

DYNAMICAL ANALYSIS OF A DISCRETE COMMENSALISM MODEL WITH MICHAELIS–MENTEN TYPE HARVESTING*

Zuzhi Cai¹, Fengde Chen^{1,†}, Lijuan Chen¹ and Zhong Li¹

Abstract In this work, we formulate and analyze a discrete-time commensalism model in which the first species is subject to Michaelis–Menten type harvesting. We first investigate the existence, stability, and global attractivity of all feasible fixed points. Our results demonstrate that when the two species coexist stably, increasing the harvesting intensity leads to the extinction of the harvested species. We then establish the conditions under which various bifurcations occur, including transcritical, pitchfork, and fold bifurcations, with particular emphasis on the period-doubling route to chaos. In addition, a comprehensive analysis of the global dynamics is conducted. Numerical simulations highlight the critical influence of the commensalism strength: Moderate commensalism ensures stable coexistence of species and increases population density, whereas excessive commensalism destabilizes the system, triggering a period-doubling bifurcation cascade to chaos. Furthermore, the intrinsic stability of the host species is shown to profoundly modulate the dynamical complexity of the commensal species. Under certain conditions, instability of the host species can advance the onset of chaos in the commensal species.

Keywords Michaelis–Menten type harvesting, commensalism, global attractivity, bifurcation, chaos.

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1. Introduction

In nature, species commonly engage in various forms of interaction. Among these, commensalism represents a particular form of asymmetric association in which one species derives benefits from the interaction while the other experiences neither gain nor harm. The dynamical properties of commensal systems have attracted growing attention in the mathematical biology literature [3, 6, 10, 15, 26, 32].

Sun and Sun [31] proposed a two-species model with commensalism as follows,

$$\begin{cases} \frac{dx}{dt} = r_1x \left(1 - \frac{x}{K_1} + a \frac{y}{K_1} \right), \\ \frac{dy}{dt} = r_2y \left(1 - \frac{y}{K_2} \right), \end{cases} \quad (1.1)$$

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where $x(t)$ and $y(t)$ represent the densities of the two species, respectively; r_1 and K_1 denote the intrinsic growth rate and carrying capacity of species x , respectively; r_2 and K_2 represent the intrinsic growth rate and carrying capacity of species y , respectively. The parameter a represents the beneficial effect of species y on x . The authors proved that the system has four fixed points $E_1(0, 0)$, $E_2(K_1, 0)$, $E_3(0, K_2)$, $E_4(K_1 + aK_2, K_2)$, where E_1 , E_2 , E_3 are unstable fixed points and E_4 is a stable node. The impact of harvesting on population dynamics is a significant theme in ecological management [2, 14, 16, 21, 24, 28–30]. Compared to linear harvesting, nonlinear harvesting functions provide a more realistic description of the relationship between harvesting effort and population density. Clark and Mangel [7] first proposed the Michaelis–Menten type harvesting function $h(E, x) = \frac{qEx}{m_1E + m_2x}$, where q is the catchability coefficient, E denotes the external effort spent on harvesting, and m_1 and m_2 are positive constants associated with the saturation characteristics of the harvesting process. Numerous studies have demonstrated the critical impact of this harvesting function on species survival and population dynamics. For example, Feng et al. [12] and Liu et al. [23] systematically investigated a single-species logistic model with seasonal Michaelis–Menten type harvesting, revealing the critical roles of harvesting timing and harvesting intensity in population persistence and extinction, and establishing the existence, stability, and bifurcation behavior of periodic solutions; Pal [25] studied a Hassell–Varley predator–prey model incorporating time delay and Michaelis–Menten type harvesting. This study analyzes how harvesting effort and time delay jointly affect system stability and bifurcation behavior. The results indicate that when the time delay exceeds a critical threshold, the positive fixed point loses its stability through a Hopf bifurcation, giving rise to stable limit cycle oscillations. Numerical simulations indicated that Michaelis–Menten harvesting is a key factor inducing unstable fixed points and chaotic dynamics.

A growing body of research has examined models that combine commensalism with harvesting [4, 11, 17, 18, 21, 34, 37]. Fang and Chen [11] analyzed a continuous-time Lotka–Volterra commensalism model with Allee effect and linear harvesting. They showed that the interplay between the Allee effect and harvesting can induce saddle-node bifurcations, and that a stronger Allee effect may elevate the equilibrium prey density. Jawad [17] proposed and analyzed a commensalism model with Michaelis–Menten type harvesting on the first species, where the second species provides commensal benefits. The author systematically analyzed the existence, local stability, and bifurcation behavior of fixed points, and demonstrated that commensalism can prevent the first species from going extinct under harvesting. Building on Jawad’s framework, Chen et al. [4] carried out a more comprehensive investigation of the same model. By combining comparison-based techniques with the asymptotically autonomous systems framework, they established sharper persistence criteria and global attractivity results for both the boundary and coexistence fixed points, substantially extending the results of [17].

More recently, Chen [3] proposed and analyzed a continuous-time commensalism model where the first species is subject to Michaelis–Menten harvesting:

$$\begin{cases} \frac{dx}{dt} = r_1x \left(1 - \frac{x}{K_1} + a\frac{y}{K_1} \right) - \frac{qEx}{m_1E + m_2x}, \\ \frac{dy}{dt} = r_2y \left(1 - \frac{y}{K_2} \right). \end{cases} \quad (1.2)$$

They analyzed the local and global stability of the system and proved that under limited harvesting, the system possesses a unique globally stable positive fixed point. However, under excessive harvesting, provided that the commensalism coefficient (a) and the carrying capacity (K_2) of

the second species are sufficiently large, the two species can still coexist stably; otherwise, the first species is driven to extinction.

In many ecological systems, population censuses and management interventions are conducted at discrete time intervals, making discrete-time models particularly suitable for populations with non-overlapping generations, seasonal reproduction, or periodic harvesting [8, 13, 20, 33]. Nevertheless, discrete commensalism models incorporating harvesting remain relatively understudied, with only a few contributions available [10, 37]. Zhou et al. [37] proposed a discrete commensalism model with Michaelis–Menten type harvesting, where the second species is subject to Michaelis–Menten type harvesting. They proved the existence of positive periodic solutions when the harvesting intensity does not exceed a certain threshold. Ditta et al. [10] investigated a discrete-time commensalism system with non-selective harvesting. They demonstrated that harvesting intensity is a key parameter triggering period-doubling bifurcation and chaos in the system. Their results indicate that high harvestable proportions stabilize the system, while low proportions induce bifurcations and chaos, potentially leading to ecosystem collapse. However, their work did not thoroughly explore the dynamic effects of commensalism intensity itself.

Motivated by these considerations, this paper investigates the discrete analog of the system (1.2). Discrete time models are often more appropriate for populations with non-overlapping generations and can exhibit richer dynamical behaviors. Our aim is to explore how the interplay between commensalism and Michaelis–Menten harvesting shapes these complex dynamics. First, we introduce the following transformation to the continuous system (1.2),

$$\bar{x} = \frac{1}{K_1}x, \quad \bar{y} = \frac{a}{K_1}y, \quad \bar{t} = r_1t.$$

After dropping the bars, system (1.2) becomes

$$\begin{cases} \frac{dx}{dt} = x \left(1 - x + y - \frac{\alpha}{\gamma + x} \right), \\ \frac{dy}{dt} = y \left(\delta - \beta y \right), \end{cases} \quad (1.3)$$

where $\alpha = \frac{qE}{r_1K_1m_2}$, $\beta = \frac{K_1r_2}{ar_1K_2}$, $\gamma = \frac{m_1E}{m_2K_1}$, $\delta = \frac{r_2}{r_1}$. Common approaches to discretizing continuous-time population models include the forward and backward Euler methods, and the piecewise constant argument method. In discrete commensalism models, both the forward Euler method [10, 32] and the piecewise constant argument method [6] have been employed. The forward Euler method is simple and explicit, but positivity is not guaranteed without suitable step-size restrictions, and the step size may affect the stability and bifurcation properties of the resulting discrete system [1, 9, 35]. The backward Euler method is implicit and generally requires nonlinear algebraic equations to be solved at each step [22]. In contrast, the piecewise constant argument method directly yields an explicit exponential map whose positive multipliers preserve the nonnegative quadrant and its coordinate axes. Moreover, its multiplicative form retains the one-way commensal structure and the biological interpretation of the model terms. Therefore, following the exponential-map form studied by Jiang and Rogers [19], we discretize system (1.3) as follows:

$$\begin{cases} x_{n+1} = x_n \exp \left(1 - x_n + y_n - \frac{\alpha}{\gamma + x_n} \right), \\ y_{n+1} = y_n \exp \left(\delta - \beta y_n \right). \end{cases} \quad (1.4)$$

Note that once the birth rates and carrying capacities of the two species are given, we can use α and $\frac{\delta}{\beta}$ to represent the harvesting pressure on species x and the commensal effect of species y on species x , respectively.

The remainder of this paper is organized as follows. Sections 2 and 3 address the existence and local stability of fixed points, respectively. Sections 4 and 5 investigate the persistence and global attractivity of system (1.4). Section 6 presents the bifurcation analysis, and Section 7 provides numerical simulations that corroborate the theoretical results. Finally, Section 8 summarizes the main findings and discusses their ecological implications.

2. Existence of fixed points

A fixed point (x, y) of (1.4) satisfies

$$x = x \exp\left(1 - x + y - \frac{\alpha}{\gamma + x}\right), \quad y = y \exp(\delta - \beta y). \quad (2.1)$$

By direct computation, system (1.4) admits two boundary fixed points $E_0(0, 0)$ and $E_1(0, \frac{\delta}{\beta})$. For other possible boundary fixed point $(x, 0)$, x is a positive root of $F(x) = 0$, where

$$F(x) = x^2 + (\gamma - 1)x + \alpha - \gamma.$$

Let Δ denote the discriminant of $F(x)$:

$$\Delta = (\gamma + 1)^2 - 4\alpha.$$

We first determine whether the axis of symmetry $x = \frac{1-\gamma}{2}$ of $F(x)$ is positive or negative. When $\frac{1-\gamma}{2} \leq 0$, i.e., $\gamma \geq 1$, for $F(x)$ to have a positive root, we require $F(0) = \alpha - \gamma < 0$, i.e., $\alpha < \gamma$. In this case, system (1.4) has a boundary fixed point $E_{12}(x_{12}^*, 0)$, where $x_{12}^* = \frac{1-\gamma+\sqrt{\Delta}}{2}$.

When $0 < \gamma < 1$, the sign of Δ is determined by

$$\Delta \begin{cases} < 0 & \text{if } \alpha > \alpha_1, \\ = 0 & \text{if } \alpha = \alpha_1 := \frac{(\gamma + 1)^2}{4}, \\ > 0 & \text{if } \alpha < \alpha_1. \end{cases}$$

Thus, $F(x)$ has two positive roots $x_{11}^* = \frac{1-\gamma-\sqrt{\Delta}}{2}$ and $x_{12}^* = \frac{1-\gamma+\sqrt{\Delta}}{2}$ if $0 < \alpha < \alpha_1$, while it has a unique positive root $x_{13}^* = \frac{1-\gamma}{2}$ if $\alpha = \alpha_1$. The sign of $F(0) = \alpha - \gamma$ satisfies

$$F(0) \begin{cases} > 0 & \text{if } \alpha > \gamma, \\ = 0 & \text{if } \alpha = \gamma, \\ < 0 & \text{if } \alpha < \gamma. \end{cases}$$

This implies that $F(0) > 0$ if $\alpha > \gamma$; $F(0) = 0$ if $\alpha = \gamma$; $F(0) < 0$ if $\alpha < \gamma$. Moreover, we always have $0 < \gamma < \alpha_1 < 1$ when $0 < \gamma < 1$. Based on the above analysis, we state the following theorem.

Theorem 2.1. *The boundary fixed points of system (1.4) other than E_0 and E_1 are classified as follows.*

- (i) *There is a boundary fixed point $E_{12}(x_{12}^*, 0)$ if $\alpha < \gamma$ and $\gamma \geq 1$.*
- (ii) *There is no other boundary fixed point if $\alpha > \alpha_1$, or if $\alpha \geq \gamma$ and $\gamma \geq 1$.*
- (iii) *There is a boundary fixed point $E_{13}(x_{13}^*, 0)$ if $\alpha = \alpha_1$ and $0 < \gamma < 1$.*
- (iv) *There is a boundary fixed point $E_{12}(x_{12}^*, 0)$ if $0 < \alpha \leq \gamma$ and $0 < \gamma < 1$.*
- (v) *There are two boundary fixed points $E_{11}(x_{11}^*, 0)$ and $E_{12}(x_{12}^*, 0)$ if $\gamma < \alpha < \alpha_1$ and $0 < \gamma < 1$.*

Next, we consider the positive fixed points (x, y) of the system (1.4). Obviously, $y = \frac{\delta}{\beta}$, and x is a positive root of the equation $G(x) = 0$, where

$$G(x) = x^2 + \left(\gamma - 1 - \frac{\delta}{\beta}\right)x + \left(\alpha - \gamma - \frac{\delta}{\beta}\gamma\right).$$

We first consider the sign of the axis of symmetry $x = \frac{1 + \frac{\delta}{\beta} - \gamma}{2}$ of $G(x)$. When $\frac{1 + \frac{\delta}{\beta} - \gamma}{2} \leq 0$, i.e., $\gamma \geq 1 + \frac{\delta}{\beta}$, a positive fixed point $E_{22}(x_{22}^*, \frac{\delta}{\beta})$ exists if $\alpha < \left(1 + \frac{\delta}{\beta}\right)\gamma$.

When $0 < \gamma < 1 + \frac{\delta}{\beta}$, i.e., the axis of symmetry satisfies $\frac{1 + \frac{\delta}{\beta} - \gamma}{2} > 0$, we consider the sign of $G(0) = \alpha - \gamma - \frac{\delta}{\beta}\gamma$ and the discriminant of $G(x)$, namely $\tilde{\Delta} = \left(\gamma + 1 + \frac{\delta}{\beta}\right)^2 - 4\alpha$.

$$\tilde{\Delta} \begin{cases} < 0 & \text{if } \alpha > \alpha_2, \\ = 0 & \text{if } \alpha = \alpha_2 = \frac{\left(\gamma + 1 + \frac{\delta}{\beta}\right)^2}{4}, \\ > 0 & \text{if } \alpha < \alpha_2. \end{cases}$$

Therefore, $G(x)$ has two roots $x_{21}^* = \frac{1 + \frac{\delta}{\beta} - \gamma - \sqrt{\tilde{\Delta}}}{2}$ and $x_{22}^* = \frac{1 + \frac{\delta}{\beta} - \gamma + \sqrt{\tilde{\Delta}}}{2}$ if $0 < \alpha < \alpha_2$, while $G(x)$ has a unique positive root $x_{23}^* = \frac{1 + \frac{\delta}{\beta} - \gamma}{2}$ if $\alpha = \alpha_2$.

$$G(0) \begin{cases} > 0 & \text{if } \alpha > \alpha_3, \\ = 0 & \text{if } \alpha = \alpha_3 = \left(1 + \frac{\delta}{\beta}\right)\gamma, \\ < 0 & \text{if } \alpha < \alpha_3, \end{cases}$$

which implies that $G(0) > 0$ if $\alpha > \alpha_3$; $G(0) = 0$ if $\alpha = \alpha_3$; $G(0) < 0$ if $\alpha < \alpha_3$. Moreover, we always have $0 < \alpha_3 < \alpha_2$. Based on the above analysis, we have the following results.

Theorem 2.2. *The positive fixed points of system (1.4) are classified as follows.*

- (i) *There is a positive fixed point $E_{22}\left(x_{22}^*, \frac{\delta}{\beta}\right)$ if $0 < \alpha < \alpha_3$ and $\gamma \geq 1 + \frac{\delta}{\beta}$.*
- (ii) *There is no positive fixed point if $\alpha > \alpha_2$, or if $\alpha \geq \alpha_3$ and $\gamma \geq 1 + \frac{\delta}{\beta}$.*
- (iii) *There is a unique positive fixed point $E_{23}\left(x_{23}^*, \frac{\delta}{\beta}\right)$ if $\alpha = \alpha_2$ and $\gamma < 1 + \frac{\delta}{\beta}$.*
- (iv) *There is a positive fixed point $E_{22}\left(x_{22}^*, \frac{\delta}{\beta}\right)$ if $0 < \alpha \leq \alpha_3$ and $\gamma < 1 + \frac{\delta}{\beta}$.*
- (v) *There are two positive fixed points $E_{21}\left(x_{21}^*, \frac{\delta}{\beta}\right)$ and $E_{22}\left(x_{22}^*, \frac{\delta}{\beta}\right)$ if $\alpha_3 < \alpha < \alpha_2$ and $\gamma < 1 + \frac{\delta}{\beta}$.*

3. Local stability of fixed points

The local dynamics of system (1.4) at any fixed point are determined by the eigenvalues of its Jacobian matrix. A direct computation shows that the Jacobian matrix evaluated at $E(x, y)$ is

$$J(E) = \begin{pmatrix} \left(1 - x + \frac{\alpha x}{(\gamma + x)^2}\right) \exp\left(1 - x + y - \frac{\alpha}{\gamma + x}\right) & x \exp\left(1 - x + y - \frac{\alpha}{\gamma + x}\right) \\ 0 & (1 - \beta y) \exp(\delta - \beta y) \end{pmatrix}.$$

A straightforward computation yields the following stability results.

Theorem 3.1. *The local stability of $E_0(0, 0)$ and $E_1\left(0, \frac{\delta}{\beta}\right)$ is as follows.*

(1) *The local stability of $E_0(0, 0)$:*

- (i) E_0 is a source if $\alpha < \gamma$;
- (ii) E_0 is non-hyperbolic if $\alpha = \gamma$;
- (iii) E_0 is a saddle if $\alpha > \gamma$.

(2) *The local stability of $E_1\left(0, \frac{\delta}{\beta}\right)$:*

- (i) E_1 is a source if $\delta > 2$ and $\alpha < \alpha_3$;
- (ii) E_1 is a sink if $0 < \delta < 2$ and $\alpha > \alpha_3$;
- (iii) E_1 is a saddle if $0 < \delta < 2$ and $\alpha < \alpha_3$, or if $\delta > 2$ and $\alpha > \alpha_3$;
- (iv) E_1 is non-hyperbolic if $\delta = 2$ or $\alpha = \alpha_3$.

Proof. The Jacobian matrices of $E_0(0, 0)$ and $E_1\left(0, \frac{\delta}{\beta}\right)$ are

$$J(E_0) = \begin{pmatrix} e^{1-\frac{\alpha}{\gamma}} & 0 \\ 0 & e^{\delta} \end{pmatrix}, \quad J(E_1) = \begin{pmatrix} e^{1+\frac{\delta}{\beta}-\frac{\alpha}{\gamma}} & 0 \\ 0 & 1 - \delta \end{pmatrix}.$$

Thus, the eigenvalues of $J(E_0)$ are $\lambda_1 = e^{1-\frac{\alpha}{\gamma}}$ and $\lambda_2 = e^{\delta}$. Since $\delta > 0$, $|\lambda_2| > 1$. Moreover we have $|\lambda_1| > 1$ if $\alpha < \gamma$; $|\lambda_1| = 1$ if $\alpha = \gamma$; $|\lambda_1| < 1$ if $\alpha > \gamma$. Then $E_0(0, 0)$ is a source if $\alpha < \gamma$; $E_0(0, 0)$ is non-hyperbolic if $\alpha = \gamma$; $E_0(0, 0)$ is a saddle if $\alpha > \gamma$. The proof process of the local stability of E_1 is similar to the above, so the theorem holds. $\square$

Next, we discuss the local stability of the boundary fixed points $E_{1i}(x_{1i}^*, 0)$ ($i = 1, 2, 3$). The Jacobian matrix at $E_{1i}(x_{1i}^*, 0)$ is

$$J(E_{1i}) = \begin{pmatrix} P_{1i} x_{1i}^* \\ 0 & e^{\delta} \end{pmatrix}, \quad P_{1i} = \frac{\alpha\gamma + 2\alpha x_{1i}^*}{(\gamma + x_{1i}^*)^2}.$$

The eigenvalues of $J(E_{1i})$ are P_{1i} and e^{δ} (> 1). In addition, when $\alpha = \alpha_1$, $P_{13} = 1$, so we have the following theorem.

Theorem 3.2. *The boundary fixed point E_{13} is non-hyperbolic if $\alpha = \alpha_1$ and $0 < \gamma < 1$.*

Since $\frac{dP_{1i}}{dx_{1i}^*} = -\frac{2\alpha x_{1i}^*}{(\gamma + x_{1i}^*)^3} < 0$, P_{1i} strictly decreases with x_{1i}^* . Combined with $x_{11}^* < x_{13}^* < x_{12}^*$, it can be concluded from $J(E_{11})$ that both eigenvalues of E_{11} are greater than 1. Therefore, the stability of E_{11} is established as follows.

Theorem 3.3. E_{11} is a source if $\gamma < \alpha < \alpha_1$ and $0 < \gamma < 1$.

Next, we discuss the local stability of E_{12} . The Jacobian matrix of $J(E_{12})$ has one eigenvalue $\lambda_1 = P_{12} = \frac{\alpha\gamma + 2\alpha x_{12}^*}{(\gamma + x_{12}^*)^2} \in (0, 1)$, and another eigenvalue $\lambda_2 = e^\delta > 1$. Therefore, the stability of E_{12} is established as follows.

Theorem 3.4. Assume E_{12} exists, the fixed point E_{12} is always a saddle point.

Now we proceed to discuss the stability of $E_{2i}(x_{2i}^*, \frac{\delta}{\beta})$ ($i = 1, 2, 3$). The Jacobian matrix at $E_{2i}(x_{2i}^*, \frac{\delta}{\beta})$ is given by

$$J(E_{2i}) = \begin{pmatrix} P_{2i} & x_{2i}^* \\ 0 & 1 - \delta \end{pmatrix}$$

where

$$P_{2i} = -\frac{\delta}{\beta} + \frac{\alpha\gamma + 2\alpha x_{2i}^*}{(\gamma + x_{2i}^*)^2}.$$

Evidently, P_{2i} and $1 - \delta$ are the two eigenvalues. It is clear that $|1 - \delta| > 1$ if $\delta > 2$; $|1 - \delta| = 1$ if $\delta = 2$; and $|1 - \delta| < 1$ if $0 < \delta < 2$. Furthermore, when $\alpha = \alpha_2$, we have $P_{23} = 1$. Therefore, the following conclusion is true.

Theorem 3.5. E_{23} is always non-hyperbolic if $\alpha = \alpha_2$ and $\delta > \beta\gamma - \beta$.

Since $\frac{dP_{2i}}{dx_{2i}^*} = -\frac{2\alpha x_{2i}^*}{(\gamma + x_{2i}^*)^3} < 0$, P_{2i} is a strictly decreasing function of x_{2i}^* . Combined with $x_{21}^* < x_{23}^* < x_{22}^*$, it can be concluded from $J(E_{21})$ that E_{21} always has one eigenvalue P_{21} greater than 1. Therefore, the following classification of E_{21} is established.

Theorem 3.6. If $\alpha_3 < \alpha < \alpha_2$ and $\delta > \beta\gamma - \beta$, then E_{21} is classified as follows.

- (i) E_{21} is a source if $\delta > 2$.
- (ii) E_{21} is a saddle if $0 < \delta < 2$.
- (iii) E_{21} is non-hyperbolic if $\delta = 2$.

Finally, we discuss the stability of E_{22} . The Jacobian $J(E_{22})$ has eigenvalues

$$\lambda_1 = -\frac{\delta}{\beta} + \frac{\alpha\gamma + 2\alpha x_{22}^*}{(\gamma + x_{22}^*)^2} < 1, \quad \lambda_2 = 1 - \delta.$$

To determine whether $|\lambda_1| < 1$ or $|\lambda_1| > 1$, we examine

$$\lambda_1 - (-1) = \frac{K(x_{22}^*)}{(\gamma + x_{22}^*)^2},$$

where

$$K(x_{22}^*) = \left(1 - \frac{\delta}{\beta}\right)(x_{22}^*)^2 + 2I x_{22}^* + \gamma I, \quad I = \alpha + \gamma - \frac{\delta}{\beta}\gamma,$$

with discriminant $\Delta(K) = 4\alpha I$. We consider two cases.

Case 1. $\delta \leq \beta$. In this case $K(x_{22}^*) > 0$, so $\lambda_1 \in (-1, 1)$.

Case 2. $\delta > \beta$. The sign of I requires further discussion.

- (1) When $I \leq 0$, i.e., $\alpha \leq \tilde{\alpha} = \gamma\left(\frac{\delta}{\beta} - 1\right) < \alpha_3$, we have $K(x_{22}^*) < 0$, and thus $|\lambda_1| > 1$.

- (2) When $I > 0$, i.e., $\alpha > \tilde{\alpha}$. Due to the existence of E_{22} , we only need to consider the case where $\tilde{\alpha} < \alpha < \alpha_2$, then

$$K(x_{22}^*) \begin{cases} > 0, & \text{if } 0 \leq x_{22}^* < \tilde{x}, \\ = 0, & \text{if } x_{22}^* = \tilde{x} \triangleq \frac{I + \sqrt{\alpha I}}{\frac{\delta}{\beta} - 1}, \\ < 0, & \text{if } x_{22}^* > \tilde{x}. \end{cases}$$

Therefore, we obtain

$$x_{22}^* \begin{cases} > \tilde{x}, & \text{if } \frac{\delta}{\beta} > \beta_1 \triangleq \frac{-\alpha + (\sqrt{\alpha} + \sqrt{I})\sqrt{\alpha + I}}{\sqrt{\alpha I}}, \\ = \tilde{x}, & \text{if } \frac{\delta}{\beta} = \beta_1, \\ < \tilde{x}, & \text{if } \frac{\delta}{\beta} < \beta_1. \end{cases}$$

Consequently, we have

$$|\lambda_1| \begin{cases} > 1, & \text{if } \frac{\delta}{\beta} > \beta_1, \\ = 1, & \text{if } \frac{\delta}{\beta} = \beta_1, \\ < 1, & \text{if } \frac{\delta}{\beta} < \beta_1. \end{cases}$$

Based on the above discussion, we have the following conclusion.

Theorem 3.7. *Suppose the positive fixed point E_{22} exists, then the following statements hold.*

- (1) *If $\delta \leq \beta$, then E_{22} is*
- (i) *a sink if $0 < \delta < 2$;*
 - (ii) *a saddle if $\delta > 2$;*
 - (iii) *non-hyperbolic if $\delta = 2$.*
- (2) *If $\delta > \beta$, then the topological classification of E_{22} is summarized in Table 1.*

Remark 3.1. Based on the analysis in Theorems 2.1, 3.1, and 3.3, when $0 < \gamma < 1$, as α increases through γ , a stability exchange occurs between E_0 and E_{11} : When $\alpha < \gamma$, E_0 is a source and E_{11} does not exist; when $\alpha = \gamma$, E_{11} coincides with E_0 and the eigenvalue λ_1 at E_0 equals 1; when $\gamma < \alpha < \alpha_1$, E_0 becomes a saddle while E_{11} emerges as a source. This collision and exchange of stability is characteristic of a transcritical bifurcation. Similarly, when $\gamma \geq 1$, the fixed points E_0 and E_{12} collide at $\alpha = \gamma$, and a transcritical bifurcation may also occur at E_0 .

4. Persistence of system (1.4)

The following result on the persistence of the second population is taken from Theorem 7 in [36].

Table 1. Local stability of the positive fixed point E_{22} when $\delta > \beta$.

Range of δ	Harvesting pressure	Commensal effect	Type of E_{22}
$0 < \delta < 2$	$0 < \alpha \leq \tilde{\alpha}$		Saddle
	$\tilde{\alpha} < \alpha < \alpha_2$	$\delta/\beta > \beta_1$	Saddle
		$\delta/\beta = \beta_1$	Non-hyperbolic
		$\delta/\beta < \beta_1$	Sink
$\delta = 2$	$0 < \alpha < \alpha_2$		Non-hyperbolic
$\delta > 2$	$0 < \alpha \leq \tilde{\alpha}$		Source
	$\tilde{\alpha} < \alpha < \alpha_2$	$\delta/\beta > \beta_1$	Source
		$\delta/\beta = \beta_1$	Non-hyperbolic
		$\delta/\beta < \beta_1$	Saddle

Theorem 4.1. *The second population $y(n)$ of system (1.4) is always persistent, and satisfies*

$$U_1 \leq \liminf_{n \rightarrow +\infty} y(n) \leq \limsup_{n \rightarrow +\infty} y(n) \leq U_2,$$

where $U_2 = \frac{\exp(\delta-1)}{\beta}$ and $U_1 = \frac{\delta}{\beta} \exp(\delta - \beta U_2)$.

Theorem 4.2. *If $1 - M_1 + U_1 - \frac{\alpha}{\gamma} \geq 0$, then system (1.4) is persistent and satisfies*

$$M_1 \leq \liminf_{n \rightarrow +\infty} x(n) \leq \limsup_{n \rightarrow +\infty} x(n) \leq M_2,$$

where

$$M_2 = \max_{x>0} x \exp\left(1 - x + U_2 - \frac{\alpha}{\gamma + x}\right), \quad M_1 = \left(1 + U_1 - \frac{\alpha}{\gamma}\right) \exp\left(1 - M_2 + U_1 - \frac{\alpha}{\gamma}\right).$$

Proof. (1) We first prove that $\limsup_{n \rightarrow +\infty} x(n) \leq M_2$.

By Theorem 4.1, $\limsup_{n \rightarrow +\infty} y(n) \leq U_2$. Hence for any $\epsilon > 0$, there exists a positive integer N_1 such that

$$y(n) < U_2 + \epsilon \quad \text{for all } n \geq N_1. \quad (4.1)$$

Define the function

$$f_\epsilon(x) = x \exp\left(1 - x + U_2 + \epsilon - \frac{\alpha}{\gamma + x}\right), \quad x > 0.$$

Since f_ϵ is continuous on $(0, +\infty)$, positive, and satisfies $\lim_{x \rightarrow 0^+} f_\epsilon(x) = \lim_{x \rightarrow +\infty} f_\epsilon(x) = 0$, it attains a finite maximum $M_2(\epsilon)$ on $(0, +\infty)$. From the first equation of system (1.4) and inequality (4.1), for all $n \geq N_1$,

$$x(n+1) = x(n) \exp\left(1 - x(n) + y(n) - \frac{\alpha}{\gamma + x(n)}\right) < f_\epsilon(x(n)) \leq M_2(\epsilon).$$

Hence $\limsup_{n \rightarrow +\infty} x(n) \leq M_2(\epsilon)$. Since $\epsilon > 0$ is arbitrary, letting $\epsilon \rightarrow 0^+$ yields

$$\limsup_{n \rightarrow +\infty} x(n) \leq M_2,$$

where $M_2 = \max_{x>0} f(x)$ with $f(x) = x \exp\left(1 - x + U_2 - \frac{\alpha}{\gamma+x}\right)$.

(2) Next, we prove that

$$\liminf_{n \rightarrow +\infty} x(n) \geq M_1.$$

First, suppose there exists an integer l such that $x(l+1) \leq x(l)$, then

$$x(l+1) = x(l) \exp\left(1 - x(l) + y(l) - \frac{\alpha}{\gamma+x(l)}\right) \leq x(l),$$

which implies $1 - x(l) + y(l) - \frac{\alpha}{\gamma+x(l)} \leq 0$, and hence $x(l) \geq 1 + y(l) - \frac{\alpha}{\gamma+x(l)} \geq 1 + U_1 - \frac{\alpha}{\gamma}$. Consequently,

$$\begin{aligned} x(l+1) &= x(l) \exp\left(1 - x(l) + y(l) - \frac{\alpha}{\gamma+x(l)}\right) \\ &\geq \left(1 + U_1 - \frac{\alpha}{\gamma}\right) \exp\left(1 - M_2 + U_1 - \frac{\alpha}{\gamma}\right) \\ &= M_1. \end{aligned}$$

We claim that $x(n) \geq M_1$ for all $n \geq l$. Suppose for contradiction that there exists $t_0 > l$ with $x(t_0) < M_1$, then $t_0 > l + 2$. Let $\tilde{t}_0 > l + 2$ be the smallest such integer, so that $x(\tilde{t}_0) < M_1 \leq x(\tilde{t}_0 - 1)$. But the preceding argument applied at $\tilde{t}_0 - 1$ gives $x(\tilde{t}_0) \geq M_1$, a contradiction. Hence $x(n) \geq M_1$ for all $n \geq l$.

Now suppose $x(n+1) > x(n)$ for all $n \in \mathbb{N}$, and let $\underline{x} = \lim_{n \rightarrow \infty} x(n)$. We claim $\underline{x} \geq 1 + U_1 - \frac{\alpha}{\gamma}$. Suppose for contradiction that $\underline{x} < 1 + U_1 - \frac{\alpha}{\gamma}$. Taking the limit $n \rightarrow +\infty$ in the first equation of system (1.4) gives $\lim_{n \rightarrow +\infty} \left(1 - x(n) + y(n) - \frac{\alpha}{\gamma+x(n)}\right) = 0$. However, for sufficiently large n ,

$$\liminf_{n \rightarrow +\infty} \left(1 - x(n) + y(n) - \frac{\alpha}{\gamma+x(n)}\right) \geq 1 - \underline{x} + U_1 - \frac{\alpha}{\gamma} > 0,$$

a contradiction. Hence the claim holds.

Since $1 - M_1 + U_1 - \frac{\alpha}{\gamma} \geq 0$ by assumption, we have $M_1 \leq 1 + U_1 - \frac{\alpha}{\gamma} \leq \underline{x}$, and therefore

$$\liminf_{n \rightarrow +\infty} x(n) \geq M_1.$$

□

Remark 4.1. In the persistence condition of Theorem 4.2, the terms 1 and U_1 represent the scaled intrinsic growth of species x and the guaranteed asymptotic commensal support supplied by species y , respectively, whereas M_1 represents density dependence at the lower comparison level. Moreover, $\frac{\alpha}{\gamma}$ is the maximum per-capita harvesting loss in the low-density limit. Hence, $1 - M_1 + U_1 - \frac{\alpha}{\gamma} \geq 0$ means that, when species x is near its lower comparison level, its intrinsic growth together with the guaranteed commensal support is sufficient to offset density dependence and the maximal harvesting loss. Ecologically, sufficient commensal support relative to harvesting pressure enables species x to recover from low density and favors the persistence of both species. Since U_1 , M_1 , and M_2 are comparison bounds, this is a sufficient and possibly conservative persistence condition.

5. Global attractivity of system (1.4)

This section establishes the global attractivity of the fixed points E_{22} and E_1 by employing Lemmas 3–5 from [5]. We begin by considering the second equation of system (1.4)

$$y(n+1) = y(n) \exp(\delta - \beta y(n)). \quad (5.1)$$

From Lemma 4 in [5], the following result is obtained.

Theorem 5.1. *If $0 < \delta < 2$ and $y(0) > 0$, then*

$$\lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}.$$

Theorem 5.2. *Suppose $0 < \alpha < \alpha_3$, $0 < \delta < 2$, $1 + \frac{\delta}{\beta} - \frac{\alpha}{\gamma + M_2} < M_2$, and $\frac{\delta}{\beta} < \frac{\alpha}{\gamma + M_2}$, then the positive fixed point $E_{22} \left(x_{22}^*, \frac{\delta}{\beta} \right)$ is globally attractive, i.e.,*

$$\lim_{n \rightarrow \infty} x(n) = x_{22}^*, \quad \lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}.$$

Proof. From Theorem 5.1, we have $\lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}$. It remains to prove that $\lim_{n \rightarrow \infty} x(n) = x_{22}^*$.

Since $\lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}$ and $\limsup_{n \rightarrow +\infty} x(n) \leq M_2$, for any sufficiently small $\epsilon > 0$, there exists $N_1 > 0$ such that for all $n \geq N_1$,

$$\frac{\delta}{\beta} - \epsilon < y(n) < \frac{\delta}{\beta} + \epsilon, \quad x(n) \leq M_2.$$

Let $F_1 = \frac{\delta}{\beta} - \epsilon$ and $G_1 = \frac{\delta}{\beta} + \epsilon$ and define

$$P := \limsup_{n \rightarrow \infty} x(n), \quad Q := \liminf_{n \rightarrow \infty} x(n).$$

To prove $\lim_{n \rightarrow \infty} x(n) = x_{22}^*$, it suffices to show that $P = Q = x_{22}^*$.

If there exist sequences $\{P_n\}$ and $\{Q_n\}$ satisfying

$$Q_n \leq Q \leq P \leq P_n,$$

and

$$\lim_{n \rightarrow \infty} P_n = \lim_{n \rightarrow \infty} Q_n = x_{22}^*,$$

then by the squeeze theorem, $\lim_{n \rightarrow \infty} x(n) = x_{22}^*$. We construct these two sequences using an iterative method as follows.

Iteration 1 (i): We first find $P_1 > 0$ such that $P \leq P_1$. From the first equation of system (1.4), for $n \geq N_1$,

$$\begin{aligned} x(n+1) &= x(n) \exp \left(1 - x(n) + y(n) - \frac{\alpha}{\gamma + x(n)} \right) \\ &\leq x(n) \exp \left(1 + G_1 - \frac{\alpha}{\gamma + M_2} - x(n) \right). \end{aligned}$$

Consider the auxiliary equation

$$u(n+1) = u(n) \exp \left(1 + G_1 - \frac{\alpha}{\gamma + M_2} - u(n) \right). \quad (5.2)$$

Since $\frac{\delta}{\beta} < \frac{\alpha}{\gamma + M_2}$ and ϵ is sufficiently small, we have $\frac{\delta}{\beta} + \epsilon < \frac{\alpha}{\gamma + M_2}$, which implies $1 + G_1 - \frac{\alpha}{\gamma + M_2} < 1$. Moreover, from $\alpha < \alpha_3 = \left(1 + \frac{\delta}{\beta}\right) \gamma$, it follows that $1 + G_1 - \frac{\alpha}{\gamma + M_2} > 0$. By Lemma 4 in [5], any positive solution $u(n)$ of (5.2) with initial value $u(N_1) > 0$ satisfies $u(n) \leq 1$ for $n \geq N_1$ and $\lim_{n \rightarrow \infty} u(n) = 1 + G_1 - \frac{\alpha}{\gamma + M_2}$. By Lemma 3 in [5], $g(u) = u \exp \left(1 + G_1 - \frac{\alpha}{\gamma + M_2} - u \right)$ is non-decreasing on $(0, 1]$. Then, by Lemma 5 in [5], for all $n \geq N_1$, we have $x(n) \leq u(n)$, where $u(n)$ is the solution of (5.2) with initial value $u(N_1) = x(N_1)$. Consequently,

$$P = \limsup_{n \rightarrow \infty} x(n) \leq \lim_{n \rightarrow \infty} u(n) = 1 + G_1 - \frac{\alpha}{\gamma + M_2}.$$

Therefore, for the above $\epsilon > 0$, there exists $N_2 > N_1$ such that for $n \geq N_2$,

$$x(n) \leq 1 + G_1 - \frac{\alpha}{\gamma + M_2} + \epsilon := P_1.$$

Since $1 + \frac{\delta}{\beta} - \frac{\alpha}{\gamma + M_2} < M_2$, by choosing $\epsilon > 0$ sufficiently small, we have $P_1 = 1 + \frac{\delta}{\beta} - \frac{\alpha}{\gamma + M_2} + 2\epsilon < M_2$.

Iteration 1 (ii): Next, we find $Q_1 > 0$ such that $Q \geq Q_1$. From the first equation of system (1.4), for $n \geq N_2$,

$$\begin{aligned} x(n+1) &= x(n) \exp \left(1 - x(n) + y(n) - \frac{\alpha}{\gamma + x(n)} \right) \\ &\geq x(n) \exp \left(1 + F_1 - \frac{\alpha}{\gamma} - x(n) \right). \end{aligned}$$

Consider the auxiliary equation

$$u(n+1) = u(n) \exp \left(1 + F_1 - \frac{\alpha}{\gamma} - u(n) \right). \quad (5.3)$$

Since $\frac{\delta}{\beta} < \frac{\alpha}{\gamma}$, for sufficiently small $\epsilon > 0$, we have $0 < 1 + F_1 - \frac{\alpha}{\gamma} \leq 1$. By Lemma 4 in [5], any positive solution $u(n)$ of (5.3) with initial value $u(N_2) > 0$ satisfies $u(n) \leq 1$ for $n \geq N_2$ and $\lim_{n \rightarrow \infty} u(n) = 1 + F_1 - \frac{\alpha}{\gamma}$. By Lemma 3 in [5], $g(u) = u \exp \left(1 + F_1 - \frac{\alpha}{\gamma} - u \right)$ is non-decreasing on $(0, 1]$. Then, by Lemma 5 in [5], for all $n \geq N_2$, we have $x(n) \geq u(n)$, where $u(n)$ is the solution of (5.3) with initial value $u(N_2) = x(N_2)$. Consequently,

$$Q = \liminf_{n \rightarrow \infty} x(n) \geq \lim_{n \rightarrow \infty} u(n) = 1 + F_1 - \frac{\alpha}{\gamma}.$$

Therefore, for the above $\epsilon > 0$, there exists $N_3 > N_2$ such that for $n > N_3$,

$$x(n) \geq 1 + F_1 - \frac{\alpha}{\gamma} - \epsilon := Q_1.$$

Iteration 2 (i): We now find $P_2 > 0$ such that $P \leq P_2 \leq P_1$. Since $\lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}$, for the above $\epsilon > 0$, there exists $N_4 > N_3$ such that for $n \geq N_4$,

$$0 < \frac{\delta}{\beta} - \frac{\epsilon}{2} < y(n) < \frac{\delta}{\beta} + \frac{\epsilon}{2}.$$

Let $F_2 := \frac{\delta}{\beta} - \frac{\epsilon}{2}$ and $G_2 := \frac{\delta}{\beta} + \frac{\epsilon}{2}$. From the first equation of system (1.4), for $n \geq N_4$,

$$\begin{aligned} x(n+1) &= x(n) \exp \left(1 - x(n) + y(n) - \frac{\alpha}{\gamma + x(n)} \right) \\ &\leq x(n) \exp \left(1 + G_2 - \frac{\alpha}{\gamma + P_1} - x(n) \right). \end{aligned}$$

Consider the auxiliary equation

$$u(n+1) = u(n) \exp \left(1 + G_2 - \frac{\alpha}{\gamma + P_1} - u(n) \right). \quad (5.4)$$

Clearly, $0 < 1 + G_2 - \frac{\alpha}{\gamma + P_1} < 1 + G_1 - \frac{\alpha}{\gamma + M_2} < 1$. By Lemma 4 in [5], any positive solution $u(n)$ of (5.4) with initial value $u(N_4) > 0$ satisfies $u(n) \leq 1$ for $n \geq N_4$ and $\lim_{n \rightarrow \infty} u(n) = 1 + G_2 - \frac{\alpha}{\gamma + P_1}$. Moreover, $g(u) = u \exp \left(1 + G_2 - \frac{\alpha}{\gamma + P_1} - u \right)$ is non-decreasing on $(0, 1]$. Then, for all $n \geq N_4$, we have $x(n) \leq u(n)$, where $u(n)$ is the solution of (5.4) with initial value $u(N_4) = x(N_4)$. Consequently,

$$P = \limsup_{n \rightarrow \infty} x(n) \leq \lim_{n \rightarrow \infty} u(n) = 1 + G_2 - \frac{\alpha}{\gamma + P_1}.$$

Therefore, for the above $\epsilon > 0$, there exists $N_5 > N_4$ such that for $n \geq N_5$,

$$x(n) \leq 1 + G_2 - \frac{\alpha}{\gamma + P_1} + \frac{\epsilon}{2} := P_2.$$

Iteration 2 (ii): Next, we find $Q_2 > 0$ such that $Q \geq Q_2 \geq Q_1$. From the first equation of system (1.4), for $n \geq N_5$,

$$\begin{aligned} x(n+1) &= x(n) \exp \left(1 - x(n) + y(n) - \frac{\alpha}{\gamma + x(n)} \right) \\ &\geq x(n) \exp \left(1 + F_2 - \frac{\alpha}{\gamma + Q_1} - x(n) \right). \end{aligned}$$

Consider the auxiliary equation

$$u(n+1) = u(n) \exp \left(1 + F_2 - \frac{\alpha}{\gamma + Q_1} - u(n) \right). \quad (5.5)$$

Since $M_2 > x(n) > Q_1$, we have $0 < 1 + F_2 - \frac{\alpha}{\gamma + Q_1} \leq 1$. By Lemma 4 in [5], any positive solution $u(n)$ of (5.5) with initial value $u(N_5) > 0$ satisfies $u(n) \leq 1$ for $n \geq N_5$ and $\lim_{n \rightarrow \infty} u(n) = 1 + F_2 - \frac{\alpha}{\gamma + Q_1}$. Moreover, $g(u) = u \exp \left(1 + F_2 - \frac{\alpha}{\gamma + Q_1} - u \right)$ is non-decreasing on $(0, 1]$. Then, for all $n \geq N_5$, we have $x(n) \geq u(n)$, where $u(n)$ is the solution of (5.5) with initial value $u(N_5) = x(N_5)$. Consequently,

$$Q = \liminf_{n \rightarrow \infty} x(n) \geq \lim_{n \rightarrow \infty} u(n) = 1 + F_2 - \frac{\alpha}{\gamma + Q_1}.$$

Therefore, for the above $\epsilon > 0$, there exists $N_6 > N_5$ such that for $n > N_6$,

$$x(n) \geq 1 + F_2 - \frac{\alpha}{\gamma + Q_1} - \frac{\epsilon}{2} := Q_2.$$

Iteration k ($k \geq 3$): Continuing this iterative process, we obtain two sequences $\{P_n\}$ and $\{Q_n\}$ defined by

$$P_n = 1 + G_n - \frac{\alpha}{\gamma + P_{n-1}} + \frac{\epsilon}{n}, \quad Q_n = 1 + F_n - \frac{\alpha}{\gamma + Q_{n-1}} - \frac{\epsilon}{n}, \quad (5.6)$$

where

$$F_n = \frac{\delta}{\beta} - \frac{\epsilon}{n}, \quad G_n = \frac{\delta}{\beta} + \frac{\epsilon}{n}.$$

These sequences satisfy

$$Q_n \leq Q \leq P \leq P_n.$$

Claim: The sequence $\{P_n\}$ is monotonically decreasing, and $\{Q_n\}$ is monotonically increasing.

We prove this claim by mathematical induction. Clearly, $P_1 \geq P_2$ and $Q_1 \leq Q_2$. Assuming $P_{k-1} \geq P_k$ and $Q_{k-1} \leq Q_k$, we have

$$\begin{aligned} P_k &= 1 + G_k - \frac{\alpha}{\gamma + P_{k-1}} + \frac{\epsilon}{k} \geq 1 + G_{k+1} - \frac{\alpha}{\gamma + P_k} + \frac{\epsilon}{k+1} = P_{k+1}, \\ Q_k &= 1 + F_k - \frac{\alpha}{\gamma + Q_{k-1}} - \frac{\epsilon}{k} \leq 1 + F_{k+1} - \frac{\alpha}{\gamma + Q_k} - \frac{\epsilon}{k+1} = Q_{k+1}. \end{aligned}$$

Thus, the claim holds. Since $\{P_n\}$ is decreasing and bounded below, and $\{Q_n\}$ is increasing and bounded above, both sequences converge. Let

$$\lim_{n \rightarrow \infty} P_n = X_1, \quad \lim_{n \rightarrow \infty} Q_n = X_2.$$

Taking the limit as $n \rightarrow \infty$ in (5.6), we obtain

$$X_1 = 1 + \frac{\delta}{\beta} - \frac{\alpha}{\gamma + X_1}, \quad X_2 = 1 + \frac{\delta}{\beta} - \frac{\alpha}{\gamma + X_2}.$$

Since $\lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}$, both $(X_1, \frac{\delta}{\beta})$ and $(X_2, \frac{\delta}{\beta})$ satisfy the equations of system (1.4). However, under the assumptions of Theorem 5.2, system (1.4) admits a unique positive fixed point $(x_{22}^*, \frac{\delta}{\beta})$. Therefore, $X_1 = X_2 = x_{22}^*$, which implies $P = Q = x_{22}^*$. This completes the proof. $\square$

Remark 5.1. The conditions in Theorem 5.2 reflect an ecological balance among commensal support, density dependence, and harvesting pressure. The restriction $0 < \delta < 2$ ensures that species y converges to $\frac{\delta}{\beta}$, thereby providing a stable asymptotic commensal benefit to species x . Since $\alpha < \alpha_3$ is equivalent to $1 + \frac{\delta}{\beta} - \frac{\alpha}{\gamma} > 0$, species x retains a positive per-capita logarithmic growth rate at low density, indicating that harvesting is not too strong to prevent its recovery.

On the other hand, $\frac{\delta}{\beta} < \frac{\alpha}{\gamma + M_2}$ indicates that even the weakest per-capita harvesting pressure within the ultimate bounded region exceeds the asymptotic commensal contribution, thereby limiting excessive net growth induced by the commensal benefit. Moreover, $1 + \frac{\delta}{\beta} - \frac{\alpha}{\gamma + M_2} < M_2$ means that, when species x approaches the upper comparison level M_2 , density dependence and harvesting loss exceed intrinsic growth and commensal support, making its per-capita logarithmic growth rate negative. Thus, these conditions describe a suitable intermediate harvesting pressure that favors stable coexistence: Harvesting is sufficiently weak to permit population recovery at low density, yet sufficiently strong, together with intraspecific density dependence, to restrain excessive growth at high density.

Theorem 5.3. Suppose $0 < \delta < 2$, $\alpha > \alpha_2$, and $\gamma < 1 + \frac{\delta}{\beta}$. Then the boundary fixed point $E_1\left(0, \frac{\delta}{\beta}\right)$ is globally attractive, i.e.,

$$\lim_{n \rightarrow \infty} x(n) = 0, \quad \lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}.$$

Proof. From Theorem 5.1, $\lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}$. It remains to prove that $\lim_{n \rightarrow \infty} x(n) = 0$.

Since $\alpha > \alpha_2 = \frac{\left(1 + \frac{\delta}{\beta} + \gamma\right)^2}{4}$, for sufficiently small $\epsilon > 0$,

$$\alpha > \frac{\left(1 + \frac{\delta}{\beta} + \gamma\right)^2}{4} + 8(\gamma + M_2)\epsilon.$$

For this ϵ , there exists $N > 0$ such that $y(n) < \frac{\delta}{\beta} + \epsilon$ for all $n \geq N$. From the first equation of system (1.4), for $n \geq N$,

$$\begin{aligned} \ln \frac{x(n+1)}{x(n)} &= 1 - x(n) + y(n) - \frac{\alpha}{\gamma + x(n)} \\ &< 1 + \frac{\delta}{\beta} + \epsilon - x(n) - \frac{\left(1 + \frac{\delta}{\beta} + \gamma\right)^2 + 8(\gamma + M_2)\epsilon}{4(\gamma + x(n))} \\ &= \frac{h(x(n))}{4(\gamma + x(n))} - \frac{2(\gamma + M_2)}{\gamma + x(n)}\epsilon + \epsilon \\ &< \frac{h(x(n))}{4(\gamma + x(n))} - \epsilon, \end{aligned}$$

where

$$h(x) = -4x^2 + 4\left(1 + \frac{\delta}{\beta} - \gamma\right)x + 4\gamma\left(1 + \frac{\delta}{\beta}\right) - \left(1 + \frac{\delta}{\beta} + \gamma\right)^2.$$

Since $\gamma < 1 + \frac{\delta}{\beta}$, the function $h(x)$ attains its maximum at $x = \frac{1 + \frac{\delta}{\beta} - \gamma}{2} > 0$, and

$$\max_{x > 0} h(x) = h\left(\frac{1 + \frac{\delta}{\beta} - \gamma}{2}\right) = 0.$$

Therefore $\ln \frac{x(n+1)}{x(n)} < -\epsilon$, which gives

$$x(n) < x(N) e^{-(n-N)\epsilon}, \quad n > N.$$

Since $x(n) \geq 0$, we conclude $\lim_{n \rightarrow \infty} x(n) = 0$. □

Remark 5.2. Theorems 5.1–5.3 reveal that when $y(n)$ is globally asymptotically stable and the commensal effect $\left(\frac{\delta}{\beta}\right)$ of species y on species x is weak, the following conclusions hold: If the harvesting on species x (measured by α) is small, both species coexist stably, as illustrated in Figure 1(a); however, as the harvesting intensity on species x exceeds the critical threshold α_2 , species x is driven to extinction, as shown in Figure 1(b). These findings are consistent with the conclusions obtained by Chen in [3].

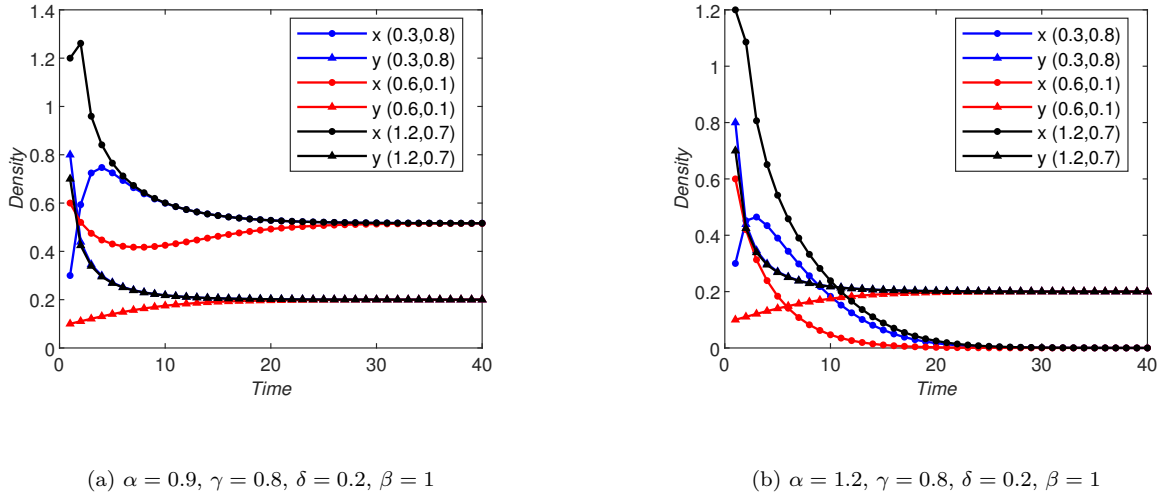


Figure 1. (a) Global attractivity of $E_{22}\left(x_{22}^*, \frac{\delta}{\beta}\right)$; (b) global attractivity of $E_1\left(0, \frac{\delta}{\beta}\right)$.

6. Bifurcation analysis

6.1. Transcritical and pitchfork bifurcations at E_0

As noted in Remark 3.1, when $\alpha = \gamma$, the Jacobian at E_0 has a simple eigenvalue $\lambda_1 = 1$ with $\lambda_2 \neq \pm 1$, suggesting that system (1.4) may undergo a transcritical bifurcation or a pitchfork bifurcation at E_0 when the parameters lie in the set Ω_a , where

$$\Omega_a := \{(\alpha, \beta, \gamma, \delta) : \alpha = \gamma > 0, \beta > 0, \delta > 0\}.$$

We now verify the transversality conditions for these bifurcations.

Taking α as the bifurcation parameter and introducing a small perturbation ξ with $|\xi| \ll 1$, system (1.4) can be written as the following map

$$\begin{pmatrix} x \\ y \end{pmatrix} \mapsto \begin{pmatrix} x \exp\left(1 - x + y - \frac{\alpha + \xi}{\gamma + x}\right) \\ y \exp(\delta - \beta y) \end{pmatrix}. \quad (6.1)$$

By setting $u = x$ and $v = y$ and expanding the Taylor series around $(u, v, \xi) = (0, 0, 0)$ to the third order, then the map (6.1) becomes

$$\begin{pmatrix} u \\ v \end{pmatrix} \mapsto \begin{pmatrix} 1 & 0 \\ 0 & e^\delta \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} f_1(u, v, \xi) \\ g_1(u, v, \xi) \end{pmatrix}, \quad (6.2)$$

where

$$\begin{aligned} f_1(u, v, \xi) &= a_{100}u^2 + a_{101}uv + a_{102}u\xi + a_{103}u^3 + a_{104}u^2v + a_{105}u^2\xi \\ &\quad + a_{106}uv^2 + a_{107}uv\xi + a_{108}u\xi^2 + O((|u| + |v| + |\xi|)^4), \\ g_1(u, v, \xi) &= -\beta e^\delta v^2 + \frac{\beta^2 e^\delta}{2} v^3 + O((|u| + |v| + |\xi|)^4), \end{aligned}$$

and

$$\begin{aligned} a_{100} &= \frac{1}{\gamma} - 1, & a_{101} &= 1, & a_{102} &= -\frac{1}{\gamma}, & a_{103} &= \frac{\gamma^2 - 2\gamma - 1}{2\gamma^2}, \\ a_{104} &= \frac{1}{\gamma} - 1, & a_{105} &= \frac{1}{\gamma}, & a_{106} &= \frac{1}{2}, & a_{107} &= -\frac{1}{\gamma}, & a_{108} &= \frac{1}{2\gamma^2}. \end{aligned}$$

From the center manifold theorem, there exists a center manifold $W_1^c(0, 0, 0)$, which can be expressed as

$$W_1^c(0, 0, 0) = \{(u, v, \xi) \in \mathbb{R}^3 : v = t_{11}u^2 + t_{21}u\xi + t_{31}\xi^2 + O(|u| + |\xi|^3)\}.$$

The function v must satisfy the invariance condition

$$v(u + f_1(u, v, \xi), \xi) = e^\delta v + g_1(u, v, \xi).$$

Substituting $v = t_{11}u^2 + t_{21}u\xi + t_{31}\xi^2 + O(|u| + |\xi|^3)$ into the above equation and comparing coefficients, we obtain $t_{11} = t_{21} = t_{31} = 0$. Consequently, the map restricted to the center manifold is given by

$$F^* : u \mapsto u + a_{100}u^2 + a_{102}u\xi + a_{103}u^3 + a_{105}u^2\xi + a_{108}u\xi^2 + O(|u| + |\xi|^4).$$

A direct computation yields

$$\begin{aligned} F^*(0, 0) &= 0, & \frac{\partial F^*}{\partial u}(0, 0) &= 1, & \frac{\partial F^*}{\partial \xi}(0, 0) &= 0, \\ \frac{\partial^2 F^*}{\partial u^2}(0, 0) &= \frac{2}{\gamma} - 2, & \frac{\partial^2 F^*}{\partial u \partial \xi}(0, 0) &= -\frac{1}{\gamma} \neq 0, \\ \frac{\partial^3 F^*}{\partial u^3}(0, 0) &= \frac{3(\gamma^2 - 2\gamma - 1)}{\gamma^2} \neq 0. \end{aligned}$$

Based on the above analysis and the bifurcation theory for discrete dynamical systems [20, 33], the following conclusions are established.

Theorem 6.1. *Suppose $(\alpha, \beta, \gamma, \delta) \in \Omega_a$ and $\gamma = 1$, then system (1.4) undergoes a pitchfork bifurcation at $E_0(0, 0)$.*

Theorem 6.2. *Suppose $(\alpha, \beta, \gamma, \delta) \in \Omega_a$ and $\gamma \neq 1$, then system (1.4) undergoes a transcritical bifurcation at $E_0(0, 0)$.*

6.2. Transcritical and pitchfork bifurcations at E_1

In this subsection, we investigate the bifurcation behavior of system (1.4) at the boundary fixed point $E_1\left(0, \frac{\delta}{\beta}\right)$. According to Theorem 3.1, when $\alpha = \gamma\left(1 + \frac{\delta}{\beta}\right)$, the fixed point E_1 is non-hyperbolic with eigenvalues $\lambda_1 = 1$ and $\lambda_2 = 1 - \delta \neq \pm 1$ if $\delta \neq 2$. This suggests that system (1.4) may undergo a codimension-one bifurcation at E_1 when the parameters belong to the set Ω_b , where

$$\Omega_b := \left\{ (\alpha, \beta, \gamma, \delta) : \alpha = \gamma\left(1 + \frac{\delta}{\beta}\right), \beta > 0, \gamma > 0, \delta > 0, \delta \neq 2 \right\}.$$

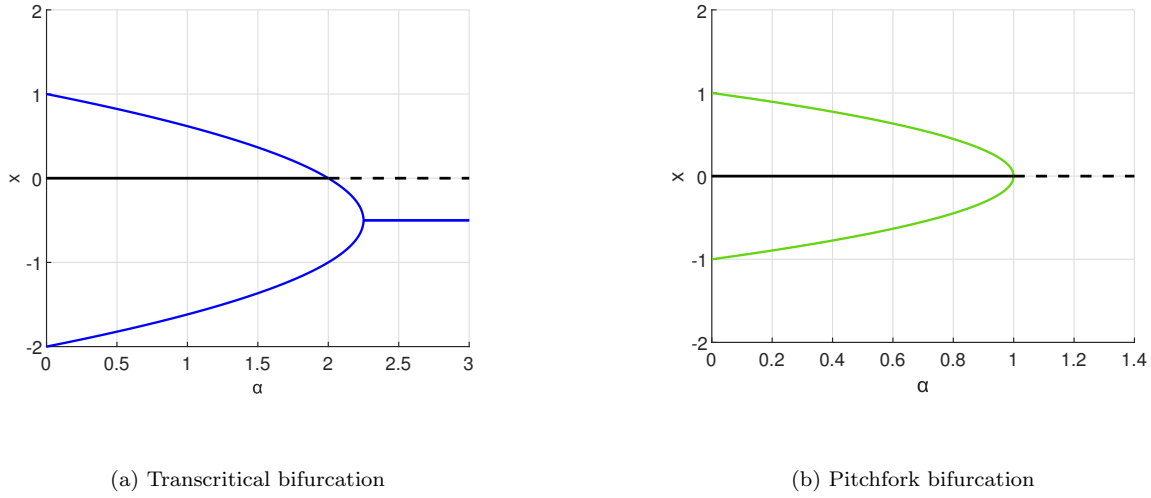


Figure 2. Bifurcation diagrams in the α - x plane: (a) Transcritical bifurcation with $\beta = 1$, $\gamma = 2$, $\delta = 1$; (b) pitchfork bifurcation with $\beta = 1$, $\gamma = 1$, $\delta = 1$.

Taking α as the bifurcation parameter and introducing a small perturbation ξ with $|\xi| \ll 1$, system (1.4) can be written as the following map:

$$\begin{pmatrix} x \\ y \end{pmatrix} \mapsto \begin{pmatrix} x \exp\left(1 - x + y - \frac{\alpha + \xi}{\gamma + x}\right) \\ y \exp(\delta - \beta y) \end{pmatrix}. \quad (6.3)$$

To facilitate the analysis, we shift the fixed point $E_1\left(0, \frac{\delta}{\beta}\right)$ to the origin by introducing the coordinate transformation $u = x$ and $v = y - \frac{\delta}{\beta}$. Under this transformation, the map (6.3) becomes

$$\begin{pmatrix} u \\ v \end{pmatrix} \mapsto \begin{pmatrix} 1 & 0 \\ 0 & 1 - \delta \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix} + \begin{pmatrix} f_2(u, v, \xi) \\ g_2(u, v, \xi) \end{pmatrix}, \quad (6.4)$$

where

$$\begin{aligned} f_2(u, v, \xi) &= b_{100}u^2 + b_{101}uv + b_{102}\xi u + b_{103}u^3 + b_{104}u^2v \\ &\quad + b_{105}u^2\xi + b_{106}uv^2 + b_{107}\xi uv + b_{108}\xi^2u + O((|u| + |v| + |\xi|)^4), \\ g_2(u, v, \xi) &= \frac{\beta(\delta - 2)v^2}{2} - \frac{\beta^2(\delta - 3)v^3}{6} + O((|u| + |v| + |\xi|)^4), \end{aligned}$$

and

$$\begin{aligned} b_{100} &= -\gamma^2 + \gamma\left(1 + \frac{\delta}{\beta}\right), \quad b_{101} = 1, \quad b_{102} = -\frac{1}{\gamma}, \quad b_{106} = \frac{1}{2}, \quad b_{107} = -\frac{1}{\gamma}, \\ b_{108} &= \frac{1}{2\gamma^2}, \quad b_{104} = (-\gamma^2 + \gamma\left(1 + \frac{\delta}{\beta}\right)), \quad b_{105} = \gamma^2 - \gamma\left(1 + \frac{\delta}{\beta}\right) + \gamma, \\ b_{103} &= \frac{\gamma^4 - 2\gamma^3\left(1 + \frac{\delta}{\beta}\right) + \gamma^2\left(1 + \frac{\delta}{\beta}\right)^2 - 2\gamma^2\left(1 + \frac{\delta}{\beta}\right)}{2\gamma^4}. \end{aligned}$$

From the center manifold theorem, the center manifold $W_2^c(0,0,0)$ of map (6.4) at the origin can be locally represented as

$$W_2^c(0,0,0) = \{(u, v, \xi) \in \mathbb{R}^3 : v = c_{11}u^2 + c_{21}u\xi + c_{31}\xi^2 + O(|u| + |\xi|)^3)\}.$$

The function v must satisfy the invariance condition

$$v(u + f_2(u, v, \xi), \xi) = (1 - \delta)v + g_2(u, v, \xi). \quad (6.5)$$

Substituting (6.5) into the above equation and comparing coefficients, we obtain $c_{11} = c_{21} = c_{31} = 0$. Consequently, the restriction of map (6.4) to the center manifold is given by

$$R^* : u \mapsto u + b_{100}u^2 + b_{102}u\xi + b_{103}u^3 + b_{105}u^2\xi + b_{108}u\xi^2 + O(|u| + |\xi|)^4).$$

To verify the transversality conditions for bifurcation, we compute the following partial derivatives,

$$\begin{aligned} R^*(0,0) &= 0, \quad \frac{\partial R^*}{\partial u}(0,0) = 1, \quad \frac{\partial R^*}{\partial \xi}(0,0) = 0, \\ \frac{\partial^2 R^*}{\partial u^2}(0,0) &= 2b_{100} = 2\gamma \left(1 + \frac{\delta}{\beta} - \gamma\right), \quad \frac{\partial^2 R^*}{\partial u \partial \xi}(0,0) = b_{102} = -\frac{1}{\gamma} \neq 0, \\ \frac{\partial^3 R^*}{\partial u^3}(0,0) &= 6b_{103} = \frac{3 \left[\gamma^2 - 2\gamma \left(1 + \frac{\delta}{\beta}\right) + \left(1 + \frac{\delta}{\beta}\right)^2 - 2 \left(1 + \frac{\delta}{\beta}\right) \right]}{\gamma^2}. \end{aligned}$$

We observe that

- When $\gamma = 1 + \frac{\delta}{\beta}$, we have $\frac{\partial^2 R^*}{\partial u^2}(0,0) = 0$ and $\frac{\partial^3 R^*}{\partial u^3}(0,0) = -\frac{6 \left(1 + \frac{\delta}{\beta}\right)}{\gamma^2} \neq 0$.
- When $\gamma \neq 1 + \frac{\delta}{\beta}$, we have $\frac{\partial^2 R^*}{\partial u^2}(0,0) \neq 0$.

Based on the above analysis and the bifurcation theory for discrete dynamical systems [20,33], we establish the following results.

Theorem 6.3. Suppose $(\alpha, \beta, \gamma, \delta) \in \Omega_b$ and $\gamma = 1 + \frac{\delta}{\beta}$, then system (1.4) undergoes a pitchfork bifurcation at the boundary fixed point $E_1 \left(0, \frac{\delta}{\beta}\right)$.

Theorem 6.4. Suppose $(\alpha, \beta, \gamma, \delta) \in \Omega_b$ and $\gamma \neq 1 + \frac{\delta}{\beta}$, then system (1.4) undergoes a transcritical bifurcation at the boundary fixed point $E_1 \left(0, \frac{\delta}{\beta}\right)$.

Remark 6.1. The transcritical bifurcation at E_1 has significant ecological implications. When $\alpha < \gamma \left(1 + \frac{\delta}{\beta}\right)$, the positive fixed point E_{22} exists and is stable, indicating the coexistence of both species. As the harvesting coefficient α increases and crosses the critical value $\gamma \left(1 + \frac{\delta}{\beta}\right)$, the fixed points E_1 and E_{22} collide and exchange stability through a transcritical bifurcation. Beyond this threshold, the positive fixed point E_{22} disappears, and only E_1 remains stable, implying the extinction of species x due to overharvesting.

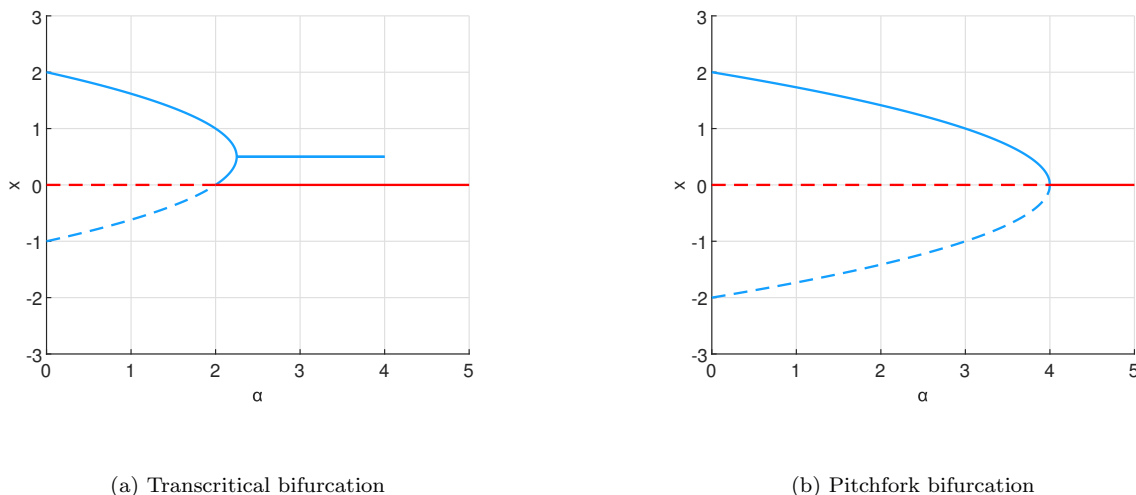


Figure 3. Bifurcation diagrams at E_1 in the α - x plane: (a) Transcritical bifurcation with $\beta = 1$, $\gamma = 1$, $\delta = 1$; (b) pitchfork bifurcation with $\beta = 1$, $\gamma = 2$, $\delta = 1$.

6.3. Fold bifurcation at E_{23}

In this subsection, we investigate the fold bifurcation of system (1.4) at the positive fixed point E_{23} . According to Theorem 2.2, when $\alpha_3 < \alpha < \alpha_2$, system (1.4) possesses two distinct positive fixed points E_{21} and E_{22} . As α increases toward the critical value α_2 , these two fixed points approach each other and eventually collide at E_{23} when $\alpha = \alpha_2$. For $\alpha > \alpha_2$, both positive fixed points disappear. This phenomenon is characteristic of a fold bifurcation.

Furthermore, from Theorem 3.5, when $\alpha = \alpha_2$, the eigenvalues of the Jacobian matrix at E_{23} are $\lambda_1 = 1$ and $\lambda_2 = 1 - \delta$. When $\delta \neq 2$, we have $|\lambda_2| < 1$ and $\lambda_2 \neq \pm 1$, which suggests that system (1.4) may undergo a fold bifurcation at E_{23} . In what follows, we verify the transversality conditions for this bifurcation.

Taking α as the bifurcation parameter and introducing a small perturbation ζ with $|\zeta| \ll 1$, we set $\alpha = \alpha_2 + \zeta$. Then system (1.4) can be written as the following map,

$$\begin{pmatrix} x \\ y \end{pmatrix} \mapsto \begin{pmatrix} x \exp \left(1 - x + y - \frac{\alpha_2 + \zeta}{\gamma + x} \right) \\ y \exp(\delta - \beta y) \end{pmatrix}. \quad (6.6)$$

To facilitate the bifurcation analysis, we shift the fixed point $E_{23} \left(x_{23}^*, \frac{\delta}{\beta} \right)$ to the origin by introducing the coordinate transformation $U = x - x_{23}^*$ and $V = y - \frac{\delta}{\beta}$. Expanding the resulting map in Taylor series around the origin, we obtain

$$\begin{pmatrix} U \\ \zeta \\ V \end{pmatrix} \mapsto \begin{pmatrix} 1 & c_{010} & x_{23}^* \\ 0 & 1 & 0 \\ 0 & 0 & 1 - \delta \end{pmatrix} \begin{pmatrix} U \\ \zeta \\ V \end{pmatrix} + \begin{pmatrix} f_3(U, V, \zeta) \\ 0 \\ g_3(U, V, \zeta) \end{pmatrix}, \quad (6.7)$$

where

$$f_3(U, V, \zeta) = c_{200}U^2 + c_{020}V^2 + c_{002}\zeta^2 + c_{110}UV$$

$$+ c_{101}U\zeta + c_{011}V\zeta + O(|U| + |V| + |\zeta|)^3),$$

$$g_3(U, V, \zeta) = \frac{\beta(\delta - 2)}{2}V^2 + O(|U| + |V| + |\zeta|)^3),$$

and

$$c_{010} = c_{011} = -\frac{x_{23}^*}{\gamma + x_{23}^*}, \quad c_{002} = \frac{x_{23}^*}{2}, \quad c_{020} = \frac{x_{23}^*}{2(\gamma + x_{23}^*)^2},$$

$$c_{101} = \frac{-\gamma^2 x_{23}^* - 2\gamma(x_{23}^*)^2 - (x_{23}^*)^3 + \alpha_2 x_{23}^* + \gamma^2 + 2x_{23}^* \gamma}{(\gamma + x_{23}^*)^2},$$

$$c_{110} = -\frac{-\gamma^2 x_{23}^* - 2\gamma(x_{23}^*)^2 - (x_{23}^*)^3 + \alpha_2 x_{23}^* + \gamma^2 + x_{23}^* \gamma}{(\gamma + x_{23}^*)^3},$$

$$c_{200} = \frac{1}{2(\gamma + x_{23}^*)^4} \left(\gamma^4 x_{23}^* + 4\gamma^3 (x_{23}^*)^2 + 6\gamma^2 (x_{23}^*)^3 + 4\gamma (x_{23}^*)^4 + (x_{23}^*)^5 \right. \\ \left. - 2\alpha_2 \gamma^2 x_{23}^* - 4\alpha_2 \gamma (x_{23}^*)^2 - 2\alpha_2 (x_{23}^*)^3 - 2\gamma^4 - 8\gamma^3 x_{23}^* \right. \\ \left. - 12\gamma^2 (x_{23}^*)^2 - 8\gamma (x_{23}^*)^3 - 2(x_{23}^*)^4 + \alpha_2^2 x_{23}^* + 2\alpha_2 \gamma^2 + 2\alpha_2 \gamma x_{23}^* \right).$$

Next, we apply the invertible transformation

$$\begin{pmatrix} U \\ \zeta \\ V \end{pmatrix} = \begin{pmatrix} -1 & 0 & 1 \\ 0 & -\frac{1}{c_{010}} & 0 \\ 0 & 0 & -\frac{\delta}{x_{23}^*} \end{pmatrix} \begin{pmatrix} X \\ \tilde{\zeta} \\ Y \end{pmatrix}.$$

Under this transformation, map (6.7) becomes

$$\begin{pmatrix} X \\ \tilde{\zeta} \\ Y \end{pmatrix} \mapsto \begin{pmatrix} 1 & 1 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 - \delta \end{pmatrix} \begin{pmatrix} X \\ \tilde{\zeta} \\ Y \end{pmatrix} + \begin{pmatrix} f_4(X, \tilde{\zeta}, Y) \\ 0 \\ g_4(X, \tilde{\zeta}, Y) \end{pmatrix}, \quad (6.8)$$

where

$$f_4(X, \tilde{\zeta}, Y) = d_{200}X^2 + d_{002}Y^2 + d_{020}\tilde{\zeta}^2 + d_{101}XY \\ + d_{110}X\tilde{\zeta} + d_{011}Y\tilde{\zeta} + O(|X| + |Y| + |\tilde{\zeta}|)^3),$$

$$g_4(X, \tilde{\zeta}, Y) = -\frac{x_{23}^* \beta(\delta - 2)Y^2}{2\delta} + O(|X| + |Y| + |\tilde{\zeta}|)^3),$$

and

$$d_{110} = \frac{(-\gamma^2 x_{23}^* - 2x_{23}^* \gamma - x_{23}^*{}^3 + \alpha_2 x_{23}^* + \gamma^2 + x_{23}^* \gamma)}{(\gamma + x_{23}^*)^3},$$

$$d_{011} = \frac{x_{23}^*}{\gamma + x_{23}^*}, d_{020} = -\frac{x_{23}^*}{2(\gamma + x_{23}^*)^2},$$

$$\begin{aligned}
d_{101} &= -\frac{(-\gamma^2 x_{23}^* - 2x_{23}^{*2} \gamma - x_{23}^{*3} + \alpha x_{23}^* + \gamma^2 + 2x_{23}^* \gamma + x_{23}^{*2})}{(\gamma + x_{23}^*)^2}, \\
d_{002} &= -\frac{x_{23}^*}{2} - \frac{x_{23}^* \beta (\delta - 2)}{2\delta}, \\
d_{200} &= -\frac{1}{2(\gamma + x_{23}^*)^4} (\gamma^4 x_{23}^* + 4\gamma^3 x_{23}^{*2} + 6\gamma^2 x_{23}^{*3} + 4\gamma x_{23}^{*4} \\
&\quad + x_{23}^{*5} - 2\alpha \gamma^2 x_{23}^* - 4\alpha \gamma x_{23}^{*2} \\
&\quad - 2\alpha x_{23}^{*3} - 2\gamma^4 - 8\gamma^3 x_{23}^* - 12\gamma^2 x_{23}^{*2} - 8\gamma x_{23}^{*3} \\
&\quad - 2x_{23}^{*4} + \alpha^2 x_{23}^* + 2\alpha \gamma^2 + 2\alpha \gamma x_{23}^*).
\end{aligned}$$

The center manifold $W_3^c(0, 0, 0)$ of map (6.8) at the origin can be locally represented as

$$W_3^c(0, 0, 0) = \left\{ (X, \tilde{\zeta}, Y) \in \mathbb{R}^3 : Y = k_1 X^2 + k_2 X \tilde{\zeta} + k_3 \tilde{\zeta}^2 + O\left((|X| + |\tilde{\zeta}|)^3\right) \right\}.$$

The function Y must satisfy the invariance condition. Substituting the expression for Y into map (6.8) and comparing coefficients of like powers, we obtain $k_1 = k_2 = k_3 = 0$. Consequently, the restriction of map (6.8) to the center manifold is given by

$$Q^* : X \mapsto X + \tilde{\zeta} + p_1 X^2 + p_2 X \tilde{\zeta} + p_3 \tilde{\zeta}^2 + O\left((|X| + |\tilde{\zeta}|)^3\right),$$

where

$$p_1 = d_{200}, \quad p_2 = \frac{1}{c_{010}^2} = \frac{(\gamma + x_{23}^*)^2}{(x_{23}^*)^2}, \quad p_3 = \frac{1}{c_{010}} = -\frac{\gamma + x_{23}^*}{x_{23}^*}.$$

To verify the transversality conditions for a fold bifurcation, we compute the following partial derivatives at the origin:

$$\begin{aligned}
Q^*(0, 0) &= 0, \quad \frac{\partial Q^*}{\partial X}(0, 0) = 1, \quad \frac{\partial Q^*}{\partial \tilde{\zeta}}(0, 0) = 1 \neq 0, \\
\frac{\partial^2 Q^*}{\partial X^2}(0, 0) &= 2p_1 = 2d_{200} \neq 0, \quad \frac{\partial^2 Q^*}{\partial X \partial \tilde{\zeta}}(0, 0) = p_2 = \frac{(\gamma + x_{23}^*)^2}{(x_{23}^*)^2} \neq 0.
\end{aligned}$$

Based on the above analysis, we establish the following result.

Theorem 6.5. Suppose $0 < \delta < 2$, $\gamma < 1 + \frac{\delta}{\beta}$, and $\alpha = \alpha_2$, system (1.4) undergoes a fold bifurcation at $E_{23}\left(x_{23}^*, \frac{\delta}{\beta}\right)$.

6.4. Period-doubling bifurcations at E_{22} and E_1

Period-doubling bifurcation is a fundamental mechanism through which discrete dynamical systems transition from steady-state behavior to periodic oscillations and eventually to chaos. In this subsection, we investigate the period-doubling bifurcations of system (1.4) at both the positive fixed point E_{22} and the boundary fixed point E_1 .

We first consider the period-doubling bifurcation at the positive fixed point E_{22} when the second species y is stable (i.e., $0 < \delta < 2$). According to Theorem 3.7, when $\frac{\delta}{\beta} = \beta_1$, the

eigenvalues at E_{22} are $\lambda_1 = -1$ and $\lambda_2 = 1 - \delta$. This suggests that system (1.4) may undergo a period-doubling bifurcation at E_{22} . We define the parameter region for this bifurcation as

$$\Omega_c \triangleq \left\{ (\alpha, \beta, \gamma, \delta) \in \mathbb{R}^4 : \frac{\delta}{\beta} = \beta_1, 0 < \alpha < \alpha_2, 0 < \gamma < 1 + \frac{\delta}{\beta}, 0 < \delta < 2 \right\}.$$

Taking β as the bifurcation parameter and introducing a small perturbation μ with $|\mu| \ll 1$, system (1.4) can be written as the following map

$$\begin{pmatrix} x \\ y \end{pmatrix} \mapsto \begin{pmatrix} x \exp \left(1 - x + y - \frac{\alpha}{\gamma + x} \right) \\ y \exp (\delta - (\beta + \mu)y) \end{pmatrix}. \quad (6.9)$$

To facilitate the bifurcation analysis, we shift the fixed point $E_{22} \left(x_{22}^*, \frac{\delta}{\beta} \right)$ to the origin by introducing the coordinate transformation $u_3 = x - x_{22}^*$ and $v_3 = y - \frac{\delta}{\beta}$. Expanding the resulting map in Taylor series around the origin, we obtain

$$\begin{pmatrix} u_3 \\ v_3 \end{pmatrix} \mapsto \begin{pmatrix} -1 & x_{22}^* \\ 0 & 1 - \delta \end{pmatrix} \begin{pmatrix} u_3 \\ v_3 \end{pmatrix} + \begin{pmatrix} f_5(u_3, v_3, \mu) \\ g_5(u_3, v_3, \mu) \end{pmatrix}, \quad (6.10)$$

where

$$\begin{aligned} f_5(u_3, v_3, \mu) &= j_1 u_3^2 + j_2 u_3 v_3 + \frac{x_{22}^*}{2} v_3^2 + O(|u_3| + |v_3| + |\mu|)^3, \\ g_5(u_3, v_3, \mu) &= \frac{\delta^2}{\beta^2} \mu + \frac{\beta(\delta - 2)}{2} v_3^2 + \frac{\delta(\delta - 2)}{\beta} \mu v_3 \\ &\quad + \frac{\delta^3}{2\beta^3} \mu^2 + O(|u_3| + |v_3| + |\mu|)^3, \end{aligned}$$

and

$$\begin{aligned} j_1 &= \frac{1}{2(\gamma + x_{22}^*)^4} \left(\gamma^4 x_{22}^* + 4\gamma^3 (x_{22}^*)^2 + 6\gamma^2 (x_{22}^*)^3 + 4\gamma (x_{22}^*)^4 + (x_{22}^*)^5 \right. \\ &\quad \left. - 2\alpha\gamma^2 x_{22}^* - 4\alpha\gamma (x_{22}^*)^2 - 2\alpha (x_{22}^*)^3 - 2\gamma^4 - 8\gamma^3 x_{22}^* - 12\gamma^2 (x_{22}^*)^2 \right. \\ &\quad \left. - 8\gamma (x_{22}^*)^3 - 2(x_{22}^*)^4 + \alpha^2 x_{22}^* + 2\alpha\gamma^2 + 2\alpha\gamma x_{22}^* \right), \\ j_2 &= -\frac{\gamma^2 x_{22}^* + 2\gamma (x_{22}^*)^2 + (x_{22}^*)^3 - \alpha x_{22}^* - \gamma^2 - 2\gamma x_{22}^* - (x_{22}^*)^2}{(\gamma + x_{22}^*)^2}. \end{aligned}$$

Next, we apply the invertible transformation

$$\begin{pmatrix} u_3 \\ v_3 \end{pmatrix} = \begin{pmatrix} -1 & 1 \\ 0 & \frac{2 - \delta}{x_{22}^*} \end{pmatrix} \begin{pmatrix} u_4 \\ v_4 \end{pmatrix}. \quad (6.11)$$

Under this transformation, map (6.10) becomes

$$\begin{pmatrix} u_4 \\ v_4 \end{pmatrix} \mapsto \begin{pmatrix} -1 & 0 \\ 0 & 1 - \delta \end{pmatrix} \begin{pmatrix} u_4 \\ v_4 \end{pmatrix} + \begin{pmatrix} f_6(u_4, v_4, \mu) \\ g_6(u_4, v_4, \mu) \end{pmatrix}, \quad (6.12)$$

where

$$\begin{aligned} f_6(u_4, v_4, \mu) &= -\frac{\delta^2 x_{22}^*}{\beta^2(2-\delta)}\mu - j_1 u_4^2 - j_2 u_4 v_4 - \frac{x_{22}^*(1+\beta)}{2}v_4^2 - \frac{\delta}{\beta}\mu v_4 \\ &\quad + \frac{\delta^3 x_{22}^*}{2\beta^3(2-\delta)}\mu^2 + O(|u_4| + |v_4| + |\mu|)^3, \\ g_6(u_4, v_4, \mu) &= -\frac{\delta^2 x_{22}^*}{\beta^2(2-\delta)}\mu - \frac{\beta x_{22}^*}{2}v_4^2 - \frac{\delta}{\beta}\mu v_4 \\ &\quad + \frac{\delta^3 x_{22}^*}{2\beta^3(2-\delta)}\mu^2 + O(|u_4| + |v_4| + |\mu|)^3. \end{aligned}$$

In a small neighborhood of $\mu = 0$, the center manifold $W_4^c(0, 0, 0)$ of map (6.12) at the origin can be locally represented as

$$W_4^c(0, 0, 0) = \{(u_4, v_4, \mu) \in \mathbb{R}^3 : v_4 = m_1\mu + m_2u_4^2 + m_3u_4\mu + m_4\mu^2 + O(|u_4| + |\mu|)^3)\},$$

where

$$m_1 = -\frac{\delta x_{22}^*}{\beta^2(2-\delta)}, \quad m_2 = m_3 = 0, \quad m_4 = \frac{\delta}{\beta^3} \left(1 - \frac{x_{22}^*}{2}\right) + \frac{\delta^2 x_{22}^*}{2\beta^3(2-\delta)}.$$

Consequently, the restriction of map (6.12) to the center manifold is given by

$$\begin{aligned} Z^* : u_4 \mapsto & -u_4 - \frac{\delta^2 x_{22}^*}{\beta^2(2-\delta)}\mu - j_1 u_4^2 + \left(2j_1 m_1 + j_2 \frac{2-\delta}{x_{22}^*} m_1\right) u_4 \mu \\ & + \left[-\frac{\delta(2-\delta)}{\beta x_{22}^*} m_1 - \frac{(1+\beta)(2-\delta)^2}{2x_{22}^*} m_1^2 - j_2 \frac{2-\delta}{x_{22}^*} m_1^2 + \frac{\delta^3 x_{22}^*}{2\beta^3(2-\delta)}\right] \mu^2 \\ & - j_1 u_4^3 + \left(3j_1 m_1 + j_2 \frac{2-\delta}{x_{22}^*} m_1\right) u_4^2 \mu + O(|u_4| + |\mu|)^4. \end{aligned}$$

To verify the transversality conditions for a period-doubling bifurcation, we compute the following discriminants:

$$\begin{aligned} \mathfrak{L}_1 &= \left(\frac{\partial^2 Z^*}{\partial u_4 \partial \mu} + \frac{1}{2} \frac{\partial Z^*}{\partial \mu} \frac{\partial^2 Z^*}{\partial u_4^2} \right) \Big|_{(u_4, \mu)=(0,0)} = -\frac{\delta}{\beta^2} (j_1 x_{22}^* + j_2), \\ \mathfrak{L}_2 &= \left(\frac{1}{6} \frac{\partial^3 Z^*}{\partial u_4^3} + \left(\frac{1}{2} \frac{\partial^2 Z^*}{\partial u_4^2} \right)^2 \right) \Big|_{(u_4, \mu)=(0,0)} = j_1^2 - j_1. \end{aligned}$$

Based on the above analysis and the bifurcation theory for discrete dynamical systems [20, 27], we establish the following result.

Theorem 6.6. *Suppose $(\alpha, \beta, \gamma, \delta) \in \Omega_c$. If $\mathfrak{L}_1 \neq 0$ and $\mathfrak{L}_2 \neq 0$, then system (1.4) undergoes a period-doubling bifurcation at the positive fixed point $E_{22} \left(x_{22}^*, \frac{\delta}{\beta} \right)$ when the parameter β varies in a small neighborhood of $\frac{\delta}{\beta_1}$. Moreover, the bifurcating period-2 orbit is stable if $\mathfrak{L}_2 > 0$, and unstable if $\mathfrak{L}_2 < 0$.*

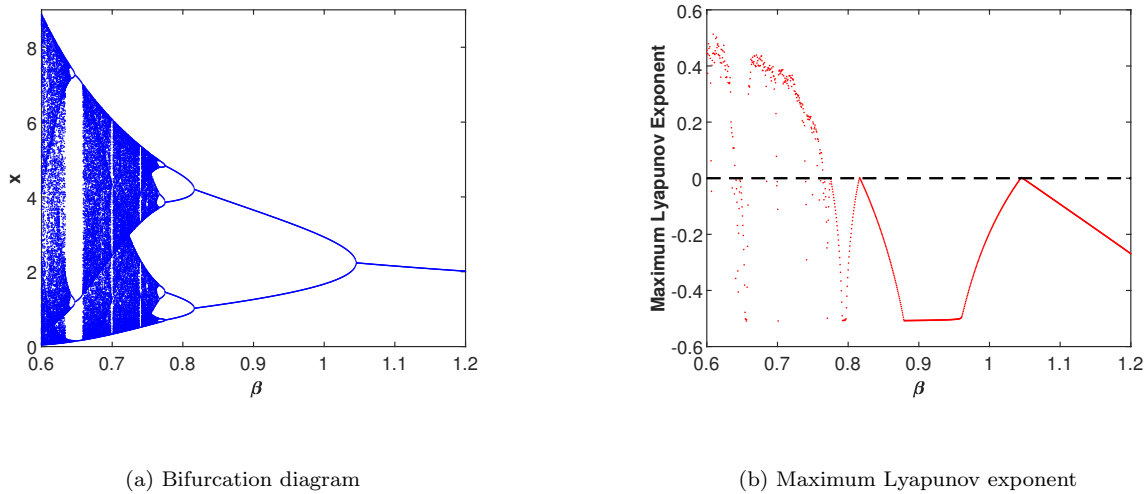


Figure 4. Period-doubling bifurcation at E_{22} in the β - x plane with $\alpha = 0.8$, $\gamma = 0.5$, $\delta = 1.6$, and initial value $(3.47, 2.68)$: (a) Bifurcation diagram; (b) maximum Lyapunov exponent.

Next, we consider the case when the second species y undergoes a period-doubling bifurcation.

When $\delta = 2$ and $\gamma - 1 < \frac{\delta}{\beta} < \beta_1$, the positive fixed point E_{22} exists, and the eigenvalues at E_{22} are $\lambda_1 \neq \pm 1$ (with $|\lambda_1| < 1$) and $\lambda_2 = 1 - \delta = -1$. This indicates that a period-doubling bifurcation may occur at E_{22} even when $(\alpha, \beta, \gamma, \delta) \notin \Omega_c$. We define the corresponding parameter region as

$$\Omega_d \triangleq \left\{ (\alpha, \beta, \gamma, \delta) \in \mathbb{R}^4 : \delta = 2, 0 < \alpha < \alpha_2, \gamma - 1 < \frac{\delta}{\beta} < \beta_1, \beta > 0, \gamma > 0 \right\}.$$

Taking δ as the bifurcation parameter and introducing a small perturbation ζ with $|\zeta| \ll 1$, system (1.4) can be written as the following map:

$$\begin{pmatrix} x \\ y \end{pmatrix} \mapsto \begin{pmatrix} x \exp \left(1 - x + y - \frac{\alpha}{\gamma + x} \right) \\ y \exp (2 + \zeta - \beta y) \end{pmatrix}. \quad (6.13)$$

Shifting the fixed point $E_{22} \left(x_{22}^*, \frac{\delta}{\beta} \right)$ to the origin by setting $u_5 = x - x_{22}^*$ and $v_5 = y - \frac{\delta}{\beta}$, we obtain

$$\begin{pmatrix} u_5 \\ v_5 \end{pmatrix} \mapsto \begin{pmatrix} \lambda_1 & x_{22}^* \\ 0 & -1 \end{pmatrix} \begin{pmatrix} u_5 \\ v_5 \end{pmatrix} + \begin{pmatrix} f_7(u_5, v_5, \zeta) \\ g_7(u_5, v_5, \zeta) \end{pmatrix}, \quad (6.14)$$

where $\lambda_1 = -\frac{2}{\beta} + \frac{\alpha\gamma + 2\alpha x_{22}^*}{(\gamma + x_{22}^*)^2}$, and the nonlinear terms are given by

$$\begin{aligned} f_7(u_5, v_5, \zeta) &= K_{200}u_5^2 + K_{110}u_5v_5 + K_{020}v_5^2 + K_{300}u_5^3 + K_{210}u_5^2v_5 \\ &\quad + K_{120}u_5v_5^2 + K_{030}v_5^3 + O((|u_5| + |v_5| + |\zeta|)^4), \\ g_7(u_5, v_5, \zeta) &= \frac{2}{\beta}\zeta - \zeta v_5 + \frac{1}{\beta}\zeta^2 + \frac{\beta^2}{6}v_5^3 - \frac{1}{2}\zeta^2v_5 + \frac{1}{3\beta}\zeta^3 + O((|u_5| + |v_5| + |\zeta|)^4), \end{aligned}$$

and

$$K_{200} = \frac{1}{2(\gamma + x_{22}^*)^4} \left(\gamma^4 x_{22}^* + 4\gamma^3 (x_{22}^*)^2 + 6\gamma^2 (x_{22}^*)^3 + 4\gamma (x_{22}^*)^4 + (x_{22}^*)^5 \right. \\ \left. - 2\alpha\gamma^2 x_{22}^* - 4\alpha\gamma (x_{22}^*)^2 - 2\alpha (x_{22}^*)^3 - 2\gamma^4 - 8\gamma^3 x_{22}^* - 12\gamma^2 (x_{22}^*)^2 \right. \\ \left. - 8\gamma (x_{22}^*)^3 - 2(x_{22}^*)^4 + \alpha^2 x_{22}^* + 2\alpha\gamma^2 + 2\alpha\gamma x_{22}^* \right),$$

$$K_{110} = K_{120} = \lambda_1, \quad K_{020} = \frac{x_{22}^*}{2}, \quad K_{030} = \frac{x_{22}^*}{6}.$$

To diagonalize the linear part of map (6.14), we apply the invertible transformation

$$\begin{pmatrix} u_5 \\ v_5 \end{pmatrix} = \begin{pmatrix} -1 & 1 \\ 0 & d_1 \end{pmatrix} \begin{pmatrix} u_6 \\ v_6 \end{pmatrix}, \quad (6.15)$$

where $d_1 = -\frac{\lambda_1+1}{x_{22}^*}$. Under this transformation, map (6.14) becomes

$$\begin{pmatrix} u_6 \\ v_6 \end{pmatrix} \mapsto \begin{pmatrix} \lambda_1 & 0 \\ 0 & -1 \end{pmatrix} \begin{pmatrix} u_6 \\ v_6 \end{pmatrix} + \begin{pmatrix} f_8(u_6, v_6, \zeta) \\ g_8(u_6, v_6, \zeta) \end{pmatrix}, \quad (6.16)$$

where

$$f_8(u_6, v_6, \zeta) = -f_7(-u_6 + v_6, d_1 v_6, \zeta) + \frac{1}{d_1} g_7(-u_6 + v_6, d_1 v_6, \zeta),$$

$$g_8(u_6, v_6, \zeta) = \frac{1}{d_1} g_7(-u_6 + v_6, d_1 v_6, \zeta).$$

In a small neighborhood of $\zeta = 0$, the center manifold $W_5^c(0, 0, 0)$ of map (6.16) at the origin can be locally represented as

$$W_5^c(0, 0, 0) = \{(u_6, v_6, \zeta) \in \mathbb{R}^3 : u_6 = n_1 \zeta + n_2 v_6^2 + n_3 v_6 \zeta + n_4 \zeta^2 + O(|v_6| + |\zeta|^3)\},$$

where

$$n_1 = \frac{2}{(\lambda_1 - 1)d_1\beta}, \quad n_2 = -\frac{(\lambda_1 + 1)d_1}{2(\lambda_1 - 1)},$$

$$n_3 = \frac{1}{\lambda_1 - 1} + \frac{2\lambda_1}{(\lambda_1 - 1)^2\beta}, \quad n_4 = -\frac{1}{d_1\beta(\lambda_1 - 1)} + \frac{4K_{200}}{\beta^2 d_1^2 (\lambda_1 - 1)^2}.$$

Consequently, the restriction of map (6.16) to the center manifold is given by

$$T^* : v_6 \mapsto -v_6 + \frac{2}{\beta d_1} \zeta - \zeta v_6 + \frac{1}{\beta d_1} \zeta^2 + \frac{\beta^2 d_1^2}{6} v_6^3 - \frac{1}{2} \zeta^2 v_6 + \frac{1}{3\beta d_1} \zeta^3 + O(|v_6| + |\zeta|^4).$$

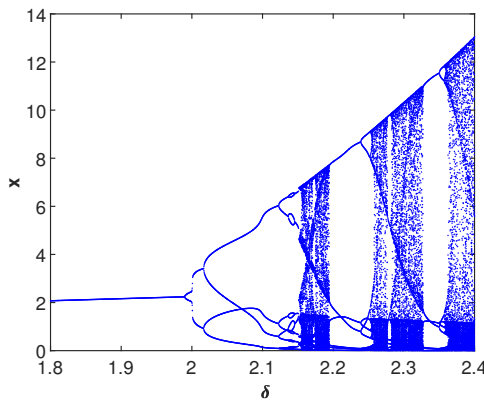
To verify the transversality conditions for a period-doubling bifurcation, we compute the following discriminants:

$$\omega_1 = \left(\frac{\partial^2 T^*}{\partial v_6 \partial \zeta} + \frac{1}{2} \frac{\partial T^*}{\partial \zeta} \frac{\partial^2 T^*}{\partial v_6^2} \right) \Big|_{(v_6, \zeta) = (0, 0)} = -1,$$

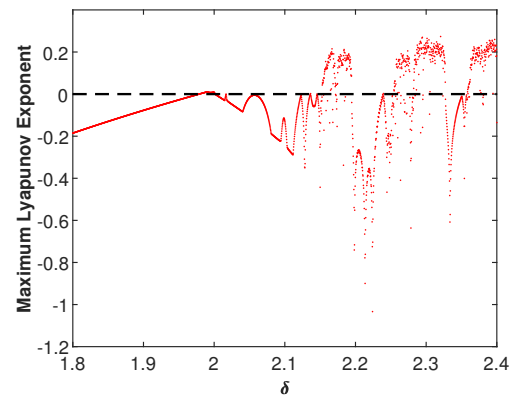
$$\omega_2 = \left(\frac{1}{6} \frac{\partial^3 T^*}{\partial v_6^3} + \left(\frac{1}{2} \frac{\partial^2 T^*}{\partial v_6^2} \right)^2 \right) \bigg|_{(v_6, \zeta) = (0,0)} = \frac{\beta^2 d_1^2}{6}.$$

Since both $\omega_1 \neq 0$ and $\omega_2 > 0$, the transversality conditions are satisfied. Based on the above analysis and the bifurcation theory for discrete dynamical systems [20, 27], we establish the following result.

Theorem 6.7. Suppose $(\alpha, \beta, \gamma, \delta) \in \Omega_d$. When the parameter δ varies in a small neighborhood of 2, system (1.4) undergoes a period-doubling bifurcation at the positive fixed point $E_{22} \left(x_{22}^*, \frac{\delta}{\beta} \right)$, and the bifurcating period-2 orbit is stable.



(a) Bifurcation diagram



(b) Maximum Lyapunov exponent

Figure 5. Period-doubling bifurcation at E_{22} in the δ - x plane with $\alpha = 0.8$, $\beta = 1.3$, $\gamma = 0.5$, and initial value $(0.5, 0.5)$: (a) Bifurcation diagram; (b) maximum Lyapunov exponent.

Note that when $\alpha \neq \alpha_3$ and $\delta = 2$, the eigenvalues at the boundary fixed point E_1 are $\lambda_1 = e^{1 + \frac{\delta}{\beta} - \frac{\alpha}{\gamma}} \neq \pm 1$ and $\lambda_2 = 1 - \delta = -1$. Through a similar discussion as in Theorem 6.7, we have the following theorem.

Theorem 6.8. Assume $(\alpha, \beta, \gamma, \delta) \in \Omega_e$. When the parameter δ varies in a small neighborhood of 2, system (1.4) undergoes a period-doubling bifurcation at the boundary fixed point $E_1(0, \frac{\delta}{\beta})$, and the bifurcating period-2 orbit is stable, where

$$\Omega_e \triangleq \{(\alpha, \beta, \gamma, \delta) \in \mathbb{R}^4 : \delta = 2, \alpha > 0, \alpha \neq \alpha_3, \beta > 0, \gamma > 0\}.$$

7. Numerical simulations

In this section, we conduct a comprehensive numerical investigation to corroborate and illustrate the theoretical results established in the preceding sections. The primary objective is to elucidate how the commensalism strength $\frac{\delta}{\beta}$ and the harvesting intensity α jointly govern the long-term dynamics of the harvested species x . Two ecologically distinct scenarios are examined: (i) The host population y is intrinsically stable ($0 < \delta < 2$), and (ii) the host population y is intrinsically unstable ($\delta > 2$).

7.1. Stable y population ($0 < \delta < 2$)

When $0 < \delta < 2$, Theorem 5.1 guarantees that $\lim_{n \rightarrow \infty} y(n) = \frac{\delta}{\beta}$, so the second species converges to $\frac{\delta}{\beta}$ regardless of the dynamics of x . The dynamical behavior of species x is then determined by the interplay between the harvesting intensity α and the effective commensalism strength $\frac{\delta}{\beta}$.

7.1.1. Impact under high harvesting intensity

We first examine the regime of high harvesting pressure by fixing $\alpha = 1.8$ and $\gamma = 1.3$, and systematically vary the commensalism strength by varying the parameter β .

Weak commensalism. Consider $(\alpha, \beta, \gamma, \delta) = (1.8, 1.6, 1.3, 0.6)$, which yields $\frac{\delta}{\beta} = 0.375$. A direct computation gives $\alpha > \alpha_2 = \frac{(\gamma + 1 + \frac{\delta}{\beta})^2}{4} \approx 1.7889$, and the condition $\gamma < 1 + \frac{\delta}{\beta}$ is satisfied. Hence, Theorem 5.3 applies, and the boundary fixed point $E_1(0, \frac{\delta}{\beta})$ is globally attractive. As illustrated in Figure 6, species x goes extinct, while species y stabilizes at $\frac{\delta}{\beta} = 0.375$. This demonstrates that when commensalism is too weak, it cannot offset the excessive harvesting pressure on species x .

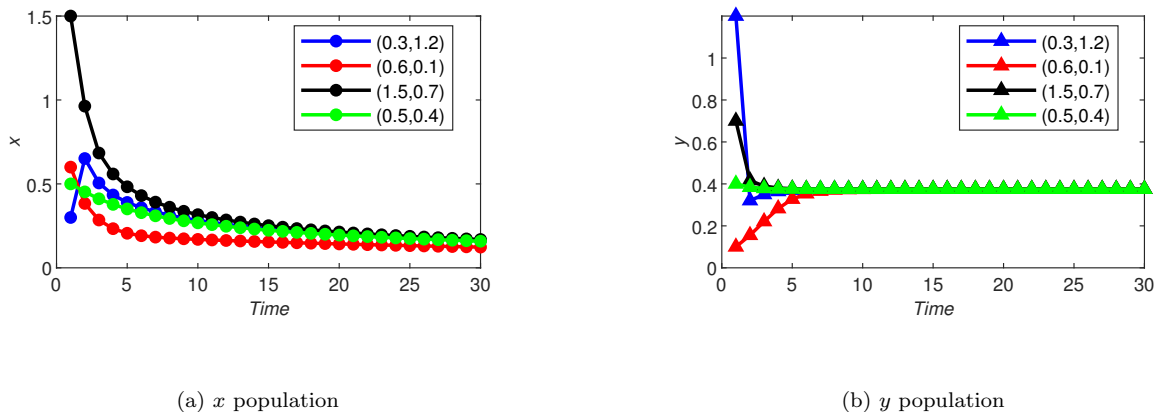


Figure 6. Global attractivity of $E_1(0, \frac{\delta}{\beta})$ under weak commensalism and high harvesting.

Moderate commensalism. Increasing the commensalism strength by reducing β to 1.2 while keeping the remaining parameters unchanged, i.e., $(\alpha, \beta, \gamma, \delta) = (1.8, 1.2, 1.3, 0.6)$, yields $\frac{\delta}{\beta} = 0.5$. In this case, $\alpha < \alpha_3 = (1 + \frac{\delta}{\beta})\gamma = 1.95$, $0 < \delta < 2$, and the conditions of Theorem 5.2 are satisfied. Consequently, the positive fixed point E_{22} is globally attractive, as confirmed by the numerical simulation in Figure 7. Both species converge to their respective equilibrium densities, confirming that moderate commensalism can counteract high harvesting pressure and sustain stable coexistence.

Strong commensalism. Further increasing the commensalism strength (by decreasing β) drives $\frac{\delta}{\beta}$ toward and beyond the critical value β_1 identified in Theorem 3.7. When $\frac{\delta}{\beta}$ reaches β_1 , the eigenvalue λ_1 of the Jacobian at E_{22} crosses -1 , and Theorem 6.6 predicts that a period-doubling bifurcation occurs. Figure 8 illustrates two representative cases:

- With $(\alpha, \beta, \gamma, \delta) = (1.8, 0.3, 1.3, 0.6)$, corresponding to $\frac{\delta}{\beta} = 2$, the positive fixed point E_{22} has lost stability and the system exhibits a stable period-2 orbit (Figure 8(a)).

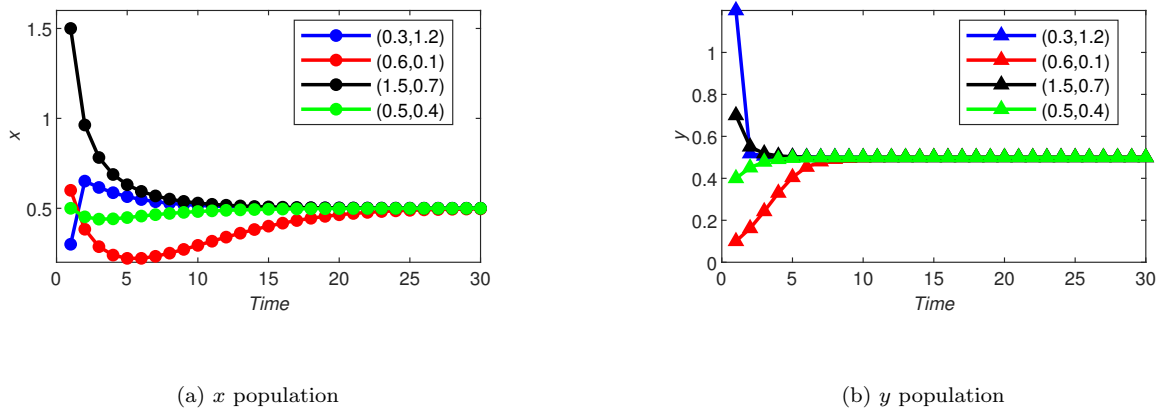


Figure 7. Global attractivity of $E_{22}(x_{22}^*, \frac{\delta}{\beta})$ under moderate commensalism and high harvesting.

- With $(\alpha, \beta, \gamma, \delta) = (1.8, 0.2, 1.3, 0.6)$, corresponding to $\frac{\delta}{\beta} = 3$, the period-doubling bifurcation has progressed to a chaotic regime, as evidenced by the irregular, aperiodic oscillations (Figure 8(b)).

These results reveal that excessively strong commensalism introduces destabilizing nonlinear feedback, ultimately undermining the regularity of population dynamics even though it elevates the mean population density of species x .

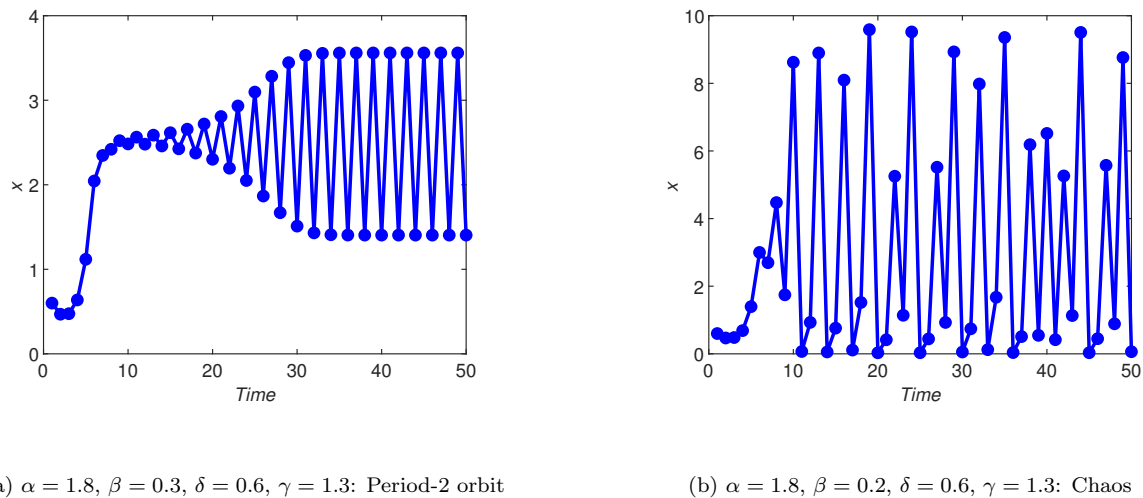


Figure 8. Time series of species x under strong commensalism and high harvesting intensity. (a) A stable period-2 cycle emerges after the first period-doubling bifurcation; (b) further increase in commensalism strength drives the system into chaos.

Bifurcation analysis with varying β . To obtain a comprehensive overview of the dynamical transitions, we fix $(\alpha, \delta, \gamma) = (1.8, 0.6, 1.3)$ and construct a bifurcation diagram by varying β over the interval $(0, 2)$, along with the corresponding maximum Lyapunov exponent (MLE). The results are presented in Figure 9. Three qualitatively distinct regimes are clearly identifiable as β decreases (equivalently, as $\frac{\delta}{\beta}$ increases):

- Extinction regime* (β large, $\frac{\delta}{\beta}$ small): Species x converges to zero, consistent with Theo-

rem 5.3.

- (ii) *Stable coexistence regime* (β moderate): The system possesses a globally attractive positive fixed point E_{22} , consistent with Theorem 5.2. As β decreases within this regime, the equilibrium density of x increases monotonically, reflecting the beneficial effect of commensalism.
- (iii) *Period-doubling cascade and chaos* (β small, $\frac{\delta}{\beta}$ large): A succession of period-doubling bifurcations occurs as $\frac{\delta}{\beta}$ passes through β_1 , consistent with Theorem 6.6. The MLE transitions from negative to positive values, confirming the onset of chaos.

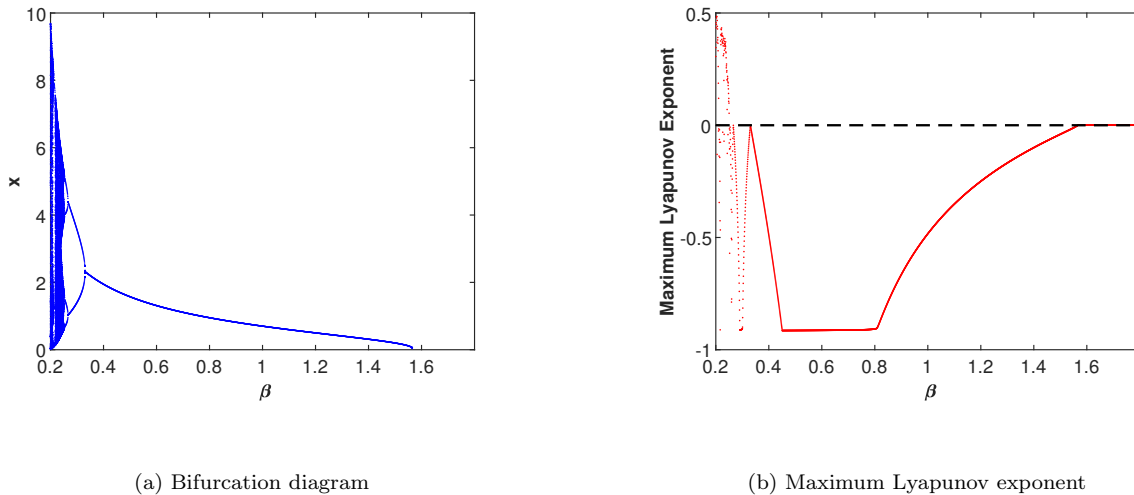


Figure 9. Bifurcation diagram and maximum Lyapunov exponent as functions of β under high harvesting: $(\alpha, \delta, \gamma) = (1.8, 0.6, 1.3)$. As β decreases (commensalism strengthens), the system transitions from species x extinction, through stable coexistence, to period-doubling bifurcation and eventually chaos.

7.1.2. Impact under low harvesting intensity

We now examine the low-harvesting regime by setting $\alpha = 1$ while keeping $\gamma = 1.3$ and $\delta = 0.6$.

Absence of commensalism. When $\frac{\delta}{\beta} = 0$ (i.e., the commensalism interaction is absent), system (1.4) degenerates into two independent models. With the parameters $(\alpha, \beta, \gamma, \delta) = (1, 1.6, 1.3, 0)$, it follows from Theorem 2 in [6] that the unique positive fixed point of the first single-species equation is locally stable, as illustrated in Figure 10. This confirms that species x can persist independently under low harvesting pressure.

Weak to moderate commensalism. With $(\alpha, \beta, \gamma, \delta) = (1, 1.6, 1.3, 0.6)$, corresponding to $\frac{\delta}{\beta} = 0.375$, one can verify that the hypotheses of Theorem 5.2 are satisfied. Accordingly, the positive fixed point E_{22} is globally attractive, as illustrated in Figure 11. Comparing the equilibrium density of x with that in the absence of commensalism, one observes an increase attributable to the commensal benefit provided by species y , consistent with the ecological expectation that commensalism elevates the population density of the beneficiary species.

Strong commensalism. As in the high-harvesting case, increasing the commensalism strength beyond the critical threshold β_1 triggers a period-doubling bifurcation at E_{22} . Figure 12 displays representative time series illustrating this phenomenon:

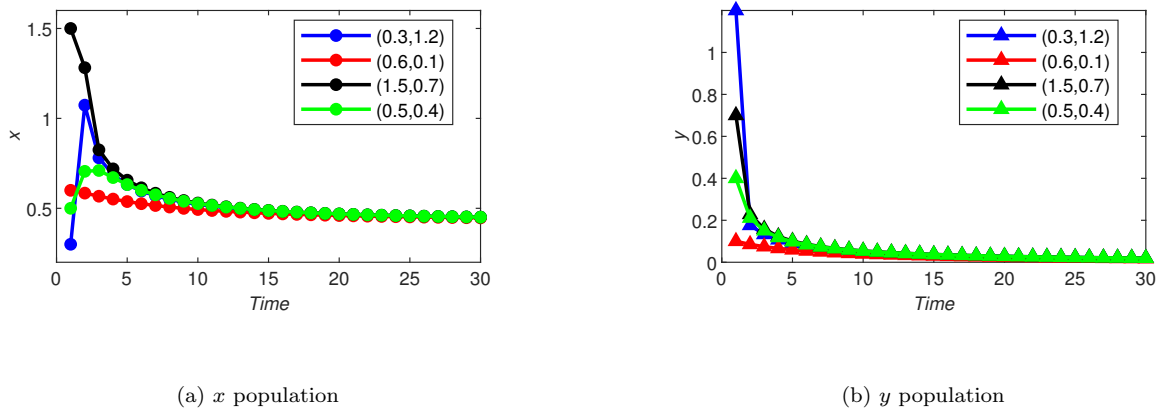


Figure 10. Stability of $E_{22}(x_{22}^*, \frac{\delta}{\beta})$ under low harvesting without commensalism.

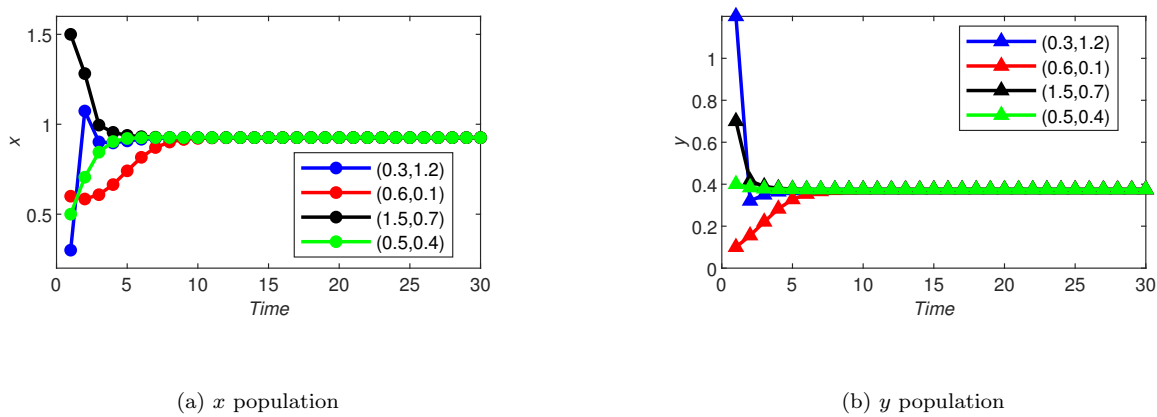


Figure 11. Global attractivity of $E_{22}(x_{22}^*, \frac{\delta}{\beta})$ under low harvesting and moderate commensalism.

- With $(\alpha, \beta, \gamma, \delta) = (1, 0.3, 1.3, 0.6)$, the system exhibits a stable period-4 cycle (Figure 12(a)), indicating that two successive period-doubling bifurcations have already occurred.
- With $(\alpha, \beta, \gamma, \delta) = (1, 0.25, 1.3, 0.6)$, the system enters a chaotic regime (Figure 12(b)).

This observation is noteworthy: Even when the harvesting pressure is relatively low and would otherwise permit stable coexistence, excessively strong commensalism alone is sufficient to destabilize the system and induce chaotic dynamics.

Bifurcation analysis with varying β . Fixing $(\alpha, \delta, \gamma) = (1, 0.6, 1.3)$ and varying β , we construct the bifurcation diagram and MLE shown in Figure 13. The overall structure is qualitatively similar to the high-harvesting case (cf. Figure 9), with two notable differences. First, the extinction regime is absent since the low harvesting intensity is insufficient to drive species x to extinction for any commensalism level. Second, the bifurcation threshold occurs at a smaller value of $\frac{\delta}{\beta}$ compared to the high-harvesting case, indicating that the system tolerates stronger commensalism before destabilization when the harvesting intensity is lower. As β decreases, the equilibrium density of x increases monotonically until the period-doubling threshold is reached, beyond which a full cascade to chaos develops.

Comparison of high and low harvesting regimes. Comparing Figures 9 and 13 reveals several key observations. Under high harvesting, there exists a critical minimum commensalism

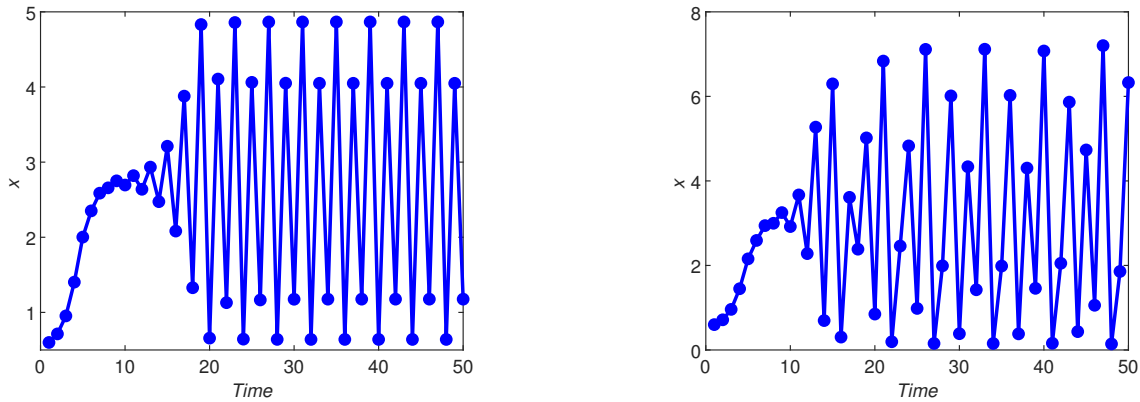
(a) $\alpha = 1$, $\beta = 0.3$, $\delta = 0.6$, $\gamma = 1.3$: Period-4 cycle(b) $\alpha = 1$, $\beta = 0.25$, $\delta = 0.6$, $\gamma = 1.3$: Chaos

Figure 12. Time series of species x under low harvesting and strong commensalism. (a) A period-4 orbit; (b) chaotic oscillations.

strength below which species x cannot survive, whereas under low harvesting, species x persists for all commensalism levels. In both cases, however, the period-doubling route to chaos is qualitatively identical, governed by the same bifurcation mechanism described in Theorem 6.6. This indicates that the commensalism-induced destabilization is a robust dynamical phenomenon that is largely independent of the harvesting intensity, although the specific parameter thresholds differ.

7.2. Unstable y population ($\delta > 2$)

When $\delta > 2$, Theorem 5.1 no longer guarantees the convergence of $y(n)$ to $\frac{\delta}{\beta}$. Instead, the second equation of system (1.4) independently undergoes a period-doubling bifurcation at $\delta = 2$ (Theorem 6.8), and for $\delta > 2$, the y -population exhibits periodic or chaotic oscillations. Since the commensal interaction is unidirectional (y influences x but not vice versa), the oscillatory dynamics of y are transmitted to species x through the term y_n in the first equation of system (1.4).

To investigate this scenario, we fix $(\alpha, \gamma, \delta) = (1.8, 1.3, 2.2)$ and vary β . The resulting bifurcation diagram and MLE are displayed in Figure 14. As β decreases (commensalism strength increases), the system undergoes the following transitions:

- (i) *Extinction of species x* (β large): Despite the oscillatory behavior of y , the commensalism strength is insufficient to sustain x under high harvesting pressure, and $x(n) \rightarrow 0$.
- (ii) *Periodic oscillations of species x* (β moderate): The system exhibits period-2 oscillations for x .
- (iii) *Higher-period oscillations and chaos* (β small): Further strengthening commensalism drives the system through successive period-doubling bifurcations into chaos.

These results demonstrate that even when the host population y is intrinsically unstable, the commensal interaction can still rescue species x from extinction, provided the commensalism strength is sufficiently large. However, the resulting dynamics of x are inevitably oscillatory or chaotic.

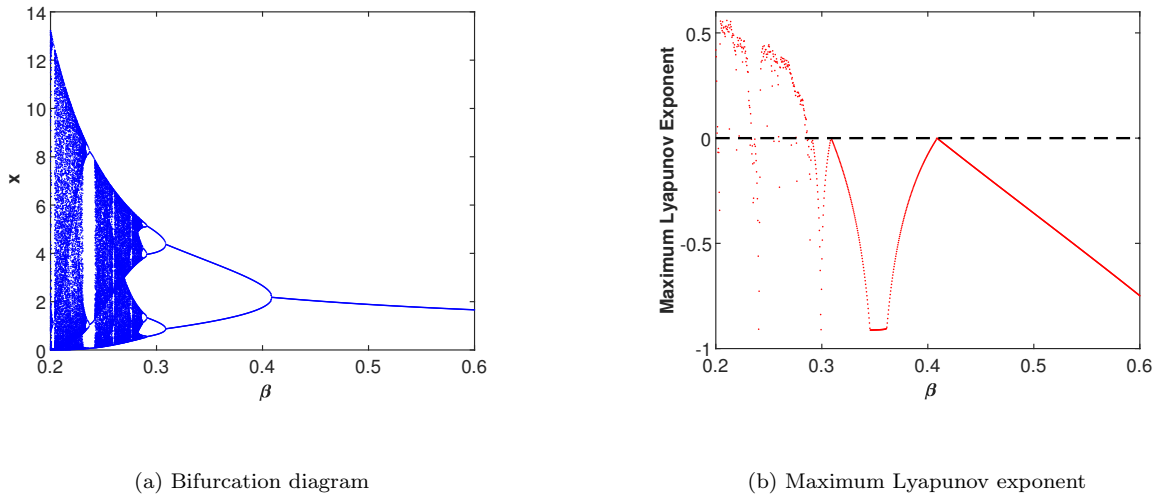


Figure 13. Bifurcation diagram and maximum Lyapunov exponent as functions of β under low harvesting: $(\alpha, \delta, \gamma) = (1, 0.6, 1.3)$. In contrast to the high-harvesting scenario, no extinction regime is present.

7.3. Transmission of instability: Effect of y population stability on x

A fundamental question raised by the preceding analysis concerns how the intrinsic stability of the host population y affects the onset of complex dynamics in species x . To address this question, we fix $(\alpha, \gamma) = (0.8, 1)$ and construct bifurcation diagrams of species x (with β as the bifurcation parameter) for several representative values of δ , spanning both the stable ($\delta < 2$) and unstable ($\delta > 2$) regimes.

The results in Figure 15 reveal a striking phenomenon: As δ increases past the critical value $\delta = 2$, the period-doubling bifurcation threshold for species x shifts to larger values of β — equivalently, to weaker commensalism strength $\frac{\delta}{\beta}$. In other words, the onset of chaos in species x occurs earlier as the host population becomes more unstable. This can be understood intuitively: When $\delta > 2$, species y oscillates with increasing amplitude (as δ increases), and these oscillations are transmitted to species x through the commensal interaction. The periodic or chaotic forcing from y effectively lowers the threshold at which the nonlinear feedback in the x -dynamics becomes destabilizing.

This observation has important ecological implications. It suggests that the stability properties of the host population serve as a critical determinant of the dynamical complexity of the entire commensal system. Even if the commensalism strength lies within the “moderate” range that would normally ensure stable coexistence, instability in the host population can push the commensal species into oscillatory or chaotic dynamics prematurely. This finding underscores the ecological principle that protecting and stabilizing the host population is essential not only for its own conservation but also for maintaining the dynamical integrity of the entire commensal community.

8. Summary and discussion

Based on the continuous-time commensalism model with Michaelis–Menten type harvesting proposed by Chen [3], this paper systematically investigates the dynamical behavior of its discrete counterpart, system (1.4). Our analysis encompasses the existence, local stability, persistence,

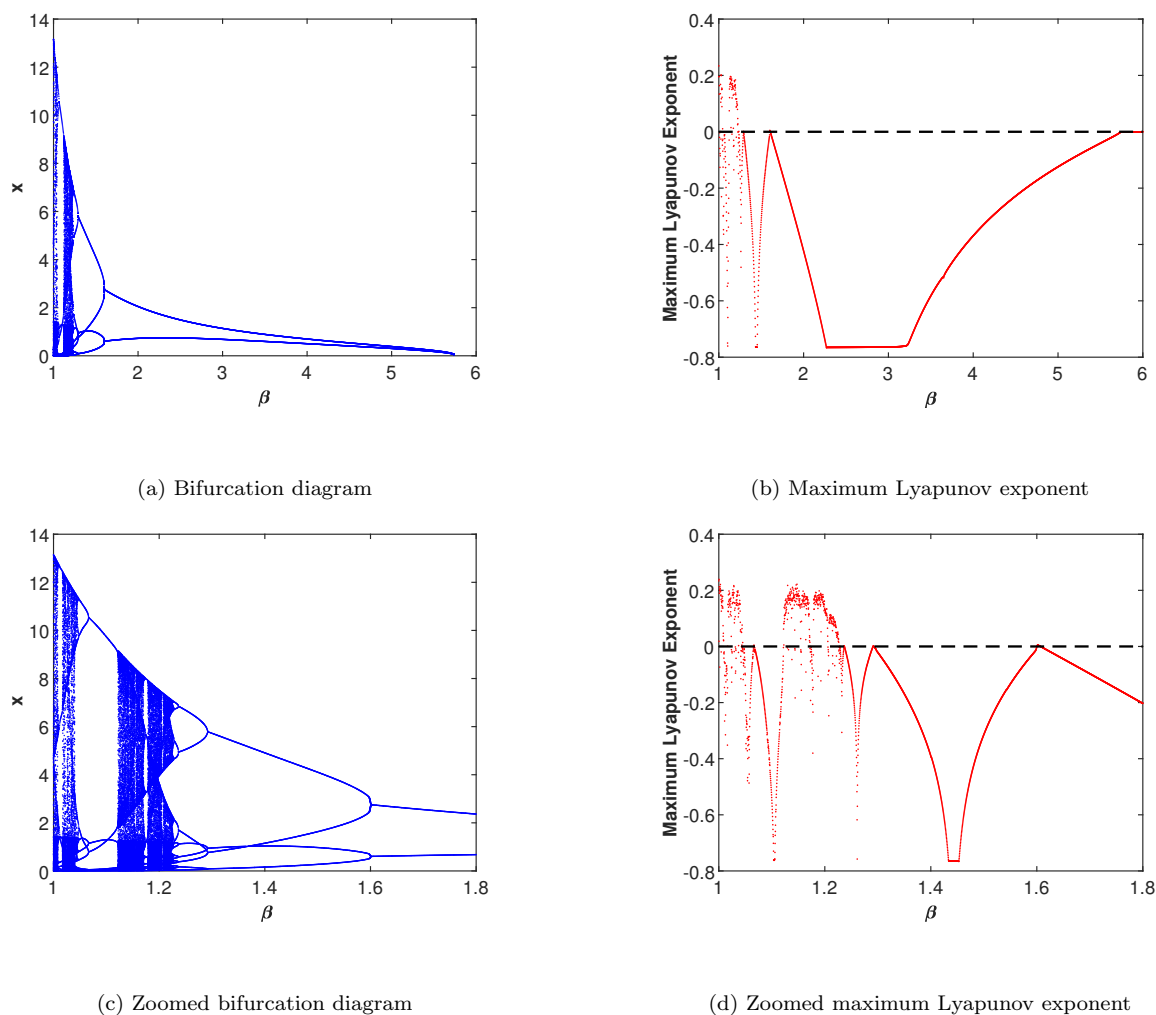


Figure 14. Bifurcation diagram and maximum Lyapunov exponent as functions of β with an unstable y population: $(\alpha, \gamma, \delta) = (1.8, 1.3, 2.2)$. Panels (c) and (d) provide magnified views of the transition region to reveal the detailed bifurcation structure.

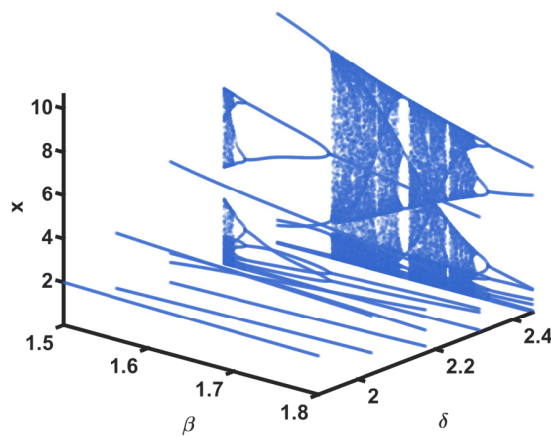


Figure 15. Bifurcation diagrams of species x in the β - x plane for increasing values of δ , with $(\alpha, \gamma) = (0.8, 1)$.

and global attractivity of fixed points (Sections 2–5), as well as the complete bifurcation structure of the system, including transcritical, pitchfork, fold, and period-doubling bifurcations (Section 6). The theoretical findings are complemented by comprehensive numerical simulations (Section 7) that elucidate the joint influence of commensalism strength and harvesting intensity on long-term population dynamics. Compared with the continuous-time model, the discrete model reveals substantially richer dynamical phenomena, particularly nonlinear behaviors induced by strong commensalism. In what follows, we synthesize the principal results, highlight the key distinctions from continuous-time models, and discuss the ecological implications.

When the commensal-providing population y is intrinsically stable ($0 < \delta < 2$), Theorems 5.2 and 5.3, together with the numerical results in Section 7, establish that the dynamic behavior of the system is governed by the interplay between the harvesting intensity α and the commensalism strength $\frac{\delta}{\beta}$. Specifically, when the harvesting intensity is below the critical threshold ($\alpha < \alpha_3$) and the commensalism strength is moderate, the system possesses a unique, globally attractive positive fixed point E_{22} , ensuring stable coexistence of both species (Figures 7 and 11). Conversely, when the harvesting intensity exceeds the threshold ($\alpha > \alpha_2$), species x is driven to extinction regardless of the commensalism level (Figure 6). The transcritical bifurcation at E_1 (Theorem 6.4 and Remark 6.1) provides a precise characterization of this transition: As α increases through the critical value $\gamma(1 + \frac{\delta}{\beta})$, the positive fixed point E_{22} collides with the boundary fixed point E_1 and disappears, leading to the extinction of species x .

The most significant finding of this study—and a fundamental departure from the conclusions of the continuous model [3]—is the discovery that excessively strong commensalism can be *detrimental* to system stability. In the continuous model (1.2), commensalism is generally beneficial: Increasing the commensal benefit always promotes species persistence and elevates the equilibrium density of the harvested species, without inducing any qualitative change in the system dynamics. In sharp contrast, the discrete model reveals the existence of an “optimal range” for the commensalism strength $\frac{\delta}{\beta}$. As demonstrated by Theorem 6.6 and the bifurcation diagrams in Figures 9 and 13, when $\frac{\delta}{\beta}$ exceeds the critical value β_1 , the positive fixed point E_{22} loses stability through a period-doubling bifurcation, and the system sequentially undergoes 2, 4, 8, ... periodic oscillations, eventually entering a chaotic state. This phenomenon is robust across different harvesting regimes: It occurs both under high harvesting intensity and under low harvesting intensity, with only the specific parameter thresholds differing between the two cases. In ecological terms, this suggests an optimal range for commensalism: Moderate interaction promotes population growth and stable coexistence, whereas excessive commensalism overwhelms the self-regulatory mechanisms of the population, ultimately generating unpredictable fluctuations that threaten long-term species persistence.

We further discovered that the intrinsic stability of the commensal-providing population is another key factor determining system dynamics. When the host population y is intrinsically unstable ($\delta > 2$), it undergoes its own period-doubling bifurcation (Theorem 6.8) and exhibits periodic or chaotic oscillations. Since the commensal interaction is unidirectional, these oscillations act as a time-varying external forcing on the dynamics of species x . The numerical results in Sections 7.2 and 7.3 (Figures 14 and 15) reveal two key consequences. First, even when the commensalism strength would normally ensure stable coexistence (in the stable- y regime), instability in the host population can prematurely push species x into oscillatory or chaotic dynamics by shifting the period-doubling bifurcation threshold to weaker commensalism strengths (Figure 15). Second, sufficiently strong commensalism from an oscillating host can rescue species x from extinction under high harvesting, although the resulting dynamics are inevitably non-stationary

(Figure 14). These findings highlight that the stability properties of the host population serve as a critical “upstream” determinant of the dynamical complexity of the entire commensal system.

Through rigorous analysis of the discrete model, this study deepens our understanding of the interaction between nonlinear harvesting and interspecific relationships. In terms of theoretical significance, we systematically characterized the complete dynamic spectrum of the discrete commensalism model, ranging from stable coexistence to periodic oscillations and chaos, and identified the central roles played by commensalism strength and host stability. Regarding management implications: First, in practice, managers should not only focus on harvesting intensity but also assess the strength of commensal relationships between species. Keeping the commensalism strength within a moderate range is crucial for avoiding detrimental oscillations and maintaining ecosystem stability. Second, protecting a species (such as the commensal-providing population y) is not only about conserving that species itself but may also have a critical “leverage effect” on the stability and sustainability of its partner species (such as the harvested population x) through interspecific interactions like commensalism. Future work could incorporate time delays, stochastic perturbations, or spatial heterogeneity to more fully characterize the complex dynamics arising from the interplay between commensalism and harvesting in realistic ecological settings.

Statements and declarations

Competing interests. The authors have no competing interests to declare.

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