

# Noise-Induced Quasi-Heteroclinic Cycle in a Rock–Paper–Scissors Game with Random Payoffs

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### Abstract

The rock–paper–scissors game is one of the main theoretical models in evolutionary game theory and has been used successfully to explain some observed phenomena in biology, economics and social science. In order to explore the influence of environmental noise on cyclic dominance in the rock–paper–scissors game, stochastic stability in a continuous-time dynamics of the game with random payoffs in pairwise interactions is investigated by using the stochastic stability theory of Itô's stochastic differential equations. After deducing a stochastic replicator equation for the strategy frequencies in a symmetric version of the game, stochastic stability conditions for constant equilibrium states are obtained and stochastic simulations of the global dynamics are performed. The main results are that (1) none of the fixation states of the system can be stochastically stable; and (2) an increase in the noise level (or stochastic fluctuation intensity) can result in the loss of stochastic stability of the constant interior equilibrium. More importantly, the simulation results not only match the theoretical predictions but also show the appearance of a noise-induced quasi-heteroclinic cycle when the constant interior equilibrium loses its stochastic stability as the noise level increases.

**Keywords** Evolutionary game theory · Cyclic dominance · Stochastic replicator equation · Stochastic stability

## **1 Introduction**

Cyclic dominance is one of the important features leading to oscillatory, chaotic, and stochastic dynamics in biology [2] as well as in social and economic systems [6–8]. The simplest theoretical model of cyclic dominance in evolutionary game theory is a children's game called the rock–paper–scissors game, where rock crushes scissors, scissors cuts paper, and paper wraps rock [9]. This simple game model has been used successfully to explain some

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observed phenomena in biology, economics and social science [9,14,21,23,33]. An example of cyclic dominance is provided by lizards with three male strategies [23,33]. Orange-throated males establish large territories holding several females. These populations are invaded by males with yellow-striped throats, which do not contribute to the defense of the territory but sneak on the females. Such a population of yellow-striped males can be invaded by bluethroated males, which defend territories large enough to hold one female against sneakers. Once yellow-striped sneakers are rare, it is advantageous to defend a large territory with several females and the cycle starts again with orange-throated males. As another example, Elowitz and Leibler [3] used three transcriptional repressor systems to build an oscillating network, termed the repressilator, in Escherichia coli. In this network, the first repressor protein, LacI from E. coli, inhibits the transcription of the second repressor gene, tetR from the tetracycline-resistance transposon Tn10, whose protein product in turn inhibits the expression of a third gene, cI from  $\lambda$  phage. Finally, cI inhibits LacI expression, completing the cycle. This negative feedback loop can lead to temporal oscillations in the concentration of each of the three components. Moreover, some studies have shown that cyclic dominance could be closely related to the maintenance of biodiversity in ecosystems [1].

Based on the replicator equation in evolutionary game theory, which describes the continuous-time dynamics for strategy frequencies in an infinite population, the dynamical properties of the rock-paper-scissors game have been studied in detail [9]. In particular, this is the case for the simplest symmetric model with the following payoffs in pairwise interactions : (1) 1 to a winning strategy against a losing strategy; (2) –*s* to a losing strategy against a winning strategy, where *s* is assumed to be positive; and (3) 0 for a tie [1,9]. It has been shown that the interior fixed point of this system (namely,  $\mathbf{x}^* = (1/3, 1/3, 1/3)$ ) is globally asymptotically stable if *s* < 1, and unstable if *s* > 1, in which case the system approaches a heteroclinic cycle near the boundary of the simplex of all three-dimensional frequency vectors [1,9].

Recently, Szolnoki et al. [26] reviewed advances on the rock–paper–scissors and related games, focusing, in particular, on the pattern formation, the impact of mobility, the spontaneous emergence of cyclic dominance, as well as mean-field and zero-dimensional models and the application of the complex Ginzburg–Landau equation. They also highlighted the importance and usefulness of statistical physics for a successful study of large-scale ecological systems, and outlined the direction for future research, related, for example, to dynamical effects of coevolutionary rules and invasion reversals owing to multi-point interactions.

One key assumption in classical evolutionary game theory is that the payoffs are constant. This supposes that the environmental conditions do not change over time. However, this assumption is unrealistic since environmental conditions in the real world are changing and uncertain. In an ecological context, May [17,18] pointed out that since real environments are uncertain and stochastic, the birth rates, carrying capacities, competition coefficients, and other parameters which characterize natural biological systems all, to a greater or lesser extent, exhibit random fluctuations. In a previous study [19], he had shown how stochastic fluctuations in carrying capacities, for instance, can profoundly influence the dynamics of a single-species population. Since then, the effects of environmental stochasticity or fluctuations on population and community ecology have been investigated by many others [15,22,24,25,28,30,31,35]. Spagnolo et al. [15,24,25], for instance, investigated some phenomena in Lotka–Volterra systems induced by environmental noise such as quasideterministic oscillations, stochastic resonance, noise-delayed extinction and spatial patterns. All these studies in ecology strongly suggest that the effects of environmental stochasticity on evolutionary dynamics should be taken into account.

Recently, in order to characterize evolutionary stability in a stochastic environment, Zheng et al. [36,37] developed the concepts of stochastic evolutionary stability (SES) and stochastic convergence stability (SCS) based on stochastic local stability (SLS) properties of fixation states as in Karlin and Liberman [12,13], but in the more general context of discrete-time linear games with two strategies and random payoffs. A SES strategy was defined as a strategy such that if all the members of the population adopt it, then the probability for any slightly perturbed strategy to invade the population under the influence of natural selection is arbitrarily low.

Note that stochastic differential equations extending the deterministic continuous-time replicator equation have already been investigated by some authors to study stochastic effects on evolutionary games, particularly linear games [4,5,11]. In these studies, the focus has been put mainly on the connection between the stochastic dynamics and evolutionarily stable strategies (ESS) in the absence of random perturbations. Moreover, random noise was added either to the replicator equation for the rate of change in the frequency of each strategy or to the average payoff for each strategy, but not to payoffs of strategies in pairwise interactions.

In this paper, our goal is to investigate how environmental noise may affect cyclic dynamical behavior in a simple continuous-time rock-paper-scissors game with random payoffs in pairwise interactions. This is done through a stochastic local stability analysis of constant equilibria. This study may reveal the evolutionary significance of environmental stochastic fluctuations in biological populations with cyclic dominance. We will use tools in stochastic differential equations, more precisely Itô's stochastic calculus [16]. This will allow us to deduce conditions for stochastic stability and apply these to the rock-paper-scissors game with random payoffs to determine whether environmental noise can induce a heteroclinic cycle.

## 2 Results

#### 2.1 Rock–Paper–Scissors Game with Random Payoffs

We consider a stochastic symmetric rock-paper-scissors game with three pure strategies, denoted by R (rock), P (paper) and S (scissors), respectively, and with a random payoff matrix at time  $t \ge 0$  given by

$$\mathbf{A}(t) = \begin{pmatrix} 0 & -s(t) & 1\\ 1 & 0 & -s(t)\\ -s(t) & 1 & 0 \end{pmatrix},$$
 (1)

where (1) the three entries on the first, second and third rows are the payoffs to strategies R, P and S, respectively, against strategies R, P and S, respectively [1,9]; and (2) for simplicity (but not without generality), the cost s(t) is a random variable given in the form  $s(t) = \bar{s} + \xi(t)$ , where  $\bar{s}$  is a constant and  $\xi(t)$  is a Gaussian noise. Here, we assume that  $\langle \xi(t) \rangle = 0$  and  $\langle \xi(t)\xi(t') \rangle = 2D\delta(t - t')$ , where  $\langle \cdot \rangle$  denotes mathematical expectation,  $\delta(\cdot)$  represents a Dirac delta function and the parameter  $D \ge 0$  measures the noise level. In other words,  $\eta(t) = \xi(t)/\sqrt{2D} = dw(t)/dt$  is a standard white noise, where w(t) stands for a standard Brownian motion, also known as a Wiener process, with  $\langle w(t) \rangle = 0$  and  $\langle w(t)w(t') \rangle = \min(t, t')$  for  $t, t' \ge 0$  [16].

Let  $x_R(t)$ ,  $x_P(t)$  and  $x_S(t)$  be the frequencies of R, P and S, respectively, at time  $t \ge 0$  in a population of infinite size. Then,  $x_R(t) + x_P(t) + x_S(t) = 1$  and, under the assumption of random pairwise interactions [9], the average payoff to strategy R is given by  $\pi_R(t) = 1$ 

 $x_S(t) - s(t)x_P(t) = x_S(t) - \bar{s}x_P(t) - x_P(t)\sqrt{2D\eta(t)}$ . Similarly, the average payoffs to strategies *P* and *S* are  $\pi_P(t) = x_R(t) - s(t)x_S(t) = x_R(t) - \bar{s}x_S(t) - x_S(t)\sqrt{2D\eta(t)}$  and  $\pi_S(t) = x_P(t) - s(t)x_R(t) = x_P(t) - \bar{s}x_R(t) - x_R(t)\sqrt{2D\eta(t)}$ , respectively. The average payoff in the whole population, denoted by  $\bar{\pi}(t)$ , is  $\bar{\pi}(t) = x_R(t)\pi_R(t) + x_P(t)\pi_P(t) + x_S(t)\pi_S(t)$ .

First, in the situation where D = 0 (that is,  $s(t) = \overline{s}$  is constant for  $t \ge 0$ ), we have the standard deterministic replicator dynamics with payoff matrix

$$\bar{\mathbf{A}} = \begin{pmatrix} 0 & -\bar{s} & 1 \\ 1 & 0 & -\bar{s} \\ -\bar{s} & 1 & 0 \end{pmatrix} ,$$

given by the equations  $\dot{x}_k = x_k(\pi_k - \bar{\pi})$  for k = R, P, S, where  $\pi_R = x_S - \bar{s}x_P, \pi_P = x_R - \bar{s}x_S$  and  $\pi_S = x_P - \bar{s}x_R$ , while  $\bar{\pi} = x_R\pi_R + x_P\pi_P + x_S\pi_S$  [9]. With respect to this deterministic dynamics, the central point  $\mathbf{x}^* = (x_R^*, x_P^*, x_S^*) = (1/3, 1/3, 1/3)$  is an interior equilibrium that does not depend on the parameter  $\bar{s}$ . Moreover, it is known that: (1) each of the three vertices of the frequency simplex  $S_3 = \{\mathbf{x} = (x_R, x_P, x_S) \text{ with } x_R, x_P, x_S \ge 0$  and  $x_R + x_P + x_S = 1\}$ , denoted by  $\mathbf{e}_R = (1, 0, 0), \mathbf{e}_P = (0, 1, 0)$  and  $\mathbf{e}_S = (0, 0, 1)$ , is a saddle fixed point if  $\bar{s} > 1$ , and an unstable fixed point if  $\bar{s} < 1$ ; (2) the interior equilibrium  $\mathbf{x}^*$  is globally asymptotically stable if  $\bar{s} < 1$ ; (3)  $\mathbf{x}^*$  is asymptotically unstable if  $\bar{s} > 1$  and then the system approaches a heteroclinic cycle near the boundary of the simplex  $S_3$ , which is formed by the three vertices  $\mathbf{e}_R$ ,  $\mathbf{e}_P$  and  $\mathbf{e}_S$  together with the edges; and (4)  $\mathbf{x}^*$  is a center if  $\bar{s} = 1$ , that is, all orbits in  $S_3$  are periodic orbits surrounding  $\mathbf{x}^*$ , in which case the game is a zero-sum game [9,34].

We now focus on the situation where D > 0 (that is, s(t) for  $t \ge 0$  is a non-degenerate stochastic process). Let  $n_R(t)$ ,  $n_P(t)$  and  $n_S(t)$  be the numbers of players using R, P and S, respectively, at time  $t \ge 0$  so that the strategy frequencies at this time are given by

$$\mathbf{x}(t) = \left(x_R(t), x_P(t), x_S(t)\right) = \frac{\left(n_R(t), n_P(t), n_S(t)\right)}{n_R(t) + n_P(t) + n_S(t)}.$$
(2)

Owing to the interpretation of payoffs as growth rates [27], the stochastic differentials of  $n_R(t)$ ,  $n_P(t)$  and  $n_S(t)$  in Itô's sense [16] are given by the equations

$$dn_R(t) = n_R(t) \left[ \pi_R(\mathbf{x}(t), \bar{s}) dt - x_P(t) \sqrt{2D} dw(t) \right],$$
(3a)

$$dn_P(t) = n_P(t) \left[ \pi_P(\mathbf{x}(t), \bar{s}) dt - x_S(t) \sqrt{2D} dw(t) \right],$$
(3b)

$$dn_{S}(t) = n_{S}(t) \left[ \pi_{S}(\mathbf{x}(t), \bar{s}) dt - x_{R}(t) \sqrt{2D} dw(t) \right], \qquad (3c)$$

respectively, where we have  $\pi_R(\mathbf{x}(t), \bar{s}) = x_S(t) - \bar{s}x_P(t), \pi_P(\mathbf{x}(t), \bar{s}) = x_R(t) - \bar{s}x_S(t)$ and  $\pi_S(\mathbf{x}(t), \bar{s}) = x_P(t) - \bar{s}x_R(t)$ .

Using the rules  $(dt)^2 = 0$ , dt dw(t) = 0 and  $(dw(t))^2 = dt$  (see, e.g., p. 36 in [16]) and expanding  $x_R(t)$  as a functions of  $n_R(t)$ ,  $n_P(t)$  and  $n_S(t)$ , we obtain

$$dx_R(t) = \frac{\partial x_R(t)}{\partial n_R(t)} dn_R(t) + \frac{\partial x_R(t)}{\partial n_P(t)} dn_P(t) + \frac{\partial x_R(t)}{\partial n_S(t)} dn_S(t) + \frac{1}{2} \frac{\partial^2 x_R(t)}{\partial n_R(t)^2} (dn_R(t))^2 + \frac{1}{2} \frac{\partial^2 x_R(t)}{\partial n_P(t)^2} (dn_P(t))^2 + \frac{1}{2} \frac{\partial^2 x_R(t)}{\partial n_S(t)^2} (dn_S(t))^2$$

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$$+ \frac{\partial^2 x_R(t)}{\partial n_R(t)\partial n_P(t)} dn_R(t) dn_P(t) + \frac{\partial^2 x_R(t)}{\partial n_P(t)\partial n_S(t)} dn_P(t) dn_S(t) + \frac{\partial^2 x_R(t)}{\partial n_R(t)\partial n_S(t)} dn_R(t) dn_S(t),$$
(4)

where

$$\frac{\partial x_R(t)}{\partial n_R(t)} = \frac{n_P(t) + n_S(t)}{(n_R(t) + n_P(t) + n_S(t))^2},\tag{5a}$$

$$\frac{\partial x_R(t)}{\partial n_P(t)} = \frac{\partial x_R(t)}{\partial n_S(t)} = -\frac{n_R(t)}{(n_R(t) + n_P(t) + n_S(t))^2},$$
(5b)

$$\frac{\partial^2 x_R(t)}{\partial n_R(t)^2} = -\frac{2(n_P(t) + n_S(t))}{(n_R(t) + n_P(t) + n_S(t))^3}$$
(5c)

$$\frac{\partial^2 x_R(t)}{\partial n_P(t)^2} = \frac{\partial^2 x_R(t)}{\partial n_S(t)^2} = \frac{2n_R(t)}{(n_R(t) + n_P(t) + n_S(t))^3},$$
(5d)

$$\frac{\partial^2 x_R(t)}{\partial n_R(t)\partial n_P(t)} = \frac{\partial^2 x_R(t)}{\partial n_R(t)\partial n_S(t)} = \frac{n_R(t) - n_P(t) - n_S(t)}{(n_R(t) + n_P(t) + n_S(t))^3},$$
(5e)

$$\frac{\partial^2 x_R(t)}{\partial n_P(t) \partial n_S(t)} = \frac{2n_R(t)}{(n_R(t) + n_P(t) + n_S(t))^3},$$
(5f)

while

$$(dn_R(t))^2 = 2Dn_R(t)^2 x_P(t)^2 dt,$$
(6a)

$$(dn_P(t))^2 = 2Dn_P(t)^2 x_S(t)^2 dt,$$
(6b)  

$$(dn_P(t))^2 = 2Dn_P(t)^2 x_S(t)^2 dt$$
(6c)

$$(dn_{S}(t))^{2} = 2Dn_{S}(t)^{2}x_{R}(t)^{2}dt,$$

$$(6c)$$

$$dn_{P}(t)dn_{P}(t) = 2Dn_{P}(t)n_{P}(t)x_{P}(t)x_{S}(t)dt$$

$$(6d)$$

$$dn_{R}(t)dn_{P}(t) = 2Dn_{R}(t)n_{P}(t)x_{S}(t)dt,$$

$$dn_{P}(t)dn_{S}(t) = 2Dn_{P}(t)n_{S}(t)x_{S}(t)x_{R}(t)dt,$$
(6e)

$$dn_R(t)dn_S(t) = 2Dn_R(t)n_S(t)x_P(t)x_R(t)dt .$$
 (6f)

We have a similar expression for  $dx_P(t)$ , while  $dx_S(t) = -dx_R(t) - dx_P(t)$  since  $x_S(t) = 1 - x_R(t) - x_P(t)$ . Then, direct calculations show that the stochastic dynamics for the strategy frequency vector  $\mathbf{x}(t) = (x_R(t), x_P(t), x_S(t))$  is described by the stochastic differential equations (SDE)

$$dx_R(t) = f_R(\mathbf{x}(t))dt + g_R(\mathbf{x}(t))dw(t), \qquad (7a)$$

$$dx_P(t) = f_P(\mathbf{x}(t))dt + g_P(\mathbf{x}(t))dw(t), \qquad (7b)$$

where

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$$f_R(\mathbf{x}) = x_R \Big[ \pi_R(\mathbf{x}, \bar{s}) - \bar{\pi}(\mathbf{x}, \bar{s}) \Big] + 2Dx_R \Big[ x_R x_P x_S - x_P^2 (x_R + x_S) + x_R^2 x_P^2 + x_P^2 x_S^2 + x_R^2 x_S^2 \Big],$$
(8a)

$$f_P(\mathbf{x}) = x_P \Big[ \pi_P(\mathbf{x}, \bar{s}) - \bar{\pi}(\mathbf{x}, \bar{s}) \Big] + 2Dx_P \Big[ x_R x_P x_S - x_S^2 (x_R + x_P) \Big]$$

$$+x_R^2 x_P^2 + x_P^2 x_S^2 + x_R^2 x_S^2 \Big],$$
(8b)

$$g_R(\mathbf{x}) = \sqrt{2D} x_R \left[ -x_P^2 + x_R x_S \right], \qquad (8c)$$

$$g_P(\mathbf{x}) = \sqrt{2D} x_P \left[ -x_S^2 + x_R x_P \right], \tag{8d}$$

with  $\bar{\pi}(\mathbf{x}, \bar{s}) = x_R \pi_R(\mathbf{x}, \bar{s}) + x_P \pi_P(\mathbf{x}, \bar{s}) + x_S \pi_S(\mathbf{x}, \bar{s}).$ 

The SDE in (7) can be considered as an extension of the classical replicator equation for the rock-paper-scissors game in a stochastic environment. It is easy to check that the vertices of the frequency simplex  $S_3$ , represented by  $\mathbf{e}_R$ ,  $\mathbf{e}_P$  and  $\mathbf{e}_S$ , are fixation states of this stochastic dynamics, and the central point  $\mathbf{x}^* = (x_R^*, x_P^*, x_S^*) = (1/3, 1/3, 1/3)$  a constant interior equilibrium. Note that  $\mathbf{e}_S$  corresponds to the zero solution of  $(x_R(t), x_P(t))$ , and  $\mathbf{x}^*$ to the zero solution of  $(x_R(t) - 1/3, x_P(t) - 1/3)$ .

## 2.2 Stochastic Stability of Equilibrium Points

In this section, we investigate the stochastic stability of the three fixation states of (7) represented by  $\mathbf{e}_R$ ,  $\mathbf{e}_P$  and  $\mathbf{e}_S$  in the simplex of frequency vectors  $S_3$  and the constant interior equilibrium  $\mathbf{x}^* = (1/3, 1/3, 1/3)$ .

We consider first the constant interior equilibrium  $\mathbf{x}^*$ . Define  $\mathbf{y}(t) = (y_1(t), y_2(t))^T$  where  $y_1(t) = x_R(t) - 1/3$  and  $y_2(t) = x_P(t) - 1/3$ . When the system state  $\mathbf{x}(t)$  is near  $\mathbf{x}^*$ , a Taylor expansion about  $\mathbf{x}^*$  leads to the stochastic differential equation

$$d\mathbf{y}(t) = \left(\mathbf{F}\mathbf{y}(t) + \mathbf{o}(||\mathbf{y}(t)|)\right) dt + \left(\mathbf{G}\mathbf{y}(t) + \mathbf{o}(||\mathbf{y}(t)|)\right) dw(t) , \qquad (9)$$

where

$$\mathbf{F} = \frac{1}{3} \begin{pmatrix} -1 & -1 - \bar{s} - 2D/3\\ 1 + \bar{s} + 2D/3 & \bar{s} + 2D/3 \end{pmatrix},$$
 (10a)

$$\mathbf{G} = \frac{1}{3} \begin{pmatrix} 0 & -\sqrt{2D} \\ \sqrt{2D} & \sqrt{2D} \end{pmatrix}.$$
 (10b)

Then, the stochastic stability of  $\mathbf{x}^*$  in (7) corresponds to the stochastic stability of the zero solution of the stochastic differential equation (9). This zero solution is stochastically stable if, for any r > 0 and any  $\epsilon$  in (0, 1), there exists  $\delta > 0$  such that

$$\mathbb{P}\left(|\mathbf{y}(t)| < r \text{ for } t \ge 0\right) \ge 1 - \epsilon \tag{11}$$

whenever  $|\mathbf{y}(0)| < \delta$ , and stochastically unstable otherwise (see [16], p. 110).

We define  $V(\mathbf{y}(t)) = \mathbf{y}(t)^T \mathbf{Q} \mathbf{y}(t)$  where we take

$$\mathbf{Q} = \begin{pmatrix} 2 & 1 \\ 1 & 2 \end{pmatrix} \,. \tag{12}$$

This matrix is positive definite, since  $\mathbf{y}^T \mathbf{Q} \mathbf{y} = y_1^2 + (y_1 + y_2)^2 + y_2^2 \ge 0$  with equality to 0 if and only if  $\mathbf{y} = (y_1, y_2)^T = (0, 0)^T$ . Actually, its eigenvalues are 3 and 1 with associated

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eigenvectors (1, 1) and (1, -1), respectively. Therefore,  $V(\mathbf{y}(t)) \ge 0$  for  $t \ge 0$  with equality to 0 if and only if  $\mathbf{y}(t) = \mathbf{0}$ , which makes it a Lyapunov candidate function. Moreover, as recalled in Supplementary Information from [16] on the basis of Itô's formula, the function  $V(\mathbf{y}(t))$  satisfies a stochastic differential equation whose drift function is given by

$$LV(\mathbf{y}(t)) = \mathbf{y}(\mathbf{t})^T \mathbf{M} \mathbf{y}(t) + \mathbf{o}(|\mathbf{y}(t)|^2), \qquad (13)$$

where

$$\mathbf{M} = \mathbf{Q}\mathbf{F} + \mathbf{F}^T \mathbf{Q} + \mathbf{G}^T \mathbf{Q}\mathbf{G} \,. \tag{14}$$

Direct calculations show that

$$\mathbf{M} = \left(\frac{3\bar{s} + 4D - 3}{9}\right)\mathbf{Q}.$$
 (15)

Since the matrix **Q** is positive definite, the matrix **M** is negative definite if  $3\bar{s} + 4D - 3 < 0$ , and positive definite if the inequality is reversed. Therefore (see Supplementary Information or [16] p. 116), the zero solution in (9), and consequently  $\mathbf{x}^*$  in (9), is stochastically stable if  $3\bar{s} + 4D - 3 < 0$ , that is,  $3\bar{s} + 4D < 3$ . Moreover, since the eigenvalues of **M** increase as  $3\bar{s} + 4D - 3$  increases, we may expect stochastic instability for  $3\bar{s} + 4D - 3 > 0$  at least large enough. Note also that these conditions reduce to  $\bar{s} < 1$  and  $\bar{s} > 1$ , respectively, when D = 0, which are the conditions for  $\mathbf{x}^*$  to be asymptotically stable and asymptotically unstable, respectively, in the deterministic model [9].

We now turn our attention to the three fixation states of (9) represented by the vertices  $\mathbf{e}_R$ ,  $\mathbf{e}_P$  and  $\mathbf{e}_S$  in the simplex of frequency vectors  $S_3$ . Note that owing to the symmetry of the payoff matrix in (1), these three vertices have the same dynamical properties. Thus, for convenience, we consider only  $\mathbf{e}_S$ . Defining  $\mathbf{y}(t) = (y_1(t), y_2(t))^T$  where  $y_1(t) = x_R(t)$  and  $y_2(t) = x_P(t)$ , and using the fact  $x_S(t) = 1 - x_R(t) - x_P(t)$ , the stochastic equation for  $\mathbf{y}(t)$  near the zero solution, which corresponds to the vertex  $\mathbf{e}_S$ , is given by (9) where

$$\mathbf{F} = \begin{pmatrix} 1 & 0\\ 0 & -\bar{s} \end{pmatrix} \,, \tag{16a}$$

$$\mathbf{G} = \begin{pmatrix} 0 & 0\\ 0 & -\sqrt{2D} \end{pmatrix} \,. \tag{16b}$$

Again, we take  $V(\mathbf{y}(t)) = \mathbf{y}(t)^T \mathbf{Q} \mathbf{y}(t)$  as a Lyapunov candidate function, but this time with

$$\mathbf{Q} = \begin{pmatrix} 1 & 0\\ 0 & 1 \end{pmatrix} \,. \tag{17}$$

Here, it is obvious that  $\mathbf{y}^T \mathbf{Q} \mathbf{y} = y_1^2 + y_2^2 \ge 0$  with equality to 0 if and only if  $\mathbf{y} = (y_1, y_2)^T = (0, 0)^T$ . Moreover, the matrix **M** in (14) takes the form

$$\mathbf{M} = \mathbf{F} + \mathbf{F}^T + \mathbf{G}^T \mathbf{G} = \begin{pmatrix} 2 & 0 \\ 0 & 2(D - \bar{s}) \end{pmatrix}.$$
 (18)

Note that **M** is indefinite if  $D < \bar{s}$ , and positive definite if  $D > \bar{s}$ . This implies that the vertex  $\mathbf{e}_S$ , and actually every vertex of the simplex  $S_3$ , is not expected to be stochastically stable in all cases when D > 0. This is also in agreement with the corresponding results in the deterministic case, since  $\bar{s} > 0$  and  $\bar{s} < 0$  are the conditions for the matrix in the linear approximation near a fixation state to be indefinite and positive definite, respectively, when D = 0.

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### 2.3 Noise-Induced Quasi-Heteroclinic Cycle

We have found conditions for stochastic stability of equilibrium points in (7), the constant interior equilibrium  $\mathbf{x}^*$  as well as the three fixation states, extend the conditions for asymptotic stability in the deterministic replicator dynamics. Moreover, as the noise level *D* increases, the condition for stochastic stability of the constant interior equilibrium  $\mathbf{x}^*$  becomes more stringent, while the fixation states are more likely to be stochastically unstable.

In order to check our theoretical predictions about the effect of an increase of D on the stability properties of the constant equilibrium points and whether these theoretical predictions accurately capture the global stochastic dynamics of the system, stochastic simulations have been performed. Of particular interest is to see what happens in the stochastic dynamical behavior of the system when the constant equilibrium point loses its stochastic stability following an increase of the noise level D. The computer simulations are based on Eq. (7) using MATLAB R2017b. Time is discretized and the length of the time step is  $10^{-4}$ . The code is given in Supplementary Information. Using  $\bar{s} = 0.7$ , the interior equilibrium  $\mathbf{x}^*$  is stochastically stable if  $D < 3(1 - \bar{s})/4 = 0.225$  and may become stochastically unstable when D exceeds this threshold value, while the fixation states are expected to be stochastically unstable for all D > 0.

The simulation results indicate that: (1) when D = 0, the constant interior equilibrium  $\mathbf{x}^*$  is asymptotically stable (Fig. 1a); (2) when D = 0.2, the constant interior equilibrium  $\mathbf{x}^*$  is stochastically locally stable (Fig. 1b); (3) when D = 0.28, 0.31 or 0.34, there may be convergence or not to the constant interior equilibrium  $\mathbf{x}^*$  starting from a nearby initial state (Fig. 1c, d for D = 0.28, Fig. 1e-f for D = 0.31 and Fig. 1g for D = 0.34, all with initial state  $x_R(0) = x_P(0) = 0.2$ ,  $x_S(0) = 0.6$ ), and the proportion of trajectories converging to  $\mathbf{x}^*$  decreases as D increases with value 0.951 for D = 0.28, value 0.062 for D = 0.31, and value 0 for D = 0.34; and (4) more generally, as D increases, the proportion of trajectories converging to  $\mathbf{x}^*$  decreases (Fig. 1h, with initial state  $x_R(0) = x_P(0) = 0.3$ ,  $x_S(0) = 0.4$ ).

Furthermore, in order to estimate the probabilities that the system state converges to the constant interior equilibrium  $\mathbf{x}^*$  for different parameter values, a heat map based on simulation results was generated on the plane  $(D, \bar{s})$  (Fig. 2). This map shows that the proportion of trajectories converging to  $\mathbf{x}^*$  is almost equal to 1 as soon as  $(D, \bar{s})$  is slightly below some straight line of negative slope, and almost equal to 0 as soon as  $(D, \bar{s})$  is slightly above the same line. Moreover, this line is close to the line of equation  $\bar{s} + D = 1$ , which is just slightly below the line of equation  $\bar{s} + (4/3)D = 1$ . This discrepancy can be explained by the fact that the condition  $\bar{s} + (4/3)D < 1$  is sufficient for stochastic stability of  $\mathbf{x}^*$  means almost convergence of the population state to  $\mathbf{x}^*$  with probability 1, and stochastic instability of  $\mathbf{x}^*$  almost convergence to  $\mathbf{x}^*$  with probability 0.

More importantly, the simulation results show the appearance of a quasi-periodic solution near the boundary of the simplex of frequency vectors  $S_3$  when the constant interior equilibrium  $\mathbf{x}^*$  loses its stochastic stability as the noise level D increases. This phenomenon shares some similarity with the appearance of a heteroclinic cycle in the deterministic rock–paper– scissors game dynamics when  $\mathbf{x}^*$  becomes unstable [9]. For this reason, the quasi-periodic solution in the stochastic dynamics is called a *noise-induced quasi-heteroclinic cycle*. The existence of this cycle has been shown by simulations and it would be interesting to prove it analytically. However, this is beyond the scope of the present paper. Moreover, we can already claim from the simulation results that, not only deterministic changes in the payoffs

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**Fig. 1** Simulation results for the stochastic differential equation in (7). Here, we take  $\bar{s} = 0.7$ . The results show that: **a** when D = 0, the constant interior equilibrium  $\mathbf{x}^* = (1/3, 1/3, 1/3)$  is asymptotically stable (where the red point represents the initial state, and the black point represents the final state); **b** when D = 0.2,  $\mathbf{x}^*$  is stochastically locally stable; **c**–**g** when D = 0.28 (panels **c** and **d**), D = 0.31 (panels **e** and **f**) and D = 0.34 (panel **g**), the proportion of trajectories converging to  $\mathbf{x}^*$  (number of times over 1000 simulations) is 0.951 for D = 0.28, but 0.062 for D = 0.31, and 0 for D = 0.34; and **h** the proportion of trajectories converging to  $\mathbf{x}^*$ 

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**Fig. 2** Estimated probabilities from simulations that the system state converges to the constant interior equilibrium  $\mathbf{x}^*$  for different parameter pairs  $(D, \bar{s})$ . The heat map shows how the stochastic stability of the system is affected by the parameter values

can lead to periodic fluctuations in a rock-paper-scissors game dynamics, but also stochastic variations as a result of environmental noise.

## **3** Conclusion

The rock–paper–scissors game is one of the most important theoretical models in evolutionary game theory, since it is the simplest game model involving cyclic dominance [9]. The continuous-time evolutionary dynamics of this model, and the corresponding theoretical results, have been used to explain not only the evolution of animal and human behaviors [2,23,33], but also to predict periodic characteristics of some gene expression dynamics [3]. In this study, we have focused our attention on the stochastic stability of equilibrium points in a continuous-time rock–paper–scissor game with random payoffs in order to show whether or not periodic dynamics can also be induced by environmental noise. We note that some previous studies on the rock–paper–scissors game in a finite population, or on a spatial network, also addressed the influence of random factors on the evolutionary dynamics [20,29,32]. However, these studies mainly focused on the effect of demographic stochasticity, especially the effect on fixation probabilities. Moreover, as shown by Hommes and Ochea [10], a stable limit cycle can occur in the rock–paper–scissors game with the logit dynamics, but this is different from the heteroclinic cycle in the classic rock–paper–scissors game with the replicator dynamics.

In this paper, we have considered a symmetric rock-paper-scissors game based on a random payoff matrix given in (2), and shown that this payoff matrix can lead to the existence of a constant interior equilibrium that does not depend on the randomness of the payoffs. Using Itô's stochastic calculus [16], we have first derived a stochastic differential equation for the rock-paper-scissors game, which extends the deterministic replicator equation when payoffs in pairwise interactions are random variables. Then we have analyzed the stochastic stability of the constant equilibrium points, the interior equilibrium point as well as the fixation states.

Our theoretical results show that: (1) none of the fixation states (i.e., the vertices  $\mathbf{e}_R$ ,  $\mathbf{e}_P$  and  $\mathbf{e}_S$ , which correspond to the three pure strategies) are expected to be stochastically stable;

and (2) as the level of random noise in payoffs increases, the constant interior equilibrium (1/3, 1/3, 1/3) may lose its stochastic stability. All our mathematical criteria for stochastic stability are in agreement with the results in the deterministic rock–paper–scissors game dynamics when random noise reduces to zero. Furthermore, we have run stochastic simulations to check the effect of random noise on the dynamics of the system. The simulation results not only match the theoretical predictions, but also show the appearance of a noise-induced quasi-heteroclinic cycle when the constant interior equilibrium loses its stochastic stability with an increase in the level of random noise. They also show that the regions for stochastic stability and stochastic instability of this equilibrium are separated by a line whose equation seems to be close to  $\bar{s} + D = 1$ , where  $\bar{s}$  is the expected cost and D the noise level. These properties would deserve further theoretical studies.

In order to further illustrate the general validity of our results, a non-symmetric rock– paper–scissors game with random payoffs where the constant interior equilibrium is not (1/3, 1/3, 1/3) has been considered too. The results in this case are shown in Supplementary Information, and they are similar.

Our analysis of the stochastic dynamics of a continuous-time rock-paper-scissors game with random payoffs might provide some possible clues for a better understanding of the evolutionary dynamics of populations in a stochastic environment.

Author contributions T-JF, JM, R-WW, SL, YT and X-DZ performed the theoretical analysis. T-JF and X-DZ ran the simulations. YT wrote the first draft. T-JF, JM, SL, YT and X-DZ revised the manuscript.

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### Declarations

Conflict of interest None declared.

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