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Limit cycles analysis and control of evolutionary game dynamics with environmental feedback[☆]



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ARTICLE INFO

Article history: Received 26 August 2021 Received in revised form 9 March 2022 Accepted 26 May 2022 Available online 29 August 2022

Keywords:
Replicator-mutator dynamics
Game-environment feedback
Limit cycles
Hopf bifurcation
Heteroclinic bifurcation
Local and global stability
Incentive-based control

ABSTRACT

Recently, an evolutionary game dynamics model taking into account the environmental feedback has been proposed to describe the co-evolution of strategic actions of a population of individuals and the state of the surrounding environment; correspondingly a range of interesting dynamic behaviors have been reported. In this paper, we provide new theoretical insight into such behaviors and discuss control options. Instead of the standard replicator dynamics, we use a more realistic and comprehensive model of *replicator-mutator dynamics*, to describe the strategic evolution of the population. After integrating the environment feedback, we study the effect of mutations on the resulting closed-loop system dynamics. We prove the conditions for two types of bifurcations, *Hopf bifurcation* and *Heteroclinic bifurcation*, both of which result in stable *limit cycles*. These limit cycles have not been identified in existing works, and we further prove that such limit cycles are in fact persistent in a large parameter space and are almost globally stable. In the end, an intuitive control policy based on incentives is applied, and the effectiveness of this control policy is examined by analysis and simulations.

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1. Introduction

Evolutionary game theory studies the evolution of strategic decision-making processes of individuals in one or multiple populations. A range of mathematical models have been extensively investigated, among which the *replicator dynamics* model is the most well-known (Hofbauer & Sigmund, 1998). Powerful theories and tools originating from evolutionary game theory facilitate the study of complex system behaviors of biological, ecological, social, and engineering fields (Komarova, 2004; Lee, Iwasa, Dieckmann, & Sigmund, 2019; Nowak, Komarova, & Niyogi, 2001; Pais, Caicedo-Nunez, & Leonard, 2013; Stella & Bauso, 2018). In the classic game setting, the payoffs in each two-player game are usually predetermined in the form of constant payoff matrices. However, in many applications, especially those involving common resources in the environment that are consumed by groups of individuals, it is recognized that the payoffs can change

over time or be affected directly by external environmental factors. Thus game-playing individuals' decisions can influence the surrounding environment, and the environment, especially its richness in resources, also acts back on the payoff distributions, which forms the so-called bi-directional game-environment feedback (Weitz, Eksin, Paarporn, Brown, & Ratcliff., 2016). Such a feedback mechanism is believed to be able to explain rich realworld complex population dynamics, including human decisionmaking, social culture evolution, plant nutrient acquisition, and natural resource harvesting. In particular, evolutionary dynamics with game-environment feedback have attracted great attention in recent years, due to its high relevance in biological and sociological systems (Lee et al., 2019; Rand, Tomlin, Bear, Ludvig, & Cohen, 2017; Tilman, Plotkin, & Akcay, 2020).

This line of research is originated in Weitz et al. (2016), where the replicator dynamics of a two-player two-strategy game are coupled with the logistic environment resource dynamics. Utilizing an elaborate environment-dependent payoff matrix, the joint game-environment dynamics exhibit interesting system behaviors. In most cases, the strategic states of the population and the environment converge to an equilibrium point on the boundary of the phase space with the zero value of environment state, which reflects the *tragedy of the commons*. The system dynamics may also show cyclic oscillations which correspond to closed periodic orbits. Particularly when the system dynamics converge to a heteroclinic cycle on the boundary, the environment state cycles between low and high values, which is referred to as the

The work of M. Cao is supported in part by the European Research Council (ERC-CoG-771687). L. Gong, W. Yao, and J. Gao are funded by China Scholarship Council (CSC). The material in this paper was partially presented at the 21st IFAC World Congress (IFAC 2020), July 12–17, 2020, Berlin, Germany. This paper was recommended for publication in revised form by Associate Editor Kostas Margellos under the direction of Editor Christos G. Cassandras.

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oscillating tragedy of commons. Since then, Weitz et al. (2016) has been followed by several extensions and variations (Gong, Gao, & Cao, 2018; Hauert, Saade, & McAvoy, 2019; Kawano, Gong, Anderson, & Cao, 2019; Lin & Weitz, 2019; Muratore & Weitz, 2021; Tilman et al., 2020). The game-environment feedback mechanism has been studied more broadly in different applications, while its theoretical settings have been adapted in different research directions, e.g. implementing different types of environment resource models and considering the structures of the populations. New meaningful dynamical behaviors have been identified, and these results are in turn helpful to understand real-world applications.

The majority of the existing studies on the game-environment framework chooses replicator dynamics to model the strategic dynamics of the game-environment system. While the replicator dynamics have been proved to be a powerful model in analyzing a variety of classical games, they do not take into account the mutation or exploration in strategies which exists ubiquitously in biological and sociological systems. Genetic mutations typically occur with small but non-negligible probabilities, and random exploration of available strategies is common in behavioral experiments (Traulsen, Hauert, Silva, Nowak, & Sigmund, 2009). Mutations and explorations can be captured by allowing individuals to spontaneously switch from one strategy to another in small probability, which results in the so-called replicator-mutator dynamics. It has also played a prominent role in evolutionary game theory and has been applied frequently in different fields (Komarova, 2004; Nowak et al., 2001; Pais et al., 2013; Pais & Leonard, 2011).

We note that although rich system behaviors, such as convergence to equilibria or heteroclinic cycles on the boundary and existence of neutral periodic orbits, have been identified in related works, the results on the limit cycle dynamics have been rarely reported in the game-environment feedback setting. Only in Tilman et al. (2020), it is shown that the time-scale difference between game and environment dynamics can result in limit cycles. When mutations are taken into account, it is of great interest to study if the coupled game and environment dynamics can exhibit limit cycles.

We also emphasize that research on how to design reasonable and effective control policies to achieve expected system behaviors in evolutionary games has attracted increasing attention (Morimoto, Kanazawa, & Ushio, 2016; Riehl & Cao, 2017; Riehl, Ramazi, & Cao, 2019; Zhu, Xia, & Wu, 2016). Specifically, using game-environment feedback, Paarporn, Eksin, Weitz, and Wardi (2018) considers optimal control problems where control takes the form of the incentives and opinions respectively. The adopted control policies can maximize accumulated resource over time. However, since the controlled system still exhibits heteroclinic oscillations, repeated collapses of the resource are inevitable. Wang, Zheng, and Fu (2020) considers adjusting the law of feedback from population states to the environment based on a slightly different co-evolutionary model of public goods games. An involved nonlinear control law is proved to be able to steer the system to evolve towards the designed behaviors, but the biological implication of such control policies still remains open to debate.

Motivated by all the unsolved issues just mentioned, in this work we study the simultaneous co-evolution of game and environment using an integrated model consisting of replicator—mutator dynamics and logistic resource dynamics. Although similar linear environment-dependent payoff matrices have been studied before, we focus on investigating the significant impact of mutations on the overall system dynamics using bifurcation theory as the main tool. In particular, we show that two different types of bifurcations, which lead to limit cycles, can take place. In sharp comparison to the marginal oscillating behaviors reported before, such as neutral periodic orbits and heteroclinic cycles, we

clarify that the identified limit cycle conditions correspond to a large space of the mutation parameter and such limit cycles are almost globally stable. In this sense, the limit cycle behavior is robust and persistent, which agrees with biological observations. Furthermore, when mutations are not too rare, the corresponding limit cycle will not be close to the boundary, and consequently the (oscillating) tragedy of commons can be averted.

Enabled by the new insight into co-evolutionary dynamics of the game and environment, we consider further a simple but effective incentive-based control policy, where the individuals receive some external incentives in the game interactions if they choose the cooperation strategy. It is shown that the controlled system dynamics can converge to certain equilibria with a high level of the environmental resource. Thus, the effectiveness of the proposed control policy is guaranteed. Compared with the proposed control policies in Paarporn et al. (2018) and Wang et al. (2020), our proposed approach is not only more effective, but also easier to implement than influencing the opinions of the individuals or realizing more complicated feedback between strategists and the environment.

Our preliminary conference paper (Gong, Yao, Gao, & Cao, 2020) considers Hopf bifurcation and limit cycles of the system dynamics in a special case where the enhancement effect and the degradation effect is balanced, but in this paper we consider general bifurcation conditions and provide a comprehensive account of the results. Moreover, the latter part about incentive-based control of this paper is not in the conference version.

The remainder of this paper is organized as follows. Section 2 provides the framework of the co-evolutionary dynamics, and introduces the integrated model with game-environment feedback. The analysis of system dynamics is presented in Section 3. The incentive-based control is applied and its performance is provided in Section 4. Finally, concluding remarks and discussion points are given in Section 5.

2. Problem formulation

Co-evolutionary game and environment dynamics occur because evolutionary game dynamics are sometimes coupled with the dynamics of the surrounding environment (see Fig. 1 for an illustrative drawing). The coupled game and environment dynamics form a closed-loop system, which consists of bi-directional actions between the environment and the population's game play: an individual's fitness depends on not only the population state, but also the state of the environment, and the state of the environment is influenced by the distribution of the choices of strategies in the population. In the following subsections, we will introduce each component of this system in turn, and then integrate them to give a complete description of our model.

2.1. Environment-dependent payoffs

We consider games played in a changing environment, which is characterized by the richness $r \in [0, 1]$ of a resource of interest; such a resource has direct influence on the payoffs that players receive. Correspondingly, the payoffs become dynamic and depend on r. We consider a two-player game with two strategies, *Cooperation* and *Defection* (C, D). Following Weitz et al. (2016), we assume that the environment-dependent payoff matrix is a convex combination of the payoff matrices from the classic Prisoner's Dilemma, i.e.,

$$A(r) = (1 - r) \begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix} + r \begin{bmatrix} R_2 & S_2 \\ T_2 & P_2 \end{bmatrix}$$

$$= \begin{bmatrix} R_1 + (R_2 - R_1)r & S_1 + (S_2 - S_1)r \\ T_1 + (T_2 - T_1)r & P_1 + (P_2 - P_1)r \end{bmatrix},$$
(1)

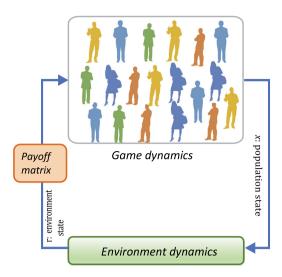


Fig. 1. The framework of evolutionary game dynamics with the environmental feedback.

where $R_1 > T_1$, $S_1 > P_1$, $R_2 < T_2$ and $S_2 < P_2$. The entries of A(r) represent the payoffs to the players at the given environment state r. For example, a C player receives the payoff of $R_1 + (R_2 - R_1)r$ and $S_1 + (S_2 - S_1)r$ when the opponent uses strategies C and D, respectively. Because of the inequalities below (1), the two matrices $\begin{bmatrix} R_2 & S_2 \\ T_2 & P_2 \end{bmatrix}$ and $\begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix}$ correspond to

the prisoner's dilemma and its inverse game, respectively. Note that the payoff matrix A(r) is the linear interpolation between the above two matrices. Thus, when r approaches 0 and 1, the mutual cooperation and defection tend to be the *Nash Equilibrium* of this dynamic game respectively. The biological interpretation is that: the individuals tend to cooperate facing the depleted environmental resource, and become more selfish and choose to defect while the resource becomes abundant.

2.2. Replicator-mutator equations

The two-player game governed by the payoff matrix A(r) in (1) are played in a well-mixed and infinite population. We denote the proportion of individuals choosing C by the variable $x \in [0,1]$. Since there are only two strategies, the population state can be represented by the vector $\mathbf{x} = [x \ 1-x]^{\mathsf{T}}$. Assume the individuals with different strategies can mutate into each other with an identical probability $\mu \in [0,1]$: a fraction of cooperators, μx , spontaneously change to choose strategy D; a fraction of defectors, $\mu(1-x)$, change to choose strategy C at the same time. We focus on the dynamics of x, which can be described by the following replicator-mutator equation

$$\dot{\mathbf{x}} = \mathbf{x}[(\mathbf{A}(r)\mathbf{x})_1 - \mathbf{x}^{\mathsf{T}}\mathbf{A}(r)\mathbf{x}] - \mu\mathbf{x} + \mu(1-\mathbf{x}),\tag{2}$$

where $(A(r)\mathbf{x})_1$ is the first entry of $A(r)\mathbf{x}$ and represents the fitness of choosing strategy C, and $\mathbf{x}^{\top}A(r)\mathbf{x}$ is the average fitness at the population state \mathbf{x} . The term $-\mu x$ represents the mutation from strategy C towards D, while $\mu(1-x)$ captures the mutation in the opposite direction.

2.3. Closed-loop system with game-environment feedback

To model the evolution of the environmental change, we use the standard logistic model

$$\dot{r} = r(1 - r)[\theta x - (1 - x)],\tag{3}$$

where the parameter $\theta>0$ represents the ratio between the enhancement effect due to cooperation and degradation effect due to defection. The influence of the population on the environment state is captured by the function $[\theta x-(1-x)]$, and the dynamics are restricted in the unit interval by r(1-r). When $\theta=1$, the enhancement effect and the degradation effect are balanced. And if $\theta>1$ or $0<\theta<1$, the enhancement effect is respectively stronger or weaker than the opposite.

Substituting (1) into (2), and then combining with (3), we obtain the closed-loop planar system describing the evolutionary game dynamics under the game-environment feedback:

$$\begin{cases} \dot{x} = x(1-x)[xr(-c+d-a+b) + x(a-b) \\ -r(d+b) + b] + \mu(1-2x) \\ \dot{r} = r(1-r)[\theta x - (1-x)], \end{cases}$$
(4)

where to simplify notations, we have used $a = R_1 - T_1$, $b = S_1 - P_1$, $c = T_2 - R_2$, and $d = P_2 - S_2$, all of which are positive because of the inequalities below (1). Note that system (4) reduces to the model considered in Weitz et al. (2016) when $\mu = 0$. Therefore, system (4) generalizes the previous model.

In view of the payoff matrix (1) and system Eqs. (4), these four parameters for re-parameterization have intuitive interpretations with respect to strategy changes when the resource is either abundant or depleted: the parameter a quantifies the incentive to stick to strategy C given that all individuals are following strategy C and the system is currently in a resource-poor state; b quantifies the incentive to switch to strategy C when the resource is depleted and all individuals enforce strategy D; in contrast, c quantifies the incentive to switch to strategy D given that all individuals enforce strategy C and the system is in a state of sufficient resource; d quantifies the incentive to stick to strategy D when the resource is abundant and all individuals are following strategy D.

3. System dynamics and bifurcations

The state space of system (4) is the unit square $\mathcal{I} = [0, 1]^2$. The interior region of this square is denoted by $\operatorname{int}(\mathcal{I}) = (0, 1)^2$. Four sides of the unit square form the boundary $\partial \mathcal{I}$. For convenience of exposition, we denote the four sides by:

$$\mathcal{B}_{t} = \{(x, r) : x \in [0, 1], r = 1\},
\mathcal{B}_{b} = \{(x, r) : x \in [0, 1], r = 0\},
\mathcal{B}_{l} = \{(x, r) : x = 0, r \in [0, 1]\},
\mathcal{B}_{r} = \{(x, r) : x = 1, r \in [0, 1]\}.$$
(5)

Then, one has $\partial \mathcal{I} := \mathcal{B}_t \cup \mathcal{B}_b \cup \mathcal{B}_l \cup \mathcal{B}_r$. It is easy to check that \mathcal{I} is invariant under the dynamics (4) for all $\mu \in [0, 1]$ by Nagumo's theorem (Blanchini & Miani, 2008, Theorem 4.7).

System (4) can have equilibria in the interior $\operatorname{int}(\mathcal{I})$; we call them *interior equilibria*. System (4) also has equilibria on the boundary $\partial \mathcal{I}$ (boundary equilibria), which will be discussed in detail in Section 3.4. It is easy to check that the interior equilibria, if they exist, must lie on the line $\{(x,r)\in\operatorname{int}(\mathcal{I}):x=1/(\theta+1)\}$. Substituting such x into the x-dynamics in (4), we have

$$0 = x(1-x)[xr(-c+d-a+b) + x(a-b) - r(d+b) + b] + \mu(1-2x),$$

which leads to

$$r = \frac{\theta a + \theta^2 b + \mu(\theta^3 + \theta^2 - \theta - 1)}{\theta(a + c + \theta b + \theta d)}.$$

Thus if the following condition holds

$$-(\theta a + \theta^2 b) < \mu(\theta^3 + \theta^2 - \theta - 1) < \theta c + \theta^2 d, \tag{6}$$

system (4) has a unique interior equilibrium

$$(x^*, r^*) = \left(\frac{1}{\theta + 1}, \frac{\theta a + \theta^2 b + \mu(\theta^3 + \theta^2 - \theta - 1)}{\theta (a + c + \theta b + \theta d)}\right). \tag{7}$$

Otherwise, no interior equilibrium exists. The interior equilibrium supports the coexistence of the two strategies under a non-depleted resource state. In view of (6), one can see that for a given θ , the existence of the interior equilibrium is determined by not only the payoff parameters but also the mutation rate.

Note that when $\theta = 1$, (x^*, r^*) is independent of the parameter μ , and (6) holds trivially for all $\mu \in [0, 1]$. This specific case has been studied in our previous conference paper (Gong et al., 2020). In this paper we do not require $\theta = 1$ and study the generic θ that takes any positive value satisfying (6).

Towards the goal of establishing conditions for the existence of limit cycles, we first present some preliminary results on the non-existence of closed orbits or limit cycles.

3.1. Non-existence of closed orbits

First, we define the \mathbf{C}^1 function $\varphi(x, r) : \operatorname{int}(\mathcal{I}) \to \mathbb{R}$ by

$$\varphi(x,r) = x^{\alpha} (1-x)^{\beta} r^{\gamma} (1-r)^{\delta} \tag{8}$$

with the parameters α , β , γ , and δ to be determined later. Note that $\varphi(x,r)$ is strictly positive in $\operatorname{int}(\mathcal{I})$ for any values of these parameters. Denote the right hand side of (4) by $f(x,r) = [f_1(x,r),f_2(x,r)]^{\top}$, and then the divergence of the modified vector field $\varphi f(x,r)$ on $\operatorname{int}(\mathcal{I})$ is given by

$$\operatorname{div} \varphi f(x, r) = \frac{\partial(\varphi f_{1})}{\partial x}(x, r) + \frac{\partial(\varphi f_{2})}{\partial r}(x, r)$$

$$= \varphi(x, r)(-(\alpha + \beta + 3)(-c + d - a + b)x^{2}r$$

$$-(\alpha + \beta + 3)(a - b)x^{2}$$

$$+ [(-c + 2d - a + 2b)\alpha + (d + b)\beta$$

$$-(\theta + 1)(\gamma + \delta + 2) + 2(-c + 2d - a + 2b)]xr$$

$$+ [(a - 2b)\alpha - b\beta + (\theta + 1)(1 + \gamma) + 2a - 4b]x$$

$$+ [-(d + b)\alpha + \gamma + \delta + 2 - b - d]r$$

$$+ \frac{\mu(1 - 2x)(\alpha - \alpha x - \beta x)}{x(1 - x)}$$

$$+ (1 + \alpha)b - (1 + \gamma) - 2\mu).$$
(9)

Let all the coefficients of the powers of x, r in (9) (except for the term containing μ) be zero, and we obtain the following set of equations

$$(\alpha + \beta + 3)(-c + d - a + b) = 0$$

$$(\alpha + \beta + 3)(a - b) = 0$$

$$(-c + 2d - a + 2b)\alpha + (d + b)\beta$$

$$-(\theta + 1)(\gamma + \delta + 2) + 2(-c + 2d - a + 2b) = 0$$

$$(a - 2b)\alpha - b\beta + (\theta + 1)(\gamma + 1) + 2a - 4b = 0$$

$$-(d + b)\alpha + \gamma + \delta + 2 - b - d = 0.$$
(10)

We first show that the equation set (10) always has solutions.

Lemma 1. There always exist some α , β , γ , and δ as solutions to (10).

The proof is omitted here due to the space limit. See the full version (Gong, Yao, Gao, & Cao, 2022) for the proof.

In fact, if one of -c + d - a + b and a - b is not zero, (10) will have exactly one solution

$$\alpha = -\frac{\zeta + c + a}{\zeta},$$

$$\beta = \frac{-2\zeta + c + a}{\zeta},$$

$$\gamma = \frac{-(a + \theta + 1)\zeta + a^2 + ac - ab - bc}{(\theta + 1)\zeta},$$

$$\delta = -\frac{(a + c)(\theta b + \theta d + d + a) + (\theta + 1 - a)\zeta}{(\theta + 1)\zeta}$$

$$(11)$$

with $\zeta = a + c + \theta b + \theta d > 0$. Otherwise, (10) will have infinitely many solutions including (11). So we fix the parameters α , β , γ , and δ at the values given in (11) such that the divergence (9) can be greatly simplified.

Then we show the non-existence of closed orbits for system (4).

Lemma 2. For system (4), the following statements hold:

- (1) when ad bc > 0, there exists some $\mu_0 > 0$ such that there are no closed orbits in \mathcal{I} for $\mu \in [\mu_0, 1]$;
- (2) when ad-bc<0, there are no closed orbits in $\mathcal I$ for $\mu\in[0,1]$;
- (3) when ad bc = 0, there are no closed orbits in \mathcal{I} for $\mu \in (0, 1]$.

Proof. The proof is direct by applying Bendixson–Dulac criterion (Wiggins, 2000, Theorem 4.1.2). Since the boundary $\partial \mathcal{I}$ contains equilibria (as shown in Section 3.4), it is not possible to have periodic orbits on it. And the sides are either invariant or repelling, so they cannot intersect with closed orbits. Now let us consider the interior $\operatorname{int}(\mathcal{I})$ which is simply connected.

In view of the fact that α , β , γ , and δ are given as in (11), one can calculate the divergence of $\varphi f(x, r)$

$$= \varphi(x,r) \left(\frac{\mu(1-2x)(3x+\alpha)}{x(1-x)} + (1+\alpha)b - (1+\gamma) - 2\mu \right)$$

$$= \varphi(x,r) \left(\frac{\mu(1-2x)(3x+\alpha)}{x(1-x)} - 2\mu - \frac{\theta(bc-ad)}{(\theta+1)^{2}} \right).$$
(12)

From (11) one knows $\alpha \in (-2, -1)$, and thus the term $g(x) := \frac{\mu(1-2x)(3x+\alpha)}{x(1-x)}$ takes its maximum value at $\bar{x} \in (0, 1)$ given by

$$\bar{x} = \begin{cases} \frac{\alpha - \sqrt{-\alpha(3+\alpha)}}{3+2\alpha}, & -1.5 < \alpha < -1, \\ 0.5, & \alpha = -1.5, \\ \frac{\alpha + \sqrt{-\alpha(3+\alpha)}}{3+2\alpha}, & -2 < \alpha < -1.5. \end{cases}$$
(13)

Rearranging (12) yields

$$\frac{\operatorname{div}\,\varphi f(x,r)}{\varphi(x,r)} \leq \frac{\mu(1-2\bar{x})(3\bar{x}+\alpha)}{\bar{x}(1-\bar{x})} - 2\mu - \frac{\theta(bc-ad)}{(\theta+1)\zeta} \\
= \frac{(1-2\alpha)\bar{x}+\alpha-4\bar{x}^2}{\bar{x}(1-\bar{x})}\mu - \frac{\theta(bc-ad)}{(\theta+1)\zeta}.$$
(14)

It is easy to check that $\frac{(1-2\alpha)\bar{x}+\alpha-4\bar{x}^2}{\bar{x}(1-\bar{x})}$ is negative for any value of $\alpha \in (-2,-1)$. Since $\varphi(x,r)$ is positive in $\mathrm{int}(\mathcal{I})$ by definition, if ad-bc>0, from (14) one has div $\varphi f(x,r)\leq 0$ when

$$\mu \ge \mu_0 := \frac{\theta(bc - ad)\bar{x}(1 - \bar{x})}{(\theta + 1)\zeta[(1 - 2\alpha)\bar{x} + \alpha - 4\bar{x}^2]}.$$
 (15)

And because the divergence is not identically zero in $\operatorname{int}(\mathcal{I})$, from the Bendixson–Dulac criterion, one knows that no closed orbits can exist in $\operatorname{int}(\mathcal{I})$ for $\mu \geq \mu_0$.

For the second case, it is easy to prove since the right hand side of (14) will always be negative for any $\mu > 0$. For the third case, the right hand side of (14) is always negative when $\mu > 0$.

In Lemma 2, it is noted that the conditions for the nonexistence of periodic orbits depend on the relationship between ad and bc. The reason is as follows: when ad - bc < 0, the divergence div $\varphi f(x,r)$ will remain positive for any $\mu \in [0,1]$ in view of (14), which excludes the possibility of periodic orbits in the phase space; when ad - bc > 0 or ad - bc = 0, there exists some μ such that div $\varphi f(x,r)$ equals 0. As a consequence, it is possible for the system to have periodic orbits in these two cases. Another point worth noting is that the only difference between the second and third cases of Lemma 2 is that system (4) may have periodic solutions for $\mu = 0$ when ad - bc = 0. This possibility has been shown in Gong et al. (2018) and Weitz et al. (2016). Despite the possibility of closed orbits under certain conditions, for $\mu = 0$ it can be proven that limit cycles (isolated closed orbits) are impossible to exist in (4) for all the parameter space as summarized below in Lemma 3.

Lemma 3. System (4) has no limit cycles in \mathcal{I} when $\mu = 0$.

The proof is presented in Gong et al. (2022). Details are omitted here to conserve space.

3.2. Hopf bifurcation at the interior equilibrium

In this section we take μ as the bifurcation parameter to study the effect of different mutation rates on the system dynamics. We investigate the possible bifurcations of the dynamics (4) as μ varies in [0, 1]. We analyze the stability of the interior equilibrium and prove that it involves a Hopf bifurcation which leads to periodic orbits.

We first invoke the Hopf bifurcation theorem (Guckenheimer & Holmes, 2000) which will be used to prove the existence of stable limit cycles.

Theorem 4 (Hopf Bifurcation Theorem). Suppose that the system $\dot{y} = F(y, \rho), y \in \mathbb{R}^2, \rho \in \mathbb{R}$ has an equilibrium (y_0, ρ_0) at which the following properties are satisfied:

(1) the Jacobian D_yF|_(y0,ρ0) has a simple pair of pure imaginary eigenvalues λ(ρ₀) and λ̄(ρ₀);
 (2) dℜ(λ(ρ)) / dρ ≠ 0.

$$(2) \frac{d \Re(\lambda(\rho))}{d \rho}|_{\rho_0} \neq 0$$

Then the dynamics undergo a Hopf bifurcation at (y_0, ρ_0) , which results in a family of periodic solutions in a sufficiently small neighborhood of (y_0, ρ_0) .

Then we make an assumption about some parameters of sys-

Assumption 5. We assume that $0 < ad - bc \le \frac{\Delta}{a^2}$.

The following theorem demonstrates that the interior equilibrium (x^*, r^*) of system (4) undergoes a Hopf bifurcation.

Theorem 6. Under Assumption 5, the interior equilibrium (x^*, r^*) of system (4) with the bifurcation parameter μ undergoes a supercritical Hopf bifurcation at $\mu = \mu_1 := \frac{\theta^2(ad-bc)}{\Delta}$, which leads to the existence of stable limit cycles for $\mu < \mu_1$ in the vicinity of μ_1 .

Proof. To prove the existence of Hopf bifurcation, we need to show that the two conditions of Theorem 4 are satisfied in system (4). The Jacobian of the vector field of (4) at (x^*, r^*) is given by

$$J^* = \begin{bmatrix} \frac{\theta^2(ad-bc) - \mu\Delta}{\theta(\theta+1)\zeta} & \frac{-\theta\zeta}{(\theta+1)^3} \\ \frac{(\theta+1)(c\theta+d\theta^2 - \mu\hat{\theta})(a\theta+b\theta^2 + \mu\hat{\theta})}{\theta^2r^2} & 0 \end{bmatrix}, \tag{16}$$

$$\hat{\theta} = (\theta^3 + \theta^2 - \theta - 1)$$

$$\Delta = (a+c)(1+\theta^2+2\theta^3) + (b+d)(2\theta+\theta^2+\theta^4).$$

Note that the off-diagonal entries

$$J_{12} = \frac{-\theta \zeta}{(\theta+1)^3} < 0$$

$$J_{21} = \frac{(\theta+1)(c\theta+d\theta^2-\mu_1\hat{\theta})(a\theta+b\theta^2+\mu_1\hat{\theta})}{\theta^2\zeta^2} > 0$$

because of (6). One can calculate the eigenvalues of I*

$$\lambda(\mu) = \frac{J_{11} \pm \sqrt{J_{11}^2 + 4J_{12}J_{21}}}{2}$$

$$= \Re(\lambda(\mu)) \pm \Im(\lambda(\mu))i.$$
(17)

It is easy to check that when $\mu = \mu_1 := \frac{\theta^2(ad-bc)}{\Lambda}$ the eigenvalues are purely imaginary, i.e.,

$$\Re(\lambda(\mu_1))=0,$$

$$\Im(\lambda(\mu_1)) = \sqrt{\frac{(c\theta + d\theta^2 - \mu\hat{\theta})(a\theta + b\theta^2 + \mu\hat{\theta})}{\theta(\theta + 1)^2\zeta}},$$

which implies that the first condition listed in Theorem 4 is satisfied. In addition, the second condition is also satisfied because

$$\left. \frac{d\Re(\lambda(\mu))}{d\mu} \right|_{\mu_1} = \frac{-\Delta}{\theta(\theta+1)\zeta} < 0.$$

Then one can conclude that the dynamics (4) undergo a Hopf bifurcation at $\mu = \mu_1$. Since μ varies in the interval (0, 1], to guarantee the occurrence of Hopf bifurcation, the critical parameter value μ_1 should also be constrained in this interval, i.e., 0 < $\mu_1 \leq 1$, which leads to

$$0 < ad - bc \le \frac{\Delta}{\theta^2},$$

which is exactly Assumption 5. The Hopf bifurcation theorem implies that a family of periodic orbits bifurcate from (x^*, r^*) for some μ in the vicinity of μ_1 . Whether the bifurcated periodic orbits are stable or not is determined by the so-called first Lyapunov coefficient ℓ_1 at (x^*, r^*) when $\mu = \mu_1$. If $\ell_1 < 0$, then these periodic orbits are stable limit cycles; if $\ell_1 > 0$, the periodic orbits are repelling. Following the computation procedure of calculating ℓ_1 as presented in Kuznetsov (2004), we obtain $\ell_1(\mu_1)$ as below

$$\ell_1(\mu_1) = \frac{\theta(bc - ad)\zeta((b+d)(\theta^3 + 2\theta) + (a+c)(2\theta^3 + 1))}{2\omega_0^3(\theta + 1)^4\Delta},$$
(18)

where $\omega_0 = \sqrt{\frac{(c\theta + d\theta^2 - \mu_1\hat{\theta})(a\theta + b\theta^2 + \mu_1\hat{\theta})}{\theta(\theta + 1)^2 \zeta}}$. (18) is negative because of (6) and Assumption 5. Thus, the bifurcated periodic orbits are stable limit cycles.

Furthermore, in view of (17), for $\mu < \mu_1$, (x^*, r^*) is unstable since the eigenvalues have positive real parts. On the other hand, the interior equilibrium is asymptotically stable for $\mu > \mu_1$ with the negative eigenvalues. Hence, the stable limit cycles exist for $\mu < \mu_1$ in the vicinity of μ_1 . Since the bifurcation is associated with stable limit cycles, it is a supercritical Hopf bifurcation. \Box

The relationship between ad and bc has played an important role in Theorem 6 in the sense that Hopf bifurcation can only

happen when ad-bc>0. In view of the Jacobian (16), when $ad-bc\leq 0$, J_{11} will remain non-positive no matter what value μ takes. Thus, as μ varies in [0, 1], the stability of the interior equilibrium does not change, which excludes the existence of a Hopf bifurcation. On the other hand, when ad-bc>0, to ensure there is a Hopf bifurcation for $\mu\in[0,1]$, Assumption 5 has to be satisfied as proved.

From the Hopf bifurcation theory, we know that the limit cycles generated from Hopf bifurcation have the amplitude of $O(\sqrt{\mu_1 - \mu})$. Since Hopf bifurcation is a local bifurcation, the obtained results only hold for μ in the vicinity of μ_1 . Next, we will show that system (4) exhibits another type of bifurcation.

3.3. Heteroclinic bifurcation

In the case $\mu=0$, it has been shown in Lemma 3 that the system (4) cannot exhibit limit cycles for any parameters. We show in this section that limit cycles may occur for $\mu>0$ in the vicinity of 0.

When $\mu = 0$, system (4) has four equilibria on the boundary $\partial \mathcal{I}$. Denote the four equilibria respectively by $E_1 = (0,0)$, $E_2 = (1,0)$, $E_3 = (1,1)$, and $E_4 = (0,1)$. Then, one can calculate the Jacobians at these points, which are

$$J_{1} = \begin{bmatrix} b & 0 \\ 0 & -1 \end{bmatrix}, \quad J_{2} = \begin{bmatrix} -a & 0 \\ 0 & \theta \end{bmatrix},$$

$$J_{3} = \begin{bmatrix} c & 0 \\ 0 & -\theta \end{bmatrix}, \quad J_{4} = \begin{bmatrix} -d & 0 \\ 0 & 1 \end{bmatrix}.$$
(19)

It is easy to see that the eigenvalues of these equilibria are indeed the diagonal entries of the associated Jacobian matrices, and thus all of these equilibria are saddle points. Next we note that the trace of each Jacobian, which is denoted by T_i , is

$$T_1 = b - 1$$
, $T_2 = \theta - a$, $T_3 = c - \theta$, $T_4 = 1 - d$.

A heteroclinic cycle on the boundary denoted by Λ , which connects the four equilibria and has the orientation $E_1 \to E_2 \to E_3 \to E_4 \to E_1$, can be identified. Its stability is determined by the payoff parameters.

Lemma 7. Consider system (4) at $\mu = 0$. There exists a heteroclinic cycle Λ , which is stable (resp. unstable) when the condition ad > bc (resp. ad < bc) is satisfied.

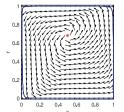
We refer to Ref. Weitz et al. (2016) for the complete proof for the case of the stable heteroclinic cycle. And the opposite case can be proved using the analogous method according to Hofbauer (1994, Corollary 2).

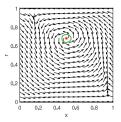
When $\mu>0$, the four corners are no longer equilibria, and the heteroclinic cycle Λ is "broken". Now we are going to show that the system (4) undergoes a heteroclinic bifurcation at $\mu=0$ when certain condition holds, and a limit cycle with the same stability of the corresponding heteroclinic cycle may be generated from Λ for $\mu>0$ sufficiently close to 0.

Definition 8. The internal σ -neighborhood of Λ is the set of all points in \mathcal{I} that are at a distance less than $\sigma > 0$ from Λ .

Theorem 9. Consider system (4). If $a > \theta$, b < 1, $c < \theta$, and d > 1, then there exist σ , $\epsilon > 0$, such that for $0 < \mu < \epsilon$, there is at most one limit cycle Γ in the internal σ -neighborhood of Λ , and Γ (if it exists) is stable.

Proof. The proof is straightforward by applying the theorem of the heteroclinic bifurcation (Luo, Wang, Zhu, & Han, 1997, Theorem 2.3.2, 2.3.3). When $a > \theta$, b < 1, $c < \theta$, and d > 1





(a) Large limit cycle

(b) Small limit cycle

Fig. 2. Phase portraits of the dynamics in (4) with payoff matrices as shown in (20). The red stars denote the unique interior equilibrium (0.5, 0.6809). The blue and green cycles show the approximated limit cycles when (a) $\mu = 0.005$; (b) $\mu = 0.1540$.

hold, which implies ad>bc. Then according to Lemma 7, there is a heteroclinic cycle when $\mu=0$ and it is stable.

In addition, all the traces T_i of the Jacobians of the equilibria are negative, while their product $\prod_{i=1}^4 T_i$ is positive. Then according to Luo et al. (1997, Theorem 2.3.3), there exist sufficiently small σ , ϵ > 0 such that for 0 < μ < ϵ , system (4) has at most one limit cycle in the internal σ -neighborhood of Λ , and this limit cycle (if it exists) is stable due to the stability of Λ . \square

When ad < bc, according to the second statement of Lemma 7, the heteroclinic cycle is unstable. It is impossible for limit cycles to be generated from this unstable heteroclinic cycle in view of Lemma 2, which claims that there are no closed orbits in \mathcal{I} for any $\mu \geq 0$ when ad - bc < 0.

Compared with the result of Hopf bifurcation, the conclusion of Heteroclinic bifurcation is relatively weaker since Theorem 9 only states that there may exist a unique limit cycle in some neighborhood of Λ . To study the exact conditions for the existence of the unique limit cycle is beyond this work.

Another difference between the limit cycles generated from Hopf bifurcation and Heteroclinic bifurcation is that the limit cycle arising from Hopf bifurcation is small in size in the phase space, as demonstrated in the simulation results in Fig. 2, while the other can be large. In these simulations the payoff matrices are given by

$$\begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix} = \begin{bmatrix} 3.5 & 1 \\ 0.5 & 0.8 \end{bmatrix}, \quad \begin{bmatrix} R_2 & S_2 \\ T_2 & P_2 \end{bmatrix} = \begin{bmatrix} 2 & 0.2 \\ 2.5 & 1.2 \end{bmatrix}. \tag{20}$$

The parameter θ is chosen to be 1, and thus the interior equilibrium is fixed and independent of μ . In view of Theorem 6, the Hopf bifurcation point is $\mu_1 = 0.1543$.

3.4. Global dynamics

As stated before, the limit cycle analysis for Hopf and Heteroclinic bifurcations are limited to the vicinity of the bifurcation points since the used methods rely mainly on linearization. To study if the limit cycle persists for $\mu \in (0, \mu_1)$, it is necessary to analyze the dynamics of (4) for all such μ .

3.4.1. Boundary equilibria and their stability

Recall that the condition (6), which involves μ , guarantees that there is a unique interior equilibrium. For some given payoff parameters and fixed values of θ , there may be some μ such that there is no interior equilibrium. In this case, the system dynamics are relatively trivial since the trajectories will converge to some limit sets on the boundary according to the Poincaré–Bendixson theorem. In the following part, we concentrate on the situation where an interior equilibrium always exists for all $\mu \in [0, 1]$. Then, we have the following assumption.

Assumption 10. We assume hereafter that $-(\theta a + \theta^2 b) < (\theta - 1)(\theta + 1)^2 < \theta c + \theta^2 d$.

Assumption 10 ensures that there is a unique interior equilibrium point for all $\mu \in [0, 1]$ in system (4). It is noted that when $\theta = 1$, Assumption 10 is satisfied trivially.

It is easy to check that the boundary $\partial\mathcal{I}:\mathcal{B}_t\cup\mathcal{B}_b\cup\mathcal{B}_l\cup\mathcal{B}_r$ itself and each of its sides are invariant under (4) in the case $\mu=0$. When $0<\mu\leq 1$, the sides \mathcal{B}_t and \mathcal{B}_b remain invariant, while \mathcal{B}_l and \mathcal{B}_r do not. As μ varies, all the possible boundary equilibria lie on the sides \mathcal{B}_t and \mathcal{B}_b , but the positions of these equilibria change. Let us try to determine the locations of the equilibria on \mathcal{B}_t and \mathcal{B}_b .

Lemma 11. There is only one equilibrium on each side \mathcal{B}_b and \mathcal{B}_t in system (4). Moreover, the equilibria are located in the sets $\{(x,r): x \in (\max\{1/2, 1/(\theta+1)\}, 1), r=0\}$ and $\{(x,r): x \in (0, \min\{1/2, 1/(\theta+1)\}), r=1\}$ respectively.

Proof. See the full version (Gong et al., 2022) for the proof. \Box

One can examine the stability of these boundary equilibria by evaluating the corresponding Jacobian matrices.

Lemma 12. All the boundary equilibria of system (4) are unstable for $\mu \in (0, 1]$.

Proof. We only show the case on the side \mathcal{B}_b . For the case of \mathcal{B}_t , one can obtain the same result analogously. Denote the equilibrium on the side \mathcal{B}_b by $(x_b^*, 0)$. We obtain its Jacobian matrix as below

$$J_b^* = \begin{bmatrix} 3x_b^{*2}(b-a) - 2\mu + b & * \\ + 2x_b^{*}(a-2b) & * \\ 0 & (\theta+1)x_b^{*} - 1 \end{bmatrix},$$
 (21)

where the symbol \star stands for $-x_b^{*3}(-c+d-a+b)-x_b^{*}(d+b)+x_b^{*2}(-c+2d-a+2b)$. As the matrix is upper triangular, the entry $(\theta+1)x_b^*-1$ is one of its eigenvalues. According to Lemma 11, one has $x_b^* \in (\max\{1/2, 1/(\theta+1)\}, 1)$. Then the eigenvalue $(\theta+1)x_b^*-1$ will be positive for any $\theta>0$, which implies that the equilibrium is unstable. \square

By checking the sign of \dot{x} on the left side \mathcal{B}_l and the right side \mathcal{B}_r , one observes that it is always positive and negative respectively. It can be easily verified that the vectors on these two sides point inwards to $\operatorname{int}(\mathcal{I})$. The sides \mathcal{B}_b and \mathcal{B}_t are positively invariant under system (4), and thus the dynamics on each side of \mathcal{B}_b and \mathcal{B}_t are easy to analyze. For example, on the side \mathcal{B}_b , one has $\dot{r}=0, \dot{x}>0$ at x=0 and $\dot{r}=0, \dot{x}<0$ at x=1. As there is only one equilibrium $(x_b^*,0)$ on the side \mathcal{B}_b , one can easily verify that $\dot{x}>0$ for $x\in[0,x_b^*)$ and $\dot{x}<0$ for $x\in(x_b^*,1]$. Thus, trajectories starting from $\mathcal{B}_b\setminus(x_b^*,0)$ will converge to the unique equilibrium $(x_b^*,0)$. The similar result can be obtained for the dynamics on \mathcal{B}_t .

In addition, we can show that the boundary $\partial \mathcal{I}$ is repelling for $\mu \in (0,1].$

Lemma 13. The boundary $\partial \mathcal{I}$ of system (4) is repelling for $\mu \in (0, 1]$.

Proof. See the full version (Gong et al., 2022) for the proof. \Box

With Lemma 13 in hand, we are ready to present some global results of the system dynamics in \mathcal{I} .

Theorem 14. Under Assumption 5, for $\mu \in (\mu_0, 1]$, the interior equilibrium (x^*, r^*) of system (4) is asymptotically stable, and all trajectories starting from $\mathcal{I} \setminus (\mathcal{B}_t \cup \mathcal{B}_b)$ will converge to (x^*, r^*) .

Proof. Recall the two critical parameter values μ_0 and μ_1 , which appear respectively in Lemma 2 and Theorem 6. One can check that $\mu_0 \geq \mu_1$ when Assumption 5 holds. Again according to Lemma 2, it is impossible for system (4) to have closed orbits in \mathcal{I} when $\mu > \mu_0$. In addition, the interior equilibrium is locally asymptotically stable in view of (16). Due to the fact that the boundary $\partial \mathcal{I}$ is repelling as shown in Lemma 13, any trajectories starting from $\operatorname{int}(\mathcal{I})\setminus\{(x^*,r^*)\}$ cannot converge to $\partial \mathcal{I}$. Then according to the Poincaré–Bendixson theorem, because of the non-existence of closed orbits or other equilibria in $\operatorname{int}(\mathcal{I})$, the trajectories with any initial points in $\operatorname{int}(\mathcal{I})\setminus\{(x^*,r^*)\}$ will converge to (x^*,r^*) . Similarly, trajectories starting from the sides \mathcal{B}_I and \mathcal{B}_r also converge to (x^*,r^*) .

So the interior equilibrium is almost globally stable in system (4), because almost all trajectories in \mathcal{I} (except for those starting from $\mathcal{B}_t \cup \mathcal{B}_b$) converge to the stable equilibrium (x^*, r^*) . We apply similar terminology to the stability of the limit cycle when it is stable and almost all trajectories converge to it.

3.4.2. Uniqueness of limit cycles in the case $\theta = 1$

Assumption 15. We assume that $\theta = 1$ henceforth.

Under Assumption 15, the enhancement effect and the degradation effect are balanced. In this case, the system can be transformed to a generalized Liénard system. However, the existence and uniqueness of limit cycles for $\mu \in (0, \mu_1]$ in the case $\theta \neq 1$ is still open.

Lemma 16. Under Assumption 5, when a + c = b + d, the system dynamics in (4) admit at most one limit cycle in $int(\mathcal{I})$ for $\mu \in (0, \mu_1)$.

Proof. Under Assumption 15, when a + c = b + d, the interior equilibrium, denoted by $q^* = (1/2, (a+b)/(2(b+d)))$, is fixed. And the system dynamics (4) are reduced to be

$$\begin{cases} \dot{x} = x(1-x)[x(d-c) - r(d+b) + b] + \mu(1-2x) \\ \dot{r} = r(1-r)(2x-1). \end{cases}$$
 (22)

We apply the transformation of the coordinates on (22), $x \rightarrow x'$, $r \rightarrow 1 - r'$, and obtain the following system

$$\left\{ \begin{array}{l} \dot{x}' = x'(1-x')[x'(d-c) + r'(d+b) - d] \\ + \mu(1-2x') \\ \dot{r}' = -r'(1-r')(2x'-1). \end{array} \right.$$

The interior equilibrium q^* of (22) now becomes $q'^* = (1/2, r'^*)$ with $r'^* = (a+b)/(2(b+d))$. By using the change of variables $x' \to \tilde{x} + 1/2$ and $r' \to \tilde{r} + r'^*$, we can shift the equilibrium q'^* to the origin of a new system as below

$$\begin{cases}
\dot{\tilde{x}} = \alpha(\tilde{x}) \left[(d+b)\tilde{r} + \frac{8\mu_1 \tilde{x}\alpha(\tilde{x}) - 2\mu\tilde{x}}{\alpha(\tilde{x})} \right] \\
\dot{\tilde{r}} = -2\beta(\tilde{r})\tilde{x},
\end{cases} (23)$$

which is defined in the region $\tilde{\mathcal{I}} = \{(\tilde{x}, \tilde{r}) : \tilde{x} \in (-1/2, 1/2), \tilde{r} \in (-\tilde{r}^*, 1 - \tilde{r}^*)\}$ with $\alpha(\tilde{x}) = (1/4 - \tilde{x}^2)$ and $\beta(\tilde{r}) = (\tilde{r} + r'^*)(1 - \tilde{r} - r'^*)$. The system is now in the form of the *generalized Liénard system* (Sabatini & Villari, 2006).

One can observe that the functions $\alpha(\tilde{x})$ and $\beta(\tilde{r})$ are always positive in the domain. Multiplying the vector field of (23) by the positive function $1/(\alpha(\tilde{x})\beta(\tilde{r}))$, we obtain

$$\begin{cases} \dot{\tilde{x}} = \varphi(\tilde{r}) - F(\tilde{x}, \tilde{r}) \\ \dot{\tilde{r}} = -g(\tilde{x}), \end{cases}$$
 (24)

where $\varphi(\tilde{r}) = \frac{(b+d)\tilde{r}}{\beta(\tilde{r})}$, $F(\tilde{x}, \tilde{r}) = \frac{2\mu\tilde{x} - 8\mu_1\tilde{x}\alpha(\tilde{x})}{\alpha(\tilde{x})\beta(\tilde{r})}$, and $g(\tilde{x}) = \frac{2\tilde{x}}{\alpha(\tilde{x})}$. The point-wise direction of the vector field of (23) is maintained in (24). Hence the existence and uniqueness of limit cycles for the two systems (23) and (24) are equivalent.

Under Assumption 5, if $0<\mu<\mu_1$ holds, it can be validated that there always exists a $\nu=\sqrt{\frac{\mu_1-\mu}{4\mu_1}}$ such that the following conditions are satisfied:

- (1) $G(-\nu) = G(\nu)$ where $G(\tilde{x}) := \int_0^{\tilde{x}} g(s) ds$; (2) $\forall \tilde{x} \in (-\nu, 0)$, the function $\tilde{r} \mapsto \frac{F(\tilde{x}, \tilde{r})}{\varphi(\tilde{r})}$ is strictly decreasing both on $0 < \tilde{r} < 1 r'^*$ and $-r'^* < \tilde{r} < 0$; $\forall \tilde{x} \in (0, \nu)$, the function $\tilde{r} \mapsto \frac{F(\tilde{x}, \tilde{r})}{\varphi(\tilde{r})}$ is strictly increasing both on $0 < \tilde{r} < 1 r'^*$ and $-r'^* < \tilde{r} < 0$;
- (3) $\forall \tilde{x} \in (-\nu, \nu), \forall \tilde{r} \in (-r'^*, 1 r'^*), \text{ one has } g(\tilde{x})F(\tilde{x}, \tilde{r}) \leq 0;$
- (4) $\forall \tilde{x} \notin (-\nu, \nu), \forall \tilde{r} \in (-r'^*, 1 r'^*), \text{ one has } F(\tilde{x}, \tilde{r}) \geq 0;$ $\forall \tilde{r} \in (-r'^*, 1 - r'^*)$, the function $\tilde{x} \mapsto F(\tilde{x}, \tilde{r})$ is increasing both on $-1/2 < \tilde{x} < -\nu$ and $\nu < \tilde{x} < 1/2$.

The detailed expressions of the functions involved in the above conditions can be found in Gong et al. (2022). It is not difficult to check these conditions, so the process is omitted here.

Then according to Sabatini and Villari (2006, Theorem 1, Corrollary 1), system (24) has at most one limit cycle in $\tilde{\mathcal{I}}$. Therefore, the original system (22) admits at most one limit cycle in $int(\mathcal{I})$. \square

It is noted that when a+c=b+d, the coefficient of the cross term xr is 0, and thus this cross term disappears in the system equations of (22). So the nonlinearity of this system is reduced. In this case, when system (22) is transformed into the Liénard form, the properties (1) - (4) listed in the proof of Lemma 16 allow us to use the Liénard system theory to prove that there is at most one limit cycle in $int(\mathcal{I})$ for $\mu \in (0, \mu_1)$. Unfortunately, those properties are not satisfied directly when $a + c \neq b + d$, and thus the existence and the number of limit cycles in this case remain unclear.

Now we are in the position to present the last result of this section about the uniqueness of limit cycle and stability of the interior equilibrium.

Theorem 17. Under Assumption 5, when a + c = b + d,

- (1) for $\mu \in (0, \mu_1)$, system (4) has exactly one limit cycle that is almost globally stable;
- (2) for $\mu \in [\mu_1, 1]$, the interior equilibrium (x^*, r^*) is almost globally stable.

Proof. Under Assumption 5, when a + c = b + d, according to Lemma 16, the system (4) has at most one limit cycle for $0 < \mu < \mu_1$. As shown in Theorem 6, the eigenvalues of the Jacobian at (x^*, r^*) have positive real parts, implying that it is repulsive. Then all trajectories starting in the small neighborhood of this equilibrium (excluding the equilibrium) will diverge, and the existence of infinite many periodic orbits in the neighborhood is excluded. From Lemma 13, one also knows that the boundary $\partial \mathcal{I}$ is repelling. According to the Poincaré-Bendixson theorem, for any initial states in $int(\mathcal{I}) \setminus \{(x^*, r^*)\}$, its ω -limit set must be a closed orbit. If there are no limit cycles in $int(\mathcal{I}) \setminus \{(x^*, r^*)\}\$, then every trajectory starting from $int(\mathcal{I}) \setminus \{(x^*, r^*)\}$ will form a periodic orbit, and an infinite number of periodic orbits will fill $int(\mathcal{I})\setminus\{(x^*,r^*)\}$. This contradicts the repulsiveness of the interior equilibrium and the boundary (Sabatini & Villari, 2006).

Suppose in $int(\mathcal{I}) \setminus \{(x^*, r^*)\}$, there is some connected region which consists of an infinite number of neutral periodic orbits and is enclosed by two periodic orbits denoted by Γ_1 and Γ_2 . Then Γ_1 and Γ_2 must be limit cycles, which contradicts Lemma 16

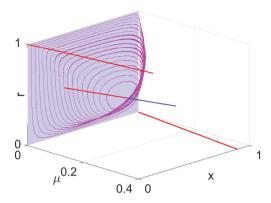


Fig. 3. The plot of a unique limit cycle of dynamics (4) with the given payoff matrices in (25). The x-axis is the mutation rate μ , the blue and red curves are stable and unstable equilibria respectively, and the magenta curves show the shape of stable limit cycles.

regarding the maximal number of limit cycles. Therefore, one can conclude that there is exactly one stable limit cycle in \mathcal{I} , and it is attractive for $\mathcal{I} \setminus (\mathcal{B}_t \cup \mathcal{B}_b \cup (x^*, r^*))$.

Note that when a + c = b + d and $\theta = 1$, we have $\mu_0 = \mu_1$. Thus, the second claim is easy to verify according to Theorems 6 and 14. □

Fig. 3 shows the plot of the unique limit cycle of system (4) when μ changes from 0 to 0.4. The payoff matrices used in the simulations are shown below, and they satisfy the condition a + c = b + d.

$$\begin{bmatrix} R_1 & S_1 \\ T_1 & P_1 \end{bmatrix} = \begin{bmatrix} 3.5 & 2 \\ 0.5 & 1 \end{bmatrix}, \quad \begin{bmatrix} R_2 & S_2 \\ T_2 & P_2 \end{bmatrix} = \begin{bmatrix} 2 & 0.2 \\ 3 & 3.2 \end{bmatrix}. \tag{25}$$

The Hopf bifurcation point is computed to be $\mu_1 = 0.1633$. It can be observed that the limit cycle "collides" with the heteroclinic cycle lying on the boundary and the interior equilibrium as μ approaches 0 and 0.1633 respectively. In addition, it disappears after μ passes 0.1633.

4. Incentive-based control

In real biological and social systems, the mutation or exploration rate is usually small. For example, an extremely high mutation rate for a biological entity may reach 1/400 per site as reported in Gago, Elena, Flores, and Sanjuán (2009). As known from Section 3, although the Hopf bifurcation point μ_1 depends on the payoff parameters, limit cycles exist in system (4) for μ < μ_1 . It means that in many situations stable limit cycles persist in the co-evolutionary dynamics of the game and environment. On the one hand, the shapes and positions of limit cycles in nonlinear systems are generally difficult to identify analytically; on the other hand, such limit cycle oscillations, although different than the (oscillating) tragedy of the commons, are not desirable from a control point of view. In addition, considering the public resource management, the issue of how to best govern commonpool resources has long been a common concern in the field of economics (Ostrom, 2015). Thus, in this section we intend to study how to design suitable control policies such that the following two objectives are attained:

- (a). alleviate or even eliminate the oscillation;
- (b). increase the environmental resource stock.

One needs to choose what the control input should be. Although multiple possible approaches have been proposed in the evolutionary games field, perhaps the most plausible control input is to offer suitable incentives to be added to the payoff of

the desired strategies (Riehl, Ramazi, & Cao, 2018). In this spirit, now we consider that in each game interaction, the cooperator receives certain constant incentive $u \ge 0$ from an external regulating authority.

Recall that the entries on the first row of A(r) are the payoffs to a C player. The external incentive will be added to the first row of (1). Thus, the control input u is incorporated into the previously defined payoff matrix (1) as follows

$$A_{u}(r) = (1 - r) \begin{bmatrix} R_{1} & S_{1} \\ T_{1} & P_{1} \end{bmatrix} + r \begin{bmatrix} R_{2} & S_{2} \\ T_{2} & P_{2} \end{bmatrix} + \begin{bmatrix} u & u \\ 0 & 0 \end{bmatrix}$$

$$= \begin{bmatrix} r(R_{2} - R_{1}) + R_{1} + u & r(S_{2} - S_{1}) + S_{1} + u \\ r(T_{2} - T_{1}) + T_{1} & r(P_{2} - P_{1}) + P_{1} \end{bmatrix}.$$
(26)

Substituting (26) into Eqs. (4) results in the following system with the control input u

$$\begin{cases} \dot{x} = x(1-x)[xr(-c+d-a+b) + x(a-b) \\ -r(d+b) + b + u] + \mu(1-2x) \\ \dot{r} = r(1-r)(2x-1). \end{cases}$$
 (27)

To emphasize the effect of the control input u on the system behaviors, we have assumed that the enhancement effect and the degradation effect are balanced by fixing the parameter θ to be 1 (under Assumption 15). In the following part we will study whether such a constant incentive can achieve the desired control objectives.

4.1. Stable equilibrium

System (27) has a unique interior equilibrium which is given by $(x_c^*, r_c^*) = (1/2, (a+b+2u)/(a+c+b+d))$ when $0 \le u < (c+d)/2$. It is noted that the interior equilibrium is shifted up vertically, i.e., the *x*-coordinate of this equilibrium is the same as the equilibrium of the system without control, while the value of the *r*-coordinate increases. Then we evaluate the Jacobian at (x_c^*, r_c^*) , which is given by

$$J_c^* = \begin{bmatrix} \frac{ad - bc + (b + d - a - c)u}{2(a + b + c + d)} - 2\mu & \frac{-(a + b + c + d)}{8} \\ \frac{2(a + b + 2u)(c + d - 2u)}{(a + b + c + d)^2} & 0 \end{bmatrix}.$$
 (28)

For this matrix, it is easy to identify that the real parts of its eigenvalues are of the same sign, which is the same as the first entry.

When $u \geq (c+d)/2$, no equilibria exist in the interior of \mathcal{I} , and all the equilibria are located on the sides \mathcal{B}_t and \mathcal{B}_b . For system (27), if $u \geq 0$, it is easy to identify that the x-coordinate of the equilibrium on \mathcal{B}_b is in the range $x \in (1/2, 1)$ by using a similar approach in Lemma 11. Then the same argument of Lemma 12 is applicable, so one can ensure that this equilibrium is unstable for $\operatorname{int}(\mathcal{I})$. Similarly, on the side \mathcal{B}_t , when 0 < u < (c+d)/2, the equilibria are located in the range $x \in (0, 1/2)$, and thus they are unstable. However, when u > (c+d)/2, the situation will be different, and we have the following statement for the equilibria.

Lemma 18. Consider system (27). When u > (c + d)/2, on the side \mathcal{B}_t , there exists one equilibrium, denoted by $(x_t^*, 1)$, satisfying $x_t^* \in (1/2, 1)$. And the other possible equilibria are all located in the set $\{(x, r) : x \in (0, 1/2), r = 1\}$.

Proof. Details are omitted here. \square

It is easy to check the stability of these equilibria by evaluating the Jacobian.

Lemma 19. When u > (c + d)/2, the boundary equilibrium $(x_t^*, 1)$ is locally asymptotically stable under system (27), while the other equilibria (if they exist) are unstable.

Proof. One can check the local stability of $(x_t^*, 1)$ by examining the Jacobian which is given by

$$J_t^* = \begin{bmatrix} 3(c-d)x_t^{*2} + 2(2d-c-u)x_t^* & \bullet \\ -d+u-2\mu & 0 & 1-2x_t^* \end{bmatrix},$$
 (29)

where the symbol \bullet stands for $-x_t^{*3}(-c+d-a+b)-x_t^*(d+b)+x_t^{*2}(-c+2d-a+2b)$. Note that the eigenvalues of J_t^* are actually the two diagonal entries. According to Lemma 18, obviously the eigenvalue $\lambda_1 = 1 - 2x_t^*$ is negative.

For the other eigenvalue $\lambda_2 = 3(c-d)x_t^{*2} + 2(2d-c-u)x_t^* - d + u - 2\mu$, one can prove it is negative in all the three cases regarding the relationship of c and d. To illustrate, we only show the case of c > d here, since the other cases are similar. Suppose $c = d + \epsilon$ with $\epsilon > 0$. We have $1/2 < x_t^* < (u-d)/\epsilon$, then one can check that

$$\lambda_2 = (3x_t^{*2} - 2x_t^{*})\epsilon + (u - d)(1 - 2x_t^{*}) - 2\mu$$

$$< (3x_t^{*2} - 2x_t^{*})\epsilon + \epsilon x_t^{*}(1 - 2x_t^{*}) - 2\mu$$

$$= (x_t^{*2} - x_t^{*})\epsilon - 2\mu$$

$$< -2\mu.$$

Thus, the eigenvalue λ_2 is negative. The fact of two negative eigenvalues ensures that the equilibrium $(x_t^*, 1)$ is locally asymptotically stable. The instability of other possible equilibria is easy to check since there is always a positive eigenvalue in view of (29). \square

Then, we define a Dulac function which is similar to that in Section $3.1\,$

$$\varphi_c(x,r) = x^{\alpha} (1-x)^{\beta} r^{\gamma - 0.5u} (1-r)^{\delta + 0.5u}, \tag{30}$$

where the parameters α , β , γ , and δ are the same as in (11) with $\theta = 1$. Denote the vector field of (27) by $f_c(x, r)$. After the multiplication of $\varphi_c(x, r)$, we compute the divergence of the modified vector field $\varphi_c f_c(x, r)$ in int(\mathcal{I}), which yields

div
$$\varphi_c f_c(x, r) = \varphi_c(x, r) [g(x)\mu - 2\mu + (1.5 + \alpha)u - \frac{(bc - ad)}{2(a + b + c + d)}],$$
(31)

with g(x) being the same as in (12), which takes the maximum value at \bar{x} as shown in (13).

Next we discuss in two cases and show that there always exists some u such that system (27) has a stable equilibrium for the whole interior.

Theorem 20. For system (27), when a+c>b+d, there exists some $u_1:=\frac{ad-bc-(4-g(\bar{x}))\mu(a+b+c+d)}{a+c-b-d}$ such that

- (1) if $u_1 < (c + d)/2$, the interior equilibrium (x_c^*, r_c^*) is almost globally stable under $u \in (u_1, (c + d)/2)$;
- (2) if $u_1 > (c+d)/2$, the boundary equilibrium $(x_t^*, 1)$ is almost globally stable under u > (c+d)/2.

Proof. When a + c > b + d, we have $\alpha = -(1 + \frac{a+c}{a+b+c+d}) \in (-2, -1.5)$, so the coefficient of the term with u in (31), i.e., $1.5 + \alpha$, is negative. Thus, if

$$u > u_1 := \frac{ad - bc - (4 - g(\bar{x}))\mu(a + b + c + d)}{a + c - b - d},$$
(32)

the right hand side of (31) is always negative, which implies that there are no closed orbits in \mathcal{I} .

By checking the Jacobian (28), one can see that the interior equilibrium (x_c^* , r_c^*) is stable when

$$u>u_2:=\frac{ad-bc-4\mu(a+b+c+d)}{a+c-b-d}.$$

As $g(\bar{x}) \geq 0$, we have $u_1 \geq u_2$. Then if $u_1 < (c+d)/2$, one can choose some $u \in (u_1, (c+d)/2)$ such that the interior equilibrium (x_c^*, r_c^*) exists and is asymptotically stable. Due to the non-existence of closed orbits in \mathcal{I} and other stable equilibria, and also because of the repulsiveness of $\partial \mathcal{I}$, one can conclude that almost all trajectories will converge to (x_c^*, r_c^*) asymptotically.

On the other hand, if $u_1 \geq (c+d)/2$, one can choose some u > (c+d)/2 which leads to the occurrence of the equilibrium $(x_t^*, 1)$. In view of (29), the equilibrium $(x_t^*, 1)$ is locally asymptotically stable. The other equilibria on \mathcal{B}_t and \mathcal{B}_b are all unstable, and they are located on the sets whose sufficient close neighborhoods in $\operatorname{int}(\mathcal{I})$ are repelling. Hence, it is impossible for trajectories starting from $\operatorname{int}(\mathcal{I})$ to converge to these points. As a consequence, $(x_t^*, 1)$ is the only ω -limit set for all initial states in $\operatorname{int}(\mathcal{I})$ from the Poincaré–Bendixson theorem. Similarly, this result extends to the sides \mathcal{B}_l and \mathcal{B}_r by following the preceding analysis. \square

Theorem 21. For system (27), when $a + c \le b + d$, the boundary equilibrium $(x_*^*, 1)$ is almost globally stable under u > (c + d)/2.

Proof. When $a+c \leq b+d$, the first entry of (28) will always be positive for any u if $\frac{ad-bc}{2(a+b+c+d)}-2\mu>0$, in which case the equilibrium will always be unstable (saddle). Thus, it is impossible to stabilize the interior equilibrium with any positive u if it is unstable in the uncontrolled system. However, one can choose some u>(c+d)/2 such that there is an equilibrium $(x_t^*,1)$ on \mathcal{B}_t which can be proved to be almost globally stable by using the same argument in the second case of Theorem 20. \square

In Theorems 20 and 21, the relationship between a+c and b+d determines whether the interior equilibrium can be stabilized or not under the positive control input u. In view of (28), one can observe that the stability of the interior equilibrium can be changed from unstable to stable when a+c>b+d under a suitable u, while the stability is not qualitatively affected by u when $a+c\leq b+d$.

When there exists an equilibrium that is globally stable for \mathcal{I} , obviously the limit cycle oscillation is eliminated, no matter whether this stable equilibrium is in the interior or on the top side. The second designed goal is also achieved, since the r-coordinates of the equilibria are higher. One can find some illustrations in Fig. 4.

4.2. Reduced amplitude of the limit cycle

For the case of a+c=b+d, although it is impossible to stabilize the interior equilibrium with a suitable u, one can observe that the amplitude of the oscillation on r-coordinate decreases under some small u.

As a+c=b+d, it is noted that the control input does not affect the stability of equilibrium (x_c^*, r_c^*) according to the Jacobian (28). However, one can transform system (27) into a form of Liénard system as (24) in the same manner. Since the listed conditions are satisfied straightforwardly, according to Lemma 16, for $\mu < (0, \mu_1)$, system (27) has a unique limit cycle when $u \in [0, (c+d)/2)$. When there is some intermediate control input $u \in (0, (c+d)/2)$, the corresponding interior equilibrium is shifted towards the top side \mathcal{B}_t . To some extent, the vector field between the interior equilibrium and the top side is "compressed". The position of the limit cycle is shifted up, and the amplitude of the cyclic oscillation on r-coordinate is reduced at the same time. In this sense, the oscillation is alleviated. Some numerical results can be found in Fig. 5.

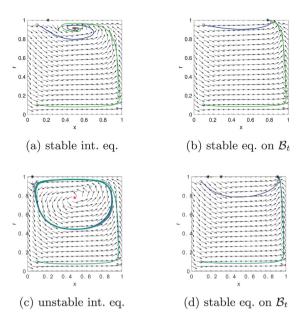


Fig. 4. Phase portraits of dynamics (27) when $a+c\neq b+d$. (a) and (b) respectively show the trajectories converge to a stable equilibrium in the interior and on the boundary with different control inputs when a+c>b+d with a=4, b=1, c=3, d=3, and $\mu=0.05$. The control inputs in (a) and (b) are 2.8 and 3.5 respectively. (c) and (d) are for the case a+c<b+d where a=2, b=3, c=1, d=4, and $\mu=0.15$. In (c) the interior equilibrium cannot be stabilized with small control input with u=1.8, but in (d) one equilibrium on the boundary is stable under a large control input with u=2.6.

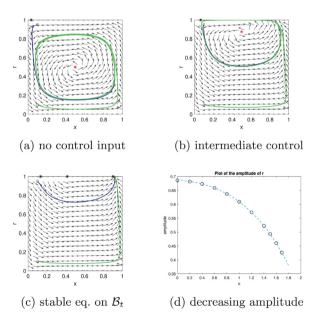


Fig. 5. Reduced amplitudes of oscillation of variable r when a+c=b+d with a=3, b=1, c=1, d=3, and $\mu=0.05$. The first three plots show the phase portraits with different values of u: (a) u=0; (b) u=1.6; (c) u=2.1. (d) shows that the amplitude of r of the limit cycle (approximated by the numerical integration) decreases as u increases.

5. Conclusions and future work

We have investigated the co-evolutionary dynamics of the game and environment when strategies' mutations are taken

into account. We used the replicator-mutator model to depict the strategic evolution. By using bifurcation theory we showed that the system at the interior equilibrium undergoes a Hopf bifurcation which generates stable limit cycles; on the other hand, we showed there is a heteroclinic bifurcation which may also generate a stable limit cycle. Our analysis highlights the important role that mutations play in the integrated system dynamics. For the co-evolutionary system, the stable limit cycle corresponds to a sustained oscillation of population's decisions and richness of the environmental resource. Compared with the neutral periodic oscillation or heteroclinic cycle oscillation that have been exhibited in previous studies using the replicator model, such limit cycle oscillations can better explain the phenomena that appear in real biological or social systems. Moreover, we proved that under certain parameter conditions, the system always admits a unique stable limit cycle which is attractive for almost the entire domain.

Such a robust limit cycle oscillation may provide implications and theoretical support for relevant studies in biology and sociology. For example, in the microbial context, some cooperating bacteria can produce costly public good, while the defecting bacteria only profit. Thus, the richness of the public good is enhanced by the cooperating bacteria and degraded by the defectors. In the process of bacterial reproduction, mutations are common. The amount of mutant offsprings can have important impact on the dynamic outcomes of the biological systems. For such microbial systems, Brown and Taddei (2007) show that the dynamics can converge to an interior equilibrium, while Weitz et al. (2016) shows that persistent heteroclinic oscillations can exist. However, the results obtained in this work theoretically reveal that a moderate limit cycle oscillation can exist in addition to the convergence to a steady state or a heteroclinic cycle. Thus, this work complements the previous studies.

We also considered the incentive-based control applied into the co-evolutionary dynamics, and showed the effectiveness of such control on maintaining the environmental resource. Namely, compared with the uncontrolled system, the incentive will increase the level of environmental resource in most cases. In particular, one can apply some intermediate incentive to let the system have an interior equilibrium that is stable for the whole interior of domain. If the interior equilibrium cannot be stabilized, some large incentive could be put into use to make the system dynamics converge to a boundary equilibrium with full environmental resource.

The obtained results in the control part of this work can provide valuable insights into many practical issues in nature, such as the common-pool resource management, environmental and sustainable development, and ecological diversity conservation. For example, the global climate change is one of the biggest challenges of our times. The strategic decisions of individuals, corporations, and governments have long-term environmental consequence that will, in turn, alter the strategic landscape those parties face (Tilman et al., 2020). To mitigate the global warming, all concerned parties are called upon to reduce greenhouse gas emissions. In such a socio-ecological system, the reduction of greenhouse gas emissions can be taken as the environmental factor of interest. Policy-makers can design and implement economic incentives aiming at adapting individual decisions to collectively agreed goals (Sullivan, 2017). Hence, the incentivebased policy proposed in this work shows the power of incentivebased control policy and leads to some directions in mitigating the global warming issue.

In this paper, we have used a more general and realistic model, replicator–mutator dynamics, to describe the strategic evolution, but the environment dynamics is still described by the simplified logistic model. Thus, it is of great interest to study the game

dynamics under different types of feedback of the practical environmental resource, such as renewing or decaying resource. The replicator or replicator–mutator equations describe the evolutionary game dynamics in an infinite well-mixed population. Due to this shortcoming, they are not suitable to study game dynamics in finite or structured populations. Therefore, another direction of future studies is to develop more appropriate individual-based models to study the game dynamics under the environmental feedback. Last but not least, in addition to the incentive-based control, there could exist other kinds of control policies that can be more effective in various specific situations.

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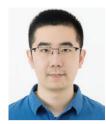
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