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Dynamics of a Producer–Grazer Model Incorporating the Effects of Phosphorus Loading on Grazer's Growth

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Abstract

Phosphorus is an essential element for all life forms, and it is also a limiting nutrient in many aquatic ecosystems. To keep track of the mismatch between the grazer's phosphorus requirement and producer phosphorus content, stoichiometric models have been developed to explicitly incorporate food quality and food quantity. Most stoichiometric models have suggested that the grazer dynamics heavily depends on the producer phosphorus content when the producer has insufficient nutrient content [low phosphorus (P):carbon (C) ratio]. However, recent laboratory experiments have shown that the grazer dynamics are also affected by excess producer nutrient content (extremely high P:C ratio). This phenomenon is known as the "stoichiometric knife edge." While the Peace et al. (Bull Math Biol 76(9):2175–2197, 2014) model has captured this phenomenon, it does not explicitly track P loading of the aquatic environment. Here, we extend the Peace et al. (2014) model by mechanistically deriving and tracking P loading in order to investigate the growth response of the grazer to the producer of varying P:C ratios. We analyze the dynamics of the system such as boundedness and positivity of the solutions, existence and stability conditions of boundary equilibria. Bifurcation diagram and simulations show that our model behaves qualitatively similar to the Peace et al. (2014) model. The model shows that the fate of the grazer population can be very sensitive to P loading. Furthermore, the structure of our model can easily be extended to incorporate seasonal P loading.

Keywords Ecological stoichiometry · Predator–prey model · Stoichiometric knife edge · Phosphorus

1 Introduction

Ecological stoichiometry, an emerging branch of ecology (Sterner and Elser 2002; Andersen et al. 2004), is defined as "the study of the balance of elements in ecological

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process" (Moe et al. 2005, p. 29). Ecological stoichiometry provides a rigorous and ubiquitous mechanistic basis for modeling population dynamics. Its principles are involved in studies of food quality, nutrition, nutrient recycling, and others, which have long histories of investigation.

Some population models implicitly assume chemical homogeneity of all trophic levels by concentrating on a single constituent. However, in an ecosystem, the macronutrients nitrogen (N), phosphorus (P), and carbon (C), along with light energy, and other nutrients are fundamental to biogeochemical processes. Moreover, the concentrations of them vary considerably among species. In aquatic ecosystems, P is usually considered one of the primary limiting nutrients (Elser et al. 2001). This means that the available quantity of P controls the pace at which algae and aquatic plants are produced. The appropriate quantities of P can be used by vegetation and soil microbes for normal growth. However, excess quantities of P lead to water quality problem such as eutrophication. When P is limiting or in excess in aquatic habitats, traditional predator–prey models, which only track the energy flow, cannot adequately describe and understand some rich and interesting aquatic observations.

In the last decades, many stoichiometric population models have been constructed to explicitly incorporate both food quality and food quantity by tracking the mismatch between P requirement in the grazer and P content in the producer. One of the popular stoichiometric predator–prey models constructed to track the food quality and the food quantity is the one proposed by Loladze, Kuang, and Elser (called the LKE model). This model describes a food quality-modified Lotka–Volterra-type producer–grazer model. The model shows that the grazer dynamics heavily depends on the P content in the producer when the producer has insufficient nutrient content (low P:C ratio). However, recent laboratory experiments show that the grazer dynamics are also affected by excess producer nutrient content (extremely high P:C ratio) (Boersma and Elser 2006; Elser et al. 2006). This phenomenon is known as the "stoichiometric knife edge."

Elser et al. (2012) and Peace et al. (2013) modified the LKE model to incorporate the stoichiometric knife-edge phenomenon. However, these models do not explicitly track P in the producer or in the media that supports the producer. For this reason, Peace et al. (2014) extended the stoichiometric knife-edge model by mechanistically deriving and tracking P in the producer and free P in the environment in order to investigate the growth response of grazer to producer of varying P:C ratios.

The Peace et al. (2014) model does not explicitly consider the effects of P loading, but it is a well-known fact that the basic cause of the eutrophication is the excessive loading of P into water bodies (Yang et al. 2008). This fact motivates our study to investigate the role of P loading in a producer–grazer system and its effects on grazer dynamics. Our model is a system of four non-smooth ordinary differential equations. The analysis of this non-smooth model is mathematically challenging due to its four minimum functions. We provide a bifurcation analysis, with respect to the P input parameter $P_{f_{in}}$, for the model with Holling type II functional response. The bifurcation analysis shows that our model behaves qualitatively similar but quantitatively different to the Peace et al. (2014) model.

The organization of this paper is as follows: In Sect. 2, the model is introduced and the biologically significant parameters are identified. In Sect. 3, the dynamics

of the system such as boundedness and positivity of the solutions and the existence and stability conditions of boundary equilibria are analyzed. In Sect. 4, bifurcation diagrams and simulations illustrating model behavior are presented. The similarities and the differences of the Peace et al. (2014) model and the stoichiometric knife-edge model with P loading are discussed systematically. In Sect. 5, the implications of our results and suggested directions for further research are discussed. Proofs of mathematical results are placed in "Appendix."

2 Model Construction

Elser et al. (2012) and Peace et al. (2013) modified the Loladze et al. (2000) model to incorporate the stoichiometric knife-edge effect:

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

$$\frac{dy}{dt} = \min \left\{ \hat{e}f(x), \frac{Q}{\theta} f(x), \hat{e}\hat{f}\frac{\theta}{Q} \right\} y - dy, \qquad (1b)$$

where $Q = (P - \theta y)/x$ describes the P:C ratio of the producer, $x(t)$ and $y(t)$ are the biomass of the producer and grazer, respectively, measured in terms of C, b is the maximum growth rate of producer, d is the specific loss rate of grazer, $\hat{e}$ (< 1) (due to the thermodynamic limitations) is maximal production efficiency of grazer, K is the producer *constant* carrying capacity (due to external constraints of C, such as light limitation), P is the total phosphorus in the system, θ is the grazer's constant P:C ratio, q is the minimal P:C in producer, and $f(x)$ is the grazer's ingestion rate, which is taken here as a Holling type II functional response. In general, the function $f(x)$ is a bounded differentiable function that satisfies $f(0) = 0$, $f'(x) > 0$, and $f''(x) < 0$ for $x \geq 0$ (Loladze et al. 2000). $f(x)$ is saturating with $\lim_{x \to \infty} f(x) = \hat{f}$. The model makes the following four assumptions.

Assumption 1 The total mass of phosphorus in the entire system is fixed; i.e., the system is closed for phosphorus with a total of P (mg P/l).

Assumption 2 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, θ (mg P/ mg C).

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

Assumption 4 At most $\hat{f}\theta$ units of phosphorus are ingested by each unit of grazer's biomass per unit time; i.e., the grazer ingests P up to the rate required for its maximal growth but not more.

Then, Peace et al. (2014) extended the stoichiometric knife-edge model to explicitly trace free P by following the procedure used by Wang et al. (2008). By this way, the

third assumption above is dropped and the following four-dimensional knife-edge model is obtained:

$$\frac{dx}{dt} = bx \min\left\{1 - \frac{x}{K}, 1 - \frac{q}{Q}\right\} - \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\} y, \tag{2a}$$

$$\frac{dy}{dt} = \min\left\{\hat{e}f(x), \frac{Q}{\theta}f(x), \hat{e}\hat{f}\frac{\theta}{Q}\right\} y - dy, \tag{2b}$$

$$\frac{dQ}{dt} = \upsilon(P_f, Q) - b \min\left\{Q\left(1 - \frac{x}{K}\right), Q - q\right\}, \tag{2c}$$

$$\frac{dP_f}{dt} = -\upsilon(P_f, Q)x + \theta dy + \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\} y \left(Q - \min\left\{\hat{e}, \frac{Q}{\theta}\right\}\theta\right), \tag{2d}$$

where $\upsilon(P_f, Q) = \frac{\hat{c}P_f}{\hat{a}+P_f}\frac{\hat{Q}-Q}{\hat{Q}-q}$ is the P uptake rate of the producer. Here, $\hat{Q}$ is the maximum of quota, $\hat{c}$ is the maximum P per C uptake of the producer, and $\hat{a}$ is phosphorus half-saturation constant of the producer.

Henceforth, we will call this model as the stoichiometric knife-edge model without P input. Notice that the assumption that total P in the system is constant allows this model to be reduced to three ODEs.

Our model is an extension of the four-dimensional knife-edge model. The major assumptions of the model are:

Assumption 5 There is a constant phosphorus concentration, $P_{f_{in}}$, in the inflow.

Assumption 6 The volume of water is constant; i.e., the inflow rate of water is equal to the outflow rate.

The stoichiometric knife-edge model with P input:

$$\frac{dx}{dt} = \underbrace{bx \min\left\{1 - \frac{x}{K}, 1 - \frac{q}{Q}\right\}}_{\substack{\text{producer growth} \\ \text{limited by light and nutrient}}} - \underbrace{\min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\} y}_{\text{uptake by grazer}} - \underbrace{\rho x}_{\text{washout}}, \tag{3a}$$

$$\frac{dy}{dt} = \underbrace{\min\left\{\overbrace{\hat{e}f(x)}^{\text{energy limitation}}, \overbrace{\frac{Q}{\theta}f(x)}^{\text{P limitation}}, \overbrace{\hat{e}\hat{f}\frac{\theta}{Q}}^{\text{P in excess}}\right\} y}_{\text{grazer growth rate}} - \underbrace{dy}_{\substack{\text{grazer death \&} \\ \text{respiration loss}}} - \underbrace{\rho y}_{\text{washout}}, \tag{3b}$$

$$\frac{dQ}{dt} = \underbrace{\upsilon(P_f, Q)}_{\text{P uptake by producer}} - \underbrace{b \min\left\{Q\left(1 - \frac{x}{K}\right), Q - q\right\}}_{\text{P consumption by producer}}, \tag{3c}$$

$$\frac{dP_f}{dt} = \underbrace{\rho(P_{f_{in}} - P_f)}_{\text{P input and washout}} - \underbrace{\upsilon(P_f, Q)x}_{\text{producer P uptake}} + \underbrace{\theta dy}_{\substack{\text{P from} \\ \text{grazer death}}}$$

$$+ \underbrace{\min \left\{ f(x), \frac{\hat{f}\theta}{Q} \right\} y \left(Q - \min \left\{ \hat{e}, \frac{Q}{\theta} \right\} \theta \right),}_{\text{P recycled by grazer}} \tag{3d}$$

where ρ is lake flushing rate (i.e., the inverse of retention time). In the rest of this paper, we assume $\rho = 0.02$/day. This specific value is selected from within the reasonable range (see Table 1).

3 Model Analysis

In this section, we present a basic analysis on the model verifying the boundedness and positivity of the solutions. We also locate boundary equilibria and develop some criteria to determine their existence and stability.

3.1 Boundedness and Positive Invariance

Let $P = Q(t)x(t) + \theta y(t) + P_f(t)$, which is the total phosphorus in system (3). Then, since $\hat{e} f(x) < \hat{f}$, the following holds true.

Table 1 All parameters are biologically realistic values obtained from Andersen (1997) and Urabe and Sterner (1996) and used by Loladze et al. (2000) and Peace et al. (2013)

Parameter	Description	Value	Units
$P_{f_{\text{in}}}$	Input concentration of P	0–0.15	mg P/l
ρ	Lake flushing rate	0–0.05	/day
$\hat{e}$	Maximal production efficiency in C terms	0.8	–
b	Maximal growth rate of the producer	1.2	/day
d	Grazer loss rate (includes respiration)	0.25	/day
θ	Grazer constant P:C	0.03	mg P/mg C
q	Producer minimal P:C	0.0038	mg P/mg C
K	Producer carrying capacity limited by light	1.5	mg C/l
$f(x)$	Grazer ingestion rate	$\frac{\hat{f}x}{a+x}$	/day
$\hat{f}$	Maximal ingestion rate of the grazer	0.81	/day
a	Half-saturation of the grazer ingestion response	0.25	mg C/l
$\hat{a}$	Phosphorus half-saturation constant of the producer	0.008	mg P/l
$\hat{c}$	Maximum P per C uptake rate of the producer	0.2	mg P/mg C/day
$\hat{Q}$	Maximum quota	2.5	mg P/mg C

The values of $\hat{c}$ and $\hat{a}$ are used in Wang et al. (2008) and are within the same orders of magnitude as those found in Andersen (1997) and Diehl (2007). The value of ρ is used in Matsumura and Sakawa (1980). The value of $P_{f_{\text{in}}}$ is used in Berger et al. (2006)

$$\frac{\mathrm{d}P}{\mathrm{d}t} = Q'(t)x(t) + Q(t)x'(t) + \theta y'(t) + P'_f(t)$$

$$= \min\left\{\hat{e}f(x), \frac{Q}{\theta}f(x), \hat{e}\hat{f}\frac{\theta}{Q}\right\}\theta y - \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\}$$

$$\min\left\{\hat{e}, \frac{Q}{\theta}\right\}\theta y - \rho Q x - \rho\theta y + \rho(P_{f_{\mathrm{in}}} - P_f)$$

$$= \min\left\{\hat{e}f(x), \frac{Q}{\theta}f(x), \hat{e}\hat{f}\frac{\theta}{Q}\right\}\theta y - \min\left\{\hat{e}f(x), \frac{Q}{\theta}f(x), \hat{e}\hat{f}\frac{\theta}{Q}\right\}\theta y$$

$$+ \rho(P_{f_{\mathrm{in}}} - P_f - Qx - \theta y)$$

$$= \rho(P_{f_{\mathrm{in}}} - P).$$

This implies

$$P^\infty \le \limsup_{t\to\infty} P(t) = P_{f_{\mathrm{in}}} \quad \text{and} \quad P(t) \le \max\left\{P_{f_{\mathrm{in}}}, P(0)\right\}.$$

Theorem 3.1 *Solutions to System* (3) *with initial conditions in the set*

$$\Omega = \left\{(x, y, Q, P_f) : 0 < x, 0 < y, q < Q < \hat{Q}, 0 < P_f, Qx + \theta y + P_f < P_{f_{\mathrm{in}}}\right\}$$
(4)

remain there for all forward time.

Proof The proof is provided in "Appendix A." □

3.2 Existence Conditions of Boundary Equilibria

System (3) has two equilibria on the boundary: the producer and grazer extinction equilibrium $E_0 = (0, 0, Q_0, P_{f_{\mathrm{in}}})$, where

$$Q_0 = \frac{(\hat{Q} - q)(\hat{a} + P_{f_{\mathrm{in}}})qb + \hat{c}P_{f_{\mathrm{in}}}\hat{Q}}{(\hat{Q} - q)(\hat{a} + P_{f_{\mathrm{in}}})b + \hat{c}P_{f_{\mathrm{in}}}} > 0,$$

and the grazer only extinction equilibrium $E_1 = (x_1, 0, Q_1, P_{f_1})$ which is obtained by considering the following cases:

Case 1 $1 - \frac{x}{K} < 1 - \frac{q}{Q}$
In this case, Eq. (3a) becomes

$$\frac{\mathrm{d}x}{\mathrm{d}t} = bx\left(1 - \frac{x}{K}\right) - \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\}y - \rho x$$

and

$$x_1 = \frac{K(b - \rho)}{b}$$

which is positive if $b > \rho$.

Equation (3c) becomes

$$\frac{\mathrm{d}Q}{\mathrm{d}t} = \frac{\hat{c}P_f}{\hat{a} + P_f} \frac{\hat{Q} - Q}{\hat{Q} - q} - bQ\left(1 - \frac{x}{K}\right)$$

and

$$Q_1 = \frac{\hat{c}P_{f_1}\hat{Q}}{(\hat{a} + P_{f_1})(\hat{Q} - q)\rho + \hat{c}P_{f_1}} > 0.$$

Equation (3d) is

$$\frac{\mathrm{d}P_f}{\mathrm{d}t} = \rho(P_{f_{\mathrm{in}}} - P_f) - \frac{\hat{c}P_f}{\hat{a} + P_f} \frac{\hat{Q} - Q}{\hat{Q} - q} x + \theta \mathrm{d}y$$

$$+ \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\} y \left(Q - \min\left\{\hat{e}, \frac{Q}{\theta}\right\}\theta\right),$$

and if the solutions of $\mathrm{d}x/\mathrm{d}t = 0$ and $\mathrm{d}Q/\mathrm{d}t = 0$ are put into Eq. (3d), then P_{f_1} is the positive root of the following equation:

$$\rho(P_{f_{\mathrm{in}}} - P_{f_1}) + \left(\frac{\rho}{b} - 1\right) \frac{\hat{c}P_{f_1}K\hat{Q}}{(\hat{a} + P_{f_1})(\hat{Q} - q)}$$

$$\left[1 - \frac{\hat{c}P_{f_1}}{P_{f_1}((\hat{Q} - q)\rho + \hat{c}) + \hat{a}\rho(\hat{Q} - q)}\right] = 0.$$

Case 2 $1 - \frac{x}{K} > 1 - \frac{q}{Q}$

In this case, Eq. (3a) becomes

$$\frac{\mathrm{d}x}{\mathrm{d}t} = bx\left(1 - \frac{q}{Q}\right) - \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\} y - \rho x$$

and

$$Q_1 = \frac{bq}{b - \rho}$$

which is positive if $b > \rho$.

Equation (3c) becomes

$$\frac{\mathrm{d}Q}{\mathrm{d}t} = \frac{\hat{c}P_f}{\hat{a} + P_f} \frac{\hat{Q} - Q}{\hat{Q} - q} - bQ\left(1 - \frac{q}{Q}\right)$$

and

$$P_{f_1} = -\frac{(q - \hat{Q})\hat{a}\rho bq}{(q - \hat{Q})(q\rho - \hat{c})b - \hat{Q}\hat{c}\rho}$$

which is positive if $(q - \hat{Q})(q\rho - \hat{c})b > \hat{Q}\hat{c}\rho$.

Equation (3d) is

$$\frac{dP_f}{dt} = \rho(P_{f_{\text{in}}} - P_f) - \frac{\hat{c}P_f}{\hat{a} + P_f}\frac{\hat{Q} - Q}{\hat{Q} - q}x + \theta dy$$

$$+ \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\} y \left(Q - \min\left\{\hat{e}, \frac{Q}{\theta}\right\}\theta\right)$$

and

$$x_1 = \frac{(b - \rho)\left(P_{f_{\text{in}}}\left((q - \hat{Q})(q\rho - \hat{c})b - \hat{Q}\hat{c}\rho\right) - (\hat{Q} - q)\hat{a}bq\rho\right)}{((q - \hat{Q})(q\rho - \hat{c})b - \hat{Q}\hat{c}\rho)qb}$$

which is positive if the following conditions are satisfied (simultaneously):

$$(q - \hat{Q})(q\rho - \hat{c})b > \hat{Q}\hat{c}\rho,$$

$$P_{f_{\text{in}}}\left((q - \hat{Q})(q\rho - \hat{c})b - \hat{Q}\hat{c}\rho\right) > (\hat{Q} - q)\hat{a}bq\rho.$$

Therefore, $E_1 = (x_1, 0, Q_1, P_{f_1})$ which takes the following form for the cases below:

$$E_1 = \begin{cases} \left(\frac{K(b-\rho)}{b}, 0, \frac{\hat{c}P_{f_1}\hat{Q}}{(\hat{a}+P_{f_1})(\hat{Q}-q)\rho+\hat{c}P_{f_1}}, P_{f_1}\right), & \text{if } 1 - \frac{x}{K} < 1 - \frac{q}{\hat{Q}} \\ \left(\frac{(b-\rho)\left(P_{f_{\text{in}}}\left((q-\hat{Q})(q\rho-\hat{c})b-\hat{Q}\hat{c}\rho\right)-(\hat{Q}-q)\hat{a}bq\rho\right)}{((q-\hat{Q})(q\rho-\hat{c})b-\hat{Q}\hat{c}\rho)qb}, 0, \frac{bq}{b-\rho}, -\frac{(q-\hat{Q})\hat{a}\rho bq}{(q-\hat{Q})(q\rho-\hat{c})b-\hat{Q}\hat{c}\rho}\right), & \text{if } 1 - \frac{x}{K} > 1 - \frac{q}{\hat{Q}} \end{cases}$$

where P_{f_1} is the positive root of the following equation:

$$\rho(P_{f_{\text{in}}} - P_{f_1}) + \left(\frac{\rho}{b} - 1\right)\frac{\hat{c}P_{f_1}K\hat{Q}}{(\hat{a} + P_{f_1})(\hat{Q} - q)}$$

$$\left[1 - \frac{\hat{c}P_{f_1}}{P_{f_1}((\hat{Q} - q)\rho + \hat{c}) + \hat{a}\rho(\hat{Q} - q)}\right] = 0.$$

Note that from the bifurcation analysis, we observe that the two equilibrium forms cannot coexist.

3.3 Stability Analysis of Boundary Equilibria

Consider the system,

$$x' = F(x, y, Q, P_f) = 0$$
$$y' = yG(x, y, Q, P_f) = 0$$
$$Q' = H(x, y, Q, P_f) = 0$$
$$P_f' = I(x, y, Q, P_f) = 0$$

To analyze the stability of equilibrium points, we use the Jacobian of the above system which is given by

$$J = \begin{pmatrix} F_x(x, y, Q, P_f) & F_y(x, y, Q, P_f) & F_Q(x, y, Q, P_f) & F_{P_f}(x, y, Q, P_f) \\ yG_x(x, y, Q, P_f) & G(x, y, Q, P_f) + yG_y(x, y, Q, P_f) & yG_Q(x, y, Q, P_f) & yG_{P_f}(x, y, Q, P_f) \\ H_x(x, y, Q, P_f) & H_y(x, y, Q, P_f) & H_Q(x, y, Q, P_f) & H_{P_f}(x, y, Q, P_f) \\ I_x(x, y, Q, P_f) & I_y(x, y, Q, P_f) & I_Q(x, y, Q, P_f) & I_{P_f}(x, y, Q, P_f) \end{pmatrix}$$

Theorem 3.2 *The producer and grazer extinction equilibrium, E_0, is unstable if $b(1 - \frac{q}{Q_0}) > \rho$.*

Proof The proof is provided in "Appendix B."   □

Theorem 3.3 *The grazer extinction equilibrium, E_1, is locally asymptotically stable if*

$$\min\left\{\hat{e}f(x_1), \frac{Q_1}{\theta}f(x_1), \hat{e}\hat{f}\frac{\theta}{Q_1}\right\} < d + \rho.$$

Proof The proof is provided in "Appendix C."   □

4 Numerical Simulations

All simulations use the Holling type II function $f(x) = \hat{f}x/(a + x)$ for the grazer ingestion rate. Parameter values are listed in Table 1. All parameters are biologically realistic values obtained from Andersen (1997) and Urabe and Sterner (1996) and used by Loladze et al. (2000) and Peace et al. (2013). The values of $\hat{c}$ and $\hat{a}$ are used in Wang et al. (2008) and within the same orders of magnitude as those found in Andersen (1997) and Diehl (2007). The value of ρ is used in Matsumura and Sakawa (1980). The value of $P_{f_{in}}$ is used in Berger et al. (2006). The initial conditions in our simulation are chosen inside the biologically meaningful region Ω [see Eq. (4)]. In our numerical experiments, we increase $P_{f_{in}}$ in an ecological meaningful range from 0 to 0.15 mg P/l. $P_{f_{in}}$ is the amount of phosphorus input in the system and affects the P:C ratio of the producer (Q) and thus the growth dynamics of the grazer.

For low phosphorus input $P_{f_{in}}$, population densities stabilize around a positive stable equilibrium (see Fig. 1a). When $P_{f_{in}}$ increases, the population densities oscillate around an unstable equilibrium. The grazer density undergoes almost near-extinction
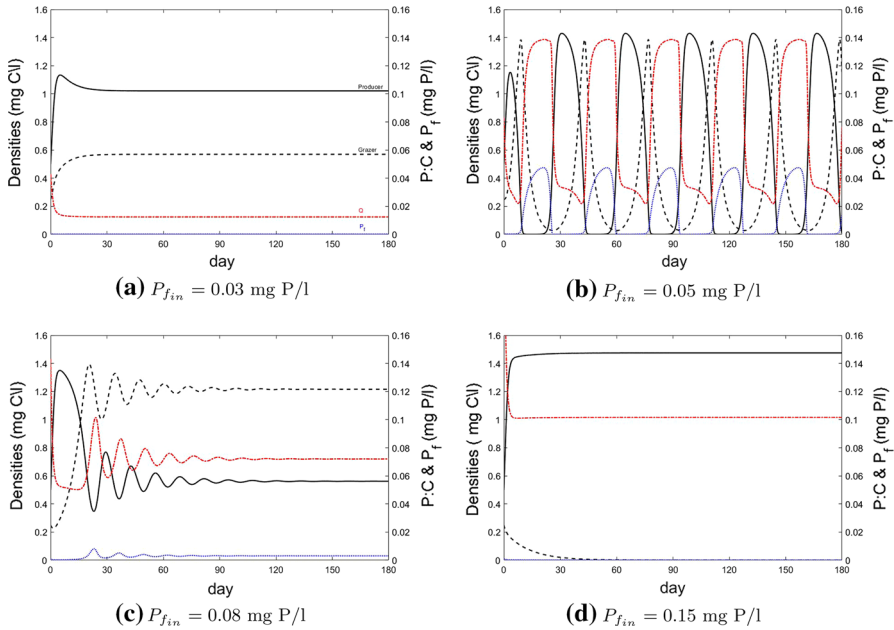
Fig. 1 Numerical simulations of the full model presented in System (3) performed using parameters found in Table 1 and varying values for $P_{f_{in}}$, **a** low phosphorus input $P_{f_{in}} = 0.03$ mg P/l, **b** $P_{f_{in}} = 0.05$ mg P/l, **c** $P_{f_{in}} = 0.08$ mg P/l, **d** excess phosphorus input $P_{f_{in}} = 0.15$ mg P/l. Producer and grazer densities (mg C/l) are given by solid and dashed lines, respectively, and Q, producer cell quota (P:C), and P_f, free phosphorus (mg P/l), are given by red dotted and blue dash-dot lines, respectively (Color figure online)

state (see Fig. 1b). When $P_{f_{in}}$ increase further, the system displays oscillations in population densities and for a while later, oscillations disappear and the positive stable equilibrium emerges (see Fig. 1c). For excess phosphorus input $P_{f_{in}}$, the grazer, despite ample food supply, is heading toward deterministic extinction. The extinction is caused by reduction in grazer growth due to high producer P:C (see Fig. 1d).

Solutions of Model (3) are compared to those of Model (2) for varying $P_{f_{in}}$ and P values in Fig. 2. For steady-state cases and $P_{f_{in}}$, $P = 0.05$ mg P/l, our model and the Peace et al. (2014) model have almost identical solutions. **(a)** coexistence at an equilibrium; **(b)** coexistence with oscillations; and **(d)** extinction of the grazer. However, for $P_{f_{in}}$, $P = 0.08$ mg P/l, they are completely different. For $P = 0.08$ mg P/l, **(c)** captures oscillations around unstable equilibrium. These oscillations have an unstable grazer density, almost nearing extinction. For $P_{f_{in}} = 0.08$ mg P/l, **(c)** captures oscillations around unstable equilibrium at the beginning, and then a little while later, oscillations damp out a positive stable equilibrium.

4.1 Bifurcation Diagrams

The bifurcation diagrams in Fig. 3 illustrate how the dynamics of the grazer in Eqs. (2) and (3) varies with P and $P_{f_{in}}$. The grazer goes extinct for extremely low values of P and $P_{f_{in}}$ because of low food quantity. As P and $P_{f_{in}}$ increase, there is a stable
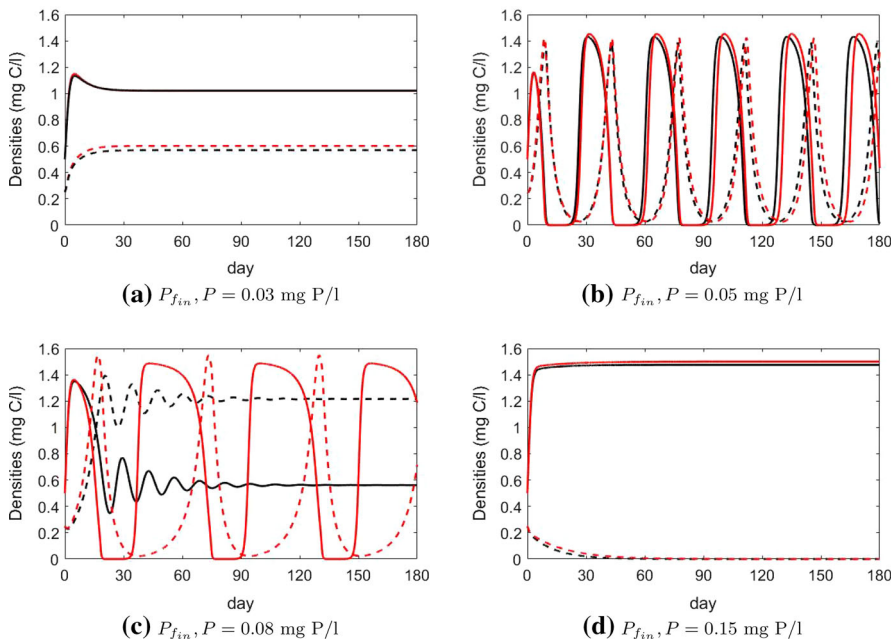
Fig. 2 Comparison of solutions of Model (3) in black and the Model (2) in red with different $P_{f_{in}}$ and P values. Solid curves depict producer densities, and dashed curves depict grazer densities (Color figure online)

equilibrium. When P and $P_{f_{in}}$ increase further, the grazer density increases until the stable equilibrium loses its stability at a saddle-node bifurcations. There is a limit cycle, and the amplitudes of the oscillations increase with P and $P_{f_{in}}$. For P and $P_{f_{in}}$ large enough, the oscillations are abruptly halted when a Hopf bifurcation occurs and another coexistence equilibrium emerges. As P and $P_{f_{in}}$ continue to increase, the grazer density starts to decrease until it reaches the second saddle-node bifurcation, and then, suddenly is driven to extinction due to low food quality. There are some subtle but important differences between the dynamics of Eqs. (2) and (3): (a) The equilibria of Eq. (3) lose their stability earlier than the corresponding ones of (2); (b) the amplitudes of the oscillations in the stoichiometric knife-edge model without P input are larger than those in the stoichiometric knife-edge model with P input; (c) the range of the oscillations in the stoichiometric knife-edge model without P input is longer than that in the stoichiometric knife-edge model with P input; (d) the coexistence equilibrium of Eq. (3) emerges earlier than the corresponding one of (2); and (e) in the stoichiometric knife-edge model with P input, the grazer density drives itself into extinction faster than that in the stoichiometric knife-edge model without P input.

Unlike the previous Model (2), Model (3) incorporates P loading dynamics. It is important to note that Model (2) is a special case of Model (3) when the lake flushing rate is zero (i.e., $\rho = 0$). Figure 4 shows the bifurcation diagram, which describes the relationship between the variable y and the parameter ρ. For low value of ρ, there are an unstable equilibrium and a stable limit cycle. As ρ increases, the unstable
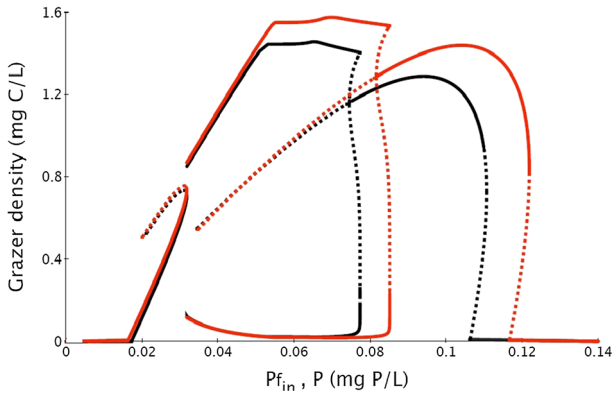
Fig. 3 Bifurcation diagram for Model (3) with respect to $P_{f_{in}}$ in black, bifurcation diagram for Peace et al. (2014) Model (2) with respect to P in red. Solid curves depict stable equilibria and extrema of stable limit cycles, and dashed curves depict unstable equilibria and extrema of unstable limit cycles. Data are generated using the bifurcation software XPPAUT (Color figure online)
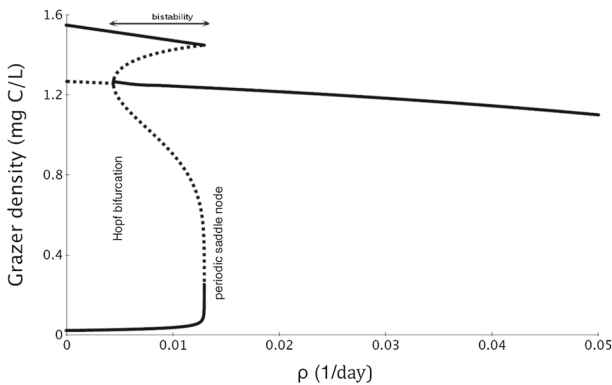

Fig. 4 Bifurcation diagram for Model (3). The grazer density (y) is the bifurcation variable, while the lake flushing rate (ρ) is the bifurcation parameter. Solid curves depict stable equilibria and extrema of stable limit cycles, and dashed curves depict unstable equilibria and extrema of unstable limit cycles. All other parameters are as in Table 1, except $P_{f_{in}}$ that is considered as a constant at 0.08 because the two models predict quantitatively different dynamics (see Fig. 2c), and it is near the observed Hopf bifurcation (Fig. 3). Data are generated by the bifurcation software XPPAUT

interior equilibrium is stabilized by a Hopf bifurcation. Immediately following this Hopf bifurcation, there is a brief region of bistability with the interior stable equilibrium and the limit cycles. As ρ increases further, this region of bistability comes to an end via a periodic saddle-node bifurcation as the limit cycles disappear. After the collapse of the limit cycles, the one interior equilibrium remains stable.

5 Conclusion and Future Directions

We constructed and analyzed a stoichiometric knife-edge model that explicitly tracks P loading. Conditions for positivity and boundedness of solutions are obtained in The-

orem 3.1. The existence and stability conditions of boundary equilibria are analyzed in Theorem 3.2 and Theorem 3.3. Bifurcation analysis of the model with P concentration in the inflow is performed. Through the bifurcation analysis, we observe that our model behaves qualitatively similar to the Peace et al. (2014) model. However, there are quantitative differences between the two models after the point where the predator limitation switches from C to P (from food quantity to food quality). Furthermore, the additional complexities of our model are justified because P loading plays an important role in controlling eutrophication of lakes and our model explicitly tracks it. Ecologist often measures environmental nutrient loads and uses them as ecological gauges for aquatic systems. This mechanistic model formulation also provides significant additional benefit; our model can be easily expanded to a seasonal model by following the procedure used by Kot et al. (1992). A seasonal extension of our model will help shed light on the major impacts seasonal P loading can have on population dynamics and ecosystem function.

Appendix A. Proof of Theorem 3.1

Proof We consider a solution $S(t) \equiv (x(t), y(t), Q(t), P_f(t))$ of System (3) with initial condition in Ω. Hence, $0 < x(0), 0 < y(0), q < Q(0) < \hat{Q}, 0 < P_f(0), Q(0)x(0) + \theta y(0) + P_f(0) < P_{f_{in}}$. Assume that there exists a time $t_1 > 0$ such that $S(t)$ touches or crosses a boundary of $\bar{\Omega}$ (closure of Ω) for the first time, and then $(x(t), y(t), Q(t), P_f(t)) \in \Omega$ for $0 \leq t < t_1$. We will have several cases to consider.

Case 1 $x(t_1) = 0$. Let $\overline{f} = f'(0) = \lim_{x \to 0} \frac{f(x)}{x}$ and $\overline{y} = \max_{t \in [0,t_1]} y(t) < \frac{P_{f_{in}}}{\theta}$. Then for every $t \in [0, t_1]$, we have

$$x' = bx \min\left\{1 - \frac{x}{K}, 1 - \frac{q}{Q}\right\} - \min\left\{f(x), \frac{\hat{f}\theta}{Q}\right\} y - \rho x$$

$$\geq -f(x)y - \rho x \geq -\bar{f}\bar{y}x - \rho x = -(\bar{f}\bar{y} + \rho)x \equiv \alpha_1 x,$$

where α_1 is a constant. Then, $x(t) \geq x(0)e^{\alpha_1 t} > 0$ for $t \in [0, t_1]$, which implies that $x(t_1) \geq x(0)e^{\alpha_1 t_1} > 0$, a contradiction. This proves that $S(t_1)$ does not reach this boundary.

Case 2 $y(t_1) = 0$. Then, for every $t \in [0, t_1]$, we have

$$y' = \min\left\{\hat{e}f(x), \frac{Q}{\theta}f(x), \hat{e}\hat{f}\frac{\theta}{Q}\right\} y - dy - \rho y,$$

$$\geq -dy - \rho y = -(d + \rho)y \equiv \alpha_2 y,$$

where α_2 is a constant. This implies that $y(t_1) \geq y(0)e^{\alpha_2 t_1} > 0$, a contradiction. This proves that $S(t_1)$ does not reach this boundary.

Case 3 $Q(t_1) = q$. Then, for every $t \in [0, t_1]$, we have

$$Q' = \upsilon(P_f, Q) - b \min \left\{ Q \left(1 - \frac{x}{K} \right), Q - q \right\}$$

$$\geq -b \min \left\{ Q \left(1 - \frac{x}{K} \right), Q - q \right\}$$

$$\geq -b(Q - q).$$

This implies that $Q(t_1) \geq q + (Q(0) - q)e^{-bt_1} > q$, a contradiction. This proves that $S(t_1)$ cannot cross this boundary.

Case 4 $Q(t_1) = \hat{Q}$. Since $\upsilon(P_f(t_1), Q(t_1)) = 0$

$$\left. \frac{dQ}{dt} \right|_{t_1} = -b \min \left\{ Q(t_1) \left(1 - \frac{x(t_1)}{K} \right), Q(t_1) - q \right\} < 0.$$

Thus, $S(t_1)$ cannot cross this boundary.

Case 5 $P_f(t_1) = 0$. Since $\upsilon(P_f(t_1), Q(t_1)) = 0$ and $\rho(P_{f_{\text{in}}} - P_f(t_1)) = \rho P_{f_{\text{in}}}$

$$\left. \frac{dP_f}{dt} \right|_{t_1} = \rho P_{f_{\text{in}}} + \theta dy(t_1) + \min \left\{ f(x(t_1)), \frac{\hat{f}\theta}{Q(t_1)} \right\}$$

$$y(t_1) \left(Q(t_1) - \min \left\{ \hat{e}, \frac{Q(t_1)}{\theta} \right\} \theta \right) > 0.$$

Thus, $S(t_1)$ cannot cross this boundary.

Case 6 $P_f(t_1) + Q(t_1)x(t_1) + \theta y(t_1) = P_{f_{\text{in}}}$. Let $z(t) = P_{f_{\text{in}}} - P_f(t) - Q(t)x(t) - \theta y(t)$, then $z(t_1) = 0$ and $z(t) > 0$ for $0 \leq t < t_1$. Then for every $t \in [0, t_1]$, we have

$$z' = -P_f' - Q'x - Qx' - \theta y'$$

$$= -\rho(P_{f_{\text{in}}} - P_f - Qx - \theta y)$$

$$= -\rho z,$$

where ρ is a constant. This implies that $z(t_1) = e^{-\rho t_1} z(0) > 0$, a contradiction. This proves that $S(t_1)$ cannot cross this boundary. □

Appendix B. Proof of Theorem 3.2

Proof At $E_0 = (0, 0, Q_0, P_{f_{\text{in}}})$, the Jacobian matrix is

$$J(E_0) = \begin{pmatrix} b \left(1 - \frac{q}{Q_0} \right) - \rho & 0 & 0 & 0 \\ 0 & -d - \rho & 0 & 0 \\ 0 & 0 & \left. \frac{d\upsilon}{dQ} \right|_{E_0} & -b \left. \frac{d\upsilon}{dP_f} \right|_{E_0} \\ \left. -\upsilon(Q, P_f) \right|_{E_0} & \theta d & 0 & -\rho \end{pmatrix}$$

where $\dfrac{dv}{dQ}\Big|_{E_0} - b = -\dfrac{\hat{c}P_{fin}}{(\hat{a}+P_{fin})(\hat{Q}-q)} - b < 0$. The eigenvalues of $J(E_0)$ are $b(1 - \frac{q}{Q_0}) - \rho$, $-d - \rho$, $\dfrac{dv}{dQ}\Big|_{E_0} - b$, and $-\rho$.

If $b(1 - \frac{q}{Q_0}) > \rho$, then the distinct real eigenvalues are of opposite signs. So E_0 is unstable in the form of a saddle. $\qquad\square$

Appendix C. Proof of Theorem 3.3

Proof Assume that $\min\left\{\hat{e}f(x_1), \frac{Q_1}{\theta}f(x_1), \hat{e}\hat{f}\frac{\theta}{Q_1}\right\} < d + \rho$. To prove that E_1 is locally asymptotically stable, we consider two cases ($1 - \frac{x}{K} < 1 - \frac{q}{Q}$ and $1 - \frac{x}{K} > 1 - \frac{q}{Q}$) where we look at the linearized system and use the Routh–Hurwitz criterion.

Case 1 $1 - \frac{x}{K} < 1 - \frac{q}{Q}$

Here, $E_1 = (x_1, 0, Q_1, P_{f_1}) = \left(\dfrac{K(b-\rho)}{b}, 0, \dfrac{\hat{c}P_{f_1}\hat{Q}}{(\hat{a}+P_{f_1})(\hat{Q}-q)\rho+\hat{c}P_{f_1}}, P_{f_1}\right)$ by Sect. 3.2 and the Jacobian takes the following form:

$$J(E_1) = \begin{pmatrix} \rho - b & F_y(E_1) & 0 & 0 \\ 0 & G(E_1) & 0 & 0 \\ H_x(E_1) & 0 & \dfrac{dv}{dQ}\Big|_{E_1} - \rho & \dfrac{dv}{dP_f}\Big|_{E_1} \\ -v(P_f, Q)\Big|_{E_1} & I_y(E_1) & -\dfrac{K(b-\rho)}{b}\dfrac{dv}{dQ}\Big|_{E_1} & -\rho - \dfrac{K(b-\rho)}{b}\dfrac{dv}{dP_f}\Big|_{E_1} \end{pmatrix}$$

where $G(E_1) = \min\left\{\hat{e}f(x_1), \frac{Q_1}{\theta}f(x_1), \hat{e}\hat{f}\frac{\theta}{Q_1}\right\} - d - \rho$.

Let $\rho < b$, $G(E_1) < 0$, $\alpha_1 = \dfrac{dv}{dQ}\Big|_{E_1} = -\dfrac{\hat{c}P_f}{(\hat{a}+P_f)(\hat{Q}-q)}\Big|_{E_1} < 0$, and $\alpha_2 = \dfrac{dv}{dP_f}\Big|_{E_1} = \dfrac{\hat{c}\hat{a}(\hat{Q}-Q)}{(\hat{a}+P_f)^2(\hat{Q}-q)}\Big|_{E_1} > 0$. The eigenvalues of $J(E_1)$ are $\rho - b$, $G(E_1)$, $-\rho$, and $-\dfrac{K(b-\rho)}{b}\alpha_2 + \alpha_1 - \rho$, which are all negative. Thus, E_1 is locally asymptotically stable for this case.

Case 2 $1 - \frac{x}{K} > 1 - \frac{q}{Q}$

Here, $E_1 = (x_1, 0, Q_1, P_{f_1}) = \left(\dfrac{(b-\rho)\left(P_{fin}\left((q-\hat{Q})(q\rho-\hat{c})b-\hat{Q}\hat{c}\rho\right)-(\hat{Q}-q)\hat{a}bq\rho\right)}{((q-\hat{Q})(q\rho-\hat{c})b-\hat{Q}\hat{c}\rho)qb}, 0, \dfrac{bq}{b-\rho}, -\dfrac{(q-\hat{Q})\hat{a}\rho bq}{(q-\hat{Q})(q\rho-\hat{c})b-\hat{Q}\hat{c}\rho}\right)$ by Sect. 3.2 and the Jacobian takes the following form:

$$J(E_1) = \begin{pmatrix} 0 & F_y(E_1) & F_Q(E_1) & 0 \\ 0 & G(E_1) & 0 & 0 \\ 0 & 0 & \dfrac{dv}{dQ}\Big|_{E_1} - b & \dfrac{dv}{dP_f}\Big|_{E_1} \\ -v(P_f, Q)\Big|_{E_1} & I_y(E_1) & I_Q(E_1) & I_{P_f}(E_1) \end{pmatrix}$$

where

$$F_Q(E_1) = \frac{bqx_1}{Q_1^2},$$

$$G(E_1) = \min\left\{\hat{e}f(x_1), \frac{Q_1}{\theta}f(x_1), \hat{e}\hat{f}\frac{\theta}{Q_1}\right\} - d - \rho,$$

$$I_Q(E_1) = -x_1\frac{dv}{dQ}\bigg|_{E_1} = x_1\frac{\hat{c}P_{f_1}}{(\hat{a}+P_{f_1})(\hat{Q}-q)},$$

and

$$I_{P_f}(E_1) = -\rho - x_1\frac{dv}{dP_f}\bigg|_{E_1} = -\rho - x_1\frac{\hat{c}\hat{a}(\hat{Q}-Q_1)}{(\hat{a}+P_{f_1})^2(\hat{Q}-q)}.$$

Let $\alpha = \frac{\hat{c}}{(\hat{a}+P_{f_1})(\hat{Q}-q)} > 0$. Then, the Jacobian simplifies down to

$$J(E_1) = \begin{pmatrix} 0 & F_y(E_1) & F_Q(E_1) & 0 \\ 0 & G(E_1) & 0 & 0 \\ 0 & 0 & -\alpha P_{f_1} - b & \frac{(\hat{Q}-Q_1)\hat{a}\alpha}{\hat{a}+P_{f_1}} \\ -\alpha P_{f_1}(\hat{Q}-Q_1) & I_y(E_1) & x_1 P_{f_1}\alpha & -\rho - x_1\frac{(\hat{Q}-Q_1)\hat{a}\alpha}{\hat{a}+P_{f_1}} \end{pmatrix}$$

One of the eigenvalues of $J(E_1)$ is $G(E_1) = \min\left\{\hat{e}f(x_1), \frac{Q_1}{\theta}f(x_1), \hat{e}\hat{f}\frac{\theta}{Q_1}\right\} - d - \rho$ and the remaining three eigenvalues are given by the eigenvalues of the matrix $J'(E_1)$ written as:

$$J'(E_1) = \begin{pmatrix} 0 & F_Q(E_1) & 0 \\ 0 & -\alpha P_{f_1} - b & \frac{(\hat{Q}-Q_1)\hat{a}\alpha}{\hat{a}+P_{f_1}} \\ -\alpha P_{f_1}(\hat{Q}-Q_1) & x_1 P_{f_1}\alpha & -\rho - x_1\frac{(\hat{Q}-Q_1)\hat{a}\alpha}{\hat{a}+P_{f_1}} \end{pmatrix}$$

The characteristic equation of the above matrix is given by :

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0,$$

where

$$A_1 = -tr(J'(E_1)) = \frac{-Q_1\hat{a}\alpha x_1 + \hat{Q}\hat{a}\alpha x_1 + P_{f_1}^2\alpha + P_{f_1}\hat{a}\alpha + P_{f_1}b + P_{f_1}\rho + \hat{a}b + \hat{a}\rho}{\hat{a} + P_{f_1}},$$

$$A_2 = \frac{-Q_1\hat{a}\alpha bx_1 + \hat{Q}\hat{a}\alpha bx_1 + P_{f_1}^2\alpha\rho + P_{f_1}\hat{a}\alpha\rho + P_{f_1}b\rho + \hat{a}b\rho}{\hat{a} + P_{f_1}},$$

$$A_3 = -\det(J'(E_1)) = \frac{P_{f_1} Q_1^2 \hat{a} \alpha^2 b q x_1 - 2 P_{f_1} Q_1 \hat{Q} \hat{a} \alpha^2 b q x_1 + P \hat{Q}^2 \hat{a} \alpha^2 b q x_1}{Q_1^2 (\hat{a} + P_{f_1})}.$$

Now by Routh–Hurwitz criterion, E_1 is locally asymptotically stable for this case whenever the following conditions are satisfied:

$$
\begin{cases}
A_1 A_2 > A_3, \\
A_i > 0, \quad i = 1, 2, 3 \quad \text{and} \\
\min\left\{ \hat{e} f(x_1), \frac{Q_1}{\theta} f(x_1), \hat{e} \hat{f} \frac{\theta}{Q_1} \right\} - d - \rho < 0.
\end{cases}
\tag{C.1}
$$

$\square$

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