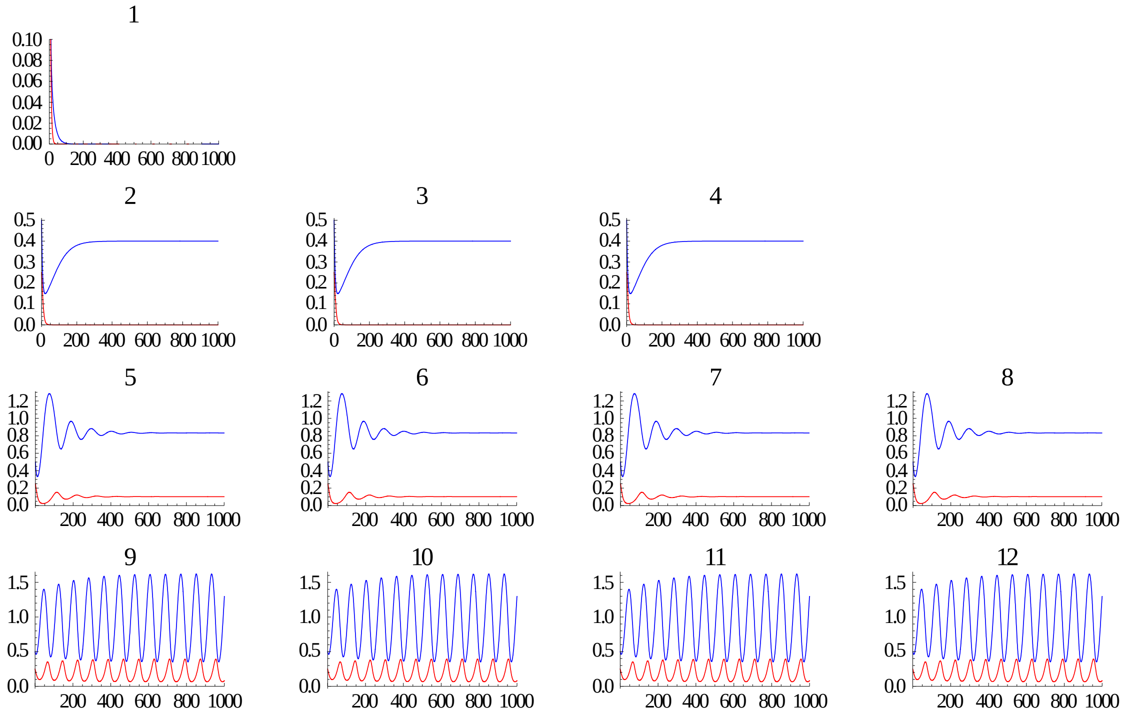
The software used here is *Mathematica*: Following the above calculation, we know first transcritical bifurcation is located at b=0.1. The second transcritical and Hopf bifurcations are at b=0.14167 and b=0.2083. For high and low producer nutrient ratio dividing lines, we set p:P=0.05 and p:P=0.0038 and used *Mathematica* to get the function of p:P=0.05 and p:P=0.0038 in the form of b versus IN. For consumer carbon ratio dividing line, we use same method to set c:C=0.031 and use *Mathematica* to get the solution in the form of IN as a function of b.

Time series analysis

According to different nutrient levels and bifurcations, the IN vs b bifurcation diagram is divided into different regions. We pick one representative point from each region to perform time series analysis.

Producer and Consumer

The first set of time series is for producer and consumer carbon in each region. Blue represents the population of the producer and red the population of the consumer. Point 1 is picked in the no life region, so both producer and consumer die out. Points 2, 3 and 4 are in monoculture areas with different nutrient levels, so the consumer of these points still dies out. Points 5, 6, 7 and 8 are in the stable coexistence equilibrium area, where both producer and consumer stably persist. We can observe that both producer and consumer approach stable equilibrium with time increasing. The last four points 9, 10, 11 and 12 are in the periodic coexistence area. These points have periodic solutions so the population of producer and consumer oscillate and never converge to equilibrium.

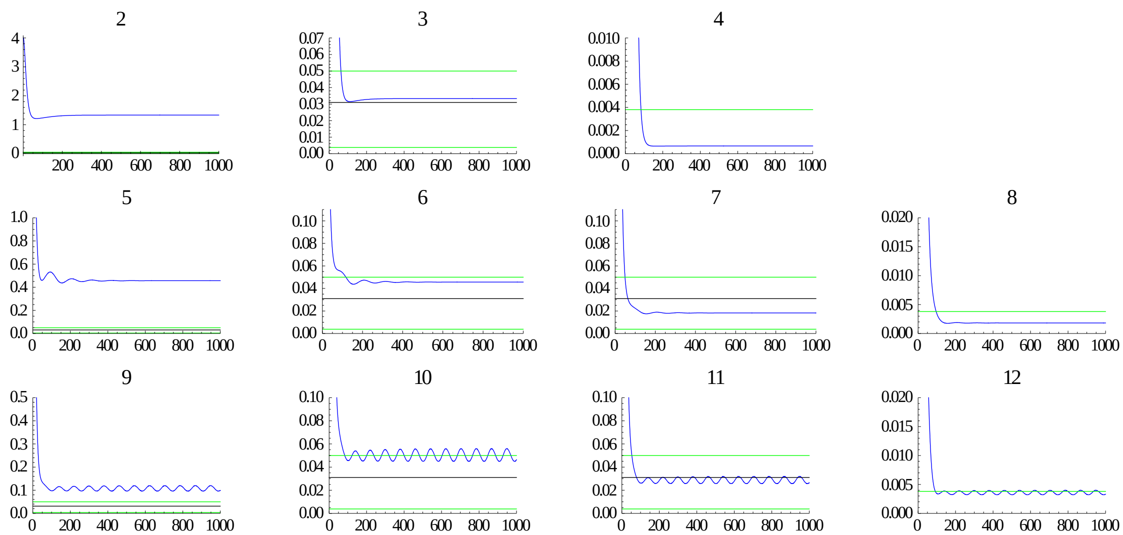


Producer Stoichiometry

The second set of time series is for producer stoichiometry: the blue curve stands for the ratio of p:P. The corresponding parameter values chosen are the same as those used for the first set of time series above. It starts from point 2 as there is no life at point 1 so p and P are both 0. The horizontal green lines stand for high nutrient to carbon standard for producer (p:P=0.05) and low nutrient to carbon standard for producer (p:P=0.0038). The middle black one is for consumer nutrient to carbon ratio (c:C=0.031) and we just add it here for comparison with later bifurcation diagrams.

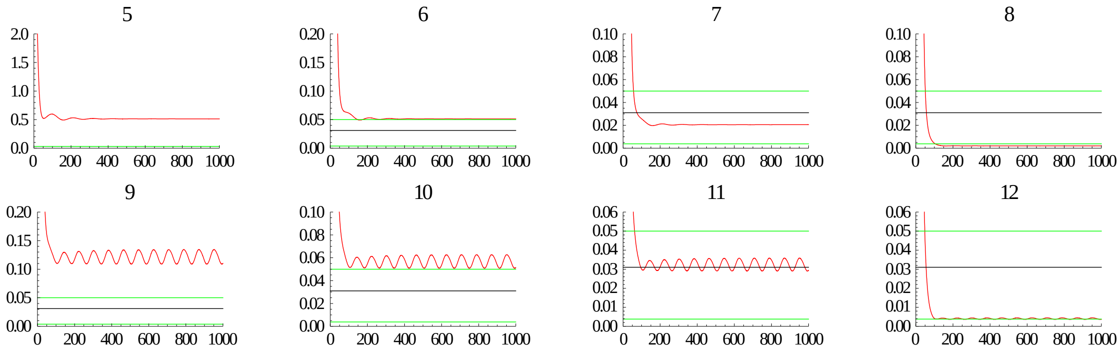
The first three points 2, 3 and 4 are from the monoculture area. 2 is in high nutrient of producer so the blue curve stays above the green line. 3 belongs to medium nutrient level of producer so the blue curve stays between the two green lines which are high standard and low for producer nutrient. 4 is in low level so the blue curve stays below the bottom green level. It also applies for the next four points 5, 6, 7 and 8. 5 is at high nutrient for producer, 6 and 7 for medium and 8 for low.

The last four points 9, 10, 11 and 12 are from the periodic coexistence area. 9 is in high producer nutrient, 10 and 11 are in medium producer nutrient, 12 is low producer nutrient. But as their solutions are periodic points, their producer nutrient to carbon ratio classification does not necessarily stay constant. The blue curve bounces up and down. Some stay in the supposed area like 9 and 11, but some just keep bouncing on the dividing line.



Consumer Stoichiometry

The third set of time series is for evaluating consumer stoichiometry. The red curve is the result of c:C of the points in the first time series analysis. Time series analysis starts from point 5 as in monoculture and no-life c and C equal 0. First 4 points 5, 6, 7, 8 are in stable coexistence stage. Point 5 and 6 are in high consumer nutrient so the red curve stays above the black horizontal line (c:C = 0.031), while 7 and 8 have low consumer nutrient so that red curve stay below black horizontal line. The last 4 points are from periodic points, We can also observe that some cross the dividing line and some do not, which is consistent with the property of periodic points.



4.2 Model with Stoichiometric Elimination

Zimmermann's stoichiometric elimination model is given:

$$\frac{dP}{dt} = bP - lP^2 - \frac{mP}{h+P}\cdot C - d_P P - m_1\left(P - \frac{p}{\theta_3}\right)^+$$

$$\frac{dp}{dt} = \mu P s - d_P p - \frac{p}{P}\cdot\frac{mP}{h+P}\cdot C - m_3(p - \theta_4 P)^+$$

$$\frac{dC}{dt} = e_c\cdot\frac{mP}{h+P}\cdot C - d_e C - d_C C - m_2\left(C - \frac{c}{\theta_c}\right)^+$$

$$\frac{dc}{dt} = e_n\cdot\frac{mP}{h+P}\cdot C\frac{p}{P} - d_e c - d_C c - m_4(c - \theta_c C)^+$$

$$\frac{dS}{dt} = d_P P + d_C C - d_s S + (1-e_c)\cdot\frac{mP}{h+P}\cdot C + m_1\left(P - \frac{p}{\theta_3}\right)^+ + m_2\left(C - \frac{c}{\theta_c}\right)^+$$

$$\frac{ds}{dt} = d_C c + d_P p + IN - d_s s - \mu P s + (1-e_n)\cdot\frac{mP}{h+P}\cdot C\cdot\frac{p}{P} + m_3(p - \theta_4 P)^+ + m_4(c - \theta_c C)^+$$

Equilibria

As in the nonstoichiometric case, there are three types of equilibria: no life, producer monoculture, and coexistence.

No-Life Equilibrium

Through setting $\frac{dP}{dt}=\frac{dC}{dt}=\frac{dc}{dt}=\frac{dp}{dt}=\frac{ds}{dt}=0$, we can find the first equilibrium under no life situation is

$$(P,\ p,\ C,\ c,\ S,\ s)=\left(0,\ 0,\ 0,\ 0,\ 0,\ \frac{IN}{d_s}\right)$$

Monoculture Equilibrium:

Setting $C=c=0$, we have monoculture equilibrium in three cases

Case 1 Low nutrient:

When $p-\theta_3P<0, m_3(p-\theta_4P)^+=0, \frac{m_1}{\theta_3}(\theta_3P-p)^+=\frac{m_1}{\theta_3}(\theta_3P-p)$

The model reduces to

$$\frac{dP}{dt}=bP-lP^2-d_PP-\frac{m_1}{\theta_3}(\theta_3P-p)$$

$$\frac{dp}{dt}=\mu Ps-d_Pp$$

$$\frac{dS}{dt}=d_PP-d_sS+m_1(P-\frac{p}{\theta_3})$$

$$\frac{\mathrm{ds}}{\mathrm{dt}}=\mathrm{d_Pp}+\mathrm{IN}-\mathrm{d_ss}-\mu\mathrm{Ps}$$

Then the monoculture equilibrium when it is under low nutrient situation is:

$$(\mathrm{P},\mathrm{p},\mathrm{S},\mathrm{s})$$

$$=(\frac{\mathrm{b}-\mathrm{d_P}-\mathrm{m_1}+\frac{\mathrm{m_1\mu IN}}{\theta_3\mathrm{d_Pd_s}}}{\mathrm{l}},\ \ \frac{\mu\,\mathrm{IN}\left(\mathrm{m_1\mu IN}+\mathrm{b}\theta_3\mathrm{d_Pd_s}-\mathrm{m}\theta_3\mathrm{d_Pd_s}+\theta_3\mathrm{d_P}^2\mathrm{d_s}\right)}{\mathrm{ld_P}^2\mathrm{d_s}^2\theta_3},$$

$$-\frac{(-\mathrm{INm_1}\mu+\mathrm{m_1}\theta_3\mathrm{d_pd_s}+\theta_3\mathrm{d_p^2d_s})(-\mathrm{INm_1}\mu+(-\mathrm{b}+\mathrm{m_1})\theta_3\mathrm{d_pd_s}+\theta_3\mathrm{d_p^2d_s})}{\mathrm{l}\theta_3{}^2\mathrm{d_p^2d_s^3}},\frac{\mathrm{IN}}{\mathrm{d_s}})$$

$$0<IN<\frac{\theta_3(\mathrm{b}+\mathrm{m_1}-\mathrm{d_p})\mathrm{d_pd_s}}{\mathrm{m_1}\mu}$$

Case 2 High nutrient:

When nutrient is at a high level, means $p-\theta_4P>0, m_3(p-\theta_4P)^+=m_3(p-\theta_4P)$, $\frac{m_1}{\theta_3}(\theta_3P-p)^+=0$

The model reduces to

$$\frac{dP}{dt} = bP - lP^2 - d_P P$$

$$\frac{dp}{dt} = \mu Ps - d_P p - m_3(p - \theta_4 P)$$

$$\frac{dS}{dt} = d_P P - d_s S$$

$$\frac{ds}{dt} = d_P p + IN - d_s s - \mu Ps + m_3(p - \theta_4 P)$$

Then the monoculture equilibrium when nutrient is at a high level is:

$$(P,\ p,\ S,\ s) = (\frac{b-d_P}{l},\ \frac{\left(\mu\frac{IN}{d_S}+m_3\theta_4\right)(b-d_P)}{l(d_P+m_3)}, \frac{(b-d_p)d_p}{ld_s},\ \frac{IN}{d_S}) \quad IN > \frac{d_P d_s \theta_4}{\mu}$$

Case 3 Intermediate nutrient:

When nutrient is at an intermediate level, means $\theta_3 P < p < \theta_4 P$, $m_3(p - \theta_4 P)^+ = \frac{m_1}{\theta_3}(\theta_3 P - p)^+ = 0$

The model will be exactly same as the model without stoichiometric elimination, the monoculture equilibrium is given:

$$(P,\ p,\ S,\ s) = (\frac{b-d_P}{l},\ \frac{\mu(b-d_P)IN}{ld_P\, d_s}, \frac{(b-d_p)d_p}{ld_s}, \frac{IN}{d_s})$$

$$\frac{\theta_3(b + m_1 - d_p)d_p d_s}{m_1\mu} < IN < \frac{d_P d_s \theta_4}{\mu}$$

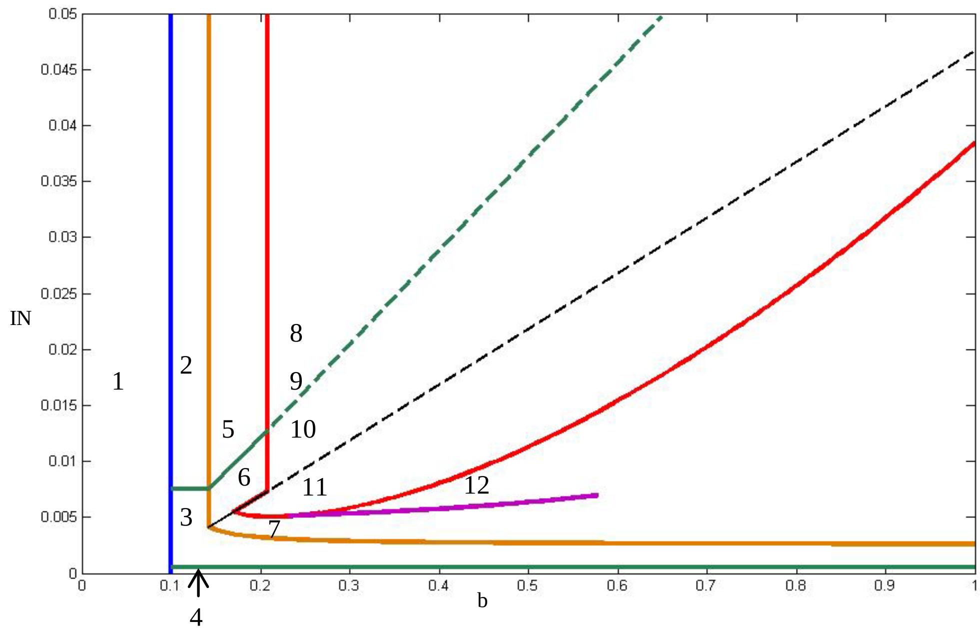
Coexistence Equilibrium:

We have not computed analytical expressions of equilibrim in all 6 cases of the coexistence stage, but the formulas for P and C from section 4.1 apply to cases 1 and 3 from Section 3.

4.3 Bifurcation Diagram and time series analysis

We now compute the bifurcation diagram and perform time series analysis on model with stoichiometric elimination when setting the elimination coefficient $m_2 = m_4 = 10$. For high nutrient, we use the formulas we computed above for the two transcritical bifurcations. Other bifurcation curves are computed with software Auto[1]. We use the same parameter values as above.

IN vs b Bifurcation Diagram (m_2=$m_4 = 10$)



In IN vs b plane (m_2=$m_4 = 10$), the first transcritical bifurcation is the first vertical line (b=0.1) which is same non-stoichiometric model. The second transcritical and Hopf bifurcations, though their upper parts are still vertical lines (b=0.14167 & b=0.2083), but their lower part becomes the curve up to the right. The cut-off line (black) is where the equilibrium value of c:C=0.031. As when c:C > 0.031, $m_2(C - \frac{c}{\theta_c})^+ = 0$, like the non-stoichiometric model, the differential equations for P and C decouple from the rest of the system. When c:C < 0.031, $m_2(C - \frac{c}{\theta_c})^+ > 0$, this new term makes these two bifurcation curves head to the right; it leaves the part near the b axis as part of the monoculture area; that's the reason the bottom line horizontal green line (p:P=0.0038) extends to the right.

An interesting point is the existence of a small curve of saddle-node of limit cycles (purple). It connects to the Hopf curve. The region between these two curves is a bistable area. The points in this area have a special property that trajectories from different initial starting points can either approach a stable equilibrium or a periodic orbit. The lower boundary of the bistable region, a saddle-node of limit cycles, is computed through AUTO[1] software. Due to periodic orbits on which the producer and consumer both pass very close to zero, AUTO[1] continuation failed when *b* was between 0.5 and 0.6. But we expect the curve continues.

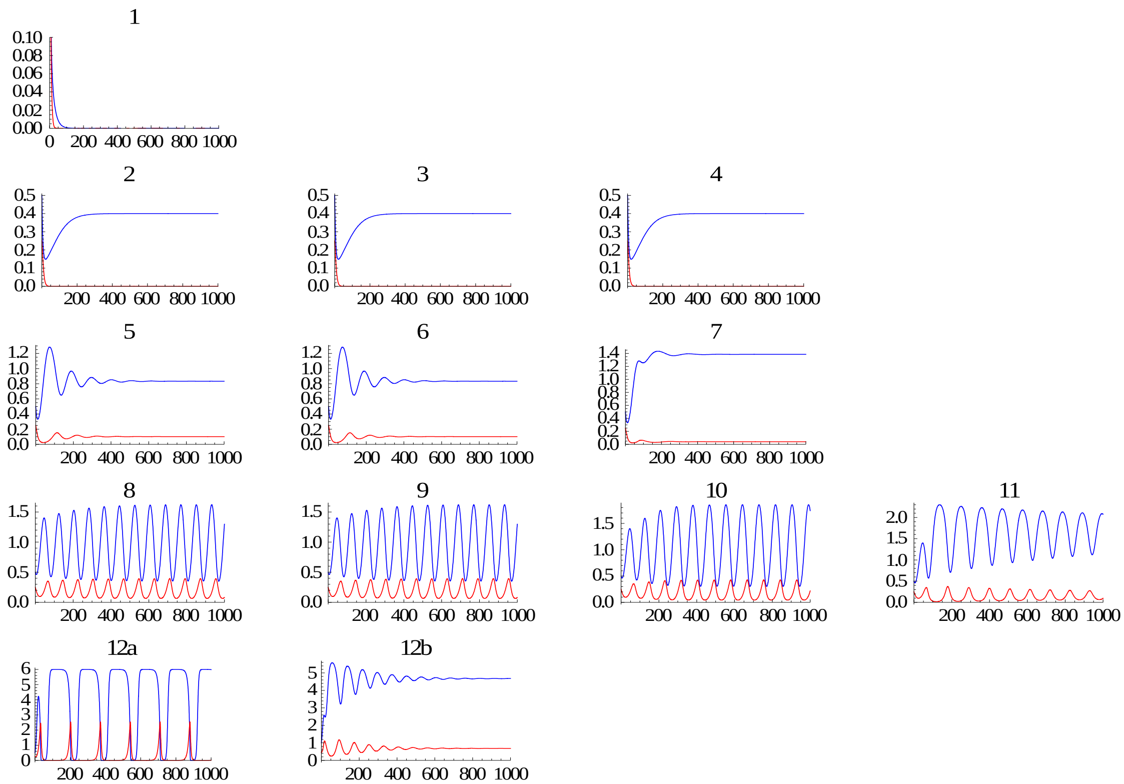
In order to compute the bifurcation diagram, we use AUTO[1] to compute the points on the transcritical, Hopf and saddle-node of limit cycles bifurcations when $c:C < \theta_c$. When $c:C \geq \theta_c$, the model is the same for the carbon terms as the one without stoichiometric elimination whose bifurcation values we already computed above. After we compute the function corresponding to equilibria with $c:C = \theta_c$ in the form of IN as a function of b, which acts as a border line in this diagram, we combine the bifurcation curves we get from software when $c:C < \theta_c$ and the result of the model without stoichiometry when $c:C \geq \theta_c$ to form the whole bifurcation diagram. Note that there is a jump between the two parts of Hopf bifurcation which are connected along the c:C dividing line. This is caused by the nonsmoothness of the system due to the use of the ``positive part'' function.

For the producer nutrient dividing line, we simply set p:P=0.05 and p:P=0.0038 and compute the equilibria through *Mathematica* in the both circumstances of $c:C \geq \theta_c$ and $c:C < \theta_c$. Then the result shows the high producer target stoichiometry level (p:P=0.05) is in the region where $c:C \geq \theta_c$,while the low producer target stoichioimetry level (p:P=0.0038) is in the region where $c:C < \theta_c$.

Time series analysis

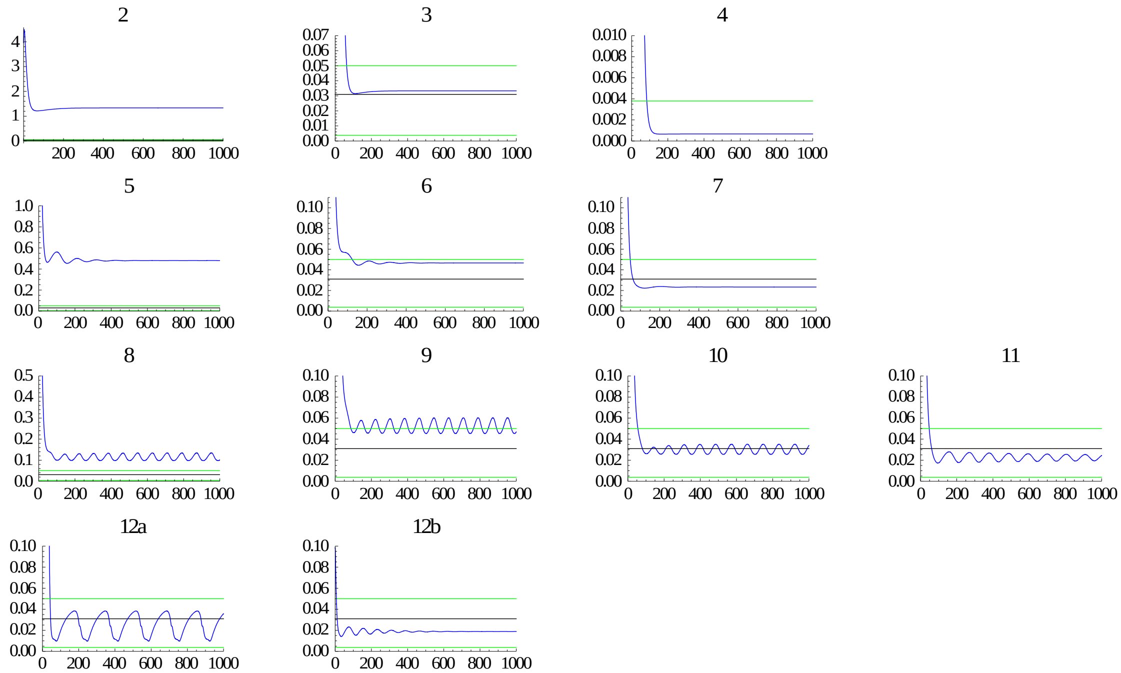
The IN vs b plane ($m_2 = m_4 = 0$) is divided it into different regions by the bifurcation curves and by the stoichiometric classification of the producer & consumer.. We pick one representative point from each region to show the resulting time series.

Producer and Consumer



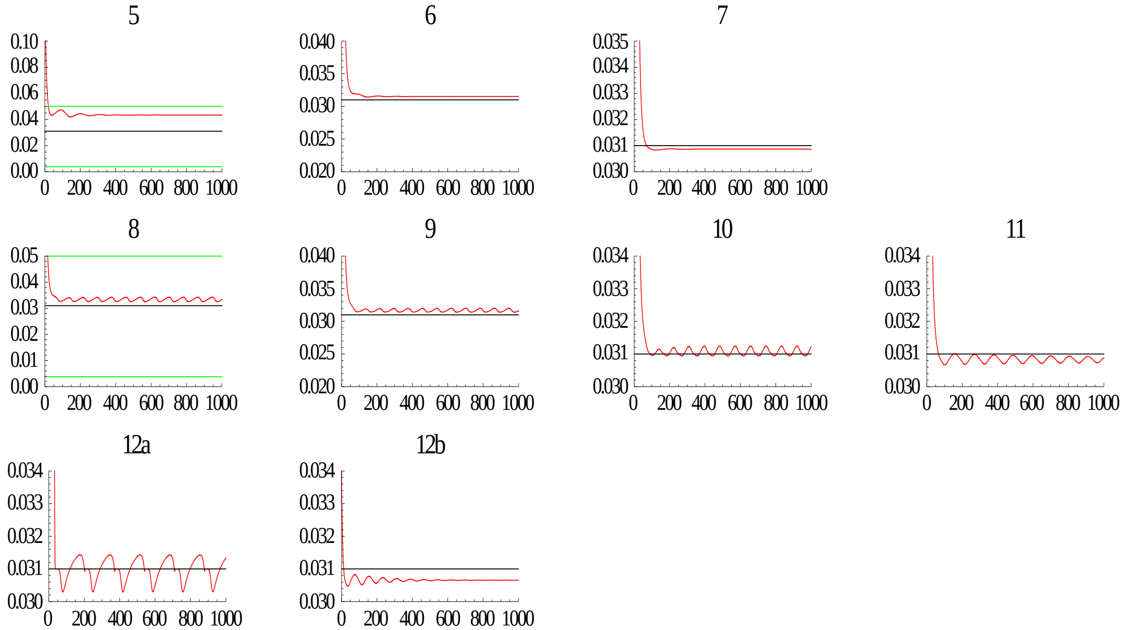
The first set of time series is for producer and consumer in different regions. The first point is from the no-life stage, so both producer (blue) and consumer (red) die out. The points of the second row are from the monoculture stage with different producer nutrient level. Points 5, 6 and 7 are in the stable coexistence equilibrium area while the next four points 8, 9, 10 and 11 are in the periodic coexistence area. The last two sub graphs 12a and 12b actually are time series for the same point 12 in the “bistability” area. We can observe that when changing initial starting point, solutions can either go to stable equilibrium or become periodic. And the amplitude of the oscillation is very high, almost driving the producer and consumer to extinction.

Producer stoichiometry



The second set of time series is for producer stoichiometry. The blue curve stands for p:P of above points. The horizontal green lines stand for p:P=0.05 and p:P=0.0038. And the middle black lines are for c:C=0.031 and we just add it here for reference. We can observe among periodic points, some cross nutrient dividing lines while some do not. 12a and 12b are from point 12 in the bistability area; one as approaches a periodic solution and the other approaches equilibrium.

Consumer stoichiometry



Time series analysis for consumer stoichiometry starts from point 5 as in the monoculture and no-life cases, both c and C equal 0. The next three points 5, 6, 7 are in the stable coexistence stage. The last four points are from the periodic orbit region. Some cross the black reference line and some stay on one side. 12a and 12b are from the same parameter point in the bistability area. One approaches a periodic solution and keeps crossing consumer nutrient dividing line, and the other one stays below the black line.

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5 4-Dimensional Reduction

We now try to reduce the 5-Dimensional system with stoichiometric elimination model to a 4-Dimensional system through letting m_2 and m_4 go to infinity. Recall that, for simplicity, we have set the producer elimination rates, m_1 and m_3, equal to 0.

When m_2 goes to infinity and $c: C \le \theta_c$, $\frac{dC}{dt}$ goes to negative infinity, and the consumers will eliminate extra carbon more and more quickly.

When m_4 goes to infinity and $c: C \ge \theta_c$, $\frac{dc}{dt}$ goes to negative infinity, and the consumers will eliminate extra nutrient more and more quickly..

5.1 Development of the 4-Dimensional Model

We start from 5D system

1. $\frac{dP}{dt} = bP - lP^2 - \frac{mP}{h+P} \cdot C - d_P P$
2. $\frac{dp}{dt} = \mu P s - d_P p - \frac{p}{P} \cdot \frac{mP}{h+P} \cdot C$
3. $\frac{dC}{dt} = e_c \cdot \frac{mP}{h+P} \cdot C - d_e C - d_C C - m_2 (C - \frac{c}{\theta_c})^+$
4. $\frac{dc}{dt} = e_n \cdot \frac{mP}{h+P} \cdot c \frac{p}{P} - d_e c - d_C c - m_4 (c - \theta_c C)^+$
5. $\frac{ds}{dt} = d_2 c + d_P p + IN - d_s s - \mu P s + (1 - e_n) \cdot \frac{mP}{h+P} \cdot C \frac{p}{P} + m_4 (c - \theta_c C)^+$

Here we set $m_2 = m_4$ and let $m_4 \to +\infty$, that means when $\theta_c C - c > 0, c < \theta_c C$, and $m_2 (C - \frac{c}{\theta_c})^+$ goes to positive infinity.

When $\theta_c C - c < 0, c > \theta_c C$, and $m_4 (c - \theta_c C)^+$ goes to positive infinity.

If the starting initial point is $\theta_c C - c > 0$, $\frac{dC}{dt} \to -\infty$ and C decreases until $\theta_c C = c$

When$\theta_c C - c < 0$, then $\frac{dc}{dt} \to -\infty$ and c decreases until $\theta_c C = c$

The system will stabilize only when $c = \theta_c C$.

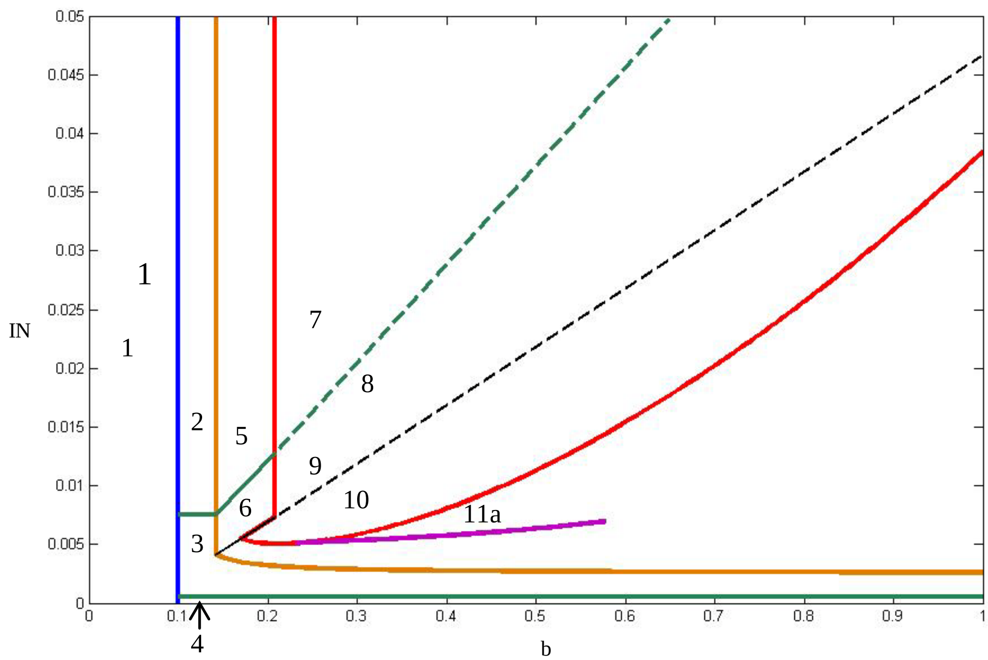
As m_2 and m_4 go to positive infinity, the system will eliminate whatever is in excess - carbon or nutrient – immediately, to stabilize the system at $\theta_c C = c$. That means the nutrient of the system must be proportional to the carbon in the system with the ratio θ_c. So in the differential equations for c and C: $e_n \cdot \frac{mP}{h+P} \cdot c\frac{p}{P} - d_e c - d_C c$ must be proportional to $e_c \cdot \frac{mP}{h+P} \cdot C - d_e C - d_C C$. $d_e c + d_C c$ is already proportional to $d_e C + d_C C$. When the arrival ratio $e_n \cdot \frac{mP}{h+P} \cdot c\frac{p}{P}$: $e_c \cdot \frac{mP}{h+P} \cdot C > \theta_c$, there is excess nutrient arriving, so the system will eliminate excess nutrient and the arrival rate of carbon remains the same. When $e_n \cdot \frac{mP}{h+P} \cdot c\frac{p}{P}$: $e_c \cdot \frac{mP}{h+P} \cdot C < \theta_c$, the system will eliminate excess carbon, and will drag down the carbon arrival rate to $e_n \cdot \frac{mP}{h+P} \cdot c\frac{p}{P} / \theta_c$. In order to satisfy these two situations simultaneously, the arrival rate of carbon $e_c \cdot \frac{mP}{h+P} \cdot C$ will change to $e_c \cdot \frac{mP}{h+P} \cdot C \cdot \min(\frac{e_n p}{e_c \theta_C P}, 1)$, and correspondingly, the elimination of excess carbon, $(1 - e_n) \cdot \frac{mP}{h+P} \cdot C\frac{p}{P}$, will change to $e_c \cdot \frac{mP}{h+P} \cdot C \cdot \theta_c \cdot (\frac{e_n p}{e_c P \theta_c} - 1)^+$

The result in our new 4D Model:

1. $\frac{dP}{dt} = bP - lP^2 - \frac{mP}{h+P} \cdot C - d_p P$
2. $\frac{dC}{dt} = e_c \cdot \frac{mP}{h+P} \cdot C \cdot min(\frac{e_n p}{e_c \theta_C P}, 1) - (d_C + d_e)C$
3. $\frac{dp}{dt} = \mu Ps - d_p p - \frac{p}{P} \cdot \frac{mP}{h+P} \cdot C$
4. $\frac{ds}{dt} = d_C c + d_p p + IN - d_s s - \mu Ps + (1 - e_n) \cdot \frac{mP}{h+P} \cdot C\frac{p}{P} + e_c \cdot \frac{mP}{h+P} \cdot C \cdot \theta_c \cdot (\frac{e_n p}{e_c P \theta_c} - 1)^+$

5.2 IN vs b bifurcation diagram and time series analysis

IN vs b Bifurcation Diagram

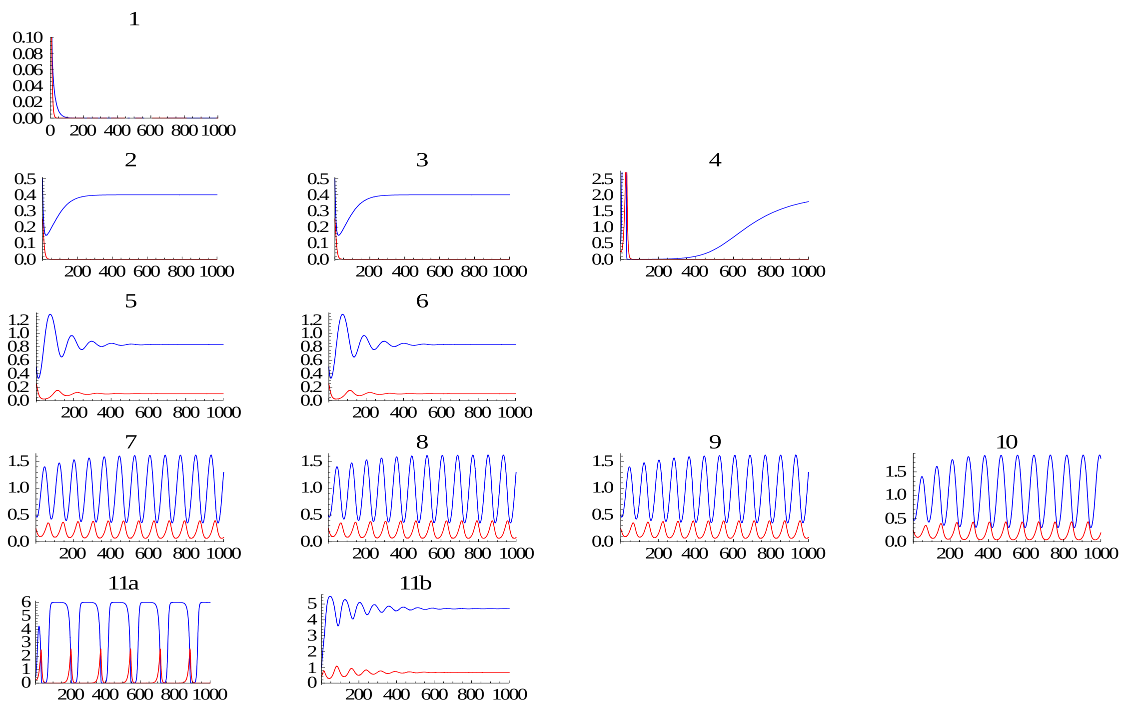


The IN vs b bifurcation diagram for the 4D system is similar with the bifurcation diagram of the 5D stoichiometric model when m_2=$m_4 = 10$. The first transcritical bifurcation is the first vertical line when b equal 0.1. While the upper parts of second transcritical and Hopf bifurcations are vertical lines (b=0.14167 & b=0.2083), their lower parts change to the curves numerically computed with AUTO[1]. The black consumer stoichiometric reference line occurs when $\frac{e_n p}{e_c P\theta_c} = 1$, which makes $\min\left(\frac{e_n p}{e_c\theta_C P}, 1\right) = 1$ and $(\frac{e_n p}{e_c P\theta_c} - 1)^+ = 0$. Exactly on that line, our new model is the same as the non-stoichiometric model despite the change from 5D to 4D. And that cutoff line is same as c:C=0.031 in the 5D model. The 4D model's bifurcation diagram also has a bistable area between lower parts of the second transcritical and the Hopf transcritical bifurcations, bounded by a saddle-node of limit cycles curve and the Hopf curve.

The numerical methods we used here is the same as what we used in the 5D model. We computed the line of $\frac{e_n p}{e_c \theta_C P} = 1$ on the IN vs b plane as a border line, then combined the bifurcation curves computed from software (below the black reference line) and bifurcation obtained through analytic work (above the black reference line) to make the whole bifurcation diagram.

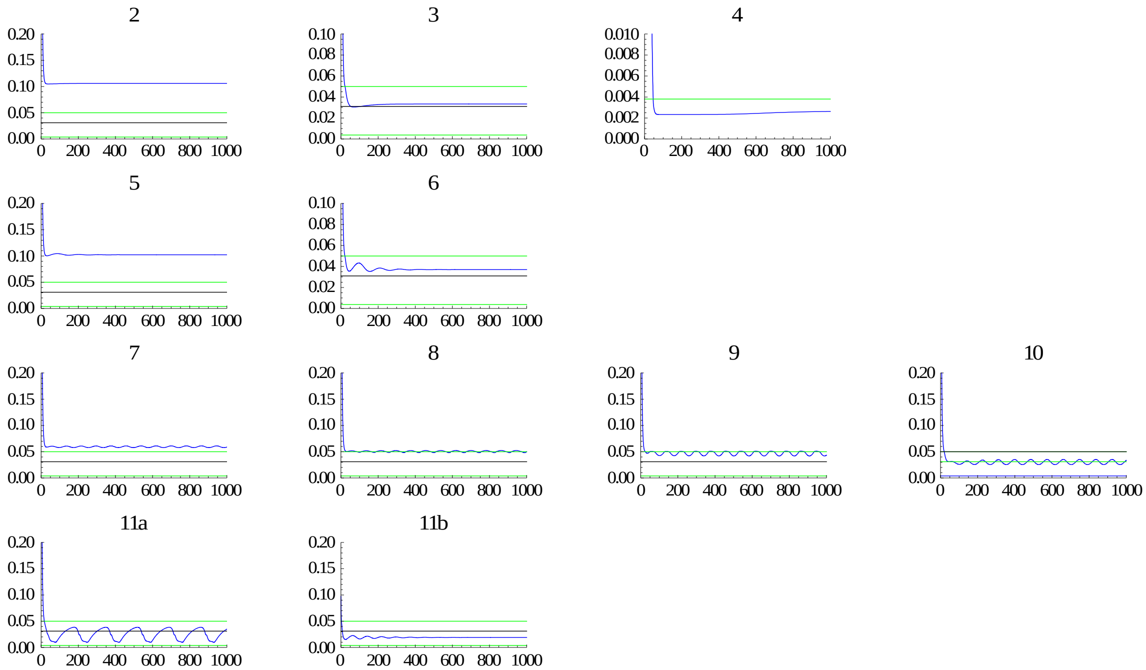
Time series analysis

Producer and consumer



Here the blue represents producer and red is for consumer, the first point is in no-life stage. There points of second row are picked in monoculture stage with different producer nutrient level. The third row represents different parameter points in the stable coexistence area and the fourth row represents different parameter regions in the periodic coexistence area. The parameter for the final row 11a&11b are picked from point 11 in the bistability area.

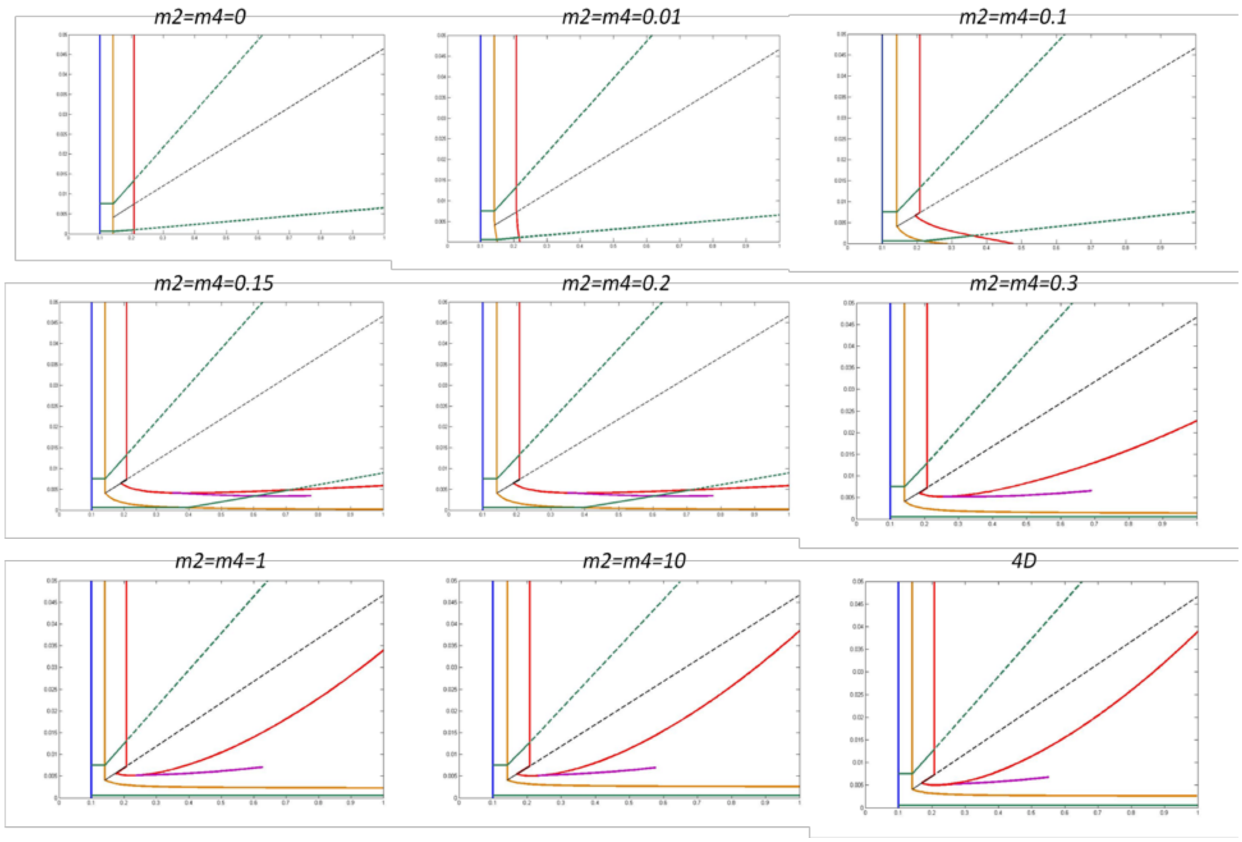
Producer nutrient



The second set of time series is for producer stoichiometry which is similar with 5D model when $m_2 = m_4 = 10$. The only difference is that the middle black lines are for $\frac{e_n p}{e_c P \theta_c}$ exactly equals 1, we just add it here for reference. We can observe among periodic points, some cross stoichiometric classification lines while some do not. 11a and 11b are from point 11 in the bistability area. One approaches a periodic solution and the other approaches coexistence equilibrium

5.3 Varying Elimination Rates

In order to provide another way to corroborate the process of developing 4D model in theoretical part, we managed to compute a series of IN vs b bifurcation diagrams of 5D model with different value of m_2 and m_4. We can observe the change of IN vs b bifurcation diagram with m_2 and m_4 increasing.



When $m_2 = m_4 = 10$, IN vs b bifurcation diagrams of 5D stoichiometric model ($m_2 = m_4 = 10$) and 4D model are almost the same. Further increase of m_2 and m_4 results in almost no change in the corresponding bifurcation diagrams. This result is consistent with our model reduction as we allowed m_2 and m_4 to approach infinity when developing our 4D model.

Second, since the elimination rate is increasing, we can see that the lower part of the bifurcation diagram (below the diagonal blue consumer stoichiometry reference line) changes from a vertical line to a sloping curve. At some value of m_2 and m_4, the second transcritical bifurcation curve ceases to reach the b axis anymore. At a later value of m_2 and m_4 the Hopf bifurcation curve also misses the b axis. As the second transcritical bifurcation curve (yellow) changes to a curve heading to the right, it will leave a monoculture region near the b axis., The low producer stoichiometry classification level becomes a horizontal line which extends to the right.

In general, when one starts from the 5D stoichiometric model with small m_2 and m_4, the IN vs b bifurcation diagram is close to the 5D non-stoichiometric bifurcation diagram ($m_2 = m_4$=0), and as m_2 and m_4 increases, the IN vs b bifurcation diagram approaches the 4D bifurcation diagram.

6 Ecological Implications

6.1 Experimental Design

The bifurcation diagram is also useful for practical experiments. For example, if we control the birth rate at 0.18 and increase the input of nutrient step by step. At initial time when we set IN equals 0, the system is in monoculture stage with low producer nutrient which is shown on the bifurcation diagram ($m_2 = m_4 = 10$). When we start to increase the input of nutrient, it's still in monoculture stage but changed to medium producer nutrient level. With the increase of input of nutrient, the experiment goes through stable coexistence and periodic coexistence. The interesting part of this experiment is that after it enters the area of periodic coexistence, it will cross the "jump" part of Hopf bifurcation which is along nutrient cut off line of consumer and then back to stable coexistence. Finally, it will continue move up to high producer nutrient with monoculture behavior.

6.2 Time Series Observation

In IN vs b plane (m_2=$m_4 = 10$), points 10 and 12 are the most interesting because p:P oscillates between being above and below the standard consumer c:C. That means that along the stable limit cycle, the consumer must alternatively eliminate carbon (when p:P > standard c:C) and nutrient (when p:P > standard c:C). Therefore, at different points on the limit cycle the consumer is either adding nutrient to the sediment or causing carbon to be added to the sediment.

7 Model Limitations and Future Work

There are, of course, many limitations due to the model's simplifying assumptions. Some future work may be needed. Here we mention two of them

1. First, when computing our IN vs b bifurcation diagrams and related time series, we didn't eliminate excess producer nutrient. Though that part does not appear to be an important factor influencing the bifurcation diagram, it would be interesting to see how the bifurcation diagrams change when we put excess producer nutrient in it.

2. Second, we noticed that in the periodic coexistence stage, some points keep crossing producer and consumer nutrient cutoff line and some not. We could investigate the border line in the bifurcation diagram between these two kinds of behaviors.

8 Summary

The model developed and studied in this paper is a model of one producer and one consumer, altered to model the stoichiometric effects of food quality. Stoichiometric limitation is modeled by restricting the conversion efficiency from producer to consumer when the food quality is low.

The main goal of our analysis has been to perform a bifurcation analysis to study enrichment. We located four primary bifurcations: TC1, TC2, Hopf, and a saddle-node of limit cycles. We computed nutrient to carbon ratios of the producer and consumer in different regions of the bifurcation diagram. We performed time series analysis on a representative point of each region to explain the classifications from our bifurcation diagrams. We observed the phenomenon of bistability, and periodic orbits along which the stoichiometric classification changes. We also observed that as the elimination rate increases, the behavior of the stoichiometric elimination model approaches the behavior of a lower dimensional model with a minimum function for its biomass conversion. Similar minimum functions have been used in previous studies.

In summary, the behavior of producer and consumer model is quite different when introducing stoichiometric elimination.

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