Rich and realistic dynamics of resource quality based population models

ICERM's MCB

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Introduction

Overview

Biomass production is essentially a mass transfer process that requires more than just energy. It is crucially dependent on the chemical compositions of both the consumer species and food resources. *There maybe many ways cells or individual may die, but only one way (cell division) to grow.*

The basis of most life on earth is photosynthesis. Photoautotrophic organisms can exhibit a very wide range of physiological plasticity in elemental composition. In contrast, animals have almost constant chemical composition. The stoichiometric formula for an average human being is: $H_{375,000,000}O_{132,000,000}C_{85,700,000}N_{6,430,000}Ca_{1,500,000}P_{1,020,000}S_{206,000}Na_{183,000}K_{177,000}Cl_{127,000}Mg_{40,000}Si_{38,600}Fe_{2,680}Zn_{2,110}Cu_{76}I_{14}Mn_{13}F_{13}Cr_{7}Se_{4}Mo_{3}Co_{1}$

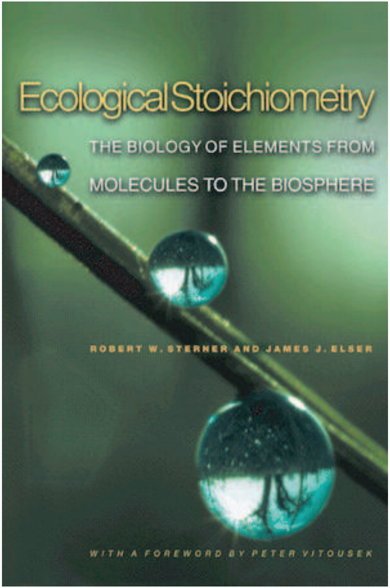
Ecological Stoichiometry

Chemistry is fundamental to truly understanding biology.

Stoichiometry is the accounting, or math, behind chemistry. It deals with the balance of multiple chemical elements in chemical reactions.

Ecological stoichiometry is the study of the balance of energy and multiple chemical resources (elements) in ecological interactions.

Growth Rate Hypothesis

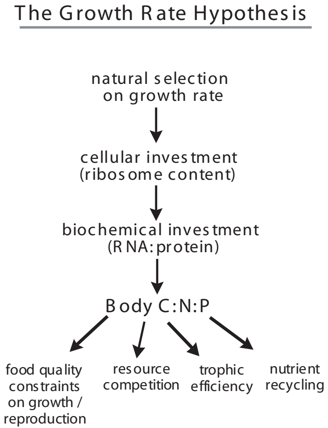


Ecological Stoichiometry

THE BIOLOGY OF ELEMENTS FROM MOLECULES TO THE BIOSPHERE

ROBERT W. STERNER AND JAMES J. ELSER

WITH A FOREWORD BY PETER VITOUSEK



The Growth Rate Hypothesis

natural selection on growth rate

cellular investment (ribosome content)

biochemical investment (RNA:protein)

Body C:N:P

food quality constraints on growth / reproduction

resource competition

trophic efficiency

nutrient recycling

Based on: Elser, J.J., D.R. Dobberfuhl, N.A. MacKay, and J.H. Schampel. Organism size, life history, and N:P stoichiometry: toward a unified view of cellular and ecosystem processes. BioScience 46: 674-684.

Experimental results

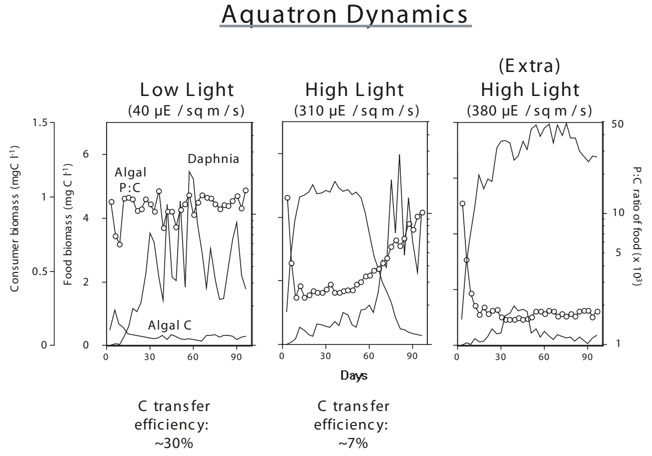


Figure 1: Urabe, J ., J .J . Elser, M. Kyle, T. Yoshida, T. Sekino and Z. Kawabata. 2002. Herbivorous animals can mitigate unfavorable ratios of energy and material supplies by enhancing nutrient recycling. Ecology Letters, 5(2):177 - 185

Accidental experimental results

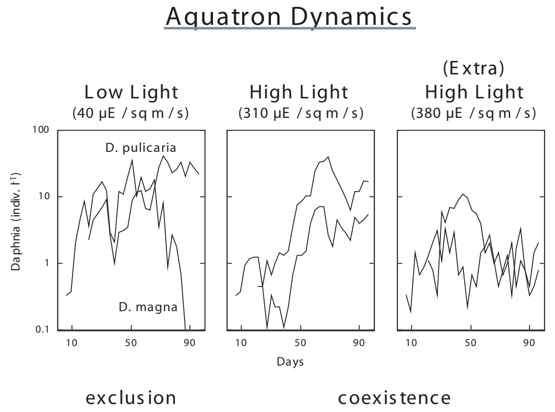


Figure 2: Urabe, J ., J .J . Elser, M. Kyle, T. Yoshida, T. Sekino and Z. Kawabata. 2002. Herbivorous animals can mitigate unfavorable ratios of energy and material supplies by enhancing nutrient recycling. Ecology Letters, 5(2):177 - 185

Our Selected Papers

Phan T, Elser JJ, Kuang Y, 2023. Rich Dynamics of a general producergrazer interaction model under shared multiple resource limitations. Applied Sciences 13, no. 7: 4150.

Loladze I, Kuang Y, Elser JJ, 2000. Stoichiometry in producer-grazer systems: Linking energy flow with element cycling, BMB 62(6): 1137-1162.

Y. Kuang, W. F. Fagan and I. Loladze 2003. Biodiversity, Habitat Area, Resource Growth Rate and Interference Competition BMB, 65; 497-518

I. Loladze, Y. Kuang, J. J. Elser and W. F. Fagan, Competition and stoichiometry: coexistence of two predators on one prey JPB, 65 (2004) 1-15.

Y. Kuang, J. Huisman and J. J. Elser, Stoichiometric ..., MBE, 1: 215 222(2004).

Hao Wang, Katherine Dunning, J. J. Elser and Y. Kuang: Daphnia species invasion, competitive exclusion, and chaotic coexistence, DCDS-B, 12, 481-493(2009).

J. J. Elser and Y. Kuang, 2011. Ecological stoichiometry, Sourcebook in Theoretical Ecology, Hastings and Gross ed. University of California Press.

A. Peace, Y. Zhao, I. Loladze, J. J. Elser and Y. Kuang, 2013. A stoichiometric producer- grazer model ... Mathematical Biosciences, 244:107-115

A. Peace, H. Wang and Y. Kuang, 2014. Dynamics of a producer-grazer model incorporating the effects of excess food-nutrient content on grazer's growth, BMB, 76:2175-2197

Very few papers on the global dynamics of stoichiometric models

1. X. Li, H. Wang, Y. Kuang, 2011. Global analysis of a stoichiometric producer-grazer model ... JMB, 63, 901-932.

2. X. Yang, X. Li, H. Wang, and Y. Kuang, 2016. Stability and bifurcation in a stoichiometric producer- grazer model with knife edge, SIAM J. on Applied Dynamical Systems 15 (4), 2051-2077.

3. M. Chen, M. Fan, Y. Kuang, 2017. Global dynamics in a stoichiometric food chain model with two limiting nutrients, Math. Biosci., 289, 919.

The First Model, 2000

Model of Loladze, Kuang and Elser (LKE model, Loladze I, Kuang Y,Elser JJ, Stoichiometry in producer-grazer systems: Linking energy flow with element cycling, 62(6): 1137-1162 (2000))

$$
\begin{aligned}
\frac{dx}{dt} &= bx\left[1 - \frac{x}{\min(K, (P-\theta y)/q)}\right] - f(x)y, \\
\frac{dy}{dt} &= c\min\left(1, \frac{P-\theta y}{\theta x}\right) f(x)y - dy.
\end{aligned}
\tag{1}
$$

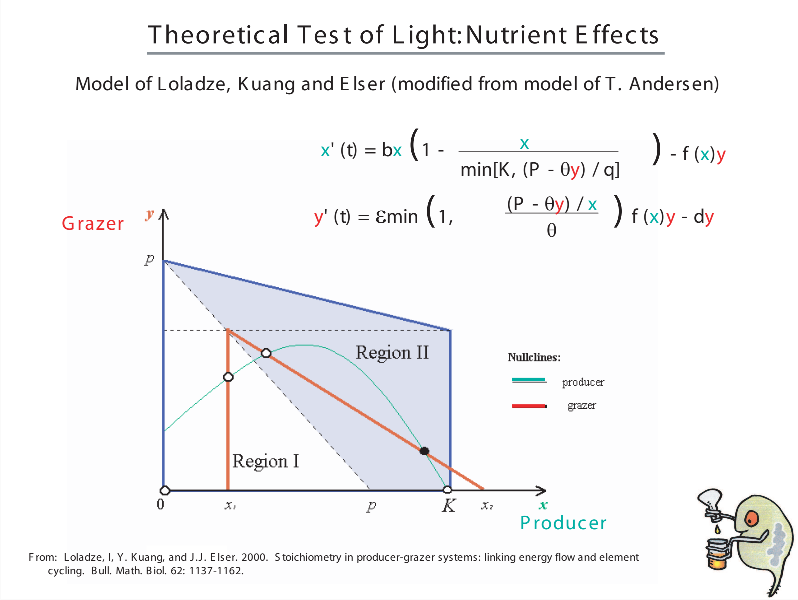
LKE Model Assumptions

A1. *The total mass of phosphorus P in the entire system is fixed, i.e. the system is closed for phosphorus with total of P* (mg P/l).

A2. *Phosphorus to carbon ratio (P:C) in the producer varies, but it never falls below a minimum q (mg P/mg C); the grazer maintains a constant P:C ratio, denoted byθ (mg P/mg C).*

A3. *All phosphorus in the system is divided into two pools: phosphorus in the grazer and phosphorus in the producer.*

LKE model dynamics



Theoretical Test of Light:Nutrient Effects

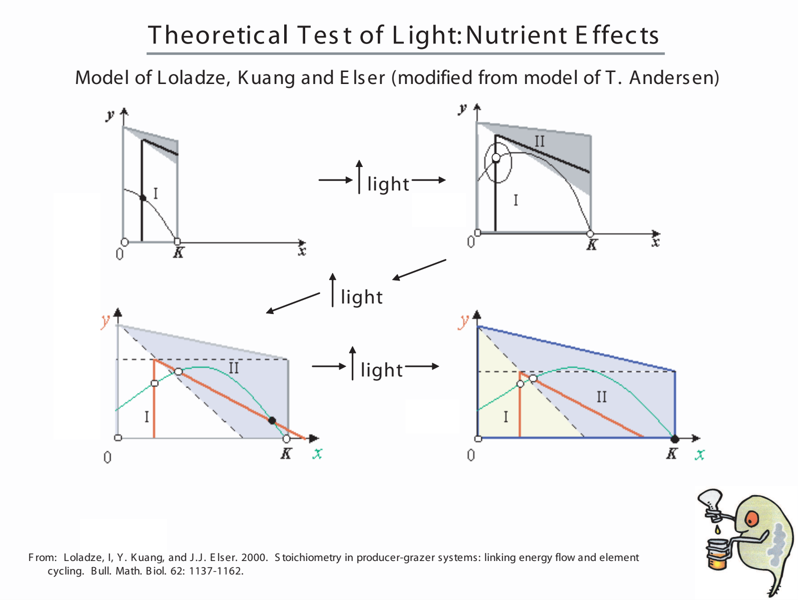
Model of Loladze, Kuang and Elser (modified from model of T. Andersen)

$$x'(t) = bx\left(1 - \frac{x}{\min[K, (P - \theta y)/q]}\right) - f(x)y$$

$$y'(t) = \varepsilon \min\left(1, \frac{(P - \theta y)/x}{\theta}\right) f(x)y - dy$$

From: Loladze, I, Y. Kuang, and J.J. Elser. 2000. Stoichiometry in producer-grazer systems: linking energy flow and element cycling. Bull. Math. Biol. 62: 1137-1162.

LKE model dynamics



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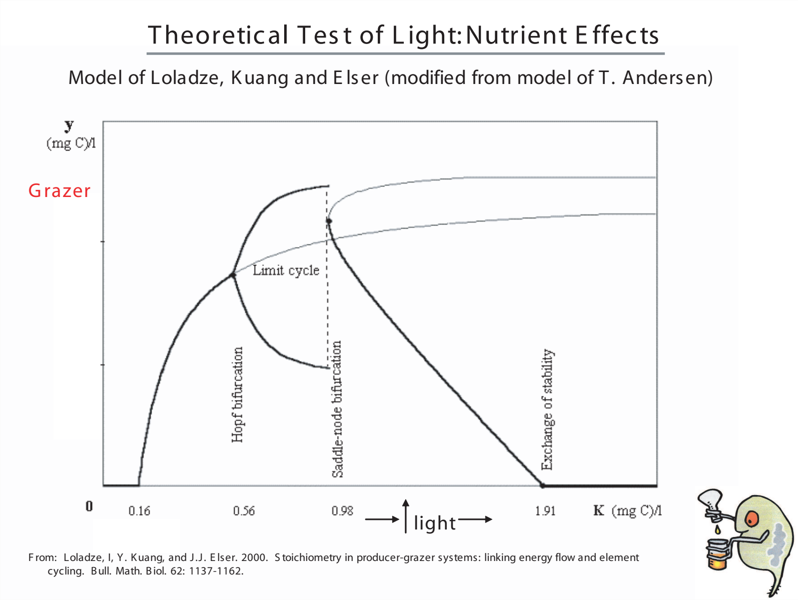
LKE model dynamics



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From: Loladze, I, Y. Kuang, and J.J. Elser. 2000. Stoichiometry in producer-grazer systems: linking energy flow and element cycling. Bull. Math. Biol. 62: 1137-1162.

Some observations

Stoichiometric models incorporate both food quantity and food quality effects in a single framework, appear to stabilize predatorprey systems while simultaneously producing rich dynamics with alternative domains of attraction and occasionally counterintuitive outcomes, such as coexistence of more than one predator species on a single-prey item and decreased herbivore performance in response to increased plant growth rate.

Stoichiometric theory has tremendous potential for both quantitative and qualitative improvements in the predictive power of mathematical population models in the study of both ecological and evolutional dynamics.

Second Model

Yang Kuang, Jef Huisman and James J. Elser: Stoichiometric plant-herbivore models and their interpretation, Math. Biosc. and Eng., 1, 215-222(2004)

If we let P_p, P_z and P_f be the phosphorous in autotroph, phosphorous in herbivore, and the free phosphorous respectively, then $P_t = P_p + P_z + P_f$. Let $x = x(t)$ be the autotroph density, $y = y(t)$ be the herbivore density and $Q = Q(t)$ be the autotroph's cell quota for P, then $P_p = Qx$ and $P_z = \theta y$. Hence

$$P_t = P_f + Qx + \theta y. \tag{2}$$

We let q be the autotroph's minimal cell quota for P, μ_m be the autotroph's true maximal growth rate, D be its death rate and $f(x)$ be the herbivore's ingestion rate.

Second Model

By **Droop** equation, we have

$$\frac{dx}{dt} = \mu_m\left(1 - \frac{q}{Q}\right)x - Dx - f(x)y. \tag{3}$$

Let e be the herbivore's yield constant and d be the specific loss rate of herbivore. If the autotroph is P poor (when $Q < \theta$), then the conversion rate becomes eQ/θ. We have

$$\frac{dy}{dt} = e\min\left(1, \frac{Q}{\theta}\right)f(x)y - dy. \tag{4}$$

Finally, we need an equation governing the dynamics of Q

$$\frac{dQ}{dt} = \alpha P_f - \mu_m(Q - q). \tag{5}$$

Special Cases for the Second Model

Since the cell metabolic process operates in a much fast pace than the growth of total biomass of either species, we approximate $Q(t)$ by the solution of

$$\alpha P_f - \mu_m(Q - q) = 0. \tag{6}$$

We have the following autotroph-herbivore model:

$$\begin{aligned} \frac{dx}{dt} &= (\mu_m - D)x\left[1 - \frac{x + \mu_m \alpha^{-1}}{[(\mu_m - D)/\mu_m][\mu_m \alpha^{-1} + (P_t - \theta y)/q]}\right] - f(x)y. \\ \frac{dy}{dt} &= e \min\left(1, \frac{Q}{\theta}\right) f(x)y - dy. \end{aligned} \tag{7}$$

Second Model

If only C limits the autotroph's growth, then the traditional autotroph equation can be used.

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{K}\right) - f(x)y \tag{8}$$

where $b = \mu_m - D$ is the net autotroph growth rate. Applying Leipig's minimum principle, we obtain the following autotroph-herbivore model with two limiting elements

$$\begin{aligned} \frac{dx}{dt} &= bx\left[1 - \max\left(\frac{x}{K}, \ \frac{x + \mu_m \alpha^{-1}}{[(\mu_m - D)/\mu_m][\mu_m \alpha^{-1} + (P_t - \theta y)/q]}\right)\right] - f(x)y. \\ \frac{dy}{dt} &= e \min\left(1, \frac{Q}{\theta}\right) f(x)y - dy. \end{aligned} \tag{9}$$

Special Cases

If we, in addition, assume that the natural autotroph death rate D is far less than its true maximal growth rate, then we can approximate the value of $(\mu_m - D)/\mu_m$ by 1. Together with the assumption α tends to ∞, the above model becomes

$$\begin{aligned} \frac{dx}{dt} &= bx\left[1 - \max\left(\frac{x}{K},\quad \frac{x}{(P_t - \theta y)/q}\right)\right] - f(x)y. \\ \frac{dy}{dt} &= e\min\left(1, \frac{Q}{\theta}\right)f(x)y - dy. \end{aligned} \tag{10}$$

Special Cases

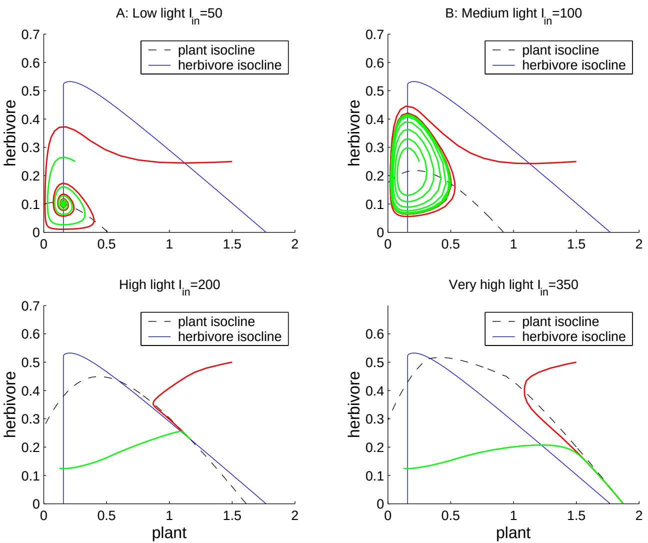
As α tends to ∞, we see that

$$Q \qquad \text{tends to} \qquad (P_t - \theta y)/x.$$

The above model s exactly the same as the LKE (Loladze, Kuang and Elser: Stoichiometry in producer-grazer systems: linking energy flow and element cycling, Bull. Math. Biol., 62, 1137-1162(2000)) model:

$$\begin{aligned} \frac{dx}{dt} &= bx\left(1 - \frac{x}{\min(K, (P_t - \theta y)/q)}\right) - f(x)y, \\ \frac{dy}{dt} &= e \min\left(1, \frac{(P_t - \theta y)/x}{\theta}\right) f(x)y - dy. \end{aligned} \tag{11}$$

Simulation


A: Low light I_{in}=50
B: Medium light I_{in}=100
High light I_{in}=200
Very high light I_{in}=350
plant isocline
herbivore isocline
herbivore
plant
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.5
1
1.5
2

Single resource with two consumers

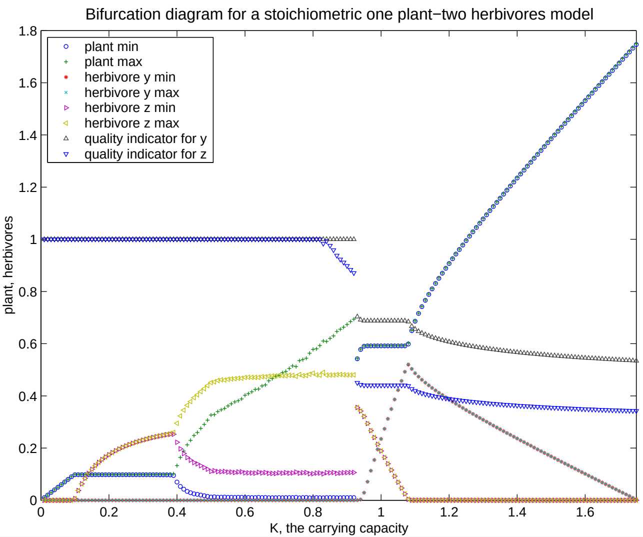
Let us start with a conventional model, which describes a system of two consumers feeding on one biotic resource.

$$\begin{aligned}
\frac{dx}{dt} &= rx\left(1 - \frac{x}{K}\right) - f_1(x)y_1 - f_2(x)y_2 \\
\frac{dy_1}{dt} &= e_1 f_1(x)y_1 - d_1 y_1 \\
\frac{dy_2}{dt} &= e_2 f_2(x)y_2 - d_2 y_2
\end{aligned} \tag{12}$$

Single resource with two consumers

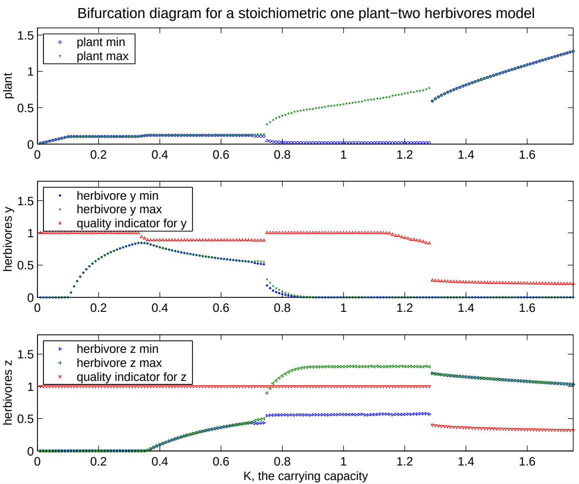
$$\begin{aligned}
\frac{dx}{dt} &= rx\left(1 - \frac{x}{\min(K, (P - s_1 y_1 - s_2 y_2)/q)}\right) - f_1(x)y_1 - f_2(x)y_2 \\
&= F(x, y_1, y_2) \\
\frac{dy_1}{dt} &= e_1 \min\left(1, \frac{(P - s_1 y_1 - s_2 y_2)}{x s_1}\right) f_1(x)y_1 - d_1 y_1 = G_1(x, y_1, y_2) \\
\frac{dy_2}{dt} &= e_2 \min\left(1, \frac{(P - s_1 y_1 - s_2 y_2)}{x s_2}\right) f_2(x)y_2 - d_2 y_2 = G_2(x, y_1, y_2)
\end{aligned} \tag{13}$$

A bifurcation diagram



Another bifurcation diagram

The coexistence of all species at a stable positive equilibrium is possible. $r = 1.4, c_1 = 0.63, c_2 = 0.6, a_1 = 0.45, a_2 = 0.36, e_1 = 0.85, e_2 = 0.8, P = 0.036, q = 0.003, s_1 = 0.038, s_2 = 0.025, d_1 = 0.1, d_2 = 0.12.$



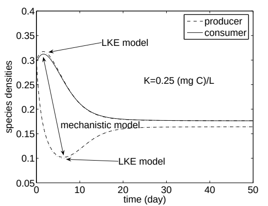
A Better Model

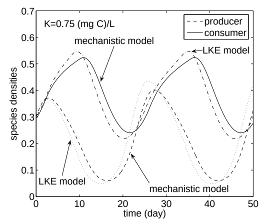
H. Wang, Y. Kuang and I. Loladze: A mechanistically derived stoichiometric producer-grazer model, J. Biological Dynamics, 2, 286-296 (2008).

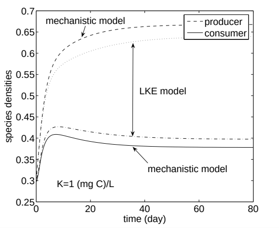
Let x be the density of carbon content in the producer, p be the density of phosphorus content in the producer, y is the density of carbon contents in the grazer, P is the density of free phosphorus in media.

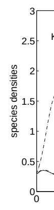
$$
\begin{aligned}
\frac{dx}{dt} &= rx\left(1-\frac{x}{\min\{K, p/q\}}\right) - f(x)y, && \text{(14a)}\\
\frac{dy}{dt} &= \hat{e}\min\left\{1, \frac{p/x}{\theta}\right\} f(x)y - \hat{d}y, && \text{(14b)}\\
\frac{dp}{dt} &= g(P)x - \frac{p}{x} f(x)y - dp, && \text{(14c)}\\
\frac{dP}{dt} &= -g(P)x + dp + \theta\hat{d}y + \left(\frac{p}{x} - \hat{e}\min\left\{\theta, \frac{p}{x}\right\}\right) f(x)y && \text{(14d)}
\end{aligned}
$$

Comparison


0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
species densities
producer
consumer
LKE model
K=0.25 (mg C)/L
mechanistic model
LKE model
0
10
20
30
40
50
time (day)


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
species densities
K=0.75 (mg C)/L
producer
consumer
mechanistic model
LKE model
LKE model
mechanistic model
0
10
20
30
40
50
time (day)

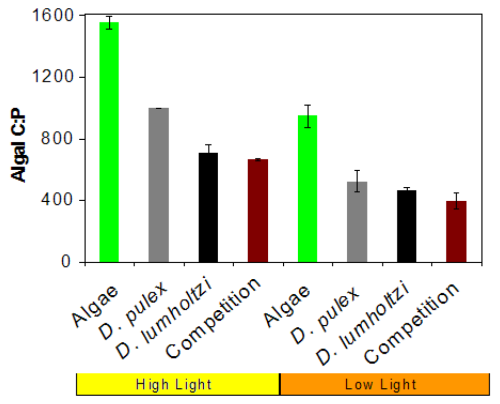

0.7
0.65
0.6
0.55
0.5
0.45
0.4
0.35
0.3
0.25
species densities
mechanistic model
producer
consumer
LKE model
mechanistic model
K=1 (mg C)/L
0
20
40
60
80
time (day)


3
2.5
2
1.5
1
0.5
0
0
species densities

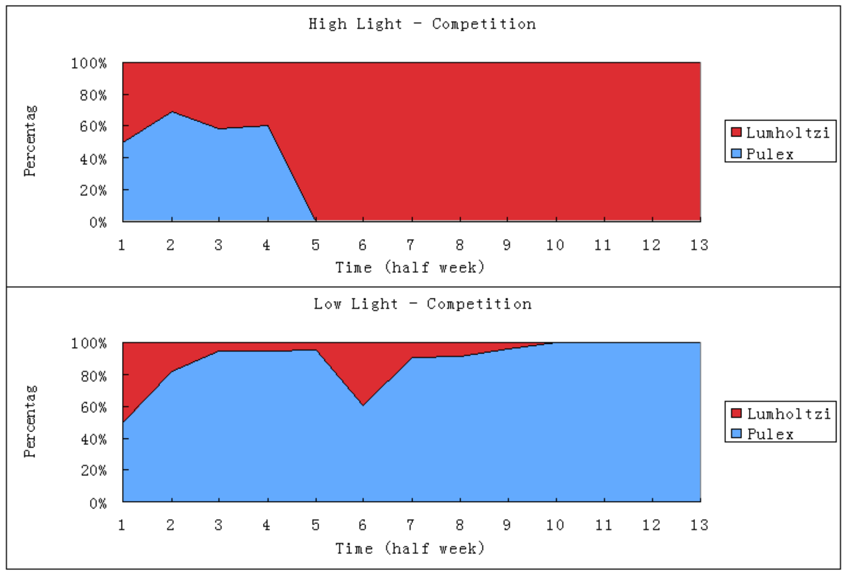
Competition

Experiment and Hypothesis We experimentally studied the competition between *D. pulex* and *D. lumholtzi* with a single food source, the green alga *Scenedesmus acutus*. There were two light conditions: high intensity and low intensity. We applied each light treatment to four test cases: a control lacking Daphnia, *D. pulex* monoculture, *D. lumholtzi* monoculture, and *D. pulex* and *D.lumholtzi* together in competition.

Competition



Competition

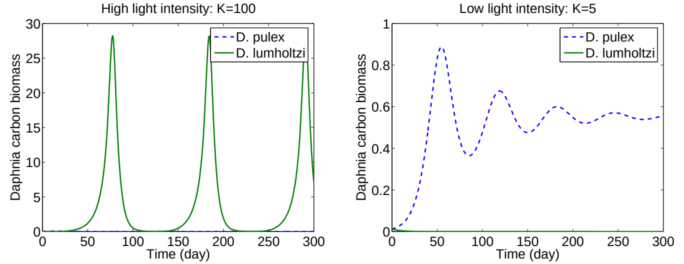


Competition

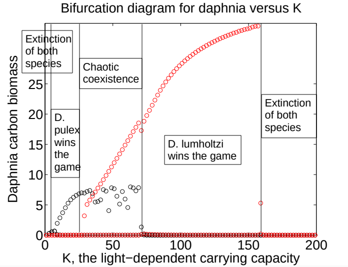
A stoichiometric competition model.

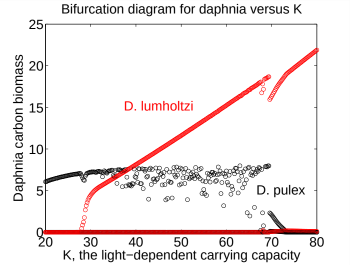
$$\begin{aligned}
\frac{dx}{dt} &= rx \min\left\{1-\frac{x}{K}, 1-\frac{q}{p/x}\right\} - \sum_{i=1}^{i=2} f_i(x)y_i, && (15)\\
\frac{dy_1}{dt} &= e_1 \min\left\{1, \frac{p/x}{\theta_1}\right\} f_1(x)y_1 - d_1 y_1, && (16)\\
\frac{dy_2}{dt} &= e_2 \min\left\{1, \frac{p/x}{\theta_2}\right\} f_2(x)y_2 - d_2 y_2, && (17)\\
\frac{dp}{dt} &= g(T-p-\theta_1 y_1-\theta_2 y_2)x - \frac{p}{x}\sum_{i=1}^{i=2} f_i(x)y_i - dp. && (18)
\end{aligned}$$

Competition

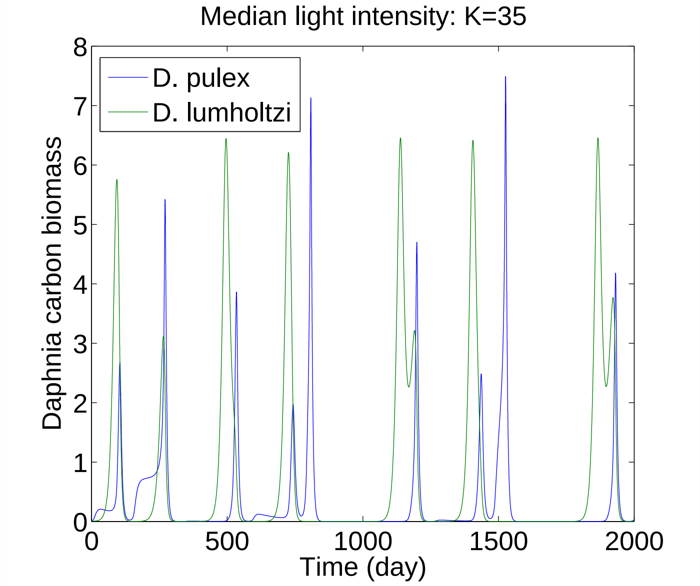


Competition

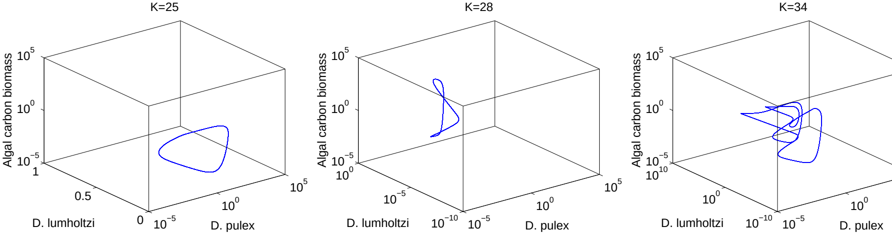




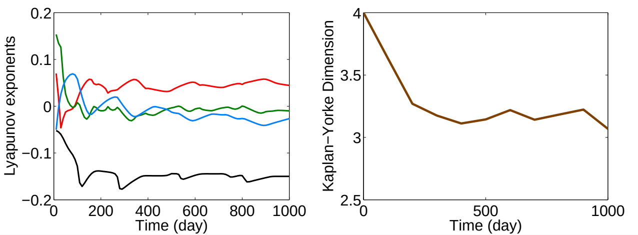
The chaotic coexistence with K=35



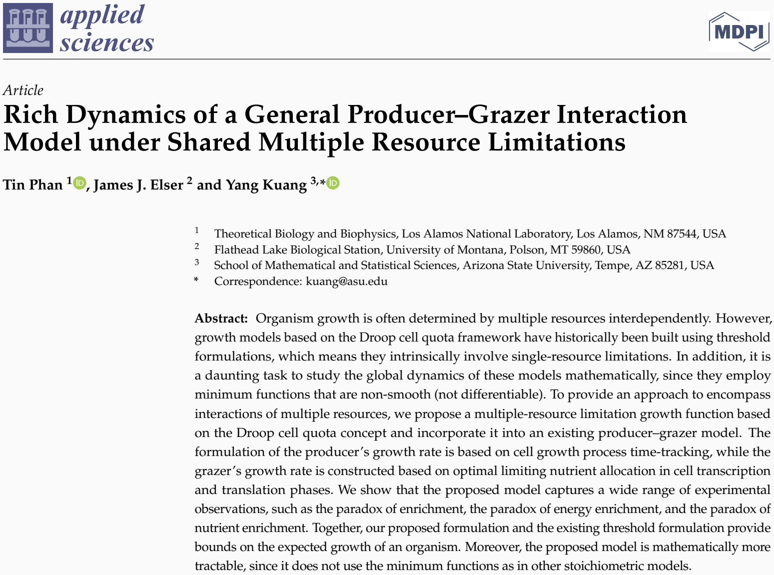
Chaos in Competition



Lyapunov exponents and the Kaplan-Yorke dimension



Third (MRL) Model



applied sciences

MDPI

Article

Rich Dynamics of a General Producer–Grazer Interaction Model under Shared Multiple Resource Limitations

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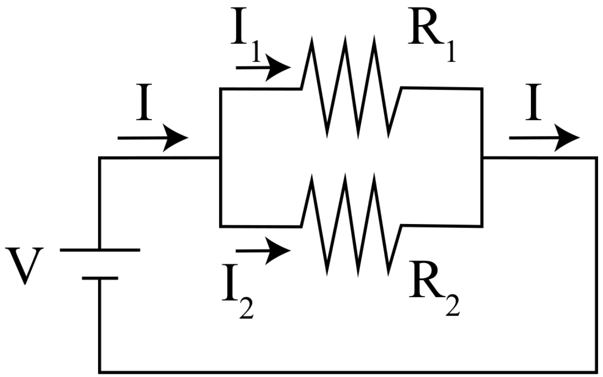
[*] Correspondence: kuang@asu.edu

Abstract: Organism growth is often determined by multiple resources interdependently. However, growth models based on the Droop cell quota framework have historically been built using threshold formulations, which means they intrinsically involve single-resource limitations. In addition, it is a daunting task to study the global dynamics of these models mathematically, since they employ minimum functions that are non-smooth (not differentiable). To provide an approach to encompass interactions of multiple resources, we propose a multiple-resource limitation growth function based on the Droop cell quota concept and incorporate it into an existing producer–grazer model. The formulation of the producer's growth rate is based on cell growth process time-tracking, while the grazer's growth rate is constructed based on optimal limiting nutrient allocation in cell transcription and translation phases. We show that the proposed model captures a wide range of experimental observations, such as the paradox of enrichment, the paradox of energy enrichment, and the paradox of nutrient enrichment. Together, our proposed formulation and the existing threshold formulation provide bounds on the expected growth of an organism. Moreover, the proposed model is mathematically more tractable, since it does not use the minimum functions as in other stoichiometric models.

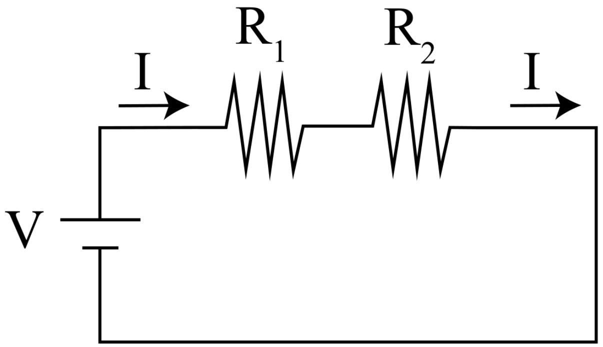
Back to the growth.

The electric circuit is a fair description of multiple resource limitation for an idealized organism. However, it can get quite confusing going back and forth between different terminologies.

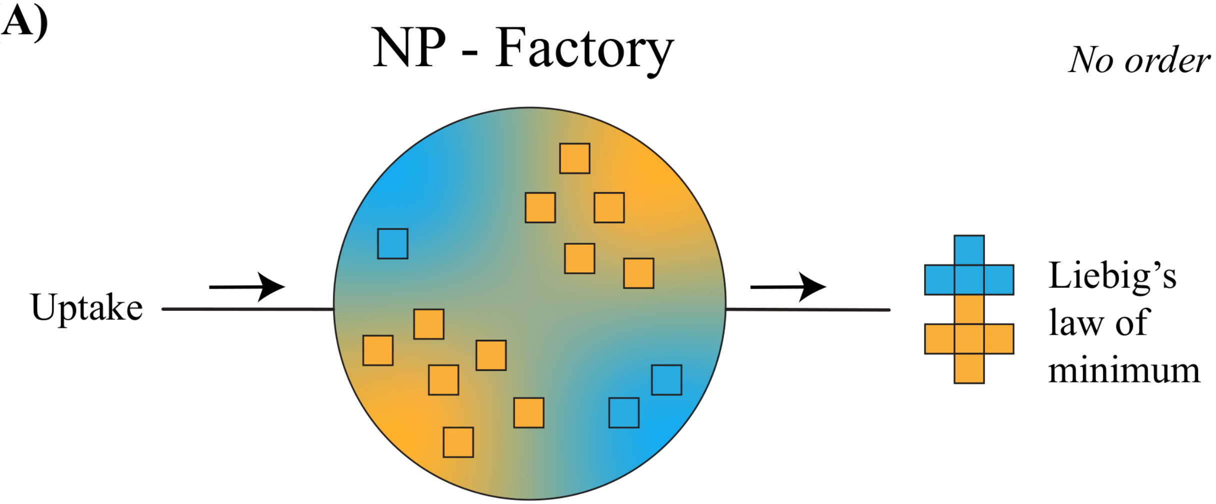
(A.1) Resistors in parallel



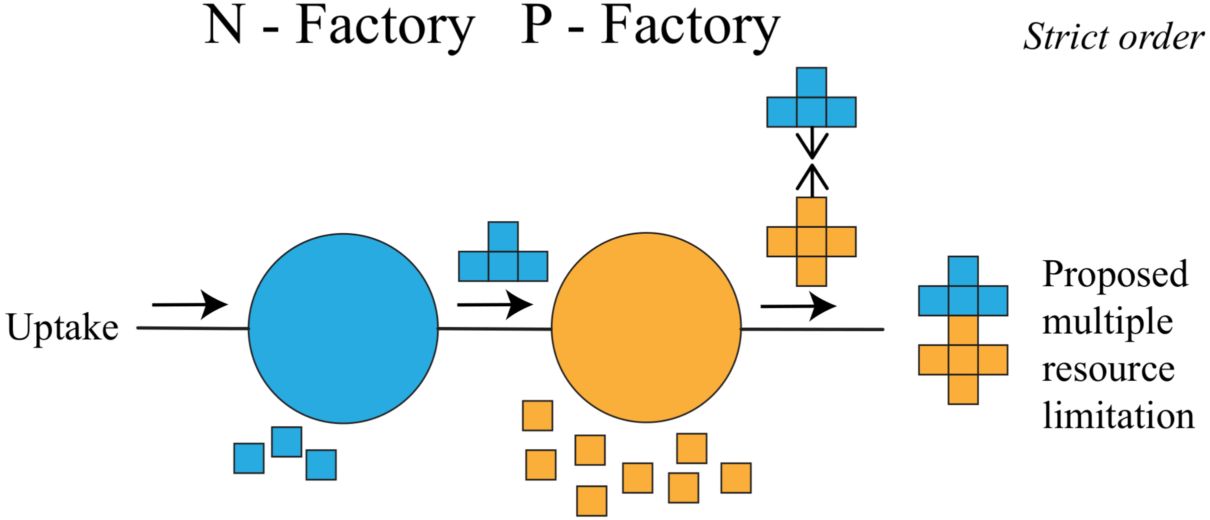
(A.2) Resistors in series



(A)



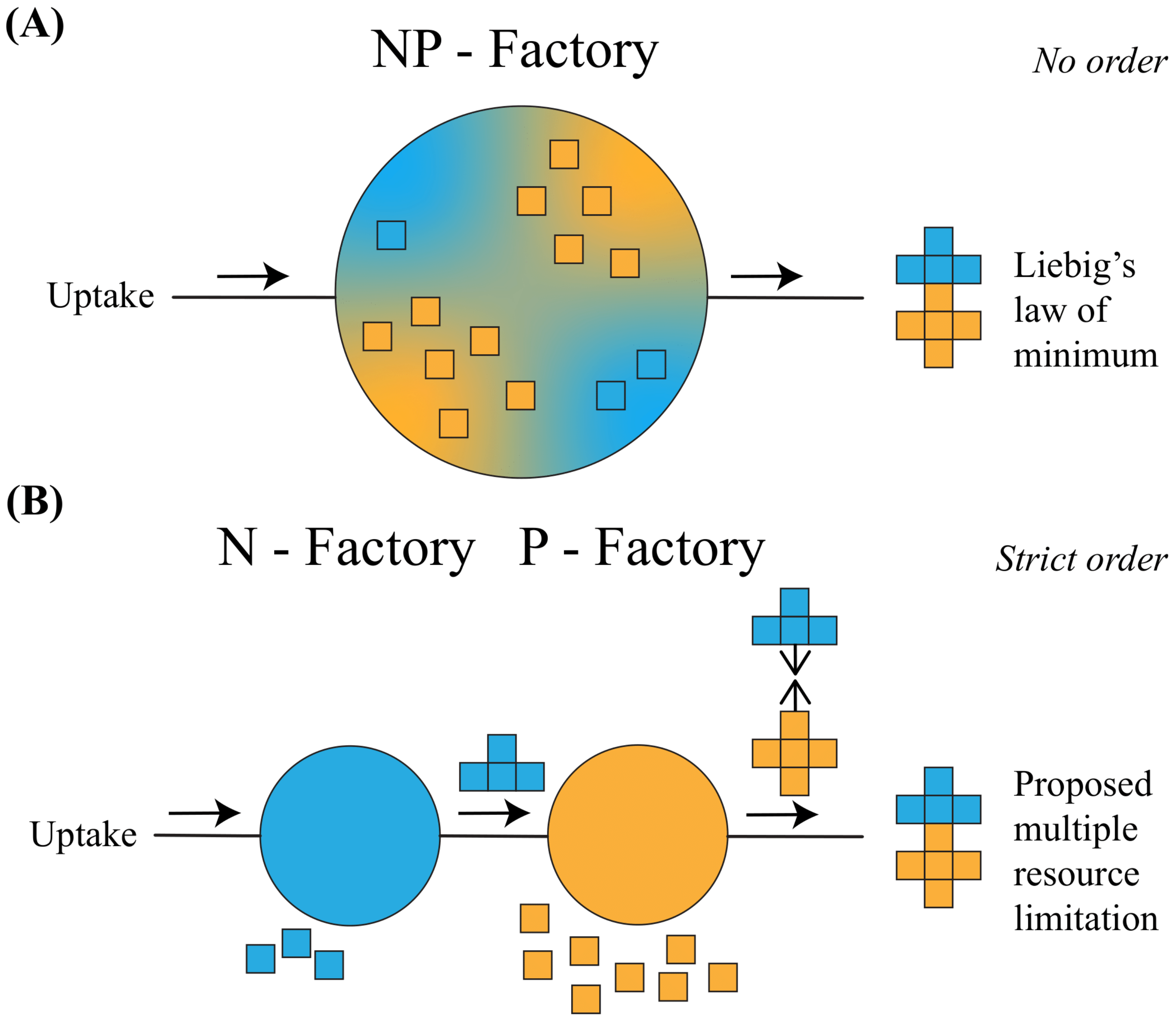
(B)



$$\mu_l = \min\{\mu_N, \mu_P\} = \mu_{max} \min\left\{\left(1 - \frac{q_N}{Q_N}\right), \left(1 - \frac{q_P}{Q_P}\right)\right\},$$

$$\mu_m = \frac{1}{T} = \frac{1}{T_N + T_P} = \frac{1}{\frac{1}{\mu_N} + \frac{1}{\mu_P}} = \frac{\mu_N \mu_P}{\mu_N + \mu_P}.$$

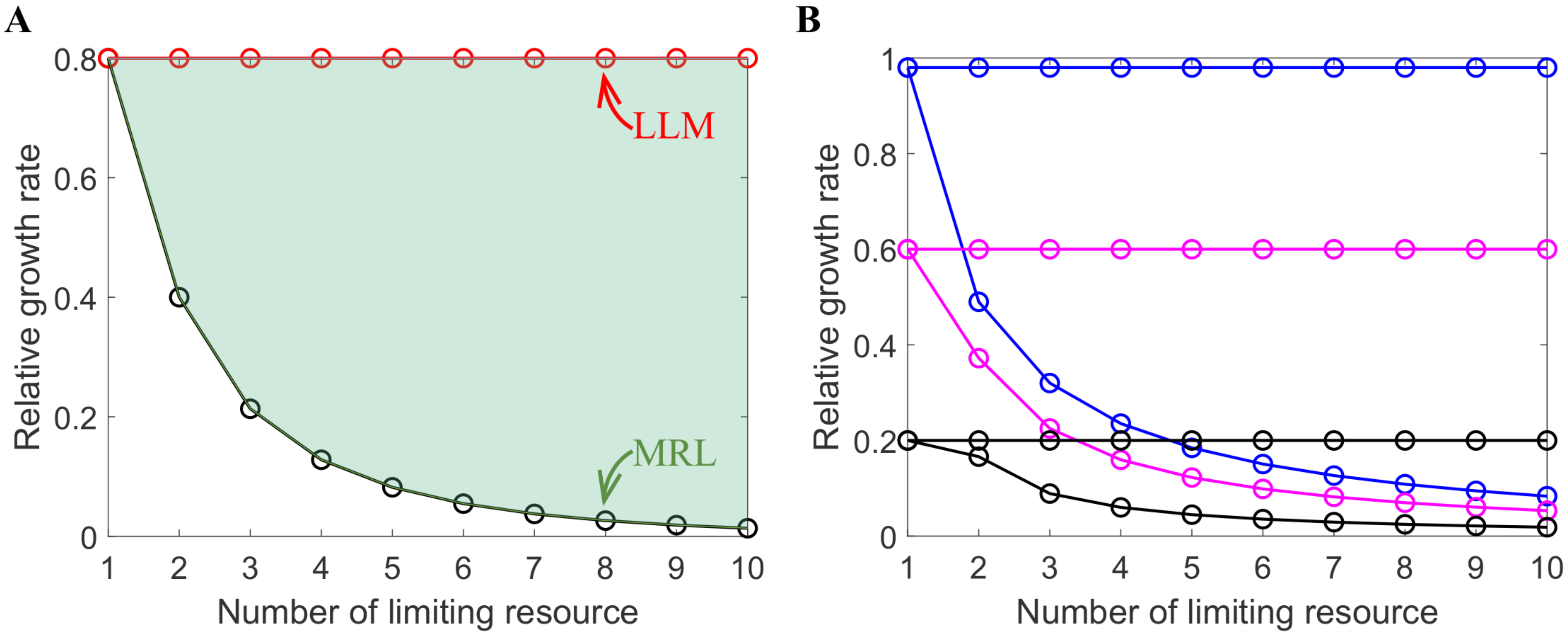
$$\mu_m < \mu < \mu_l.$$



Properties and extensions.

$$\mu_L = \min\{\mu_i : i = 1, 2, \ldots n\},$$

$$\mu_M = \frac{1}{T} = \frac{1}{T_1 + T_2 + \ldots + T_n} = \frac{1}{\frac{1}{\mu_1} + \ldots + \frac{1}{\mu_n}}$$



Liebig’s Law of Minimum:

- the growth rate is constrained by lowest stave.

Multiple resource limitation:

- the growth rate is constrained by the nutrient-specific water holes.

The growth rate of an organism is depicted here as the current water level in the barrel.

- Liebig’s law gives the upper bound on the growth rate, which is set by the lowest stave.
- The proposed multiple resource limitation gives the lower bound on the growth rate due to the combined limitation of all resources, which is described using the water holes at the bottom of the barrel.
- The true growth rate of an organism is then somewhere between these two bounds.

MRL applied to the LKE model.

1. Producer-grazer system is closed.
2. Minimum P:C ratio for producer is q.
3. P:C ratio of the grazer is fixed at θ.
4. Grazer dies at a constant rate d.
5. Density of producer is limited by light at a maximum K.
6. Intake phosphorus P_{IN} can be partitioned.
7. The energy conversion efficiency for the grazer is an increasing function of the C:P ratio in the producer. (*)

$$\begin{aligned}
\text{(Producer rate of change)} &= \text{(Growth rate)} - \text{(Predation rate)}\\
\text{(grazer rate of change)} &= \text{(Conversion to biomass)} \times \text{(Predation rate)} - \text{(Death rate)}.
\end{aligned}$$

Goal 1: determine the amount of phosphorus intake per $f(x)y$ (predation)

1. Since P:C is θ for grazer, θy is the total amount of phosphorus in the grazer population.
2. Since P is conserved in the closed system, the total amount of phosphorus in the producer population is: $P - \theta y$.
3. The P:C ratio for the producer is $\boldsymbol{Q = (P - \theta y)/x}$.
4. The total amount of phosphorus acquired from predation is $\boldsymbol{Q \times f(x)y}$.

Goal 2: find phosphorus that goes into biomass production for the grazer.

1. Not all acquired phosphorus is used for biomass production.
2. Assume that phosphorus intake (P_{IN}) is partitioned into P_R and P_P.
    - P_R is the phosphorus going into maintaining/building the existing/new machinery.
    - P_P is the phosphorus reserved for biomass synthesis (processed by P_R).
3. Let $\alpha(\cdot)$ be the optimal function that optimize the growth process by optimizing the fraction of intake phosphorus that goes into P_R and P_P.
4. Then, the most efficient division would have each P_R processes $\alpha(\cdot)$ unit of P_P to build biomass.

+ If $\alpha(\cdot)$ is small ($\ll 1$), then most of the intake resource (phosphorus) goes into maintaining the machinery.

+ If $\alpha(\cdot)$ is very large, then most of the intake P goes into making new biomass.

$$P_{IN} = P_R + P_P = P_R + \alpha(\cdot)P_R = \big(1 + \alpha(\cdot)\big)P_R.$$

$$P_R = \frac{1}{1+\alpha(\cdot)}P_{IN} \qquad \text{and} \qquad P_P = \frac{\alpha(\cdot)}{1+\alpha(\cdot)}P_{IN}.$$

$$P_P = \frac{\alpha(\cdot)}{1+\alpha(\cdot)}P_{IN} = \frac{\alpha(\cdot)}{1+\alpha(\cdot)}Qf(x)y.$$

Goal 3: find biomass synthesis from predation.
Since P:C is θ for the grazer, we have

$$(\text{Conversion to biomass}) \times (\text{Predation rate}) = \left(\frac{1}{\theta}\frac{\alpha(\cdot)}{1+\alpha(\cdot)}\right)Qf(x)y$$

The rate of change equation for the grazer population:

$$\frac{dy}{dt} = \frac{\alpha(\cdot)}{1+\alpha(\cdot)}\frac{Qf(x)y}{\theta} - dy.$$

Goal 4: apply the MRL to the growth of the producer population.

$$\mu\frac{\left(1-\frac{x}{K}\right)\left(1-\frac{q}{Q}\right)}{\left(1-\frac{x}{K}\right)+\left(1-\frac{q}{Q}\right)}$$

The rate of change equation for the producer population:

$$\frac{dx}{dt} = \mu\frac{\left(1-\frac{x}{K}\right)\left(1-\frac{q}{Q}\right)}{\left(1-\frac{x}{K}\right)+\left(1-\frac{q}{Q}\right)}x - f(x)y$$

Goal 5: Determine the biomass efficiency conversion rate.
By assumption (7), $\alpha(\cdot)$ is an increasing function of $1/Q$ (or the C:P ratio of the producer), which we assume to take the form:

$$\alpha\left(\frac{1}{Q}\right) = a\,\frac{1/Q}{m + 1/Q} = \frac{a}{mQ + 1}.$$

a is the maximum efficiency of biomass production.
m is the half-saturation of biomass production efficiency.

$$\frac{\alpha(\cdot)}{1 + \alpha(\cdot)} = \frac{a}{a + mQ + 1}$$

Goal 6: the predation functional response $f(x)$ is taken to be: $f(x) = \frac{cx}{k+x}$.

Possible mechanism for assumption 7: The energy conversion efficiency for the grazer is an increasing function of the C:P ratio in the producer.

It has been noted that a higher C:P ratio (lower P:C ratio) in the producer tends to decrease the efficiency in the transfer of energy (C) and increasing P can increase the biomass of the upper trophic species.

In our model, the P: C ratio of the producer is represented by $Q = (P - \theta y)/x$. Thus, higher Q means a lower relative energy content in the producer (lower C relative to P). Additionally, since the total quantity of P is fixed in our model, more P in the producer biomass (or higher Q) implies less P in the grazer biomass.

Since all P intake (P_{IN}) is partitioned into P_R and P_P, e.g., $P_R + \alpha(\cdot)P_P = P_{IN}$, and if we assume the ***organism prioritizes survival over growth***, then it means the cell must prioritize keeping P_R relatively constant over maximizing P_P.

$$\alpha(\cdot)P_P = P_{IN} - P_R$$

Note that the right-hand side is a decreasing function of increasing P (or Q) in the producer. The left-hand side is the amount of phosphorus going into new biomass production. Thus, as P_{IN} decreases and P_R is kept constant, the amount of phosphorus partitioned for new biomass production decreases. Therefore, $\alpha(\cdot)$ can be considered to be a decreasing function of increasing P (or increasing Q).

In other words, to account for the effect of energy, we can consider $\alpha(\cdot)$ as an increasing function of $1/Q$ (instead of a decreasing function of Q). That is, higher P in producers leads to higher Q, but lower P in the grazers (lower $1/Q$), which would lead to a lower food conversion efficiency value for $\alpha(\cdot)$ while decreasing P in producer has the opposite effect.

Theorem 1: The biological solutions of the proposed model are eventually bounded within the set

$$\Omega = \left\{(x,y): x,y > 0, x \leq \min\left\{K, \frac{P}{q}\right\}, y \leq \frac{P}{\theta}\right\}.$$

In summary, the LKE model takes the form:

$$\frac{dx}{dt} = \mu x\left(1 - \frac{x}{\min\left(K, (P-\theta y)/q\right)}\right) - \frac{cx}{k+x}y$$

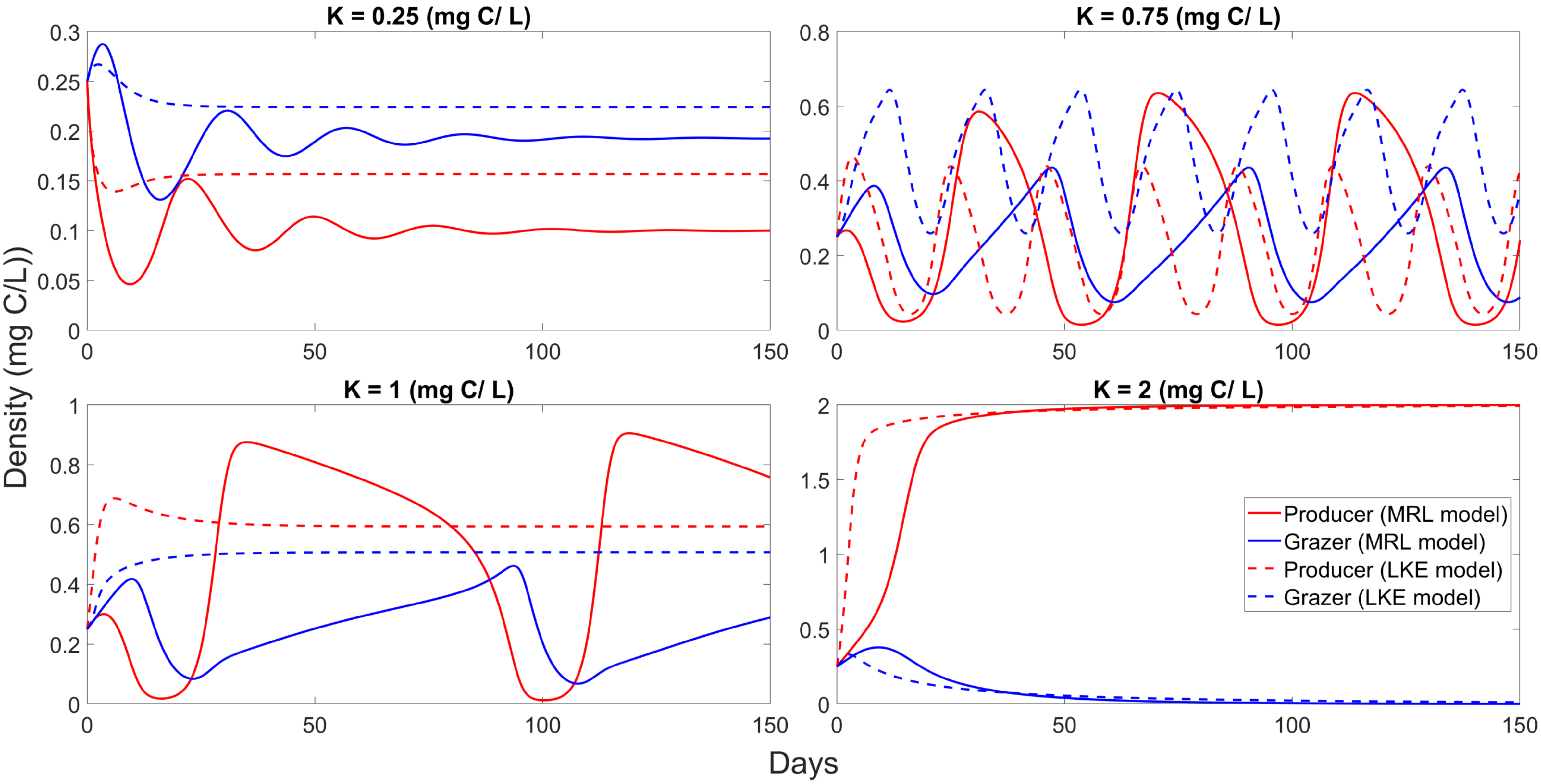
$$\frac{dy}{dt} = b_1 \min\left(1, \frac{(P-\theta y)/x}{\theta}\right)\frac{cx}{k+x}y - dy.$$

The MRL model takes on the following form for comparison purposes:

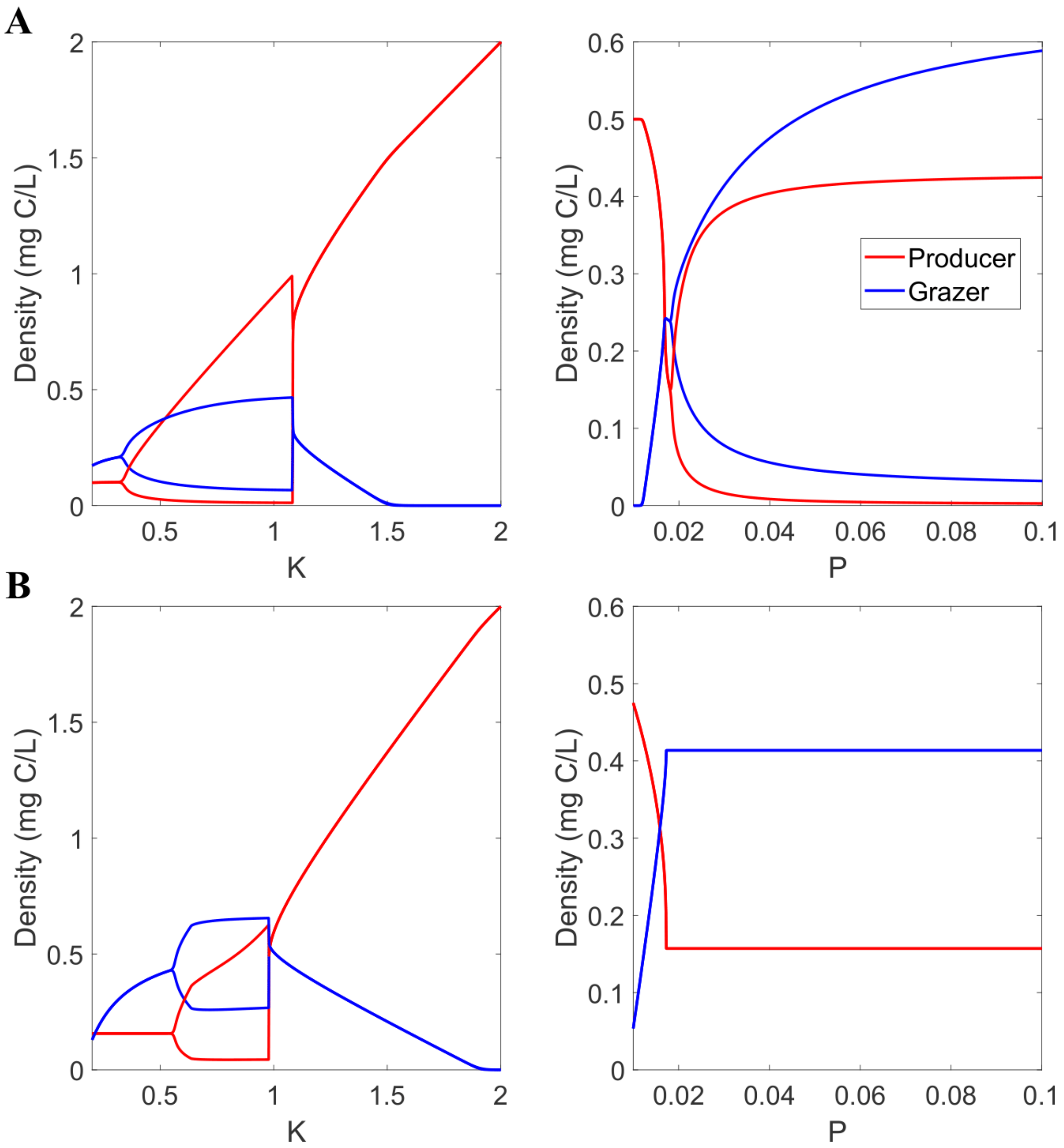
$$\frac{dx}{dt} = \mu\frac{\left(1-\frac{x}{K}\right)\left(1-\frac{q}{Q}\right)}{\left(1-\frac{x}{K}\right)+\left(1-\frac{q}{Q}\right)}x - \frac{cx}{k+x}y$$

$$\frac{dy}{dt} = \frac{a}{a+mQ+1}\frac{cx}{k+x}\frac{Q}{\theta}y - dy.$$

Comparison of model dynamics



Comparison of model bifurcation.



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THANK YOU!