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Dynamical Properties of a Predator-Prey Discrete Model with Hunting Cooperation Mechanism

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Abstract. In this paper, the effect of a hunting cooperation functional response in discrete predator-prey model is first to be studied. By surveying the existence conditions and stability of the fixed points, a preliminary foundation for bifurcation analysis is provided. Then, flip bifurcation of the nonhyperbolic fixed points is investigated, the theoretical explanation for our results from a biological perspective is presented.

Keywords. discrete model, functional response, stability, flip bifurcation

1. Introduction

Mathematical model is a vital tool to reveal the interaction and internal relationship on the population of predator and prey. The general predator-prey discrete model is of the following form

$$\begin{cases} x_{n+1} = x_n + g(x_n)x_n - f(x_n, y_n)y_n, \\ y_{n+1} = y_n + \varepsilon f(x_n, y_n)y_n + sy_n, \end{cases} \tag{1}$$

where x_n and y_n denote the densities of prey and predator in generation n, $g(x_n)$ is the net growth rate of prey in the absence of predators, s denotes death rate (if $s < 0$) or intrinsic growth rate (if $s > 0$) of predator, $f(x_n, y_n)$ is the rate of consumption of prey by a predator and ε is the rate at which captured prey becomes predators. The term $f(x_n, y_n)$ can reflect the behavior of a predator toward a prey, so, it is also called functional response. Since Maynard Smith [1] proposed Lotka-Volterra type functional response (i.e. $f(x_n, y_n) = mx_n$) in predator-prey model (1), many researchers have assumed various functional responses and studied the dynamical property of (1). Levine [2] and Liu and Xiao [3] gave Lotka-Volterra type of model (1) and analyzed the fold, flip and Neimark-Sacker bifurcations. Hadeler and Gerstmann [4] and Neubert and Kot [5] considered

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the model (1) with Holling type II functional response, of which non-hyperbolicity and codimension 1 bifurcations were completely discussed by Li and Zhang [6] and Arias et al [7]. Singh and Malik [8] studied a Leslie-Gower type with Holling II. In [9], He and Lai considered a Leslie-Gower type with Holling III and investigated its bifurcation and chaotic behaviors. In [10], Huang et al investigated the model with nonmonotonic Holling IV response and shown Bogdanov-Takens bifurcation. More research in this area can be found in [11-15] and the references cited therein.

Motivated by all the above ideas of assuming functional response functions for model (1), in this paper, we consider another functional response function as follows

$$f(x_n, y_n) = \frac{\alpha x_n y_n}{1 + x_n y_n}. \tag{2}$$

This function was first put forward by Cosner et al [16] to show the hunting cooperation mechanism by which a group of predators search, touch and kill a group of prey. Obviously, $f(x, y)$ is not just monotonically increasing for x and y and it is even upper bounded. This means that predators are more efficient when their population size is large, but not when their population size is too large, because signals between predators cannot be transmitted smoothly if their foraging queue is too long [16]. This mechanism is not like the one caused by conventional responses as mentioned above.

To the best of our knowledge, there is no literature that has proposed functional response function (2) in any discrete model and studied its effects. Therefore, The main purpose of this paper is to discuss what kind of interesting dynamics the functional response (2) brings to the model (1). By assuming $g(x)$ is the logistic prey growth rate and substituting (2) in model (1), we have

$$\begin{cases} x_{n+1} = x_n + x_n(1 - x_n) - \frac{\alpha x_n {y_n}^2}{1 + x_n y_n}, \\ y_{n+1} = y_n + \frac{\beta x_n {y_n}^2}{1 + x_n y_n} - \gamma y_n, \end{cases} \tag{3}$$

where α, β and γ are positive.

The research content is arranged as follows. The linear stability of the model fixed points are discussed in the next section. The analysis of the flip bifurcation is arranged in Section 3. Finally, the theoretical explanation of our results is given from the perspective of biology.

2. Stability of the fixed points

We write model (3) as the following planar mapping $F : \mathbf{R}^2 \mapsto \mathbf{R}^2$

$$F : \begin{pmatrix} x \\ y \end{pmatrix} \mapsto \begin{pmatrix} x(2 - x) - \frac{\alpha x y^2}{1 + xy} \\ (1 - \gamma) y + \frac{\beta x y^2}{1 + xy} \end{pmatrix}. \tag{4}$$

Then (4) has at least a trivial fixed point $E_0(0, 0)$ and a semi-trivial fixed point $E_1(1, 0)$. Moreover, (4) has interior fixed point $E^*(x, y)$ which satisfies $x > 0$, $y > 0$ and

$$x^3 - x^2 + \frac{\alpha \gamma^2}{\beta^2 - \beta\gamma} = 0, \quad y = \frac{\gamma}{\beta - \gamma} x^{-1}. \tag{5}$$

We first get the following conclusion for (4). The proof is simple and is omitted.

Lemma 1 *Assume $\beta > \gamma$ and let $\alpha_c := \frac{4}{27}\frac{\beta(\beta-\gamma)}{\gamma^2}$. If $\alpha > \alpha_c$, we have no interior fixed point; If $\alpha = \alpha_c$, we have unique interior fixed point $E_0^*(x_0, y_0)$, where $x_0 = \frac{2}{3}, y_0 = \frac{3\gamma}{2(\beta-\gamma)}$; If $\alpha < \alpha_c$, we have two interior fixed points $E_1^*(x_1, y_1), E_2^*(x_2, y_2)$ satisfying (5) and $x_2 < \frac{2}{3} < x_1$.*

The Jacobi matrix at any point $E(x,y)$ of mapping (4) is

$$J(E) = \begin{pmatrix} 2(1-x) - \frac{\alpha y^2}{1+xy} + \frac{\alpha x y^3}{(1+xy)^2} & -\frac{\alpha x y(2+xy)}{(1+xy)^2} \\ \frac{\beta y^2}{(1+xy)^2} & 1-\gamma+\frac{\beta x y(2+xy)}{(1+xy)^2} \end{pmatrix}. \tag{6}$$

Corresponding to fixed points E_0, E_1, we have

$$J(E_0) = diag(2, 1-\gamma), J(E_1) = diag(0, 1-\gamma).$$

Hence, we easily get the following conclusions (omitted proofs) on linear stability of E_0 and E_1.

Lemma 2 *The properties of fixed point E_0 hold:* (i) *if $0 < \gamma < 2$, E_0 is a saddle;* (ii) *if $\gamma > 2$, E_0 is an unstable node;* (iii) *if $\gamma = 2$, E_0 is non-hyperbolic.*

Lemma 3 *The properties of fixed point E_1 hold:* (i) *if $\gamma > 2$, E_1 is a saddle;* (ii) *if $0 < \gamma < 2$, E_1 is an stable node;* (iii) *if $\gamma = 2$, E_1 is non-hyperbolic.*

Corresponding to positive fixed points E_1^*, we have

$$J(E_1^*) = \begin{pmatrix} (2-\gamma_0)s_1 & -\alpha(1-\gamma_0^2) \\ \frac{\gamma\gamma_0}{\alpha(1-\gamma_0)}s_1 & 1+\gamma\gamma_0 \end{pmatrix},$$

where $\gamma_0 := 1 - \frac{\gamma}{\beta}$, and $s_1 := 1 - x_1$, and their characteristic polynomials

$$P(\lambda) = \lambda^2 - ((2-\gamma_0)s_1 + \gamma\gamma_0 + 1)\lambda + ((2-\gamma_0)s_1 + 3\gamma\gamma_0 s_1).$$

For the convenience, we let

$$\gamma_1 := \frac{1 + s_1\gamma_0 - 4s_1}{3s_1\gamma_0}.$$

The linear stability of E_1^* is given as follows.

Lemma 4 *If $\alpha < \alpha_c$, the following properties of fixed point E_1^* hold:*

(i) *when $-\frac{1}{3} < s_1 < \frac{1}{3}$, E_1^* is a source if $\gamma < \gamma_1$, E_1^* is a saddle if $\gamma > \gamma_1$;*
(ii) *when $s_1 < -\frac{1}{3}$, E_1^* is a source if $\gamma > \gamma_1$, E_1^* is a saddle if $\gamma < \gamma_1$;*
(iii) *when $s_1 = -\frac{1}{3}$, E_1^* is a saddle;*
(iiii) *when $s_1 \neq -\frac{1}{3}$, E_1^* is non-hyperbolic if $\gamma = \gamma_1$.*

Proof. From Lemma 1, positive fixed point E_1^* satisfies $x_1 > \frac{2}{3}$, then $s_1 < \frac{1}{3}$. We have $P(1) = \gamma\gamma_0(3s_1 - 1) < 0$, $P(-1) = 2 + 2(2-\gamma_0)s_1 + \gamma\gamma_0(1+3s_1)$. Thus, we know characteristic equation $P(\lambda) = 0$ has no conjugate complex root in view of $P(1) < 0$. Without loss generality, we suppose two real roots λ_1 and λ_2 of $P(\lambda) = 0$ satisfy $\lambda_1 < \lambda_2$.

(i) When $-\frac{1}{3} < s_1 < \frac{1}{3}$, if $\gamma < \gamma_1$, then $P(-1) < 0$. We get $\lambda_1 < -1$ and $\lambda_2 > 1$, which means that E_1^* is a source. If $\gamma > \gamma_1$, then $P(-1) > 0$. We get $-1 < \lambda_1 < 1 < \lambda_2$, which means that E_1^* is a saddle.

(ii) The proof is similar to that of (i), we may omitted it.

(iii) When $s_1 = -\frac{1}{3}$, we get $P(-1) > 0$, which means that E_1^* is a saddle.

(iiii) When $s_1 \neq -\frac{1}{3}$, we get $P(-1) = 0$ if $\gamma = \gamma_1$. It means that -1 is a root of $P(\lambda) = 0$, therefore, E_1^* is non-hyperbolic.

3. Analysis of flip bifurcation

In the following, we will use bifurcation theory to study the flip bifurcations of the above fixed points E_0, E_1 and E_1^* when the non-hyperbolic conditions are satisfied.

3.1. Flip bifurcation at E_0 and E_1

From Lemma 2 and Lemma 3, when $\gamma = 2$, the corresponding eigenvalues are $|\lambda_1| \neq 1$ and $\lambda_2 = -1$. This indicates that the mapping (4) may occur flip bifurcation at E_0 and E_1. Because of the practical implications of the model, we discuss the bifurcation at semi-trivial fixed point E_1 only. We introduce a parameter γ^* satisfying $\gamma^* = \gamma - 2$ in the following discussion.

Theorem 1 *The mapping (4) experiences a supercritical flip bifurcation at E_1 when parameter γ^* pass through* 0. *Specifically, assume $\beta < 1$ (or, $\beta > 1$), a stable period doubling point bifurcates from $(E_1, \gamma^*) = (E_1, 0)$ when $\gamma^* > 0$ (respectively, $\gamma^* < 0$). Moreover, E_1 is unstable (or, stable) when $\beta < 1$ (respectively, $\beta > 1$).*

Proof By using transformation T: $x = \mu + 1, y = \upsilon, \gamma = \gamma^* + 2$ and Taylor series expansion, the mapping (4) can be written as follows

$$F_1 : \begin{pmatrix} \mu \\ \upsilon \\ \gamma^* \end{pmatrix} \mapsto \begin{pmatrix} 0 & 0 & 0 \\ 0 & -(1+\gamma^*) & 0 \\ 0 & 0 & 1 \end{pmatrix} \begin{pmatrix} \mu \\ \upsilon \\ \gamma^* \end{pmatrix} + \begin{pmatrix} f_1(\mu, \upsilon, \gamma^*) \\ f_2(\mu, \upsilon, \gamma^*) \\ 0 \end{pmatrix} \tag{7}$$

where parameter γ^* is considered as a new independent variable, $f_1(\mu, \upsilon, \gamma^*) = -\mu^2 - \alpha\upsilon^2 - \alpha\mu\upsilon^2 + \alpha\upsilon^3 + O(\| (\mu, \upsilon, \gamma^*) \|^4)$ and $f_2(\mu, \upsilon, \gamma^*) = \beta\upsilon^2 + \beta\mu\upsilon^2 - \beta\upsilon^3 + O(\| (\mu, \upsilon, \gamma^*) \|^4)$. Hence, by the theory of [17], we have a center manifold at $(\mu, v) = (0, 0)$ in a small neighborhood of $\gamma^* = 0$, which satisfies the following condition

$$W_{loc}(0,0) = \{(\mu, \upsilon, \gamma^*) \in \mathbf{R}^3 | \ \mu = h(\upsilon, \gamma^*), h(0,0) = 0, Dh(0,0) = 0, |\upsilon| < \varepsilon, |\gamma^*| < \delta\}$$

where ε and δ are sufficiently small positive numbers. Assume that

$$\mu = h(\upsilon, \gamma^*) = c_1\upsilon^2 + c_2\upsilon\gamma^* + c_3{\gamma^*}^2 + O(\|(\upsilon, \gamma^*)\|^3).$$

From the invariance of the central manifold $\mu = h(\upsilon, \gamma^*)$, we obtain

$$\mathscr{N}(h(\upsilon, \gamma^*)) = h\Big(-(1+\gamma^*) + f_2(h(\upsilon, \gamma^*), \upsilon), \gamma^*\Big) - f_1(h(\upsilon, \gamma^*), \upsilon) = 0.$$

By comparing the coefficients of $\upsilon^2, \upsilon\gamma^*$ and γ^{*^2}, we obtain $c_1 = -\alpha, c_2 = c_3 = 0$. Thus the center manifold is

$$\mu = h(\upsilon, \gamma^*) = -\alpha\upsilon^2 + O(\|(\upsilon, \gamma^*)\|^3).$$

On the center manifold, Mapping (7) is

$$\upsilon \mapsto \tilde{f}_2(\upsilon, \gamma^*) = -(1+\gamma^*)\upsilon + \beta\upsilon^2 - \beta\upsilon^3 + O(\|(\upsilon, \gamma^*)\|^4). \tag{8}$$

Consider the second iterate of mapping (8), we have

$$\tilde{f}_2^2(\upsilon, \gamma^*) = \upsilon - 2\upsilon\gamma^* - \beta\upsilon^2\gamma^* + \upsilon\gamma^{*^2} + 2\beta\upsilon^3 - 2\beta^2\upsilon^3 + O(\|(\upsilon, \gamma^*)\|^4).$$

By computation, we have

$$\tilde{f}_2(0,0) = 0, \quad \frac{\partial \tilde{f}_2}{\partial \upsilon}(0,0) = -1, \quad \frac{\partial \tilde{f}_2^2}{\partial \gamma^*}(0,0) = 0,$$

$$\frac{\partial \tilde{f}_2^2}{\partial \upsilon}(0,0) = 1, \quad \frac{\partial^2 \tilde{f}_2^2}{\partial \gamma^* \partial \upsilon}(0,0) = -2, \quad \frac{\partial^3 \tilde{f}_2^2}{\partial \upsilon^3}(0,0) = 12\beta(1-\beta),$$

and we get nondegeneracy condition

$$\left(-\frac{\partial^3 \tilde{f}_2^2(0,0)}{\partial \upsilon^3} \bigg/ \frac{\partial^2 \tilde{f}_2^2(0,0)}{\partial \gamma^* \partial \upsilon}\right) = 6\beta(1-\beta) \neq 0.$$

According to the result in [17], the mapping (4) has flip bifurcation at E_1 and it is supercritical, if $\beta < 1$ (or, $\beta > 1$), a stable period doubling points arise at point $(E_1, \gamma^*) = (E_1, 0)$ when $\gamma^* > 0$ (respectively, $\gamma^* < 0$).

Next, we discuss the stability of E_1 if $\gamma^* = 0$. From (8), we have

$$\upsilon \mapsto \tilde{f}_2(\upsilon, 0) = -\upsilon + \beta\upsilon^2 - \beta\upsilon^3 + O(\|(\upsilon, \gamma^*)\|^4).$$

By computation, we get the Schwarizan derivative of $\tilde{f}_2(\upsilon, 0)$ is

$$S\tilde{f}_2(\upsilon, 0) = \frac{\tilde{f}_2^{(3)}(\upsilon, 0)}{\tilde{f}_2'(\upsilon, 0)} - \frac{3}{2}\left(\frac{\tilde{f}_2''(\upsilon, 0)}{\tilde{f}_2'(\upsilon, 0)}\right)^2 = 6\beta(1-\beta)$$

From Theorem 2.3 (ii) in [18], we get E_1 is unstable (or, stable) when $\beta < 1$ (or, $\beta > 1$).

3.2. *Flip bifurcation at E_1^**

From Lemma 4, if $\gamma = \gamma_1$ the characteristic equation at fixed point $E_1^*(x_1, y_1)$ has two roots $\lambda_1 = -1$ and $\lambda_2 = 2 + s_1(2-\gamma_0) + \gamma_1\gamma_0$ when $s_1 \neq -\frac{1}{3}$. By selecting γ as a bifurcation parameter and using a transformation of

$$x = \mu + x_1^*, \quad y = \upsilon + y_1^*, \quad \gamma = \gamma_1 + \gamma^*,$$

we change mapping (4) into the following Taylor series form at origin $(\mu, \upsilon, \gamma^*) = (0,0,0)$

$$F_3 : \begin{pmatrix} \mu \\ \upsilon \end{pmatrix} \mapsto \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix} \begin{pmatrix} \mu \\ \upsilon \end{pmatrix} + \begin{pmatrix} f_1(\mu,\upsilon,\gamma^*) \\ f_2(\mu,\upsilon,\gamma^*) \end{pmatrix} \tag{9}$$

where

$$\begin{aligned} f_1(\mu,\upsilon,\gamma^*) &= c_{13}\mu^2 + c_{14}\mu\upsilon + c_{15}\upsilon^2 + e_1\mu^3 + e_2\mu^2\upsilon + e_3\mu\upsilon^2 + e_4\upsilon^3 \\ &\quad + O(\|(\mu,\upsilon,\gamma^*)\|^4), \\ f_2(\mu,\upsilon,\gamma^*) &= c_{23}\mu^2 + c_{24}\mu\upsilon + c_{25}\upsilon^2 + d_1\gamma^* + d_2\mu\gamma^* + d_3\upsilon\gamma^* + d_4\mu^2\gamma^* + d_5\mu\upsilon\gamma^* \\ &\quad + d_6\upsilon^2\gamma^* + q_1\mu^3 + q_2\mu^2\upsilon + q_3\mu\upsilon^2 + q_4\upsilon^3 + O(\|(\mu,\upsilon,\gamma^*)\|^4), \end{aligned}$$

and the concrete expressions of all coefficients will be omitted for reducing the size of the page.

Constructing an invertible linear transformation

$$\begin{pmatrix} \mu \\ \upsilon \end{pmatrix} = \begin{pmatrix} c_{12} & c_{12} \\ -1-c_{11} & \lambda_2 - c_{11} \end{pmatrix} \begin{pmatrix} \xi \\ \eta \end{pmatrix}. \tag{10}$$

we convert the mapping F_3 to

$$\begin{pmatrix} \xi \\ \eta \end{pmatrix} \mapsto \begin{pmatrix} -1 & 0 \\ 0 & \lambda_2 \end{pmatrix} \begin{pmatrix} \xi \\ \eta \end{pmatrix} + \begin{pmatrix} g_1(\xi,\eta,\gamma^*) \\ g_2(\xi,\eta,\gamma^*) \end{pmatrix} \tag{11}$$

where

$$\begin{aligned} g_1(\xi,\eta,\gamma^*) &= \tfrac{1}{c_{12}(1+\lambda_2)}(D_{13}\mu^2 + D_{14}\mu\upsilon + D_{15}\upsilon^2 + c_{12}\mu\gamma^* + E_{11}\mu^3 + E_{12}\mu^2\upsilon \\ &\quad + E_{13}\mu\upsilon^2 + E_{14}\upsilon^3) + O(\|(\xi,\eta,\gamma^*)\|^4), \\ g_2(\xi,\eta,\gamma^*) &= \tfrac{1}{c_{12}(1+\lambda_2)}(F_{13}\mu^2 + F_{14}\mu\upsilon + F_{15}\upsilon^2 - c_{12}\mu\gamma^* + J_{21}\mu^3 + J_{22}\mu^2\upsilon \\ &\quad + J_{23}\mu\upsilon^2 + J_{24}\upsilon^3) + O(\|(\xi,\eta,\gamma^*)\|^4), \end{aligned}$$

and the concrete expressions of all coefficients will be omitted for reducing the size of the page.

Similar proof as of Theorem 1, on center manifold, the mapping (11) is

$$\xi \mapsto g_{1c}(\xi,\gamma^*) = -\xi + l_1\xi^2 + l_2\xi\gamma^* + l_3\xi^2\gamma^* + l_4\xi^3 + O(\|(\xi,\gamma^*)\|^3) \tag{12}$$

where the expressions of $l_i, (i = 1,2,3,4)$ are omitted for reducing the size of the page.

In order to get the condition of mapping (12) undergoing flip bifurcation, we compute

$$\left(\frac{\partial^2 g_{1c}}{\partial\gamma^*\partial\xi} + \frac{1}{2}\frac{\partial g_{1c}}{\partial\gamma^*}\frac{\partial^2 g_{1c}}{\partial\xi^2} \right)\Bigg|_{(0,0)} = l_2, \qquad \left(\frac{1}{6}\frac{\partial^3 g_{1c}}{\partial\xi^3} + \left(\frac{1}{2}\frac{\partial^2 g_{1c}}{\partial\xi^2} \right)^2 \right)\Bigg|_{(0,0)} = l_4 + l_1^2.$$

By Theorem 3.5.1 in [19], we get bifurcation result of mapping (4) at $E_1^*(x_1,y_1)$.

Theorem 2 *If $l_2 \neq 0$ and $l_4 + l_1^2 \neq 0$, when γ^* is perturbed in a sufficiently small neighborhood of the origin, the mapping (4) undergoes flip bifurcation at $E_1^*(x_1,y_1)$. Moreover, if $l_4 + l_1^2 > 0 (< 0)$, the bifurcation is supercritical (subcritical), that is, the period doubling orbit bifurcating from $E_1^*(x_1,y_1)$ is stable (unstable).*

4. Biological explanation

According to Theorem 1, the flip bifurcation undergoes at $E_1(1,0)$, which means there is no predator, the number of prey will oscillate with period-2 around the maximum environmental capacity, and the oscillation is stable (or, unstable) with $\gamma > 2$ (or, $\gamma < 2$). From Theorem 2, flip bifurcation arises at $E_1^*(x_1, y_1)$, which indicates the coexistence of prey and predator with period doubling oscillation when $l_2 \neq 0$ and $l_4 + l_1^2 > 0$. Therefore, the effect of the hunting cooperation mechanism determines the fluctuation stability of predator and prey populations.

5. Simulations

First, if let $\alpha = 0.7$, $\beta = 0.73$ and initial value $(x_0, y_0) = (0.98, 0.14)$, we get the bifurcation diagram (see Fig. 1). From Fig. 1, we know that when γ cross through 2, a stable periodic-2 points bifurcate from point $(1,0)$. Moreover, when γ continues to grow through 2.4, a stable periodic-4 points will occur.

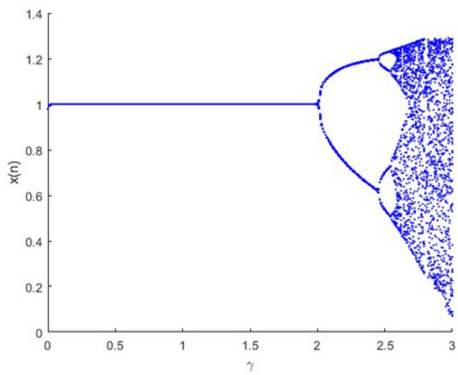

Fig. 1 Bifurcation diagram at point $E_1(1,0)$ with $\alpha = 0.7$, $\beta = 0.73$

Second, if let $\alpha = 0.9765$, $\beta = 3.00$ and $\gamma = 0.9$, then we have $\gamma_0 = 0.7$, $E_1^*(x_1, y_1) = (0.8074, 0.5308)$ and $\alpha_c = 1.152$, so, $\alpha < \alpha_c$ which satisfies the condition of Lemma 4. By tedious calculation, we get $l_1 \approx 1.0533$, $l_2 \approx 18.0752$ and $l_4 \approx -4.0813$. So, the conditions of Theorem 2 will be satisfied, i.e., $l_2 \neq 0$ and $l_4 + l_1^2 < 0$. Therefore, from Fig. 2, we see that as γ cross through 0.9, an unstable period-2 orbit bifurcates from E_1^*.

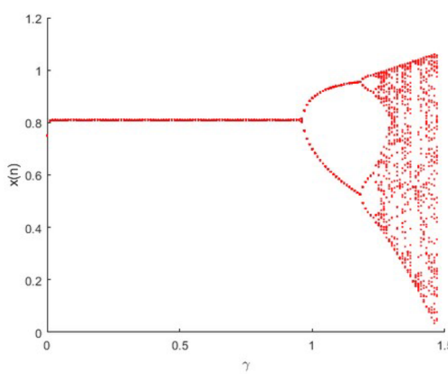

Fig. 2 Bifurcation diagram at point $E_1^* = (0.8074, 0.5308)$ with $\alpha = 0.9765$, $\beta = 3.00$ and $\gamma = 0.9$

Competing interests

The authors declare that they have no competing interests.

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