### ORIGINAL PAPER



### **Evolutionary games with two species and delayed reciprocity**

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**Abstract** In the rich variety of biological interaction patterns, the state of an individual often does not depend solely on immediate factors but is significantly associated also with interactions or circumstances from

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the past. In evolutionary game theory with the focus on the evolution of cooperation, these phenomena frequently fall under the umbrella of delayed reciprocity. Especially in populations or systems where multiple species are considered there is significant asymmetry in the different types of interaction returns, but also in various delayed effects incurred by different species. With this motivation, this paper studies three different two-species evolutionary models: the intraspecific payoff delay model, the interspecific payoff delay model, and the all-payoff delay model. It is found that if the delay applies only to interspecific interactions, it only affects the convergence time of the cooperation rate but not the stability of the equilibrium points. In contrast, once the delay applies to intraspecific interactions, then the system transitions from asymptotic stability to oscillations around the equilibrium point as the time delay period increases. Lastly, increasing the delay value postpones convergence when the internal equilibrium point is asymptotically stable, and increases the amplitude when the system is oscillating.

**Keywords** Evolutionary game · Delayed reciprocity · Multiple species · Stability

### 1 Introduction

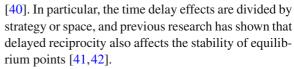
Over the past few decades, research using evolutionary game theory has provided many explanations as to why natural selection might favor the evolution of



cooperation [1–8]. Among these, reciprocity has perhaps been most widely studied and this in various forms [9]. In general, reciprocity can be divided into two categories, namely direct and indirect reciprocity [10,11]. The former relies only on the performance in repeated direct interactions [12,13], while the latter also takes into account the experiences of others [14–16], possibly in social networks [17,18], or related to reputation in general [19]. In many other cases, altruism typically does not bring any immediate paybacks, rather on the contrary, but it does provide long-term benefits; hence, the term delayed reciprocity for this type of interactions [20,21].

The significance of time delays in action is readily understood in biological systems and has been demonstrated to possibly affect the stability of equilibrium points as well as the evolution of cooperation [22–26]. Likewise, the effect has been shown to be valid within the framework of evolutionary game theory. Specifically, the stability of the interior equilibrium of the pure strategy model under this long-term effect depends not only on the properties of the payoff matrix, but also on the effect of time delays [27]. Thereafter, the impact of strategy-related asymmetric delays, on the evolutionary dynamics of the system's equilibrium point, has received further attention and examination [28]. The uncertainty of the existence of delay periods in realistic interactions and its consequent consideration as a random variable appear in the study of evolutionary game theory. The results reveal that the interior equilibrium point is asymptotically stable for any rate parameter value under an exponential delay distribution; they also derive sufficient conditions for asymptotic stability under the uniform and Erlang distributions [29].

In addition to the classical evolutionary game theory explorations noted above, research including coevolution [30] has also received much attention in recent years [31–33]. In environmental feedback games [34–38] involving resource growth, the introduction of delay effects may lead to the system oscillating between depleted and replenished environments and between cooperation and defection behavior [39]. When the relevant coevolutionary issues are revisited, the nature of the growable resource or environment becomes the simple abstraction of other species involved in secondary interactions, which further influences the study of multi-group competition. In multi-population approaches, individuals may engage in different types of interactions with opponents from different groups



Inspired by the differentiated patterns of interaction in different biological systems [43,44], a realization was made that delay effects may also be species-dependent and that immediate and delayed reciprocity may co-exist. Aiming to address these issues, the replicator dynamics were developed for three scenarios: interspecific payoff delay systems and all-payoff delay systems. The results show that if the delay effect acts only on interspecific interactions, it only affects the convergence time of the cooperation rate but not the stability of the equilibrium point. In contrast, once the delay effect acts on intraspecific payoffs, the system transitions from asymptotic stability to oscillation around the equilibrium point as the time delay period increases.

### 2 Replicator dynamics in two species

To introduce the main framework of the multi-species evolutionary game, in this section, it is assumed that the population sizes of both species (A and B) are infinitely large( $N_{A,B} \to +\infty$ ). Interactions within and among populations are considered as randomly matched pairwise games. At each time step, each individual may interact with an opponent from the same species with probability p or from another species with probability 1-p. For the pairwise game, each participant can choose cooperation(C) or defection(D), and the corresponding payoff matrices can be described as:

$$M_{1} = \begin{matrix} C_{A} & D_{A} & & C_{B} & D_{B} \\ M_{1} = \begin{matrix} C_{A} & \begin{pmatrix} R_{1} & S_{1} \\ T_{1} & P_{1} \end{pmatrix}, & M_{2} = \begin{matrix} C_{A} & \begin{pmatrix} R_{2} & S_{2} \\ T_{2} & P_{2} \end{pmatrix}, \\ C_{A} & D_{A} & & C_{B} & D_{B} \end{matrix}$$

$$M_{3} = \begin{matrix} C_{B} & \begin{pmatrix} R_{3} & S_{3} \\ T_{3} & P_{3} \end{pmatrix}, & M_{4} = \begin{matrix} C_{B} & \begin{pmatrix} R_{4} & S_{4} \\ T_{4} & P_{4} \end{pmatrix}.$$

where  $M_1$  and  $M_4$  are used for describing the intraspecific payoffs of species A and B, while  $M_2$  and  $M_3$  are used for the interspecific payoffs. Specifically, when the four matrices are identical, the system is consistent with classical single-species replicator dynamics. The more general case is that species variability often leads to asymmetric payoff patterns. Thus, it can be



**Table 1** Parameters in the model

| Value                               |
|-------------------------------------|
| $p(R_1 + P_1 - S_1 - T_1)$          |
| $(1-p)(R_2+P_2-S_2-T_2)$            |
| $(1-p)(R_3+P_3-S_3-T_3)$            |
| $p(R_4 + P_4 - S_4 - T_4)$          |
| $p(S_1 - P_1) + (1 - p)(S_2 - P_2)$ |
| $(1-p)(S_3-P_3)+p(S_4-P_4)$         |
|                                     |

derived the following expected payoffs, relying on different payoff matrices:

$$\begin{cases} P_A^C = p[R_1x + S_1(1-x)] + (1-p)[R_2y + S_2(1-y)] \\ P_A^D = p[T_1x + P_1(1-x)] + (1-p)[T_2y + P_2(1-y)] \\ P_B^C = (1-p)[R_3x + S_3(1-x)] + p[R_4y + S_4(1-y)] \\ P_B^D = (1-p)[T_3x + P_3(1-x)] + p[T_4y + P_4(1-y)] \end{cases}$$

where x and y represent the cooperation frequency of species A and B. The replicator dynamics in two species can be written as follows:

$$\begin{cases} \dot{x} = x(1-x)(P_A^C - P_A^D) \\ \dot{y} = y(1-y)(P_R^C - P_R^D) \end{cases}$$
 (2)

By substituting the expected payoffs in Eq.(1) into Eq.(2), it is derived as follows:

$$\begin{cases} \frac{dx}{dt} = x(1-x)[a_1x + a_2y + b_1] \\ \frac{dy}{dt} = y(1-y)[a_3x + a_4y + b_2] \end{cases}$$
(3)

where the parameters are shown in Table 1.

The dynamic system in Eq.(3) has a unique interior equilibrium point  $(x^*, y^*) = (\frac{a_4b_1 - a_2b_2}{a_2a_3 - a_1a_4}, \frac{a_3b_1 - a_1b_2}{a_1a_4 - a_2a_3})$ . In addition, there are other four vertex fixed points, namely  $(x^*, y^*) = (0, 0), (0, 1), (1, 0), (1, 1)$ , and four boundary fixed points, namely,  $(0, -\frac{b_2}{a_4})$ ,  $(1, -\frac{a_3+b_2}{a_4})$ ,  $(-\frac{b_1}{a_1}, 0)$ ,  $(-\frac{a_2+b_1}{a_1}, 1)$ . In order to simplify the simulations required later,

In order to simplify the simulations required later, only a few parameters are chosen to characterize the asymmetric patterns of competition and reciprocity that exist in multi-species interactions. It is worth emphasizing that the payoff coupling and the setting of parameter values here are unrelated to the interactions of real biological systems but merely provide a basis for verifying the validity of the theoretical approach and demon-

strating specific evolutionary dynamics. Specifically, the payoff matrix can be expressed as:

$$M_{1} = \begin{matrix} C_{A} & D_{A} & & C_{B} & D_{B} \\ D_{A} & \begin{pmatrix} 1 & \alpha S \\ T & 0 \end{pmatrix}, & M_{2} = \begin{matrix} C_{A} & \begin{pmatrix} 1 & \alpha S \\ T & 0 \end{pmatrix}, \\ C_{A} & D_{A} & & C_{B} & D_{B} \\ M_{3} = \begin{matrix} C_{B} & \begin{pmatrix} 1 & S \\ \alpha T & 0 \end{pmatrix}, & M_{4} = \begin{matrix} C_{B} & \begin{pmatrix} 1 & S \\ \alpha T & 0 \end{pmatrix}. \end{matrix}$$

where  $\alpha$  is used to control asymmetry between species.

Subsequently, we construct the evolutionary game models for different time delay effects and analyze the stability of their interior equilibrium points, respectively.

## 3 Replicator dynamics of intraspecific payoffs delay

This section explores the situation when the delay is applied to intraspecific payoffs, which means the expected intraspecific payoff of species A(B) at time t depends on the interaction at time  $t - \tau_1(t - \tau_2)$ . Thus, the expected payoffs in Eq.(1) can be rewritten as:

$$\begin{cases} P_A^C(t) = p[R_1x(t-\tau_1) + S_1(1-x(t-\tau_1))] \\ + (1-p)[R_2y(t) + S_2(1-y(t))] \\ P_A^D(t) = p[T_1x(t-\tau_1) + P_1(1-x(t-\tau_1))] \\ + (1-p)[T_2y(t) + P_2(1-y(t))] \\ P_B^C(t) = (1-p)[R_3x(t) + S_3(1-x(t))] \\ + p[R_4y(t-\tau_2) + S_4(1-y(t-\tau_2))] \\ P_B^D(t) = (1-p)[T_3x(t) + P_3(1-x(t))] \\ + p[T_4y(t-\tau_2) + P_4(1-y(t-\tau_2))] \end{cases}$$

$$(4)$$

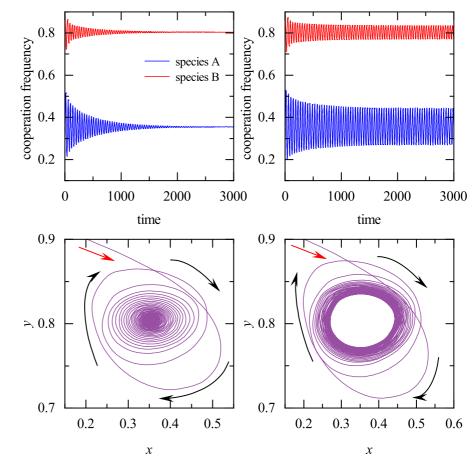
By substituting the terms in Eq.(4) to the replicator dynamics in Eq.(2), the delay differential system is transformed as follows:

$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} = x(t)(1-x(t))[a_1x(t-\tau_1) + a_2y(t) + b_1] \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} = y(t)(1-y(t))[a_3x(t) + a_4y(t-\tau_2) + b_2] \end{cases}$$
(5)

Next, we investigate the stability of the interior equilibrium of the system in Eq. (5). The linearized approximation around  $x = x^*$  and  $y = y^*$  can be given by:

$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} \approx \delta_1 x(t - \tau_1) + \delta_2 y(t) \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} \approx \delta_3 x(t) + \delta_4 y(t - \tau_2) \end{cases}$$
 (6)

Fig. 1 Simulation results for the intraspecific payoff delay model when  $\tau_1 = \tau_2$ . Since  $\tau^* \approx 10.465$  is calculated,  $\tau = 10.2$  is adopted in the left column and  $\tau = 10.6$  in the right column, and thereby observe the evolutionary dynamics of the interior equilibrium point under stability and instability. The other parameters are S = 0.5, T = 1.5,  $\alpha = 0.8$ , p = 0.8



where  $\delta_1 = a_1 x^* (1 - x^*)$ ,  $\delta_2 = a_2 x^* (1 - x^*)$ ,  $\delta_3 = a_3 y^* (1 - y^*)$ , and  $\delta_4 = y^* (1 - y^*) a_4$ .

We first investigate the symmetric delay ( $\tau_1 = \tau_2 = \tau$ ) by applying the Laplace transform to system (6); there is the following characteristic equation:

$$(\lambda^2 - \delta_2 \delta_3) e^{\lambda \tau} + \delta_1 \delta_4 e^{-\lambda \tau} - \lambda (\delta_1 + \delta_4) = 0.$$
 (7)

Let  $\lambda = iw$  and substitute it into the characteristic equation, by separating the real and imaginary parts, then it follows that

$$\begin{cases} (w^2 + \delta_2 \delta_3 - \delta_1 \delta_4) \cos(\tau w) = 0\\ (w^2 + \delta_2 \delta_3 + \delta_1 \delta_4) \sin(\tau w) = -(\delta_1 + \delta_4)w \end{cases}$$
(8)

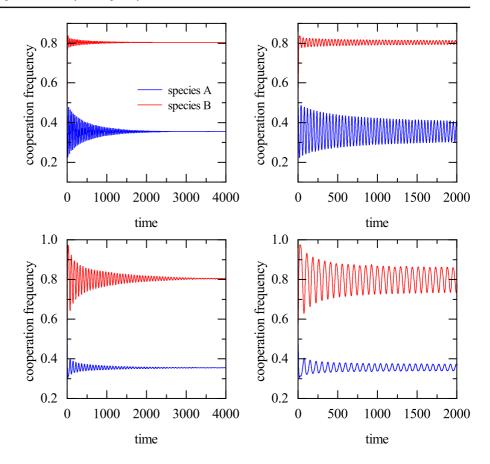
From Eq.(8), it can be derived that  $\tau^* = \frac{\pi}{2w}$  is the threshold for the transition through a Hopf bifurcation, where  $w = \frac{1}{2} \left( \pm (\delta_1 + \delta_4) \pm \sqrt{\delta_1^2 - 2\delta_1 \delta_4 + \delta_4^2 - 4\delta_2 \delta_3} \right)$ . Thus, when  $\tau < \tau^*$ , the unique interior equilibrium point is asymptotically stable.

With the parameters setting in Fig. 1, it can be calculated that  $w \approx 0.150$  and  $\tau^* \approx 10.465$ . The interior equilibrium point  $(x^*, y^*) \approx (0.354, 0.804)$  is asymptotically stable when applying  $\tau = 10.2 < \tau^*$  (in the left panel), and it is unstable when  $\tau = 10.6 > \tau^*$  (in the right panel). It can be found that asymptotic stability is associated with the phenomenon of the cooperation rate gradually converging individually to its interior fixed point over time, whereas instability implies that the cooperation rate persists in periodic oscillations within a specific range. In addition, the evolutionary trace on the left shows them spiraling toward and eventually into the interior equilibrium point, while the case on the right shows them not approaching nor moving away and finally forming a limit ring. Note that the red arrows in the diagram indicate the initial point, while the black arrows indicate the direction of evolution.

For the case of asymmetric delays between two species, if  $\tau_1 \neq \tau_2$ , then the following characteristic equation holds:



Fig. 2 Simulation results for the intraspecific payoff delay model when  $\tau_1 \neq \tau_2$ . When  $\tau_2 = 5(\tau_1 = 5)$  is a fixed value, hence  $\tau_1^* \approx 9.774 (\tau_2^* \approx 17.222).$ In the top row, the values of  $\tau_1$  in the left and right panels are taken as 9.6 and 9.8, respectively, while in the bottom row, the left and right panels take  $\tau_2$  equal to 17 and 17.5, respectively. The other parameters are  $S = 0.5, T = 1.5, \alpha =$ 0.8, p = 0.8



$$\lambda^2 - \lambda(\delta_1 e^{-\lambda \tau_1} + \delta_4 e^{-\lambda \tau_2}) + \delta_1 \delta_4 e^{-\lambda(\tau_1 + \tau_2)} - \delta_2 \delta_3 = 0 \tag{9}$$

Similarly let  $\lambda = i w$ . Then

$$\begin{cases}
-w^2 - w\delta_1 \sin(w\tau_1) - w\delta_4 \sin(w\tau_2) \\
-\delta_1\delta_4 \cos[w(\tau_1 + \tau_2)] = 0 \\
-w\delta_1 \cos(w\tau_1) - w\delta_4 \cos(w\tau_2) \\
-\delta_1\delta_4 \sin[w(\tau_1 + \tau_2)] = 0
\end{cases}$$
(10)

Compared to Eq. (8), there is an additional unknown time delay variable in Eq. (10), and therefore only if one of the values is fixed does the other have a solution. Let  $\tau_1^*(\tau_2^*)$  be the critical value of the transition when the value of  $\tau_2(\tau_1)$  is given, then:

$$\begin{cases} \sin(w\tau_1^*) = -\frac{\frac{\delta_2\delta_3(\delta_4\sin(\tau_2w) + w)}{\delta_4^2 + w^2 + 2\delta_4w\sin(\tau_2w)} + w}{\delta_1} \\ \cos(w\tau_1^*) = \frac{\delta_2\delta_3\delta_4\cos(\tau_2w)}{\delta_1(\delta_4^2 + w^2 + 2\delta_4w\sin(\tau_2w))} \\ \sin(w\tau_2^*) = -\frac{w^3 + \delta_1(\delta_2\delta_3 + 2w^2)\sin(\tau_1w) + \delta_1^2w + \delta_2\delta_3w}{\delta_4(\delta_1^2 + w^2 + 2\delta_1w\sin(\tau_1w))} \\ \cos(w\tau_2^*) = \frac{\delta_1\delta_2\delta_3\cos(\tau_1w)}{\delta_4(\delta_1^2 + w^2 + 2\delta_1w\sin(\tau_1w))} \end{cases}$$

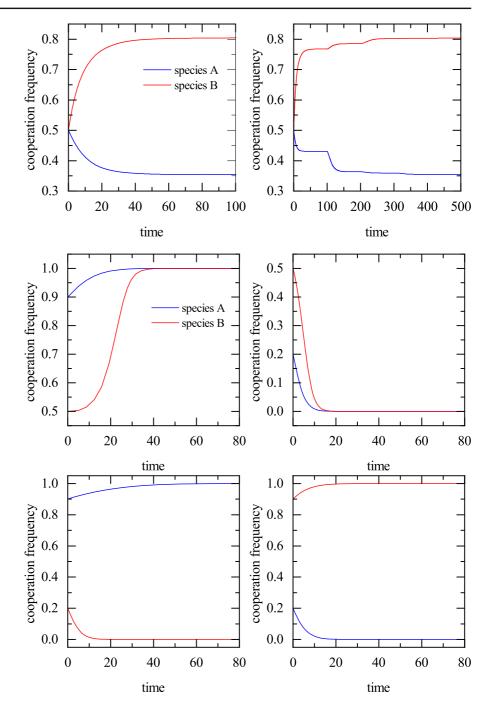
The solution is that 
$$\tau_1^* = \arccos\left(\frac{\delta_2\delta_3\delta_4\cos(\tau_2w)}{\delta_1(\delta_4^2+w^2+2\delta_4w\sin(\tau_2w))}\right)/w$$
, and  $\tau_2^* = \arccos\left(\frac{\delta_1\delta_2\delta_3\cos(\tau_1w)}{\delta_4(\delta_1^2+w^2+2\delta_1w\sin(\tau_1w))}\right)/w$ . It is worth mentioning that the solutions for  $w$  are different when solving separately for  $\tau_1^*$  and  $\tau_2^*$ . Furthermore, when  $\tau_2$  is given, the interior equilibrium point  $(x^*, y^*)$  is asymptotically stable if  $\tau_1 < \tau_1^*$ ; alternatively, when  $\tau_1$  is given, it is asymptotically stable if  $\tau_2 < \tau_2^*$ .

In Fig. 2, numerical simulations are carried out with the same parameter values as in Fig. 1 to examine the effect of asymmetric time delays on stability. By fixing  $\tau_2 = 5$  ( $\tau_1 = 5$ ), it can be calculated that  $\tau_1^* \approx 9.774$  ( $\tau_2^* \approx 17.22$ ). In the panels, the evolutionary dynamics are shown when values are taken around the critical values. In the left column, the cooperation frequencies eventually converge to the asymptotically stable interior equilibrium points after sufficient relaxation ( $\tau_1 = 9.6$  in the top panel and  $\tau_2 = 17$  in the bottom panel), while in the right column, the system is continuously in an unstable state of periodic oscillations



**Fig. 3** A comparison of non-delay systems  $(\tau_1 = \tau_2 = 0 \text{ in the left})$  panel) with interspecific payoff delay systems  $(\tau_1 = \tau_2 = 50 \text{ in the right})$  panel). The simulation results show that the delay effect does not affect the stability of the system, but rather postpones the convergence time. The other parameters are  $S = 0.5, T = 1.5, \alpha = 0.8, p = 0.8$ 

**Fig. 4** Evolutionary multistability resulting from different initial points. Based on a non-time delay system, the simulation demonstrates that the unstable interior equilibrium is attracted to other different equilibria, resulting in multi-stable evolutionary dynamics. The other parameters are S = -0.5, T = 0.8,  $\alpha = 0.8$ , p = 0.8



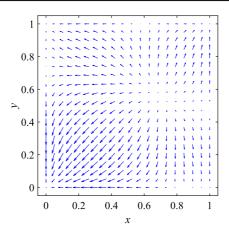
( $\tau_1 = 9.8$  in the top panel and  $\tau_2 = 17.5$  in the bottom panel).

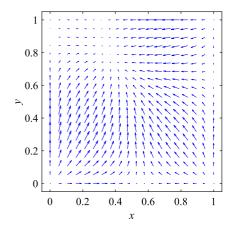
# 4 Replicator dynamics of interspecific payoffs delay

In this section, we study the replicator dynamics when interspecific payoffs are delayed, i.e., the interspecific payoffs of species A(B) at time t in dependence on interactions at time  $t - \tau_1(t - \tau_2)$ , whereas intraspecific



Fig. 5 The evolutionary trajectory of instability (left panel) and stability (right panel). The parameters on the left are T=0.8, S=0.5 and the right are T=1.5, S=0.5. The common parameter values include  $\alpha=0.8$ , p=0.8





payoffs are obtained immediately. Then, the expected payoff in Eq.(1) can be rewritten as follows:

$$\begin{cases} P_A^C(t) = p[R_1x(t) + S_1(1 - x(t))] \\ + (1 - p)[R_2y(t - \tau_1) + S_2(1 - y(t - \tau_1))] \\ P_A^D(t) = p[T_1x(t) + P_1(1 - x(t))] \\ + (1 - p)[T_2y(t - \tau_1) + P_2(1 - y(t - \tau_1))] \\ P_B^C(t) = (1 - p)[R_3x(t - \tau_2) + S_3(1 - x(t - \tau_2))] \\ + p[R_4y(t) + S_4(1 - y(t))] \\ P_B^D(t) = (1 - p)[T_3x(t - \tau_2) + P_3(1 - x(t - \tau_2))] \\ + p[T_4y(t) + P_4(1 - y(t))] \end{cases}$$

$$(11)$$

By substituting the terms in Eq. (11) to the replicator dynamics in Eq. (2), one has the following system:

$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} = x(t)(1 - x(t))[a_1x(t) + a_2y(t - \tau_1) + b_1] \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} = y(t)(1 - y(t))[a_3x(t - \tau_1) + a_4y(t) + b_2] \end{cases}$$
(12)

Next, we investigate the stability of the interior equilibrium of the system. The linearized system in Eq.(12) around  $x = x^*$ , and  $y = y^*$  is:

$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} \approx \delta_1 x(t) + \delta_2 y(t - \tau_1) \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} \approx \delta_3 x(t - \tau_2) + \delta_4 y(t) \end{cases}$$
(13)

By means of the Laplace transformation, the following characteristic equation is obtained:

$$\lambda^{2} + a\lambda + b\lambda e^{-\lambda(\tau_{1} + \tau_{2})} + c + de^{-\lambda(\tau_{1} + \tau_{2})} = 0 \quad (14)$$

where  $a = -(\delta_1 + \delta_4)$ , b = 0,  $c = \delta_1 \delta_4$ ,  $d = -\delta_2 \delta_3$ . As  $b^2 + 2c - a^2 < 0$ , and when  $0 < x^* < y^*$ ,  $0 < y^* < 1$  is satisfied, it gives  $c^2 - d^2 > 0$ . Hence, there is no purely imaginary solution for this equation, and the stability of the interior equilibrium point is unaffected by the time delay terms. As shown in Fig. 3, the evolutionary dynamics without and with time delay terms are shown in the left and right panels, respectively. It can be observed that the cooperation rate with the identical initial condition (0.5, 0.5) ultimately evolves to the same state, namely the stable interior equilibrium point  $(x^*, y^*)$ , and the time delay effect is mainly in postponing the time for the system to evolve into a steady state.

Although the stability is unaffected by the delayed interspecific returns, it is still of significant value to explore the stability of the unique interior equilibrium point. The simple simulations in Fig. 4 reveal the existence of multiple stability when the interior fixed point is unstable. Specifically, the identical parameter values settings were applied in the four subplots; however, the unique variation of the initial cooperation rate ultimately resulted in the system being attracted to four different vertex points, namely (1, 1), (0, 0), (1, 0) and (0, 1).

We subsequently analyze the stability of systems in the absence of time delays. Applying Lyapunov's stability discriminant, the Jacobian matrix can be written as:

$$J = \begin{bmatrix} \delta_1 & \delta_2 \\ \delta_3 & \delta_4 \end{bmatrix} \tag{15}$$

The eigenvalues are solved as:



$$\begin{cases} \lambda_1 = \frac{1}{2} (-\sqrt{\delta_1^2 - 2\delta_4 \delta_1 + \delta_4^2 + 4\delta_2 \delta_3} + \delta_1 + \delta_4) \\ \lambda_2 = \frac{1}{2} (\sqrt{\delta_1^2 - 2\delta_4 \delta_1 + \delta_4^2 + 4\delta_2 \delta_3} + \delta_1 + \delta_4) \end{cases}$$
(16)

The unique interior equilibrium point  $(x^*, y^*)$  is stable when the corresponding two eigenvalues both have negative real parts, and it is unstable if any eigenvalue has a positive real part. With the same parameter values settings in Fig. 4, it is clear that the interior equilibrium point  $(x^*, y^*) \approx (0.695, 0.553)$  is unstable, as the eigenvalues are calculated as  $\lambda_1 \approx 0.089 > 0$ and  $\lambda_2 \approx 0.183 > 0$ , respectively. Moreover, the details of the evolution both for stable and unstable state are reflected in Fig. 5. In the left panel, the vector field shows an unstable interior equilibrium point, where any deviation from that equilibrium point eventually converges to one of the vertex points. In the right plot, by applying the same parameter values as in Fig. 1, it can be seen that any initial point eventually converges to the unique internal equilibrium point  $(x^*, y^*)/approx(0.354, 0.804).$ 

### 5 Replicator dynamics of all-payoffs delay

In this section, we focus on the replicator dynamics when all payoffs are delayed, which suggests that all the payoffs of species A(B) at time t are dependent on the interactions at time  $t - \tau_1(t - \tau_2)$ . The expected payoffs for the four types of players are defined as:

$$\begin{cases} P_A^C(t) = p[R_1x(t-\tau_1) + S_1(1-x(t-\tau_1))] \\ + (1-p)[R_2y(t-\tau_1) + S_2(1-y(t-\tau_1))] \\ P_A^D(t) = p[T_1x(t-\tau_1) + P_1(1-x(t-\tau_1))] \\ + (1-p)[T_2y(t-\tau_1) + P_2(1-y(t-\tau_1))] \\ P_B^C(t) = (1-p)[R_3x(t-\tau_2) + S_3(1-x(t-\tau_2))] \\ + p[R_4y(t-\tau_2) + S_4(1-y(t-\tau_2))] \\ P_B^D(t) = (1-p)[T_3x(t-\tau_2) + P_3(1-x(t-\tau_2))] \\ + p[T_4y(t-\tau_2) + P_4(1-y(t-\tau_2))] \end{cases}$$

$$(17)$$

Then, the dynamical system with time delay is given:

$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} = x(t)(1-x(t))[a_1x(t-\tau_1) + a_2y(t-\tau_1) + b_1] \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} = y(t)(1-y(t))[a_3x(t-\tau_1) + a_4y(t-\tau_1) + b_2] \end{cases}$$
(18)

In order to study the stability of the interior fixed point, the system is linearized at the equilibrium point



$$\begin{cases} \frac{\mathrm{d}x(t)}{\mathrm{d}t} = \delta_1 x(t - \tau_1) + \delta_2 y(t - \tau_1) \\ \frac{\mathrm{d}y(t)}{\mathrm{d}t} = \delta_3 x(t - \tau_2) + \delta_4 y(t - \tau_2) \end{cases}$$
(19)

When  $\tau_1 = \tau_2$ , the characteristic equation is given by:

$$(\delta_1 \delta_4 - \delta_2 \delta_3) e^{-\lambda \tau^*} - \lambda (\delta_1 + \delta_4) + \lambda^2 e^{\lambda \tau} = 0, \quad (20)$$

Letting  $\lambda = iw$  and separating the real and imaginary parts, from which one has:

$$\begin{cases} w^2 + w(\delta_1 + \delta_4)\sin(w\tau) - (\delta_1\delta_4 - \delta_2\delta_3)\cos(2w\tau) = 0\\ (\delta_1\delta_4 - \delta_2\delta_3)\sin(2w\tau) + w(\delta_1 + \delta_4)\cos(w\tau) = 0 \end{cases}$$
(21)

From Eq.(21), one can derive  $\tau^* = \frac{\pi}{2w}$ , and  $w = \frac{1}{2}(\pm\sqrt{u^2-4v}\pm v)$ , where  $u = \delta_1\delta_4 - \delta_2\delta_3$ ,  $v = \delta_1 + \delta_4$ . Therefore, the interior equilibrium point  $(x^*, y^*)$  is asymptotically stable when  $\tau < \tau^*$ . In Fig. 6, the same parameter values as in Fig. 1 are applied, whereby it is easy to obtain  $\tau^* \approx 8.966$ . The stability and instability of the interior equilibrium point and the corresponding dynamics characteristics are illustrated in the left and right columns of Fig. 6, respectively. From the left column, taking values away from the threshold  $\tau^*$  results in faster convergence of the cooperation rate, while in the right column, values of  $\tau$  away from this Hopf bifurcation point result in larger amplitudes of the cooperation rate. Moreover, the numerical simulations also prove the correctness of the theoretical derivation.

When  $\tau_1 \neq \tau_2$ , through fixing one of the time delay terms, the critical value of another one can be easily derived. From the linear dynamics shown in Eq. (19), the characteristic equation gives:

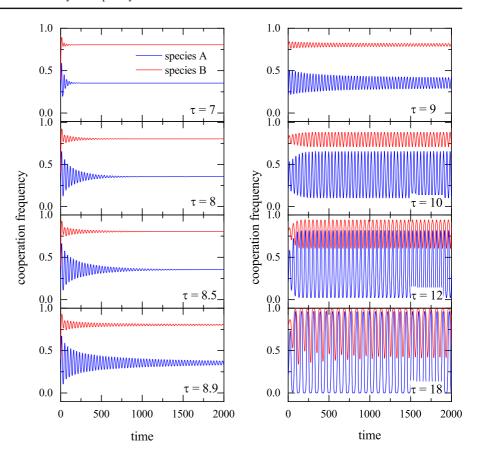
$$\lambda^2 - \lambda(\delta_1 e^{-\lambda \tau_1} + \delta_4 e^{-\lambda \tau_2}) + (\delta_1 \delta_4 - \delta_2 \delta_3) e^{-\lambda(\tau_1 + \tau_2)} = 0$$
(22)

Let  $\lambda = i w$  a pure imaginary, one has:

$$\begin{cases} \sin(w\tau_1) = -\frac{w(u(\delta_4 + w\sin(\tau_2 w)) + \delta_1 w(\delta_4 \sin(\tau_2 w) + w))}{u^2 + \delta_1^2 w^2 + 2u\delta_1 w\sin(\tau_2 w)} \\ \cos(w\tau_1) = \frac{w^2(u - \delta_1 \delta_4)\cos(\tau_2 w)}{u^2 + \delta_1^2 w^2 + 2u\delta_1 w\sin(\tau_2 w)} \\ \sin(w\tau_2) = -\frac{w(w(u\sin(\tau_1 w) + \delta_4 w) + \delta_1(u + \delta_4 w\sin(\tau_1 w)))}{u^2 + \delta_4^2 w^2 + 2u\delta_4 w\sin(\tau_1 w)} \\ \cos(w\tau_2) = \frac{w^2(u - \delta_1 \delta_4)\cos(\tau_1 w)}{u^2 + \delta_4^2 w^2 + 2u\delta_4 w\sin(\tau_1 w)} \end{cases}$$



Fig. 6 Simulation results for the interspecific payoff delay model when  $\tau_1 = \tau_2 = \tau$ . With the applied parameter values, the critical value comes to  $\tau^* \approx 8.966$ . By using  $\tau = 7, 8, 8.5$  and 8.9 in the left column and  $\tau = 9, 10, 12 \text{ and } 18 \text{ in the}$ right column, various characteristics regarding the evolutionary dynamics can be observed. Additional parameters for this figures are S = 0.5, T = 1.5,  $\alpha = 0.8, p = 0.8$ 



It can be further calculated that  $\tau_1^* = \arccos\left(\frac{w^2(u-\delta_1\delta_4)\cos(\tau_2w)}{u^2+\delta_1^2w^2+2u\delta_1w\sin(\tau_2w)}\right)/w$ ,  $\tau_2^* = \arccos\left(\frac{w^2(u-\delta_1\delta_4)\cos(\tau_1w)}{u^2+\delta_1^2w^2+2u\delta_4w\sin(\tau_1w)}\right)$ , are the critical values at which the system goes from stability to oscillation when the values of  $\tau_2$  and  $\tau_1$  are given, respectively. In the top(bottom) row of Fig. 7, the time delayed term  $\tau_2(\tau_1)$  is fixed as 5, and the critical values are worked out to be  $\tau_1^*\approx 9.653(\tau_2^*\approx 19.351)$ . The convergence and oscillations of the cooperation rate demonstrate asymptotically stable and unstable equilibria resulting from the corresponding time delay values of  $\tau_1$  and  $\tau_2$ .

#### 6 Conclusion

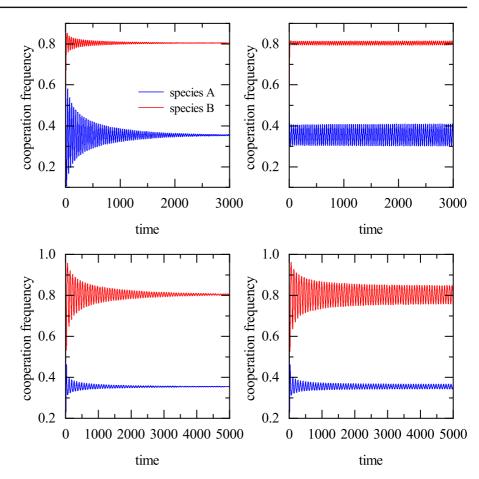
Time delay effect is prevalent in systems ranging from biology, economics to signal system and has significant impacts on their proper functioning [45–47]. Typically, delayed reciprocity, a pattern of mutual assistance in which individuals exchange altruistic behavior in the present for rewards in future moments, is eas-

ily observed in the reproductive processes of birds and mammalian organisms [21,48,49]. When individuals from multiple species interact, they need to potentially engage in both intraspecific and interspecific interactions. Due to variability across species, these interaction patterns may be asymmetric; therefore, four matrices are adopted to characterize the gains in these interactions. What's more, for individuals from any species, these different types of gains may be immediate or delayed.

To analyze the impact of delay effects on the cooperative system in the above complex scenario, three evolutionary game models based on replicator dynamics constructed in this paper are: the intraspecific payoff delay model, interspecific payoff delay model, and all-payoff delay model. The main result is that: if the delay acts on intraspecific payoffs (intraspecific payoff delay and all-payoffs delay model), the system undergoes a transition from asymptotic stability to oscillation around the internal equilibrium point as the delay period increases; otherwise, if delay applies only to interspecific interactions, it affects only the conver-



Fig. 7 Simulation results for the interspecific payoff delay model when  $\tau_1 \neq \tau_2$ . In the top and bottom rows,  $\tau_2$  and  $\tau_1$  are fixed at 5, respectively, and theoretical calculations indicate that  $\tau_1^* = 9.653$  and  $\tau_2^* = 19.351$ . In the top (bottom) row,  $\tau_1 = 9.5$  and  $9.7(\tau_2 = 19.3 \text{ and } 19.4) \text{ are}$ employed in the left and right panels, respectively. Thus, the stable and unstable evolutionary dynamics are illustrated in the left and right columns, respectively. The other parameters are  $S = 0.5, T = 1.5, \alpha =$ 0.8, p = 0.8



gence time of the cooperation rate. Moreover, it is shown that increasing the delay value postpones convergence when the internal equilibrium point is asymptotically stable, and increases the amplitude when the system is oscillating.

In summary, this paper investigated the impact of time-delay effects associated with species and interactions on cooperative systems. Although the proposed idealized model is not directly applicable to the analysis of realistic problems, it is an important addition to the study of multi-species evolutionary games. In future work, we would like to continue exploring other factors in multispecies interactions that may influence cooperation and evolutionary dynamics, such as stochastic, impulse effects [26,50,51].

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### **Declarations**

**Competing interest** The authors declare that they have no competing interest.

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