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Global analysis of a stoichiometric producer–grazer model with Holling type functional responses

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Abstract Cells, the basic units of organisms, consist of multiple essential elements such as carbon, nitrogen, and phosphorus. The scarcity of any of these elements can strongly restrict cellular and organismal growth. During recent years, ecological models incorporating multiple elements have been rapidly developed in many studies, which form a new research field of mathematical and theoretical biology. Among these models, the one proposed by Loladze et al. (Bull Math Biol 62:1137–1162, 2000) is prominent and has been highly cited. However, the global analysis of this nonsmooth model has never been done. The aim of this paper is to provide the complete global analysis for the model with Holling type I functional response and perform a bifurcation analysis for the model with Holling type II functional response.

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1 Introduction

Ecological stoichiometry is the study of the balance of energy (carbon) and multiple nutrients (such as phosphorus and nitrogen) in ecological interactions (Sterner and Elser 2002). All organisms are composed of these fundamental elements. The scarcity of any of these elements can severely restrict organismal growth. Empirical studies show that plants can be easily limited by nutrient availability, and herbivores are more nutrient-rich organisms than plants (Elser et al. 2000). The plant nutrient quality can dramatically affect the growth of herbivorous grazers and may even lead to their extinction (Urabe et al. 2002). However, historic predator–prey interaction models only consider energy/carbon flow, usually quantified by population or density. To be realistic, both food quantity and food quality need to be incorporated in modeling producer–grazer interactions.

The growing empirical studies of ecological stoichiometry facilitate a series of newly emerged stoichiometric population models (Andersen 1997; Grover 2002; Hessen and Bjerkeng 1997; Kuang et al. 2004; Loladze et al. 2000; Wang et al. 2007, 2008). One of the most popular stoichiometric producer–grazer models is the one proposed by Loladze et al. (2000):

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

$$\frac{dy}{dt} = e\min\left\{1, \frac{(P-\theta y)/x}{\theta}\right\} f(x)y - dy, \tag{2}$$

where

x	is the density of producer (mg C/l),
y	is the density of grazer (mg C/l),
b	is the intrinsic growth rate of producer (/day),
K	is the carrying capacity of producer, which is positively related to light intensity,
e	is the maximal production efficiency of grazer (no unit),
d	is the specific loss rate of grazer that includes metabolic losses and death (/day),
q	is the minimal phosphorus:carbon ratio in producer (mg P/mg C),
θ	is the constant phosphorus:carbon ratio in grazer (mg P/mg C),
P	the total mass of phosphorus in the entire system (mg P/l),
$f(x)$	is the consumption rate of grazer (/day), which is usually one of Holling type functional responses

In this model, the ratio of two essential chemical elements, phosphorus to carbon, represents producer quality.

The model in Loladze et al. (2000) is nonsmooth and has complex dynamics with multiple internal equilibria, limit cycles, and bistability. Saddle-node bifurcation, transcritical bifurcation, supercritical and subcritical Hopf bifurcations appear in this model, especially, at one bifurcation point of light intensity (i.e., K) both subcritical Hopf bifurcation and saddle-node bifurcation occur. Loladze et al. (2000) presented graphical tests for the local stability of all equilibria and plotted a bifurcation diagram showing how dynamics change as light intensity varies. In this paper, we provide a rigorous mathematical analysis for local and global stability results of all equilibria and the existence of limit cycles. For the model with Holling type I functional response, we present complete analytical results. For the model with Holling type II functional response, we provide a rigorous bifurcation analysis for the parameter K.

2 Global analysis of the model with Holling type I functional response

Basic assumptions for the type I model are the following:

(i) $f(x) = \alpha x$ (Holling type I functional response);
(ii) $q < \theta$ (biologically reasonable for most plants and their corresponding herbivores);
(iii) $e < 1$ (due to thermodynamic limitations).

For simplicity, we scale the system by

$$P/\theta \to P, \quad q/\theta \to q, \quad \alpha dt \to dt, \quad b/\alpha \to b, \quad d/\alpha \to d$$

to obtain the new system

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{\min\{K, (P-y)/q\}}\right) - xy \triangleq xF(x, y), \tag{3}$$

$$\frac{dy}{dt} = e\min\{x, P-y\}\, y - dy \triangleq yG(x, y). \tag{4}$$

Here,

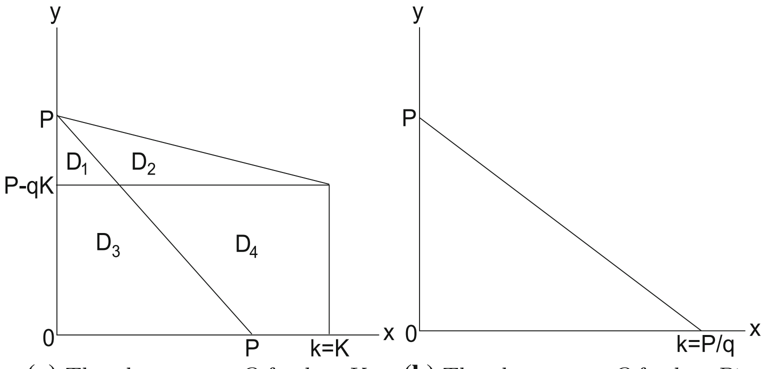
$$F(x, y) = b\left(1 - \frac{x}{\min\{K, (P-y)/q\}}\right) - y = \begin{cases} b - \frac{bx}{K} - y, & y \le P - qK; \\ b - \frac{bqx}{P-y} - y, & y > P - qK. \end{cases}$$

$$G(x, y) = e\min\{x, P-y\} - d = \begin{cases} ex - d, & x + y \le P; \\ eP - d - ey, & x + y > P. \end{cases}$$

Let

$$k = \min\{K, P/q\} = \begin{cases} K, & K < P/q; \\ P/q, & K \ge P/q, \end{cases}$$

$$\Omega = \{(x, y) : 0 < x < k, 0 < y < P, qx + y < P\}.$$



(a) The phase space Ω for $k = K$. **(b)** The phase space Ω for $k = P/q$.

Fig. 1 When $k = K$, Ω is an *open trapezoid*, while when $k = P/q$, Ω is an *open triangle*

When $k = K$, Ω is an open trapezoid (see Fig. 1a). In this case, we define

$$\begin{aligned}
D_1 &= \{(x, y) \in \Omega : y > P - qK, x + y < P\},\\
D_2 &= \{(x, y) \in \Omega : y > P - qK, x + y > P\},\\
D_3 &= \{(x, y) \in \Omega : y < P - qK, x + y < P\},\\
D_4 &= \{(x, y) \in \Omega : y < P - qK, x + y > P\}.
\end{aligned}$$

When $k = P/q$, Ω is an open triangle (see Fig. 1b).

2.1 Basic results

In this section, we prove the dissipativity and the nonexistence of limit cycles.

Theorem 1 (Dissipativity) Ω *is positively invariant for the semiflow generated by system* (3)–(4).

Proof We only prove the invariance for the case $k = K$ since the other case $k = P/q$ is simpler to prove.

The positive x-axis and the positive y-axis are both invariant. On the right boundary of Ω, $x = k, 0 \le y \le P - qk$, we have $dx/dt = -ky < 0$. Therefore, all orbits starting from Ω cannot escape Ω from these three boundaries. To show that solutions starting from Ω cannot escape Ω from the upper boundary, we define

$$z = qx + y.$$

Then on the upper boundary, $qx + y = P, 0 \le x \le k$, we have

$$dz/dt = qdx/dt + dy/dt = -(1 - e)qxy - edy,$$

where we use the assumption (ii), i.e. $q < 1$ after scaling, which guarantees that all points (x, y) on the upper boundary satisfy $x+y > P$ and thus $G(x, y) = eP-d-ey$

on the upper boundary. According to the assumption (iii), $e < 1$, we have $dz/dt < 0$ on the upper boundary. Hence, all orbits starting from Ω will stay in Ω for all forward times. □

Theorem 2 *System* (3)–(4) *has no nontrivial periodic solutions in* Ω.

Proof The vector field defined by system (3)–(4) is locally Lipschitz-continuous in Ω, which guarantees the existence and uniqueness of solutions of system (3)–(4). However, this vector field is not C^1, so the classical Dulac's criterion cannot be applied. Fortunately, there is a generalized Dulac's criterion for locally Lipschitz-continuous planar systems

$$\frac{d\mathbf{x}}{dt} = f(\mathbf{x}), \quad \mathbf{x} \in D \subset \mathbb{R}^2. \tag{5}$$

If D is a simply connected, bounded, open subset of $\mathbb{R}^2$, and there exist a C^1 function $\chi : D \to \mathbb{R}$ and a constant $c > 0$ such that

$$\mathrm{div}(\chi(\mathbf{x}) f(\mathbf{x})) \leq -c, \quad a.e. \quad \text{in} \quad D,$$

then every compact limit set of (5) in D consists of equilibria and every compact invariant set of (5) in D is a set of equilibria and heteroclinic orbits containing no heteroclinic cycles, for instance, see Theorem 9 in Sanchez (2005); here a heteroclinic cycle is a Jordan curve that consists of equilibria and heteroclinic (or homoclinic) orbits of (5).

Similar to Theorem 1, we only consider the case: Ω is an open trapezoid. Choose

$$\chi(x, y) = \frac{1}{xy}.$$

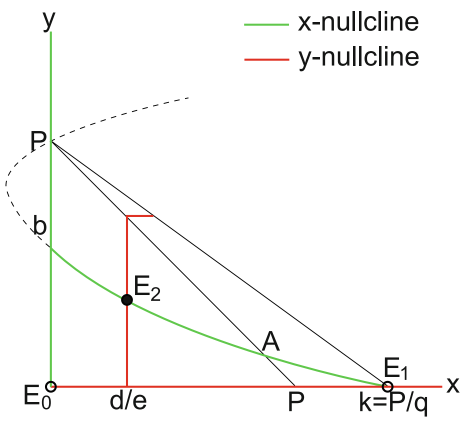
Simple computations yield that

$$\mathrm{div}(\chi(x, y) f(x, y)) = \begin{cases} \frac{-qb}{y(P-y)}, & \text{in region } D_1, \\ \frac{-qb}{y(P-y)} - \frac{e}{x}, & \text{in region } D_2, \\ -\frac{b}{K}, & \text{in region } D_3, \\ -\frac{b}{K} - \frac{e}{x}, & \text{in region } D_4, \end{cases}$$

where the regions D_1, D_2, D_3, D_4 are defined in Fig. 1a. Define $c = \min\{c_1, c_2, c_3, c_4\}$, where

$$\begin{aligned} c_1 &= \min_{(x,y)\in D_1} \left(\frac{qb}{y(P-y)} \right), \\ c_2 &= \min_{(x,y)\in D_2} \left(\frac{qb}{y(P-y)} + \frac{e}{x} \right), \\ c_3 &= \frac{b}{K}, \\ c_4 &= \min_{(x,y)\in D_4} \left(\frac{b}{K} + \frac{e}{x} \right). \end{aligned}$$

Fig. 2 The nullclines and equilibria for $K \geq P/q$ and $b < P$



It is easy to see that $c > 0$. Hence, the generalized Dulac's criterion can be applied to system (3)–(4) in Ω and thus the proof is completed. □

2.2 The case $K \geq P/q$

Basic facts in this case are as follows:

1. $k = \min\{K, P/q\} = P/q$ (so Ω is an open triangle).
2. $F(x, y) = b - \frac{bqx}{P-y} - y$.
3. $G(x, y) = \begin{cases} ex - d, & x + y \leq P; \\ (eP - d) - ey, & x + y > P. \end{cases}$
4. $F_x = -\frac{bq}{P-y} < 0, \qquad F_y = -\frac{bqx}{(P-y)^2} - 1 < 0.$
5. $G_x = \begin{cases} e, & x + y \leq P; \\ 0, & x + y > P. \end{cases} \qquad G_y = \begin{cases} 0, & x + y \leq P; \\ -e, & x + y > P. \end{cases}$

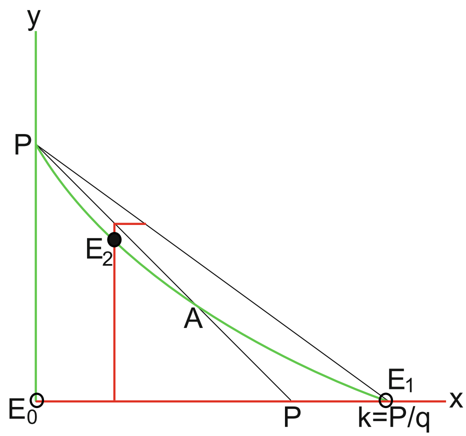
We first examine the nullclines of the system.
x-**nullcline**: $x = 0$ and $F(x, y) = 0$, where $F(x, y) = 0$ implies

$$y = (1/2)\left[b + P - \sqrt{(b-P)^2 + 4bqx}\right] \triangleq g(x).$$

If $b < P$, we have $g(0) = b$, $g(k) = 0$. That is, x-nullcline is the positive y-axis and a monotone decreasing smooth curve connecting the starting point $(0, b)$ and the ending point $(k, 0)$ (see Fig. 2).

If $b \geq P$, then $g(0) = P$, $g(k) = 0$, and x-nullcline is the positive y-axis and a monotone decreasing smooth curve connecting $(0, P)$ and $(k, 0)$ with the exception of a biologically insignificant point $(0, P)$ (at this point the grazer contains all phosphorus and thus the producer is absent from the system) (see Fig. 3).

Fig. 3 The nullclines and equilibria for $K \geq P/q$ and $P \leq b < P/(1-q)$



Denote by A the intersection point of the curve: $y = g(x)$ and the line $x + y = P$, then the coordinate of A is

$$x_A = P - b + bq, \quad y_A = b - bq.$$

If $b < \frac{P}{1-q}$, then $x_A > 0$; if $b \geq \frac{P}{1-q}$, then $x_A \leq 0$.
y**-nullcline**: $y = 0$ and $G(x, y) = 0$.
If $\frac{d}{e} < P$, $G(x, y) = 0 \Rightarrow \begin{cases} x = \frac{d}{e}, & 0 < y \leq P - \frac{d}{e}; \\ y = P - \frac{d}{e}, & \frac{d}{e} \leq x \leq \frac{d}{qe}. \end{cases}$ That is, in this case y-nullcline is the positive x-axis and a right-angle line (see Figs. 2, 3).
If $\frac{d}{e} = P$, $G(x, y) = 0 \Rightarrow y = 0$, $\frac{d}{e} = P \leq x \leq k$.
If $\frac{d}{e} > P$, then for any $(x, y) \in \Omega$, $G(x, y) < 0$.
Next, we examine the stability of equilibria on the boundary.
To find equilibria, we solve

$$xF(x, y) = 0,$$
$$yG(x, y) = 0.$$

The boundary equilibria are $E_0 = (0, 0)$ and $E_1 = (k, 0)$.

To determine the local stability of these equilibria, we consider the Jacobian matrix of system (3)–(4):

$$J(x, y) = \begin{pmatrix} F(x, y) + xF_x(x, y) & xF_y(x, y) \\ yG_x(x, y) & G(x, y) + yG_y(x, y) \end{pmatrix}.$$

At the origin, it takes the form $J(E_0) = \begin{pmatrix} b & 0 \\ 0 & -d \end{pmatrix}$. Since the determinant is negative, the eigenvalues have different signs. Thus, the origin E_0 is always unstable in the form of a saddle, whose stable manifold is y-axis and unstable manifold is x-axis.

At E_1, the Jacobian matrix is

$$J(E_1) = \begin{pmatrix} F(k,0) + kF_x(k,0) & kF_y(k,0) \\ 0 & G(k,0) \end{pmatrix} = \begin{pmatrix} -b & -\frac{b+P}{q} \\ 0 & eP - d \end{pmatrix}.$$

If $eP - d > 0$, i.e., $d/e < P$, then the eigenvalues of $J(E_1)$ have different signs. Thus, E_1 is always unstable in the form of a saddle, whose stable manifold is x-axis and unstable manifold direction is

$$y = -\frac{q(eP - d + b)}{b + P}(x - k).$$

Note that

$$-\frac{q(eP - d + b)}{b + P} > -q.$$

Therefore, the slope of the unstable manifold direction is larger than that of the line $qx + y = P$, which is the upper boundary of Ω, and this implies the unstable manifold lies inside Ω. In this case, we can deduce that there are internal equilibria in Ω.

If $eP - d < 0$, i.e., $d/e > P$, then the eigenvalues of $J(E_1)$ are both negative, thus E_1 is always a stable node. Moreover, E_1 is globally asymptotically stable. In fact, in this case there are only the boundary equilibria and no internal equilibria. In addition, there are no nontrivial periodic solutions (by Theorem 2), and the only direction towards the origin is y-axis, which is invariant. Hence, all orbits will eventually tend to the equilibrium E_1, and E_1 is a G.A.S node. Also we can easily deduce this fact by $dy/dt < 0$ in the whole phase space Ω.

The neutral case $d/e = P$ is a bit complicated. In this case, saddle-node bifurcation appears. When $x_A < d/e < P$, system (3)–(4) has only one internal equilibrium $E_2 = (d/e, g(d/e))$, which is a G.A.S. node (see Theorem 4 below), and we had shown that E_1 is a saddle when $d/e < P$. If d/e tends to P from the left side, then E_2 tends to E_1, and $d/e = P$ implies that E_2 collides E_1; thus, E_1 is a saddle-node, and saddle-node bifurcation appears. Interestingly, all orbits in Ω also tends to E_1 because the unstable manifold direction does not belong to Ω. Also, we can obtain this result by 1) $dy/dt < 0$ in Ω; 2) $dy/dt = 0$ if and only if $y = 0,\ P \le x \le P/q$.

Summarizing the above discussions, we obtain the following theorem.

Theorem 3 *The origin E_0 is an unstable saddle, and the only direction towards E_0 is y-axis. For the stability of the equilibrium E_1, there are three cases:*

If $d/e < P$, the equilibrium E_1 is an unstable saddle, and the only direction towards E_1 is x-axis;
If $d/e > P$, the equilibrium E_1 is a G.A.S. node;
If $d/e = P$, the equilibrium E_1 is a saddle-node, saddle-node bifurcation appears, and all orbits in Ω will eventually tend to the equilibrium E_1.

As mentioned before, system (3)–(4) has only one internal equilibrium $E_2 = (d/e, g(d/e))$ if and only if $d/e < P$. If $d/e < x_A = P - b + bq$, then E_2 lies below the line $x + y = P$; if $x_A < d/e < P$, then E_2 lies above the line $x + y = P$; if $d/e = x_A$, then E_2 lies on the line $x + y = P$ (see Figs. 2, 3). Also, the fact that the intersection point A belongs to the phase space Ω or not is very important to discuss the stability of E_2. First we will consider the case: $x_A > 0$.

2.2.1 (i) $b < \frac{P}{1-q}$

Theorem 4 *The internal equilibrium E_2 is G.A.S. whenever it exists.*

1. *If $0 < d/e < x_A = P - b(1-q)$, then E_2 is a G.A.S. equilibrium. Define*

$$\lambda \triangleq (1/4)\left[b + P + \frac{bq}{4e} - \sqrt{\left(b + P + \frac{bq}{4e}\right)^2 - \frac{2b^2q}{e}}\right] \tag{6}$$

   and

$$\mu \triangleq g^{-1}(\lambda) \tag{7}$$

   whenever λ is a real number. Then if $\frac{d}{e} < \mu$, E_2 is a G.A.S. focus. If λ is not a real number, or $\frac{d}{e} \geq \mu$, E_2 is a G.A.S. node;
2. *If $x_A < d/e < P$, then E_2 is a G.A.S. node, and there exists a heteroclinic orbit connecting E_2 and E_1.*
3. *If $d/e = x_A$, then E_2 is a G.A.S. node, and there also exists a heteroclinic orbit connecting E_2 and E_1.*

Proof For the case 1: $d/e < x_A$, at the equilibrium E_2 the Jacobian matrix takes the form

$$J(E_2) = \begin{pmatrix} xF_x & xF_y \\ yG_x & yG_y \end{pmatrix} = \begin{pmatrix} -\frac{bqx}{P-y} & -\frac{bqx^2}{(P-y)^2} - x \\ ey & 0 \end{pmatrix}$$

with $x = x_{E_2} = d/e$, $y = y_{E_2} = g(d/e)$. Its determinant and trace are respectively

$$\mathrm{Det}J(E_2) = ey\left[x + \frac{bqx^2}{(P-y)^2}\right] > 0, \qquad \mathrm{Tr}J(E_2) = -\frac{bqx}{P-y} < 0.$$

Therefore, all eigenvalues of $J(E_2)$ have negative real parts, and by Theorems 2 and 3, the equilibrium E_2 is G.A.S. To determine E_2 is a focus or a node, we need to determine the sign of the discriminant

$$\Delta(E_2) = \frac{b^2q^2x^2}{(P-y)^2} - 4ey\left[x + \frac{bqx^2}{(P-y)^2}\right]$$

with $x = x_{E_2} = d/e$, $y = y_{E_2} = g(d/e)$. In fact,

$$\begin{aligned}\Delta(E_2) = &\ (b-y)^2 - 4ey\left[\tfrac{(b-y)^2}{bq} + \tfrac{(b-y)(P-y)}{bq}\right] \\ = &\ \tfrac{4e(b-y)}{bq}\left[2y^2 - (b + P + \tfrac{bq}{4e})y + \tfrac{b^2q}{4e}\right].\end{aligned}$$

Define

$$h(y) = 2y^2 - \left(b + P + \frac{bq}{4e}\right) y + \frac{b^2 q}{4e}$$

for $y \in [0, P]$.

First we consider the case: $b < P$. Let λ be the smaller root of $h(y)$, i.e.,

$$\lambda = (1/4)\left[b + P + \frac{bq}{4e} - \sqrt{\left(b + P + \frac{bq}{4e}\right)^2 - \frac{2b^2 q}{e}}\, \right]$$

and

$$\mu = g^{-1}(\lambda).$$

Note that $h(0) > 0, h(b) < 0$, thus λ is a real number and $\lambda < b$. If $\lambda < y_{E_2}$, i.e. $\frac{d}{e} < \mu$, then $h(y_{E_2}) < 0$ which implies that $\Delta(E_2) < 0$. Thus, E_2 is a focus. Conversely, if $\lambda \geq y_{E_2}$, i.e. $\frac{d}{e} \geq \mu$, then $h(y_{E_2}) \geq 0$ which implies that $\Delta(E_2) \geq 0$. Thus, E_2 is a node.

For the second case: $P \leq b < \frac{P}{1-q}$, we also have that $h(0) > 0$ and $h(b) = b(b - P) \geq 0$. However since $h(P) = (P - \frac{bq}{4e})(P - b)$, therefore if $b < \frac{4eP}{q}$, $h(P) < 0$; if $b \geq \frac{4eP}{q}$, $h(P) \geq 0$. Thus, the case $h(P) < 0$ (or $h(y^*) < 0$ for some $y^* \in (0, P)$) is completely same as the first case: $b < P$, λ is a real number and we can obtain the same conclusion. If $h(P) \geq 0$ and for any $y \in (0, P)$, $h(y) > 0$, then $\Delta(E_2) \geq 0$ and E_2 is a node. Note that in this case λ is not a real number.

For the case 2: $P - b(1 - q) < d/e < P$, E_2 lies above the line $x + y = P$, and the Jacobian matrix $J(E_2)$ takes the form

$$J(E_2) = \begin{pmatrix} -\frac{bqx}{P-y} & -\frac{bqx^2}{(P-y)^2} - x \\ 0 & -ey \end{pmatrix}.$$

Its eigenvalues are $-bqx/(P - y)$ and $-ey$, and by Theorems 2 and 3, E_2 is a G.A.S. node. Note that, by Theorem 3, the unstable manifold direction of E_1 directs inward. Thus, there exists a heteroclinic orbit connecting E_2 and E_1.

For the case 3: $d/e = x_A = P - b(1-q)$, E_2 is the same as A and lies on the line $x + y = P$. Since G_x and G_y are not continuous on this line, we cannot compute the Jacobian matrix of E_2. Also, as in case 2, there exists a heteroclinic orbit connecting E_2 and E_1. In addition, the line: $x_A \leq x \leq (P - y_A)/q$, $y = y_A$ is also an orbit that directs to E_2. Therefore, by Theorems 2 and 3, E_2 is a G.A.S. node. $\square$

Let us discuss the case 1 in Theorem 4 more precisely to end this section. First we consider the second case: $P \leq b < \frac{P}{1-q}$. From the proof, we know that $h(P) < 0$ is equivalent to $b < \frac{4eP}{q}$. Since $b < \frac{P}{1-q}$, we have a sufficient condition $q < 4e/(1+4e)$ for $h(P) < 0$. That is, if $q < 4e/(1 + 4e)$, then $h(P) < 0$, and λ is a real number.

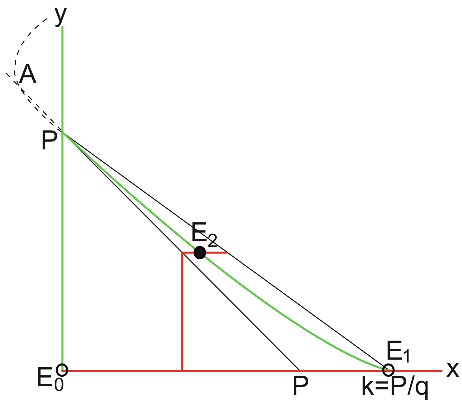


Fig. 4 The nullclines and equilibria for $K \geq P/q$ and $b \geq P/(1-q)$

Secondly, we show that if $q < 4e/(1+4e)$, then $\lambda \leq y_A = b - bq < y_{E_2}$, i.e. $\mu \geq x_A > \frac{d}{e}$. In fact, the smaller root λ of $h(y)$ is less than or equal to $b - bq$, which is equivalent to $h(b-bq) \leq 0$, i.e.,

$$\Delta(b-bq) = b^2q^2 - 4e(b-bq)[P - b + 2bq] \leq 0,$$

which implies that $q^2 - 4e(1-q)(\frac{P}{b} - 1 + 2q) \leq 0$. Since $\frac{P}{b} - 1 > -q$ (by the condition $b < \frac{P}{1-q}$), we have a sufficient condition $q^2 < 4e(1-q)q$ for $h(b-bq) \leq 0$, i.e., $q < 4e/(1+4e)$. Therefore, if the condition $q < 4e/(1+4e)$ holds, then E_2 in case 1 is a G.A.S. focus. In biology, e is in the scale 0.1 and q is in the scale 0.001, thus the sufficient condition $q < 4e/(1+4e)$ is always valid in reality.

2.2.2 *(ii)* $b \geq \dfrac{P}{1-q}$

In this subcase, the intersection point A does not belong to Ω since $x_A = P\text{–}b(1\text{–}q) \leq 0$. the equilibrium E_2 lies above the line $x + y = P$ (see Fig. 4). We obtain the conclusion by replacing x_A with $x_A = P - b + bq < 0$ in Theorem 4:

Theorem 5 *If* $0 < \dfrac{d}{e} < P$, *then* E_2 *is a G.A.S. node, and there exists a heteroclinic orbit connecting* E_2 *and* E_1.

2.3 The case $P \leq K < P/q$

Basic facts in this case are as follows:

1. $k = \min\{K, P/q\} = K$.
2. $\Omega = \{(x, y) : 0 < x < k, 0 < y < P, 0 < qx + y < P\}$ is an open trapezoid.

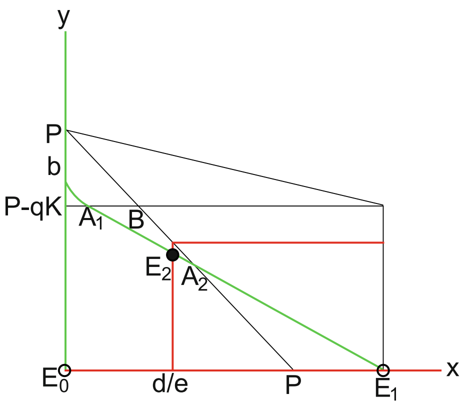


Fig. 5 The nullclines and equilibria for $P \le K < P/q$ and $P - qK < b < (P - qK)/(1 - q)$

3. $dx/dt = xF(x, y), dy/dt = yG(x, y)$, where

$$F(x, y) = \begin{cases} b(1 - \frac{x}{K}) - y, & 0 \le y \le P - qK, \\ b(1 - \frac{qx}{P-y}) - y, & P - qK < y < P; \end{cases}$$

$$G(x, y) = \begin{cases} ex - d, & 0 \le x + y \le P, \\ (eP - d) - ey, & x + y > P. \end{cases}$$

y**-nullcline** in this case is completely same as that in Sect. 2.2, which is the positive x-axis and a right-angle line, and x**-nullcline** is different from that in Sect. 2.2 according to the value of b. When $0 < b \le P - qK$, x-nullcline is the positive y-axis and a line segment connecting the starting point $(0, b)$ and the ending point $(k, 0)$. When $b > P - qK$, besides the positive y-axis, x-nullcline consists of two parts, one is the parabola $y = g(x)$, the other is a line $y = b(1 - \frac{x}{K})$ (see Fig. 5). In this case, when $P - qK < b < P$, the starting point is $(0, b)$; when $b \ge P$, the starting point is $(0, P)$.

Denote by A_1 the intersection point of x-nullcline and the line $y = P - qK$ (if it exists). That is,

$$A_1(x_1, y_1) : \begin{cases} b(1 - \frac{x}{K}) - y = 0, \\ y = P - qK. \end{cases} \Rightarrow \begin{cases} x_1 = K[1 - (P - qK)/b], \\ y_1 = P - qK. \end{cases}$$

Denote by B the intersection point of the line $x + y = P$ and the line $y = P - qK$. That is,

$$(x_B, y_B) = (qK, P - qK).$$

Denote by A the intersection point of x-nullcline and the line $x + y = P$ in the domain $\{(x, y) \in \Omega : y \ge P - qK\}$. That is,

$$A(x_A, y_A) : \begin{cases} b(1 - \frac{qx}{P-y}) - y = 0, \\ x + y = P. \end{cases} \Rightarrow \begin{cases} x_A = P - b[1 - q], \\ y_A = b - bq. \end{cases}$$

Denote by A_2 the intersection point of x-nullcline and the line $x + y = P$ in the domain $\{(x, y) \in \Omega : y < P - qK\}$. That is,

$$A_2(x_2, y_2) : \begin{cases} x + y = P, \\ b(1 - \frac{x}{K}) - y = 0. \end{cases} \Rightarrow \begin{cases} x_2 = K\frac{P-b}{K-b}, \\ y_2 = b\frac{K-P}{K-b}. \end{cases}$$

For the stability of the boundary equilibria, since

$$J(E_0) = \begin{pmatrix} b & 0 \\ 0 & -d \end{pmatrix}$$

and

$$J(E_1) = \begin{pmatrix} -b & -K \\ 0 & eP - d \end{pmatrix},$$

the stability of E_0 and E_1 are completely same as in Sect. 2.2. We omit the details.

In order to discuss the stability of the internal equilibrium E_2, we need to know the relative position relationship about these intersection points $A,\ A_1,\ A_2, B$. This case is divided into four subcases by different ranges of b:

(i) $P - qK < b < \dfrac{P - qK}{1 - q}$;
(ii) $0 < b \leq P - qK$;
(iii) $\dfrac{P - qK}{1 - q} \leq b < \dfrac{P}{1 - q}$;
(iv) $b \geq \dfrac{P}{1 - q}$.

Note that $\frac{P-qK}{1-q} \leq P$ in this case, since $P \leq K$. In the subcases (i)&(ii), the intersection A_1 is on the left side of B. In the subcases (iii) & (iv), the intersection A_1 is on the right side of the intersection B.

2.3.1 (i) $P - qK < b < \dfrac{P - qK}{1 - q}$

In this subcase, $0 < x_1 < x_B < x_2$, and A does not exist (see Fig. 5). For the stability of the internal equilibrium E_2, we have the following theorem:

Theorem 6 1. *If $0 < d/e < x_1$, then E_2 is a G.A.S. equilibrium. Moreover, if $d/e < \mu$ (see Theorem 4 for the definition of μ), then E_2 is a G.A.S. focus; if λ is not a real number (see Theorem 4 for the definition of λ), or $d/e \geq \mu$, then E_2 is a G.A.S. node.*
2. *If $d/e = x_1$, then E_2 is a G.A.S. equilibrium and there exists a heteroclinic orbit connecting E_2 and E_1.*
3. *If $x_1 < d/e < x_2$, then E_2 is a G.A.S equilibrium. Moreover, if $d/e < \frac{4eK^2}{b+4eK}$, then E_2 is a G.A.S. focus; if $d/e \geq \frac{4eK^2}{b+4eK}$, then E_2 is a G.A.S. node.*

4. *If $d/e = x_2$, then E_2 is a G.A.S. node, and there exists a heteroclinic orbit connecting E_2 and E_1.*
5. *If $x_2 < d/e < P$, then E_2 is a G.A.S. node, and there exists a heteroclinic orbit connecting E_2 and E_1.*

Proof The idea is completely same as that in Theorem 4. In fact, we only need to prove the case 3, since the others had been proven in Theorem 4. In the case 3, the Jacobian matrix at E_2 has the form:

$$J(E_2) = \begin{pmatrix} -\frac{bx}{K} & -x \\ ey & 0 \end{pmatrix}.$$

Its determinant and trace are $\mathrm{Det}J(E_2) = exy > 0$, $\mathrm{Tr}J(E_2) = -\frac{bx}{K} < 0$ respectively. Thus, E_2 is a G.A.S. equilibrium. To determine E_2 is a focus or a node, we need to compute the sign of the discriminant

$$\begin{aligned}\Delta &= \frac{b^2x^2}{K^2} - 4exy = \frac{b^2x^2}{K^2} - 4bex\left(1 - \frac{x}{K}\right)\\ &= x\left[\frac{b^2x}{K^2} + \frac{4be}{K}x - 4be\right] = x\left[\left(\frac{b^2}{K^2} + \frac{4be}{K}\right)x - 4be\right].\end{aligned}$$

From this, one can easily obtain the results in the case 3. □

2.3.2 (ii) $0 < b \le P - qK$

In this subcase, $x_1 = K[1 - (P - qK)/b] < 0$ (see Fig. 6), then we obtain the result by allowing $x_1 < 0$ in Theorem 6:

Theorem 7 1. *If $0 < d/e < x_2$, then E_2 is a G.A.S equilibrium. Moreover, if $d/e < \frac{4eK^2}{b+4eK}$, then E_2 is a G.A.S. focus; if $d/e \ge \frac{4eK^2}{b+4eK}$, then E_2 is a G.A.S. node;*
2. *If $d/e = x_2$, then E_2 is a G.A.S. node.*
3. *If $x_2 < d/e < P$, then E_2 is a G.A.S. node.*

2.3.3 (iii) $\dfrac{P - qK}{1 - q} \le b < \dfrac{P}{1 - q}$

In this subcase, the intersection point A_1 is on the right side of the intersection point B. The intersection point A_2 disappears. Furthermore, the intersection A satisfies $x_A > 0$. When $d/e < x_A$, E_2 lies below the straight line $x + y = P$; when $d/e > x_A$, E_2 lies above the straight line $x + y = P$ (see Fig. 7).

Therefore, we have the following theorem:

Theorem 8 1. *If $0 < d/e < x_A$, then E_2 is a G.A.S. equilibrium. Moreover, if $d/e < \mu$ (see Theorem 4 for the definition of μ), then E_2 is a G.A.S. focus; if λ is not a real number, or $d/e \ge \mu$, then E_2 is a G.A.S. node.*

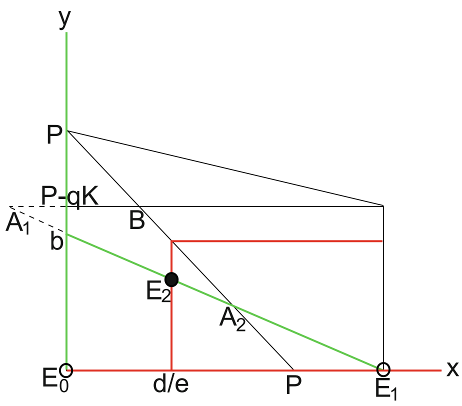


Fig. 6 The nullclines and equilibria for $P \leq K < P/q$ and $0 < b \leq P - qK$

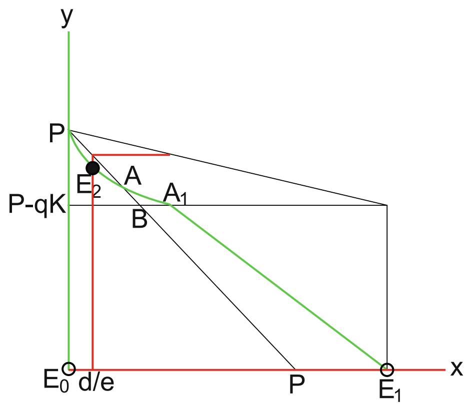


Fig. 7 The nullclines and equilibria for $P \leq K < P/q$ and $(P - qK)/(1 - q) \leq b < P/(1 - q)$

2. *If $d/e = x_A$, then E_2 is a G.A.S. node.*
3. *If $x_A < d/e < P$, then E_2 is a G.A.S. node.*

2.3.4 (iv) $b \geq \dfrac{P}{1-q}$

In this subcase, the intersection point A has negative or zero x-coordinate, that is, $x_A \leq 0$ (see Fig. 8). We have the following theorem by discussing the cases $0 < d/e < x_B$, $x_B < d/e < P$, and $d/e = x_B$:

Theorem 9 *E_2 is a G.A.S node.*

2.4 The case $K < P$

This section is completely similar to the previous section, thus we only list the results without providing details. First, we analyze the stability of the boundary equilibria E_0, E_1. At E_0, $J(E_0) = \begin{pmatrix} b & 0 \\ 0 & -d \end{pmatrix}$, and thus E_0 is always a saddle. At E_1, $J(E_1) =$

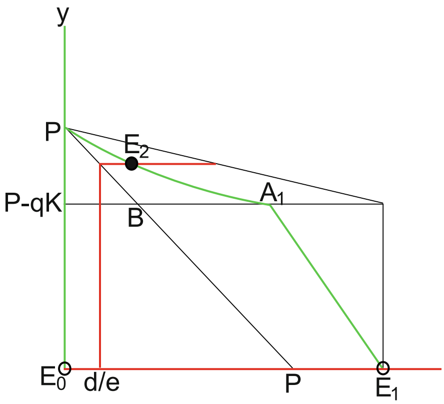


Fig. 8 The nullclines and equilibria for $P \le K < P/q$ and $b \ge P/(1-q)$

$\begin{pmatrix} -b & -K \\ 0 & eK-d \end{pmatrix}$. Therefore, if $d/e > K$, E_1 is a G.A.S. node; if $d/e < K$, E_1 is a saddle; if $d/e = K$, E_1 is a saddle-node.

In order to discuss the stability of the internal equilibrium E_2, we need to know the relative position relationship among these intersection points A, A_1, A_2, B which are defined in Section 2.3. This case is also divided into four subcases by different ranges of b:

(i) $0 < b \le P - qK$;

(ii) $P - qK < b < \dfrac{P-qK}{1-q}$;

(iii) $\dfrac{P-qK}{1-q} \le b < \dfrac{P}{1-q}$;

(iv) $b \ge \dfrac{P}{1-q}$.

2.4.1 (i) $0 < b \le P - qK$

In this subcase, all the intersection points do not exist, the x-nullcline $y = b(1 - \frac{x}{K})$ lies below the line $x + y = P$, and E_2 also lies below the lines $x + y = P$ and $y = P - qK$. Therefore, we have

Theorem 10 *If* $0 < d/e < \frac{4eK^2}{b+4eK}$, *$E_2$ is a G.A.S. focus.*
If $\frac{4eK^2}{b+4eK} \le d/e < K$, *$E_2$ is a G.A.S. node.*

2.4.2 (ii) $P - qK < b < \dfrac{P-qK}{1-q}$

In this subcase, the intersection point A_1 exists, the x-nullcline $y = b(1 - \frac{x}{K})$ lies below the line $x + y = P$, and E_2 also lies below the line $x + y = P$. Whether E_2 is above the line $y = P - qK$ depends on if d/e is smaller than $x_1 = K[1-(P-qK)/b]$ or not. Therefore, we have

Theorem 11 1. *If* $0 < d/e < x_1$*, then* E_2 *is a G.A.S. equilibrium. Moreover, if* $d/e < \mu$ *(see Theorem 4 for the definition of* μ*), then* E_2 *is a G.A.S. focus; if* λ *is not a real number, or* $d/e \geq \mu$*, then* E_2 *is a G.A.S. node.*
2. *If* $d/e = x_1$*, then* E_2 *is a G.A.S. equilibrium and there exists a heteroclinic orbit connecting* E_2 *and* E_1*.*
3. *If* $x_1 < d/e < K$*, then* E_2 *is a G.A.S equilibrium. Moreover, if* $d/e < \frac{4eK^2}{b+4eK}$*, then* E_2 *is a G.A.S. focus; if* $d/e \geq \frac{4eK^2}{b+4eK}$*, then* E_2 *is a G.A.S. node;*

2.4.3 (iii) $\dfrac{P - qK}{1-q} \leq b < \dfrac{P}{1-q}$

We have the following theorem for this subcase:

Theorem 12 1. *If* $0 < d/e < x_A$*, then* E_2 *is a G.A.S. equilibrium. Moreover, if* $d/e < \mu$ *(see Theorem 4 for the definition of* μ*), then* E_2 *is a G.A.S. focus; if* λ *is not a real number, or* $d/e \geq \mu$*, then* E_2 *is a G.A.S. node.*
2. *If* $d/e = x_A$*, then* E_2 *is a G.A.S. node.*
3. *If* $x_A < d/e < x_2$*, then* E_2 *is a G.A.S. node.*
4. *If* $d/e = x_2$*,then* E_2 *is a G.A.S. node.*
5. *If* $x_2 < d/e < K$*, then* E_2 *is a G.A.S equilibrium. Moreover, if* $d/e < \frac{4eK^2}{b+4eK}$*, then* E_2 *is a G.A.S. focus; if* $d/e \geq \frac{4eK^2}{b+4eK}$*, then* E_2 *is a G.A.S. node.*

2.4.4 (iv) $b \geq \dfrac{P}{1-q}$

We have the following theorem for this subcase:

Theorem 13 1. *If* $0 < d/e \leq x_2$*, then* E_2 *is a G.A.S. node.*
2. *If* $x_2 < d/e < K$*, then* E_2 *is a G.A.S equilibrium. Moreover, if* $d/e < \frac{4eK^2}{b+4eK}$*, then* E_2 *is a G.A.S. focus; if* $d/e \geq \frac{4eK^2}{b+4eK}$*, then* E_2 *is a G.A.S. node.*

2.5 Summary of results of type I model

It is easy to analyze boundary equilibria. We have many subcases due to the internal equilibrium E_2. As a summary, the stability results of E_2 are the following:
When $E_2 \in D_1$, it is a G.A.S focus or node by the case 1 of Theorem 4.
When $E_2 \in D_2$, it is a G.A.S node by the case 2 of Theorem 4.
When $E_2 \in D_3$, it is a G.A.S focus or node by the case 3 of Theorem 6.
When $E_2 \in D_4$, it is a G.A.S node by the case 5 of Theorem 6.

3 Global analysis of the model with Holling type II functional response

In this section, the consumption rate function $f(x) = \dfrac{cx}{a+x}$ follows the Holling type II functional response. The complexity of the type II model leads to enormously many cases for rigorous analysis, thus it is almost impossible to analyze this model with so many free parameters. Here we only analyze this model with one varying parameter K (i.e. light intensity). No rigorous bifurcation analysis has been done for this model. Our bifurcation analysis provides a rigorous mathematical proof for the numerical bifurcation diagram of light intensity. Many interesting dynamical phenomena appear in our bifurcation analysis. For instance, almost all types of bifurcation occur, and bistability of an internal equilibrium and a limit cycle occurs. We fix all parameters (except K) with realistic values: $P = 0.025, e = 0.8, b = 1.2, d = 0.25, \theta = 0.04, q = 0.004, c = 0.8, a = 0.25$; K has the range: $0-2.0$. Units can be found in Loladze et al. (2000) and Wang et al. (2008).

With the above parameter values, we have

$$f(x) = \frac{cx}{a+x} = \frac{0.8x}{0.25+x} = \frac{16x}{5+20x},$$
$$\min\left\{K, \frac{P-\theta y}{q}\right\} = \min\left\{K, \frac{25}{4} - 10y\right\},$$
$$\min\left\{1, \frac{(P-\theta y)/x}{\theta}\right\} = \min\left\{1, \frac{\frac{5}{8}-y}{x}\right\}.$$

The model becomes

$$\frac{dx}{dt} = \frac{6}{5}x\left(1 - \frac{x}{\min\{K, \frac{25}{4} - 10y\}}\right) - \frac{16xy}{5+20x}, \tag{8}$$
$$\frac{dy}{dt} = \frac{4}{5}\min\left\{x, \frac{5}{8} - y\right\}\frac{16y}{5+20x} - \frac{1}{4}y. \tag{9}$$

The phase space $\Omega = \{(x, y) : 0 < x < K, 0 < y < 5/8, x + 10y < 25/4\}$ is an open trapezoid. Similar to Theorem 1, one can easily obtain the following result.

Theorem 14 *Ω is a positively invariant set for the flow generated by system* (8)–(9).

We first examine the nullclines of the system. To simplify the analysis, we rewrite system (8)–(9) in the following form:

$$\frac{dx}{dt} = xF(x, y),$$
$$\frac{dy}{dt} = yG(x, y),$$

where

$$F(x, y) = \frac{6}{5}\left(1 - \frac{x}{\min\{K, \frac{25}{4} - 10y\}}\right) - \frac{16y}{5+20x}$$
$$= \begin{cases} \frac{6}{5}\left(1 - \frac{x}{K}\right) - \frac{16y}{5+20x}, & y \le \frac{5}{8} - \frac{K}{10}, \\ \frac{6}{5}\left(1 - \frac{x}{\frac{25}{4}-10y}\right) - \frac{16y}{5+20x}, & y > \frac{5}{8} - \frac{K}{10}, \end{cases}$$

and

$$G(x, y) = \frac{4}{5} \min\left\{x, \frac{5}{8} - y\right\} \frac{16}{5+20x} - \frac{1}{4}$$
$$= \begin{cases} \frac{64x}{25+100x} - \frac{1}{4}, & x + y \le \frac{5}{8}, \\ \frac{40-64y}{25+100x} - \frac{1}{4}, & x + y > \frac{5}{8}. \end{cases}$$

The partial derivatives of F and G exist almost everywhere on Ω:

$$F_x = \begin{cases} -\frac{6}{5K} + \frac{320y}{(5+20x)^2}, & y \le \frac{5}{8} - \frac{K}{10}, \\ -\frac{24}{125-200y} + \frac{320y}{(5+20x)^2}, & y > \frac{5}{8} - \frac{K}{10}; \end{cases}$$
$$F_y = \begin{cases} -\frac{16}{5+20x}, & y < \frac{5}{8} - \frac{K}{10}, \\ \frac{192x}{(25-40y)^2} - \frac{16}{5+20x}, & y > \frac{5}{8} - \frac{K}{10}; \end{cases}$$
$$G_x = \begin{cases} \frac{64}{(5+20x)^2}, & x + y < \frac{5}{8}, \\ \frac{64y-40}{(25+100x)^2}, & x + y > \frac{5}{8}; \end{cases}$$
$$G_y = \begin{cases} 0, & x + y < \frac{5}{8}, \\ -\frac{64}{25+100x}, & x + y > \frac{5}{8}. \end{cases}$$

The x-nullcline is $x = 0$ and $F(x, y) = 0$. If $y \le \frac{5}{8} - \frac{K}{10}$, $F(x, y) = 0$ determines a parabola

$$y = g(x) \triangleq \frac{3}{8}(1 + 4x)\left(1 - \frac{x}{K}\right).$$

The maximum of the function g is

$$y_{max} = g\left(K/2 - 1/8\right) = \frac{3}{16} + \frac{3}{8}K + \frac{3}{128}\frac{1}{K}.$$

If $K \ge \frac{35+2\sqrt{235}}{76} \approx 0.863940$, then

$$y_{max} \ge \frac{5}{8} - \frac{K}{10}.$$

That is, if $K > \frac{35+2\sqrt{235}}{76}$, the parabola $y = g(x)$ will enter the domain $\{(x, y) \in \Omega : y > \frac{5}{8} - \frac{K}{10}\}$. In this case, the x-nullcline is joint with two parts, one is the parabola $y = g(x)$, the other is a hyperbola:

$$\frac{8y}{3+12x} + \frac{4x}{25-40y} = 1.$$

More precisely, if $K > \frac{35+2\sqrt{235}}{76}$, the x-nullcline is a piecewise smooth curve $A\widehat{BCD}E_1$ (see Fig. 14), where the coordinate of A is $(0, 3/8)$, the coordinates of B and D are determined by the equations:

$$y = \frac{3}{8}(1+4x)\left(1 - \frac{x}{K}\right),$$
$$y = \frac{5}{8} - \frac{K}{10},$$

i.e., the coordinate of B is

$$\left(\frac{1}{120}\left[(60K - 15) - \sqrt{4560K^2 - 4200K + 225}\right], \frac{5}{8} - \frac{K}{10}\right)$$

and the coordinate of D is

$$\left(\frac{1}{120}\left[(60K - 15) + \sqrt{4560K^2 - 4200K + 225}\right], \frac{5}{8} - \frac{K}{10}\right),$$

the coordinate of C is determined by the equations:

$$F(x, y) = \frac{8y}{3+12x} + \frac{4x}{25-40y} - 1 = 0,$$
$$F_x(x, y) = \frac{-96y}{(3+12x)^2} + \frac{4}{25-40y} = 0,$$

i.e., the coordinate of C is

$$x_c = \frac{2}{19} + 5\sqrt{\frac{47}{28880}} \approx 0.306968,$$
$$y_c = \frac{11}{19} - \sqrt{\frac{47}{28880}} \approx 0.535514,$$

the coordinate of E_1 is $(K, 0)$.

The y-nullcline is simpler, which is the x-axis and a piecewise linear segment

$$x = 25/156, \qquad 0 < y < 145/312,$$
$$100x + 256y - 135 = 0, \qquad x > 25/156,$$

determined by $G(x, y) = 0$ (see Figs. 10, 14).

Now we start to analyze the system according to the parameter K.

- Case 1. $0 < K \leq 25/156$.
- Case 2. $25/156 < K \leq 89/156$.
- Case 3. $89/156 < K < 0.585185$.
- Case 4. $0.585185 \leq K \leq 0.654664$.
- Case 5. $0.654664 < K < 2$.

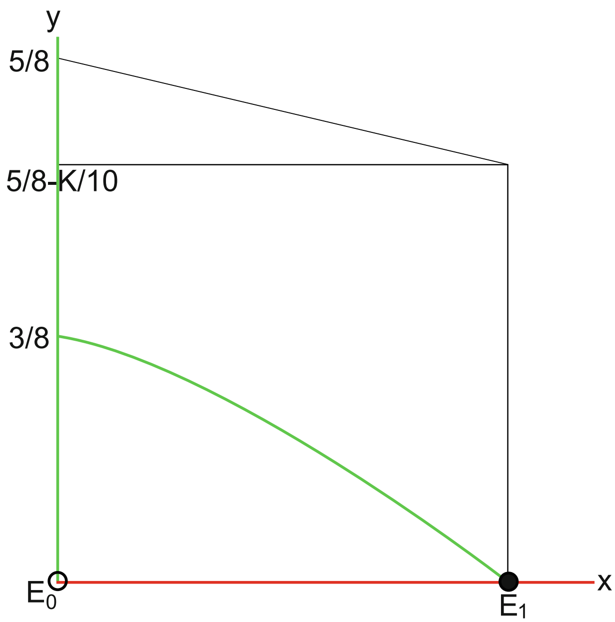


Fig. 9 The nullclines and equilibria for $0 < K \leq 25/156$

3.1 Case 1. $0 < K \leq 25/156$

The system has only the boundary equilibria $E_0 = (0, 0)$, $E_1 = (K, 0)$. No internal equilibria exist in this case (see Fig. 9). E_0 is a saddle, E_1 is G.A.S. If $0 < K < 25/156$, E_1 is a G.A.S. node; if $K = 25/156$, E_1 is a saddle-node, transcritical bifurcation appears, and all orbits in Ω tend to E_1.

3.2 Case 2. $25/156 < K \leq 89/156$

When $K = 89/156$, the straight line $x = 25/156$ is exactly the symmetric axis of the x-nullcline $y = g(x)$. The coordinate of the intersection point F of two straight lines $y = 5/8 - K/10$ and $x + y = 5/8$ is $(K/10, 5/8 - K/10)$ (see Fig. 10).

Since $89/156 < \frac{35+2\sqrt{235}}{76}$, then the x-nullcline is the parabola $y = g(x)$, which does not enter the domain $\{(x, y) \in \Omega : y > \frac{5}{8} - \frac{K}{10}\}$. In order to determine the relative position relationship between the x-nullcline and the straight line $100x+256y-135 = 0$, we need to compute the corresponding values of K such that the equations

$$y = 3/8(1 + 4x)(1 - x/K),$$
$$0 = 100x + 256y - 135$$

have a unique solution. Only if

$$K = \frac{24}{(121)^2}(199 + 8\sqrt{390}) \approx 0.585185,$$

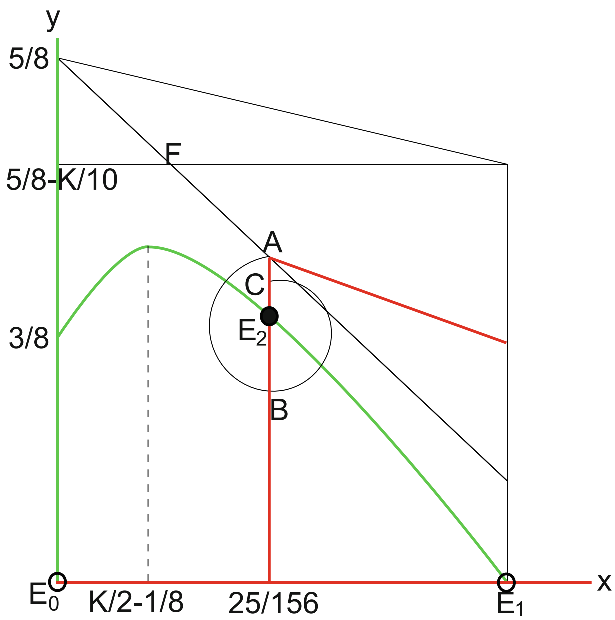


Fig. 10 The nullclines and equilibria for $25/156 < K < 89/156$

the above equations have the unique solution $x = 0.243671$ and $y = 0.432160$.

Since $89/156 < 0.585185$, the x-nullcline $y = g(x)$ only intersects the y-nullcline once, and the system has a unique internal equilibrium $E_2(x_{E_2}, y_{E_2}) = (25/156, g(25/156))$.

Now we analyze the stability of E_0, E_1, and E_2. The boundary equilibria E_0 and E_1 are saddles. At the internal equilibrium E_2, the Jacobian matrix takes the form

$$J(E_2) = \begin{pmatrix} -\frac{6x}{5K} + \frac{320xy}{(5+20x)^2} & -\frac{16x}{5+20x} \\ \frac{64y}{25(1+4x)^2} & 0 \end{pmatrix}$$

with $x = x_{E_2} = 25/156$, $y = y_{E_2} = g(25/156)$. Therefore the determinant and trace of the matrix $J(E_2)$ are respectively

$$\mathrm{Det}J(E_2) = \frac{384}{125} \frac{1 - \frac{x}{K}}{(1 + 4x)^2}, \tag{10}$$

$$\mathrm{Tr}J(E_2) = -\frac{6}{5}x \frac{8x + 1 - 4x}{K(1 + 4x)}. \tag{11}$$

When $25/156 < K < 89/156$, then $K/2 - 1/8 < x_{E_2} < K$. From this, it is easy to show that $\mathrm{Det}J(E_2) > 0$, $\mathrm{Tr}J(E_2) < 0$. Thus, E_2 is a L.A.S. equilibrium. In order to prove that E_2 is G.A.S., we consider the orbit starting from the intersection point A of the line $x = 25/156$ and the line $x + y = 5/8$ (see Fig. 10). From the property of the vector field, we know that the domain bounded by the orbit arc $\widehat{ABC}$ and the line segment $\overline{CA}$ is an attracting neighborhood of the equilibrium E_2. According to the theory of a classical predator–prey system, we know that the classical predator–prey system

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{K}\right) - \frac{cxy}{a+x} \tag{12}$$

$$\frac{dy}{dt} = e\frac{cxy}{a+x} - dy \tag{13}$$

has the only internal equilibrium E_2, which is G.A.S., if $\frac{a}{ce/d-1} < K \le a + \frac{2a}{ce/d-1}$, for example, see Lemma 4.5 in Hsu et al. (1978). Here in our case,

$$\frac{a}{ce/d-1} = 25/156, \quad a + \frac{2a}{ce/d-1} = 89/156,$$

since

$$a = 0.25, \quad c = 0.8, \quad e = 0.8, \quad d = 0.25.$$

In addition, since

$$\min\left\{1, \frac{(P-\theta y)/x}{\theta}\right\} \le 1,$$

by the standard comparison argument, any orbit of the original system (8)–(9) starting from the line $x = 25/156$ returns to some point of this line whose y-coordinate is less than that of the orbit of the classical predator–prey system (12)–(13) with the same initial point. Hence, the equilibrium E_2 is G.A.S.

When $K = 89/156$, then $K/2 - 1/8 = x_{E_2} < K$. Therefore $\mathrm{Det}J(E_2) > 0$, $\mathrm{Tr}J(E_2) = 0$. That is, the Jacobian matrix $J(E_2)$ has a pair of pure imaginary eigenvalues and the internal equilibrium E_2 is a center-type equilibrium. Fortunately, when $K = 89/156$, the equilibrium E_2 is G.A.S. for the classical predator–prey system (12)–(13) (see Lemma 4.5 in Hsu et al. 1978). As above, using the standard comparison argument, we know that the internal equilibrium E_2 is also G.A.S. for the original system (8)–(9). In fact, when $K = 89/156$, Hopf bifurcation occurs.

As a summary, we arrive at the following result.

Theorem 15 *When* $25/156 < K \le 89/156$*, the system has two boundary equilibria* E_0, E_1*, which are unstable saddles, and one internal equilibrium* E_2*, which is G.A.S. When* $K = 89/156$*, Hopf bifurcation occurs.*

3.3 Case 3. $89/156 < K < 0.585185$

Theorem 16 *When* $89/156 < K < 0.585185$*, the system has two boundary equilibria* E_0, E_1*, which are unstable saddles, and one internal equilibrium* E_2*, which is unstable, and has at least one limit cycle* (*see* Fig. 11).

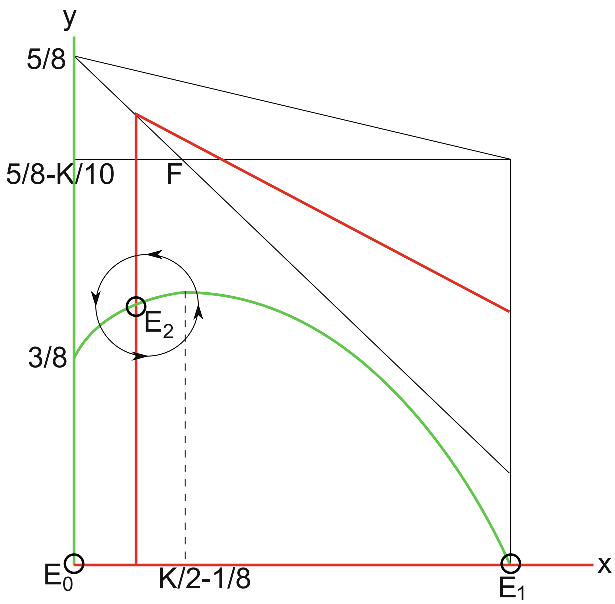


Fig. 11 The nullclines and equilibria for $89/156 < K < 0.585185$

Proof The proof of the first part is similar to Case 2. Since in this case, $x_{E_2} < K/2 - 1/8 < K$, from (10)–(11) we know that $\mathrm{Det}J(E_2) > 0$, $\mathrm{Tr}J(E_2) > 0$, and thus all eigenvalues of the Jacobian matrix $J(E_2)$ have positive real parts. Hence, E_2 is an unstable equilibrium. The existence of the limit cycle is guaranteed by Poincaré–Bendixson theorem. □

We note that the uniqueness of the limit cycle has not been established here. The uniqueness of the limit cycle seems valid in this theorem, but a rigorous proof is needed to confirm this conjecture.

3.4 Case 4. $0.585185 \leq K \leq 0.654664$

We first compute the y-coordinate of the equilibrium E_2:

$$y_{E_2} = \frac{3}{8}\left(1 + \frac{100}{156}\right)\left(1 - \frac{25}{156}\frac{1}{K}\right) = \frac{8}{13} - \frac{50}{507}\frac{1}{K}.$$

Next the y-coordinate of M (see Fig. 12) is

$$y_M = \frac{5}{8} - \frac{25}{156} = \frac{145}{312}.$$

If the y-coordinate of E_2 is larger than the y-coordinate of M, that is,

$$\frac{8}{13} - \frac{50}{507}\frac{1}{K} > \frac{145}{312},$$

which is equivalent to

$$K > \frac{5200}{7943} \approx 0.654664,$$

then the original system has no internal equilibria in the domain $\{(x, y) \in \Omega : x + y < 5/8\}$. In other words, when $0.585185 < K < 0.654664$, the system has three internal equilibria E_2, E_3, E_4, and the equilibrium E_2 lies below the line $x + y = 5/8$, the other equilibria E_3, E_4 lie above this line (see Fig. 12). By simple calculation, we know that the coordinates of these equilibria are

$$E_2 = \left(\frac{25}{156}, \frac{8}{13} - \frac{50}{507K}\right),$$

$$E_3 = \left(x_{E_3} = \frac{1}{8}\left[\frac{121}{24}K - 1 - \sqrt{\left(\frac{121}{24}K - 1\right)^2 - \frac{13}{2}K}\right], -\frac{25}{64}x_{E_3} + \frac{135}{256}\right),$$

$$E_4 = \left(x_{E_4} = \frac{1}{8}\left[\frac{121}{24}K - 1 + \sqrt{\left(\frac{121}{24}K - 1\right)^2 - \frac{13}{2}K}\right], -\frac{25}{64}x_{E_4} + \frac{135}{256}\right).$$

We also note that when $K > 0.654664$, then $x_{E_3} < 25/156$, and the system has at most one internal equilibrium E_4.

Now we discuss the stability of these equilibria. The boundary equilibria E_0 and E_1 are unstable saddles. Same as in Case 3, E_2 is an unstable equilibrium and all eigenvalues of $J(E_2)$ have positive real parts.

In order to investigate the stability of the equilibria E_3 and E_4, one can apply the criteria of local stability in Loladze et al. (2000) directly. For the reader's convenience, we here give the details. At E_3 and E_4, the Jacobian matrices are

$$J(E_i) = \begin{pmatrix} xF_x & xF_y \\ yG_x & yG_y \end{pmatrix} = \begin{pmatrix} -\frac{6x}{5K} + \frac{320xy}{(5+20x)^2} & -\frac{16x}{5+20x} \\ \frac{y(64y-40)}{(25+100x)^2} & \frac{-64y}{25+100x} \end{pmatrix}$$

with $x = x_{E_i}$, $y = y_{E_i}$, $i = 3, 4$.

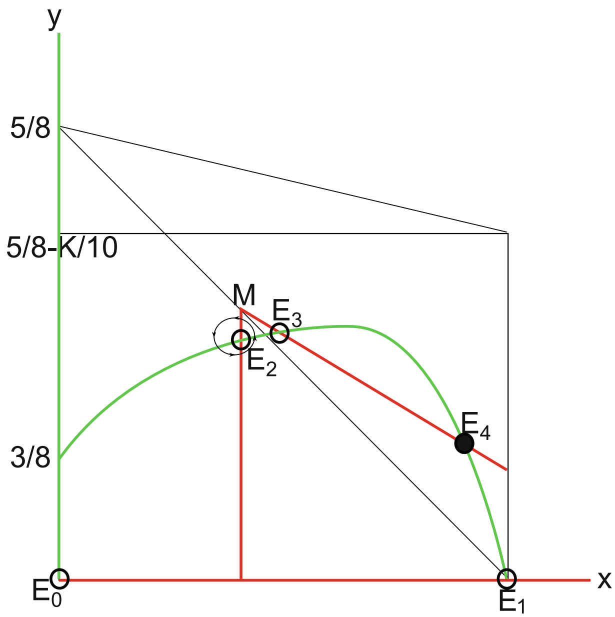


Fig. 12 The nullclines and equilibria for $0.585185 < K < 0.654664$

At E_3, since $-\frac{F_x}{F_y} > -\frac{G_x}{G_y}$, then

$$\begin{aligned}\mathrm{Sign}(\mathrm{Det}(\mathrm{J}(E_3))) &= \mathrm{Sign}(F_x G_y - F_y G_x) = \mathrm{Sign}\left(\frac{F_x G_y - F_y G_x}{F_y G_y}\right), \\ &= \mathrm{Sign}\left(-\frac{G_x}{G_y} - \left(-\frac{F_x}{F_y}\right)\right) \\ &< 0.\end{aligned}$$

Hence, E_3 is an unstable saddle.

At E_4, since $-\frac{F_x}{F_y} < -\frac{G_x}{G_y} < 0$, then $F_x < 0$ and

$$\begin{aligned}\mathrm{DetJ}(E_4) &> 0, \\ \mathrm{TrJ}(E_4) &= xF_x + yG_y < 0.\end{aligned}$$

Hence, E_4 is a L.A.S. equilibrium. In addition,

$$\begin{aligned}\Delta\mathrm{J}(E_4) &= (\mathrm{TrJ}(E_4))^2 - 4\mathrm{DetJ}(E_4) = (xF_x + yG_y)^2 - 4xy(F_x G_y - F_y G_x), \\ &= (xF_x - yG_y)^2 + 4xyF_y G_x \\ &> 0,\end{aligned}$$

which shows that E_4 is a L.A.S. node.

Same as in Case 3, the system has at least one limit cycle since E_2 is unstable. Further, from the property of the vector field, the equilibrium E_2 lies inside the limit cycle, and the equilibria E_3, E_4 lie outside the limit cycle.

When $K = 0.585185$, the x-nullcline $y = g(x)$ and the y-nullcline $100x+256y-135 = 0$ have a unique intersection point $E_{3,4}$, whose coordinates are (0.243671, 0.432160) (see Case 2). In this case, the system has two internal equilibria E_2, $E_{3,4}$. E_2 lying in the domain $\{(x, y) \in \Omega : x + y < 5/8\}$ is an unstable equilibrium and all eigenvalues of $J(E_2)$ have positive real parts as above. When K tends to 0.585185 from the right, E_3 and E_4 collide and become the equilibrium $E_{3,4}$ which lies on the line $x + y = 5/8$. Since E_3 is an unstable saddle and E_4 is a L.A.S. node, then $E_{3,4}$ is an unstable saddle-node, and saddle-node bifurcation occurs. Here we note that the node E_4 is stable. Moreover, the system has at least one limit cycle surrounding the equilibrium E_2.

When $K = 0.654664$, the system has two internal equilibria $E_{2,3}$, E_4. When K tends to 0.654664 from the left, E_2 and E_3 collide and become the equilibrium $E_{2,3}$ which lies on the line $x + y = 5/8$. Since E_2 is an unstable equilibrium and all eigenvalues of $J(E_2)$ have positive real parts, then E_2 is an unstable node or focus. Also, we note that node and focus with same stability are topologically equivalent. Thus, from the topological point of view, we can treat the equilibrium E_2 as an unstable node. On the other hand, E_3 is an unstable saddle. Therefore, the equilibrium $E_{2,3}$ is an unstable saddle-node, which is different from the saddle-node $E_{3,4}$ since the node E_2 is unstable. E_4 lying in the domain $\{(x, y) \in \Omega : x + y > 5/8\}$ is a L.A.S. node.

Next, we show that in this case the system in Ω has no limit cycles. Suppose that the system has a nontrivial periodic solution $\Gamma : (x(t), y(t))$ in Ω. Since the system has two internal equilibria $E_{2,3}$ and E_4, at least one of them lies inside the domain bounded by the closed orbit Γ. We only consider the equilibrium $E_{2,3}$ lying inside this domain (see Fig. 13) since the other two cases can be proven similarly. Therefore, Γ must intersect the x-nullcline and y-nullcline. Denote the intersections of Γ and the x-nullcline as D_3 (left) and D_2 (right); denote the intersections of Γ and y-nullcline as D_4 (left) and D_1 (right) (see Fig. 13). Since $\frac{dx}{dt} > 0$ below the x-nullcline $y = g(x)$, then the orbit Γ has the counter clockwise direction. On the other hand, since $\frac{dy}{dt} < 0$ above the y-nullcline $100x + 256y - 135 = 0$, we deduce that the y-coordinate of the point D_2 is smaller than that of the point D_1, which is a contradiction. Hence, in this case, there exists a heteroclinic orbit connecting the equilibria $E_{2,3}$, E_4, and E_4 is a G.A.S. node. Note that when $K > 0.654664$, the system in Ω also has no limit cycles.

As a summary, we obtain the following theorem.

Theorem 17 *When* $0.585185 \leq K \leq 0.654664$*, the system has two boundary equilibria* E_0, E_1*, which are unstable saddles.*

When $0.585185 < K < 0.654664$*, the system has three internal equilibria* E_2, E_3, E_4. E_2 *lying in the domain* $\{(x, y) \in \Omega : x + y < 5/8\}$ *is unstable.* E_3, E_4 *lying in the domain* $\{(x, y)\Omega : x+y > 5/8\}$ *are an unstable saddle and a stable node, respectively. Moreover, the system has at least one limit cycle surrounding the equilibrium* E_2.

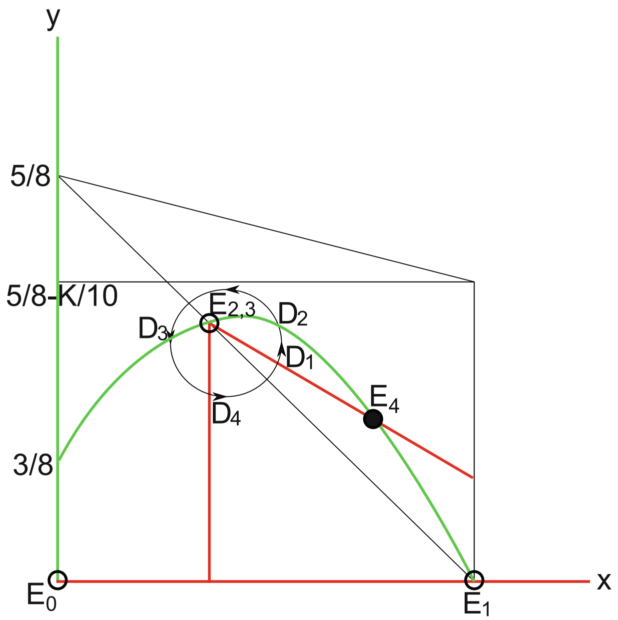


Fig. 13 The nullclines and equilibria for $K = 0.654664$

When $K = 0.585185$*, the system has two internal equilibria* E_2, $E_{3,4}$. E_2 *lying in the domain* $\{(x, y) \in \Omega : x+y < 5/8\}$ *is unstable.* $E_{3,4}$ *lying on the line* $x+y = 5/8$ *is an unstable saddle-node. Moreover, the system has at least one limit cycle surrounding the equilibrium* E_2.

When $K = 0.654664$*, the system has two internal equilibria* $E_{2,3}$, E_4. $E_{2,3}$ *lying on the line* $x + y = 5/8$ *is an unstable saddle-node.* E_4 *lying in the domain* $\{(x, y) \in \Omega : x + y > 5/8\}$ *is a G.A.S. node. Moreover, the system has no limit cycles.*

3.5 Case 5. $0.65466 < K < 2$

Theorem 18 *When* $0.654664 < K < 1.35$*, the system has two boundary equilibria* E_0, E_1 *which are unstable saddles and one internal equilibrium* E_4 *which is a G.A.S. node, and the system has no limit cycles. Moreover, there exists a heteroclinic orbit connecting* E_1 *and* E_4.

When $K = 1.35$, E_0 *is an unstable saddle,* E_4 *and* E_1 *collide and become a G.A.S. saddle-node* E_1 *(for the studied trapping region), and all orbits of the system in* Ω *tend to* E_1.

When $K > 1.35$*, the system has only the boundary equilibria* E_0, E_1 *but no internal equilibria.* E_0 *is an unstable saddle, and* E_1 *is a G.A.S. node.*

For the case 5, both subcases are plotted in Figs. 14 and 15, respectively.

Note that Figs. 9–15 are for illustration purpose. They are not accurately computed by a numerical program.

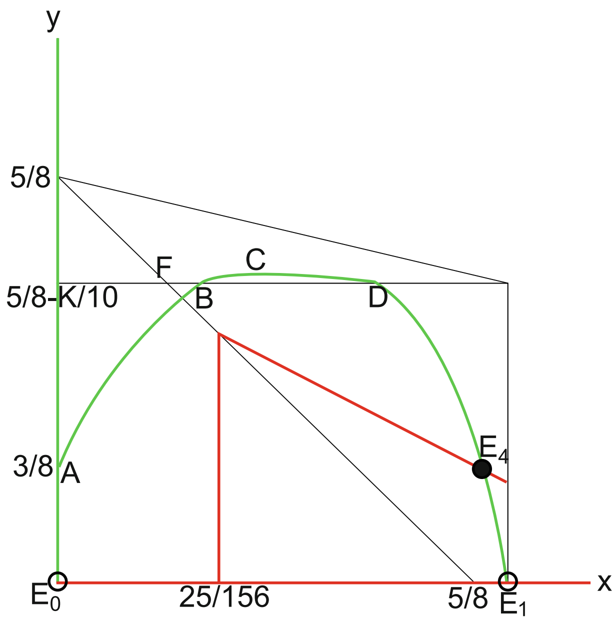


Fig. 14 The nullclines and equilibria for $0.654664 < K < 1.35$

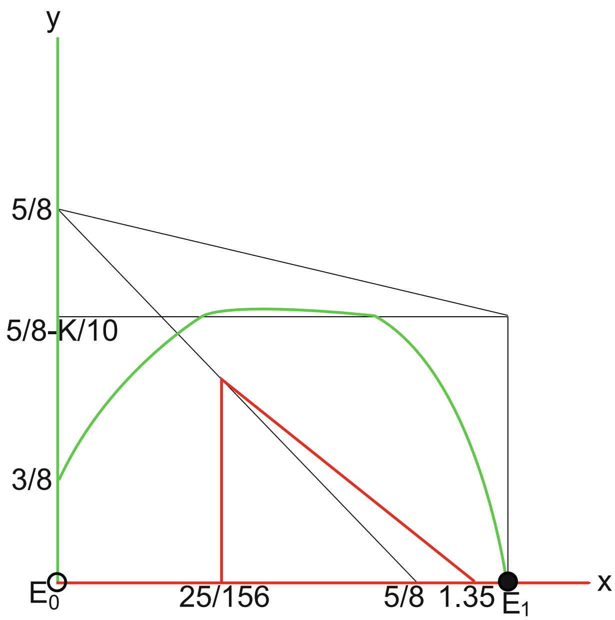


Fig. 15 The nullclines and equilibria for $1.35 < K < 2$

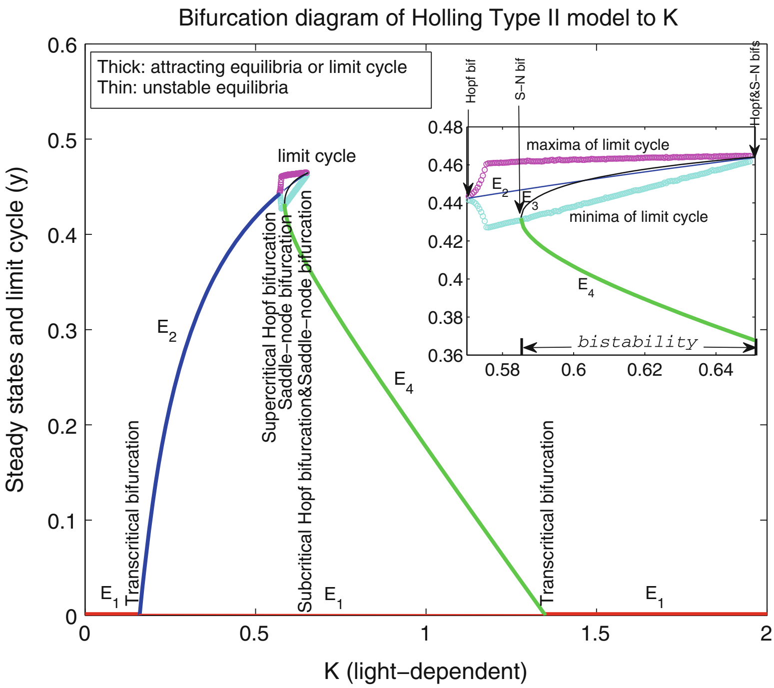


Fig. 16 The bifurcation diagram for the model with Holling type II functional response. In the bistability region, solutions tend to either the limit cycle or the internal equilibrium E_4

3.6 Bifurcation diagram

In Fig. 16, we accurately plot the bifurcation diagram with respect to the light-dependent carrying capacity of producer, K, according to the results of our mathematical analysis as follows:

- When $0 < K \leq 25/156$, there exist no internal equilibria, and the boundary equilibrium E_1 is G.A.S.
- When $25/156 < K \leq 89/156$, there exists a unique internal equilibrium E_2 which is G.A.S, and all boundary equilibria are unstable.
- When $89/156 < K < 0.585185$, there exists a unique internal equilibrium E_2 which is unstable, all boundary equilibria are also unstable, and there exists at least one limit cycle.
- When $K = 0.585185$, there exist two internal equilibria: E_2 and $E_{3,4}$ are unstable, and there exists at least one limit cycle.
- When $0.585185 < K < 0.654664$, there exist three internal equilibria: E_2 and E_3 are unstable, E_4 stable; there exists at least one limit cycle; all solutions either tend to the limit cycle or tend to E_4 (bistability).
- When $K = 0.645664$, there exist two internal equilibria: $E_{2,3}$ is unstable, E_4 is G.A.S.
- When $0.654664 < K < 1.35$, there exists a unique internal equilibrium E_4 which is G.A.S.

- When $1.35 \leq K < 2$, there exist no internal equilibria, and the boundary equilibrium E_1 is G.A.S.

Supercritical Hopf bifurcation (at $K = 89/156$), subcritical Hopf bifurcation (at $K = 0.654664$), saddle-node bifurcation (at $K = 0.585185, 0.654664$), and transcritical bifurcation (at $K = 25/156, 1.35$) occur in the bifurcation diagram. The bifurcation phenomenon is more complicated at $K = 0.65466$. As K passes through 0.654664, the limit cycle disappears via subcritical Hopf bifurcation, the internal unstable equilibrium disappears via saddle-node bifurcation, and all solutions tend to a globally attracting equilibrium E_4 outside the limit cycle. Hence, both subcritical Hopf bifurcation and saddle-node bifurcation occur at the same point $K = 0.654664$.

4 Discussion

We analyze the stoichiometric producer–grazer model proposed by Loladze et al. (2000) with Holling type functional responses. The model is nonsmooth, and thus it has complicated dynamics. We provide the complete global analysis for the Holling type I model and perform the bifurcation analysis of the light-dependent carrying capacity for the Holling type II model. Our bifurcation analysis exhibits more complicated dynamics than the one in the original paper (Loladze et al. 2000). For example, bistability of an internal equilibrium and a limit cycle occurs in the case $0.585185 < K < 0.654664$: for a fixed light intensity with the corresponding carry capacity between 0.585185 and 0.654664, the herbivore population can either stay in a steady state with high producer biomass or fluctuate periodically with low producer biomass.

For the type II model, it is intriguing to further examine the bifurcation point at $K = 0.65466$ which is caused by the nonsmoothness of the stoichiometric model. This type of bifurcation may widely exist in stoichiometric models that normally involve minimum functions due to the Liebig's Law of Minimum. Besides K, it is appealing to perform bifurcation analysis for other key parameters such as the total nutrient availability P and the nutrient:carbon ratio in grazers θ (representing their nutrient requirement). The complete global analysis of the type II model includes a considerable number of cases but may provide other fascinating dynamical phenomena besides complex bifurcations. The bifurcation analysis in this paper provides quite different results when compared to the bifurcation diagram in Loladze et al. (2000), although parameter values are only slightly different. Hence, the dependence of dynamical behaviors on parameters seems extremely high. Sensitivity analysis is needed to evaluate the robustness of all results for this stoichiometric model. For example, smaller maximal conversion efficiency of grazer e would move the vertical limb of the grazer nullcline towards the right and give the declining limb a steeper slope, and the producer nullcline always remains the same. Whether the bistability of a steady state and a limit cycle exists for smaller e strongly depends on other parameters.

A more complicated case is the stoichiometric model with Holling type III functional response. Such a model may provide more exciting dynamical behaviors. We do not incorporate the type III model in this paper because it is not as biologically relevant as types I and II for producer–grazer interactions.

The conjecture for the uniqueness of limit cycle in this paper needs a rigorous proof. The nonsmoothness of the dynamical system makes this proof much more challenging than a smooth dynamical system.

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