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SPECIAL ISSUE - CONTROL-THEORETIC APPROACHES FOR SYSTEMS IN THE LIFE SCIENCES

The Impact of Irrational Behaviours in the Optional Prisoner's Dilemma with Game-Environment Feedback

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Summary

In the optional prisoner's dilemma (OPD), players can choose to cooperate and defect as usual, but can also abstain as a third possible strategy. This strategy models the players' participation in the game and is a relevant aspect in many settings, e.g. social networks or opinion dynamics, e.g., during an election abstention is an option. In this paper, we provide a formulation of the OPD where we consider irrational behaviours in the population inspired by prospect theory. Prospect theory has gained increasing popularity in recent times because it can capture aspects such as reference dependence or loss aversion, which are common in human behaviour. This element is original in our formulation of the game and is incorporated in our framework through pairwise comparison dynamics. Recently, the impact of the environment has been studied in the form of feedback on the population dynamics. Another element of novelty in our work is the extension of the game-environment feedback to the OPD in two forms of dynamics, the replicator and the pairwise comparison. The contribution of this paper is threefold. First, we propose a modelling framework where prospect theory is used to capture irrational behaviours in an evolutionary game with game-environment feedback. Second, we carry out the stability analysis of the system equilibria and discuss the oscillating behaviours arising from the game-environment feedback. Finally, we extend our previous results to the OPD and we discuss the main differences between the model resulting from the replicator dynamics and the one resulting from the pairwise comparison dynamics.

KEYWORDS:

Evolutionary games, game theory, pairwise comparison dynamics, nonlinear dynamics, gameenvironment feedback, prospect theory.

1 | INTRODUCTION

Evolutionary game theory studies the evolution of strategic interactions in a population of rational decision makers based on suitable incentives, which are given in the form of strategy-dependent payoffs^{1,2}. The popularity of a given strategy is influenced by the system dynamics and the incentives given to an individual for choosing that strategy, thus leading to myopic behaviours where the favoured option is not the global best for the population. This is the case for the well-known prisoner's dilemma (PD), in which the dominant strategy is defection³. In the setting of finite games, many evolutionary dynamics have been used, including best response dynamics, the Brown-von Neuman-Nash dynamics and replicator dynamics to mention a few. The latter

are recognised to be the ones most widely used⁴. However, regardless of the mathematical model used, the common game setting involves fixed incentives associated with each strategy. This limitation does not consider the role of the environment in affecting the game dynamics and therefore the frequency of the strategies in the population.

A recent line of research, initiated in the work by Weitz *et al.*⁵, has attracted a great attention as it proposes a new way to model the reciprocal dependence of the payoffs on the environment and vice versa, taking into account the enhancement and degradation effects on an environmental resource. This is done through a direct dependence of the payoff matrix on the environment, giving rise to interesting system dynamics characterized by oscillatory behaviours and equilibria on the boundary of the phase space. The resulting oscillations correspond to closed periodic orbits. Limit cycles have been observed also when a time-scale difference between the game and the environment dynamics is considered⁶.

This feedback mechanism is believed to be able to explain the complexity of real-world systems for which one often observes bi-directional feedback between the state of the environment and the incentives associated to each strategy⁶. Interactions of this kind can be found in a wide range of disciplines, including sociology, economics and animal behaviour^{7,8,9,10}. An example of this in human systems is the individuals' decision to vaccinate or not, which would result in otherwise-preventable infectious diseases in children and then an increasing incentive to vaccinate^{11,12,13}. In ecology, an example can be found in plant nutrient acquisition where the competitive balance between the interactions of different species and the availability of environmental resources alter the nature of the competitive process of nitrogen fixation¹⁴.

The work by Su *et al.* has taken another direction by studying the impact of the environment and its evolution through game transitions, namely a framework where players move from playing one game and its associated payoff matrix to another one based on the environmental resource¹⁵. Chen and Szolnoki have applied the concept of game-environment feedback to punishment and inspection in the setting of governing the commons¹⁶. Finally, another line of research has explored the asymmetric aspects of this topic, both in the case of asymmetric evolutionary dynamics and in the case of asymmetrical game-environment feedback^{17,18}.

Game-environment feedback, or in general coevolutionary game theory, has generated increasing interest in the control community, where the design of adequate control policies play a crucial role in achieving a specific system behaviour^{19,20}. An example of the use of game-environment feedback in control is the work by Paarporn *et al.* where the controlled system exhibits oscillatory behaviours due to deprecation of the environmental resource²¹. Examples from such a wide range of research areas show that an understanding of the dynamics in the presence of game-environment feedback is a crucial aspect for a deeper awareness of complex real-life systems. In the life sciences, an example in the context of the collective decision-making process originating in house-hunting honeybee swarms is given by the work by Baar and Bauso, which aims to incorporate gameenvironment feedback through the parameters of the model²². Recently, the collective decision-making process in honeybees has been studied through the development of the optimal control problem, where the parameters of the corresponding mean-field game model act as an implicit environmental feedback²³. Inspired by the biological process originating in honeybees, the control community has seen an increasing interest in recent years for a range of applications, including consensus dynamics in robotics and neural correlations of brains in vertebrates, in disciplines such as behavioural ecology, psychology and neurosciences, multi-agent decision-making and network design^{24,25,26}.

Although several approaches have been adopted to study the prisoner's dilemma, including, e.g., the design of a strategy that is obtained by saturating a polynomial function in an *n*-population game setting²⁷, incorporating the evolution of the environment in the strategy profile through the payoff matrix poses a risk in limiting the likelihood of cooperation, and gives rise to an "oscillating tragedy of the commons"⁵. An additional difficulty may come when we take into consideration the corresponding optional game, i.e. the optional prisoner's dilemma (OPD), where players can choose to cooperate and defect, but also abstain from playing the game²⁸. This formulation includes the dynamics of many real-life decision-making settings, such as opinion dynamics in the context of an election campaign and duopolistic competition in marketing^{28,29}.

By extending the work on game-environment feedback to the OPD, we derive two models: one resulting from the replicator dynamics as an extension of the prior work on game-environment feedback and another one resulting from the pairwise comparison dynamics. The motivation that underpins the need for this additional model comes from the surge of interest that prospect theory has had in the past years and its continuous use in the past 30 years within behavioural economics and beyond³⁰. Prospect theory has its foundations on the work from two psychologists, Kahneman and Tversky, through which they demonstrated a systematic misalignment between the predictions conducted with utility theory and the real-life behaviour of individuals' decision-making under risk³¹. The main elements that constitute this theory are³⁰:

• reference dependence, which is a measure of utility to a reference point;

- loss aversion, which captures the idea that people are more sensitive to losses;
- diminishing sensitivity, which models losses and gains in different ways, i.e. the value function is convex in the region of losses and concave in the region of gains, respectively;
- probability weighting, which account for the addition weights that individuals assign to probabilities of events.

Through the pairwise comparison dynamics, we capture some elements of irrational or subjective behaviour that comes from the above elements of prospect theory. More formally, the model resulting from the pairwise comparison dynamics uses the flux from a pair of strategies in such a way that switching to another strategy other than the optimal is possible, as opposed to the best response dynamics where switching is possible only for the optimal strategy. Prospect theory has been applied in a range of settings, including discrimination in obsessive-compulsive disorders³², dynamics pricing for shared mobility³³ and in the context of collective decision-making through pairwise comparison dynamics³⁴. Finally, we include prospect theory in the formulation of the OPS with game-environment feedback via pairwise comparison dynamics through the use of a weighting function which gives weight zero to the probability of unfavourable events in a risk-seeking scenario.

Highlights of contributions. The contribution of this paper is threefold. First, we propose a modelling framework where we capture the irrational behaviours originating in the context of behavioural economics through Kahneman and Tversky's prospect theory. In the proposed framework, we study the game-environment feedback on replicator dynamics⁵ and we extend it to a different kind of dynamics, i.e. pairwise comparison dynamics. Second, we carry out the stability analysis of the system resulting from these dynamics and discuss its differences with the original model. Lastly, we extend the work on the PD to account for the abstain strategy via the OPD. Motivated by the importance of the abstain strategy in real-life contexts and the irrational behaviours in many decision making settings, we investigate the system resulting from the application of pairwise comparison dynamics to the optional game.

This paper is organised as follows. In Section 2, we provide the problem formulation for the PD with game-environment feedback in the case of pairwise comparison dynamics. We conduct the stability analysis of the equilibria of the system and we discuss the differences and similarities between our results and the results in previous research works. In Section 3, we extend the proposed framework with game-environment feedback to the case of the OPD, where players can choose to abstain from playing the game as a third strategy. We study the stability of the two models and discuss the main differences between them and the added value of this work in relation to the rest of the literature on this topic. Finally, in Section 5 we draw conclusions and discuss future directions of research.

2 | FEEDBACK-EVOLVING PRISONER'S DILEMMA VIA PAIRWISE COMPARISON DYNAMICS

Evolutionary game dynamics with game-environment feedback have become popular in the past few years because of the induced dependency between the population dynamics and the surrounding environment. This leads to a system where the environment changes as a consequence of the frequency of the strategies and where the population dynamics are affected by the environment in return. Figure 1 shows a diagram representation of the game-environment feedback, where the game dynamics and the environment form a closed-loop system.

2.1 | Evolutionary Game Model via Pairwise Comparison Dynamics

In this section, we extend the initial feedback evolving game framework to pairwise comparison dynamics, which are a form of innovative dynamics. We compare our results to the framework obtained via replicator dynamics by Weitz *et al.*⁵ in the context of the prisoner's dilemma (PD). The motivation for this extension is twofold: first, through pairwise comparison dynamics we can capture some aspects of irrational behaviour of individuals' decision-making under risk through prospect theory 30,31 ; second, the results presented here share similarities with the seminal work on game-environment feedback that are worth investigating, especially in terms of equilibria and stability⁵.

Let us consider the standard payoff matrix in the context of the PD where the two-player game consists of the two strategies cooperation (C) and defection (D):

$$A = \begin{bmatrix} R & S \\ T & P \end{bmatrix},\tag{1}$$

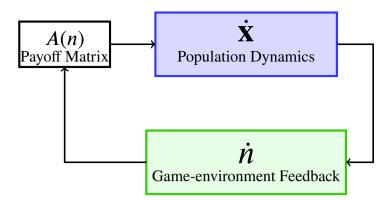


FIGURE 1 Diagram representation of the evolutionary dynamics for game-environment feedback. In general, the payoff matrix A determines the frequencies of strategies, x_i for all i, to derive the population dynamics. Through the game-environment feedback the frequencies of the strategies change the state of the environment, n, which, in turn, influences the values in the payoff matrix A(n), with explicit dependence on the environmental resource n.

where *R* is the reward for cooperating, *S* is the sucker's payoff, *T* is the payoff associated with the temptation to cheat and *P* is the punishment for cheating. In the classical formulation of the game, T > R > P > S so that mutual defection is the Nash equilibrium associated with the game. In the context of evolutionary game theory, the model associated with the above symmetric two-player game via replicator dynamics can be written as⁵

$$\dot{x} = x(1-x)(r_1(x) - r_2(x)), \tag{2}$$

where $x \equiv x_1$ because of the conservation of mass law for which $x_1 + x_2 = 1$, and where $r_1(x)$ is the fitness of player 1 and $r_2(x)$ is the fitness of player two, respectively. These are defined as:

$$r_1(x) = \sum_j a_{1j} x_j = (Ax)_1 = Rx + S(1-x),$$
(3)

$$r_2(x) = \sum_j a_{2j} x_j = (Ax)_2 = Tx + P(1-x).$$
(4)

After substituting the above into equation (2), we obtain:

$$\dot{x} = x(1-x)(Rx + S(1-x) - Tx - P(1-x)) = -x(1-x)(\delta_{TR}x + \delta_{PS}(1-x)),$$
(5)

where $\delta_{TR} = T - R$ and $\delta_{PS} = P - S$.

We can now formulate the analogous model for the PD via pairwise comparison dynamics. To this end, let us consider the following dynamics:

$$\dot{x}_i = \sum_j x_j \phi_{ji} - x_i \sum_j \phi_{ij},\tag{6}$$

where $\phi_{ij} \ge 0$ is the rate at which a player *i* changes his strategy to strategy *j* and $x_i\phi_{ij}$ is the flux from strategy *i* to strategy *j*. When ϕ_{ij} is given by the proportional rule $\phi_{ij} = [a_j - a_i]_+ = \sum_k [a_{jk} - a_{ik}]_+ x_j$, and by recalling that the notation $[\cdot]_+$ denotes the positive part defined as $[f(x)]_+ = \max(f(x), 0)$, the resulting dynamics are called pairwise comparison dynamics or pairwise difference dynamics³⁵. After a simple calculation, the model resulting from the pairwise comparison dynamics for the PD is the following:

$$\dot{x} = (1 - x)[r_1(x) - r_2(x)]_+ - x[r_2(x) - r_1(x)]_+,$$
(7)

where $r_1(x)$ and $r_2(x)$ are the fitness of player 1 and the fitness of player 2, respectively, as defined before. If we substitute the payoffs from matrix (1), we get the following model:

$$\dot{x} = (1 - x)[(\delta_{PS} - \delta_{TR})x - \delta_{PS}]_{+} - x[-((\delta_{PS} - \delta_{TR})x - \delta_{PS})]_{+}.$$

Since the argument of the positive part is the same with different sign, only one of the two terms in the above model can be present at any given time. More specifically, we obtain the following models:

$$\dot{x} = (1 - x)[(\delta_{PS} - \delta_{TR})x - \delta_{PS}], \qquad \dot{x} = -x[-((\delta_{PS} - \delta_{TR})x - \delta_{PS})], \tag{8}$$

where the left one is derived when $(\delta_{PS} - \delta_{TR})x - \delta_{PS} > 0$ and the right one is given when $(\delta_{PS} - \delta_{TR})x - \delta_{PS} < 0$.

Lemma 1. Consider system (8). This system has three fixed points: $x^* = 1$ when $(\delta_{PS} - \delta_{TR})x - \delta_{PS} > 0$, $x^* = 0$ when $(\delta_{PS} - \delta_{TR})x - \delta_{PS} < 0$ and a fixed point that is common to both models, namely $x^* = \delta_{PS}/(\delta_{PS} - \delta_{TR})$. The first two fixed points are asymptotically stable, and $x^* = \delta_{PS}/(\delta_{PS} - \delta_{TR})$ is unstable.

Proof. The existence and stability of the equilibria must be investigated by considering the two models separately. By looking at the sign of the square, we can determine that $x^* = 1$ is stable for the left model and that $x^* = 0$ is stable in the right model, whereas $x^* = \delta_{PS}/(\delta_{PS} - \delta_{TR})$ is unstable in both of them.

Example 1. Consider the following payoff matrix

$$A = \begin{bmatrix} 3 & 0 \\ 5 & 1 \end{bmatrix}$$

We can calculate the fitness of player 1 and the fitness of player 2 as in the following:

$$r_1(x) = 3x_1,$$

 $r_2(x) = 5x_1 + x_2,$

and the resulting model via replicator dynamics is

$$\dot{x} = -x(1-x)(1+x),$$

while the model resulting from the pairwise difference dynamics is

$$\dot{x} = -x(1+x).$$

In the above, regardless of the dynamics used, the only stable equilibrium point in the domain [0, 1] is $x^* = 0$, as it can be deduced from the sign as before. Within the same domain, the model obtained via replicator dynamics presents another equilibrium point $x^* = 1$, which is unstable. The equilibrium point $x^* = -1$, albeit common to both models, is not in the given domain and therefore is not considered. The dynamics for this example are depicted in Fig. 2 (top).

Example 2. In this example, we consider a situation where cooperation is favored, namely a Harmony game. Let the payoff matrix be

$$A = \begin{bmatrix} 5 & 1 \\ 3 & 0 \end{bmatrix}.$$

The fitness of player 1 and the fitness of player 2 are calculated as

$$r_1(x) = 5x_1 + x_2,$$

 $r_2(x) = 3x_1,$

and the resulting model via replicator dynamics is

$$\dot{x} = x(1-x)(1+x),$$

while the model resulting from the pairwise difference dynamics is

$$\dot{x} = (1 - x)(1 + x).$$

As in the previous example, the model via replicator dynamics has two equilibria in the domain [0, 1], namely $x^* = 0$ and $x^* = 1$, whereas the model with pairwise comparison dynamics has only one equilibrium $x^* = 1$. In both cases, the only stable equilibrium point is $x^* = 1$, meaning that cooperation is the stable strategy. The dynamics for this example are depicted in Fig. 2 (bottom).

2.2 | Game-Environment Feedback

We can now extend the above results in the context of feedback-evolving games, namely when the payoff matrix depends on an environmental resource n, in line with the work by Weitz *et al.*⁵. We define our game-environment feedback dynamics as

$$\epsilon \dot{x} = (1 - x)[r_1(x, A(n)) - r_2(x, (A(n))]_+ - x[r_2(x, A(n)) - r_1(x, A(n))]_+,$$

$$\dot{n} = n(1 - n)[(1 + \lambda)x - 1],$$
(9)

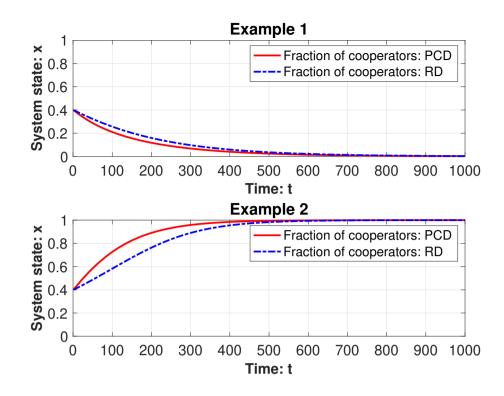


FIGURE 2 Time evolution of system (5) via replicator dynamics (RD) and pairwise comparison dynamics (PCD). The first plot (top) shows the evolution of the cooperation strategy for *Example 1*. The second plot (bottom) shows the evolution of the cooperation strategy for *Example 2*.

where the term n(1-n) is used to ensure that the state of the environment is within the domain [0, 1], ϵ denotes the rate at which the population dynamics change the environment. Let $\lambda > 0$ be the ratio between the enhancement effect due to cooperation and degradation effect due to defection. Parameter λ can take values in three sub-domains: when $\lambda < 1$, the degradation effect is stronger than the enhancement effect; when $\lambda = 1$, the two effects are in balance; when $\lambda > 1$ the enhancement effect is stronger than the degradation effect. The main difference between the above model and the one in the previous section is the environmental dependency of the payoff matrix A(n). For the purpose of studying this model, we consider the following environment-dependent matrix:

$$A(n) = (1-n) \begin{bmatrix} T & P \\ R & S \end{bmatrix} + n \begin{bmatrix} R & S \\ T & P \end{bmatrix} = \begin{bmatrix} T - n\delta_{TR} & P - n\delta_{PS} \\ R + n\delta_{TR} & S + n\delta_{PS} \end{bmatrix},$$
(10)

where $\delta_{TR} = T - R$, $\delta_{PS} = P - S$ and we assume T > R > P > S as before. Similarly to the case without the environmental feedback, we provide the two systems resulting from the pairwise comparison dynamics (pairwise difference) for the PD with game-environment feedback in the following:

$$\begin{aligned} \epsilon \dot{x} &= (1-x)[(1-2n)(\delta_{PS} + (\delta_{TR} - \delta_{PS})x)], & \epsilon \dot{x} &= -x[-(1-2n)(\delta_{PS} + (\delta_{TR} - \delta_{PS})x)], \\ \dot{n} &= n(1-n)[(1+\lambda)x-1], & \dot{n} &= n(1-n)[(1+\lambda)x-1] \end{aligned}$$
(11)

Theorem 1. The first model in (11) has the following fixed points: $(x^*, n^*) = (1, 0), (x^*, n^*) = (1, 1)$. The second model in (11) has the following fixed points: $(x^*, n^*) = (0, 0), (x^*, n^*) = (0, 1)$. Both models share the following equilibria: $(x^*, n^*) = (-\delta_{PS}/(\delta_{TR} - \delta_{PS}), 0), (x^*, n^*) = (-\delta_{PS}/(\delta_{TR} - \delta_{PS}), 1)$ and $(x^*, n^*) = (1/(\lambda + 1), 1/2)$. All fixed points are unstable, and only the last one, namely $(x^*, n^*) = (1/(\lambda + 1), 1/2)$, is neutrally stable.

Proof. To study the stability of system (11), we consider each model separately, first. The first model in (11) has the following Jacobian:

$$J_1(x,n) = \begin{bmatrix} (1-2n)(\delta_{TR} - 2\delta_{PS} - 2x(\delta_{TR} - \delta_{PS})) & -(1-x)(2x(\delta_{TR} - \delta_{PS}) + 2\delta_{PS}) \\ n(1-n)(1+\lambda) & (1-2n)((1+\lambda)x-1) \end{bmatrix}.$$
 (12)

The above Jacobian, linearized about the fixed points unique to this model, yields:

$$J_1(1,0) = \begin{bmatrix} -\delta_{TR} & 0\\ 0 & \lambda \end{bmatrix}, \quad J_1(1,1) = \begin{bmatrix} \delta_{TR} & 0\\ 0 & -\lambda \end{bmatrix}$$

Since each Jacobian has a positive eigenvalue, these equilibria are locally unstable. Similarly, for the second model the Jacobian is the following:

$$J_2(x,n) = \begin{bmatrix} (1-2n)(\delta_{PS} + 2x(\delta_{TR} - \delta_{PS})) & (2x^2(\delta_{TR} - \delta_{PS}) + 2x\delta_{PS}) \\ n(1-n)(1+\lambda) & (1-2n)((1+\lambda)x-1) \end{bmatrix}.$$
 (13)

When linearizing about the two equilibria unique to the second model, we get:

$$J_2(0,0) = \begin{bmatrix} \delta_{PS} & 0\\ 0 & -1 \end{bmatrix}, \quad J_2(0,1) = \begin{bmatrix} -\delta_{PS} & 0\\ 0 & 1 \end{bmatrix}.$$

Again, both fixed points are locally unstable. Now, we linearize each Jacobian about the common fixed points $(x^*, n^*) = (-\delta_{PS}/(\delta_{TR} - \delta_{PS}), 0), (x^*, n^*) = (-\delta_{PS}/(\delta_{TR} - \delta_{PS}), 1)$, we obtain:

$$J_1\left(\frac{-\delta_{PS}}{\delta_{PS}-\delta_{TR}},0\right) = \begin{bmatrix} \delta_{TR} & 0\\ 0 & -\frac{\lambda\delta_{PS}+\delta_{TR}}{\delta_{TR}-\delta_{PS}} \end{bmatrix}, \qquad J_1\left(\frac{-\delta_{PS}}{\delta_{PS}-\delta_{TR}},1\right) = \begin{bmatrix} -\delta_{TR} & 0\\ 0 & \frac{\lambda\delta_{PS}+\delta_{TR}}{\delta_{TR}-\delta_{PS}} \end{bmatrix} \\ J_2\left(\frac{-\delta_{PS}}{\delta_{PS}-\delta_{TR}},0\right) = \begin{bmatrix} -\delta_{PS} & 0\\ 0 & -\frac{\lambda\delta_{PS}+\delta_{TR}}{\delta_{TR}-\delta_{PS}} \end{bmatrix}, \qquad J_2\left(\frac{-\delta_{PS}}{\delta_{PS}-\delta_{TR}},1\right) = \begin{bmatrix} \delta_{PS} & 0\\ 0 & \frac{\lambda\delta_{PS}+\delta_{TR}}{\delta_{TR}-\delta_{PS}} \end{bmatrix}.$$

In all cases, due to the positive part of the system, we have at least one positive eigenvalue and therefore all fixed points are locally unstable. Finally, we can now turn our attention to the interior fixed point and calculate the Jacobian for the first model as in the following:

$$J_1\left(\frac{1}{\lambda+1},\frac{1}{2}\right) = \begin{bmatrix} 0 & -\lambda(2(\delta_{TR}-\delta_{PS})+2\delta_{PS}(\lambda+1))\\ \frac{1}{4}(\lambda+1) & 0 \end{bmatrix}$$

whose eigenvalues have no real parts, i.e. we have two purely imaginary eigenvalues. Therefore, the interior fixed point is neutrally stable. An analogous result follows from the Jacobian of the second model for the interior fixed point.

In line with Weitz *et al.*⁵, we can now analyze the global dynamics of the system and extent the local result to the entire domain. At any given time, system (9) behaves like the left or right model in (11); we focus on the first model, but an analogous demonstration can be given for the second model. Because of the separability of the factors, we have:

$$\frac{dx}{dn} = \delta_{PS} \frac{(1-x)(1-2n)(1+(\delta_{TR}/\delta_{PS}-1)x)}{\epsilon n(1-n)[(1+\lambda)x-1].}$$

From the above, it follows

$$\int \frac{(1+\lambda)x-1}{(1-x)(1+\Delta x)} dx = \int \frac{\delta_{\rm PS}}{\varepsilon} \frac{(1-2n)}{n(1-n)} dn,$$

where $\Delta = \delta_{TR}/\delta_{PS} - 1$. We can now integrate each side of the above equation by partial fractions as in the following. Integrating the right-hand side yields:

$$\frac{\delta_{PS}}{\epsilon} \left[\int \frac{1}{n} dn - \int \frac{1}{1-n} dn \right] = \frac{\delta_{PS}}{\epsilon} \left[\log(n) - \log(1-n) \right] + \text{const.}$$

Integrating the left-hand side yields:

$$\frac{\lambda}{1+\Delta} \int \frac{1}{1-x} dx - \frac{1+\Delta+\lambda}{1+\Delta} \int \frac{1}{1+\Delta x} dx = \frac{\lambda}{1+\Delta} \log(1-x) - \frac{1+\Delta+\lambda}{1+\Delta} \log(1+\Delta x) + \text{const.}$$

We identify the constant of motion

$$H(x,n) = \frac{\delta_{PS}}{\epsilon} \left[\log(n) - \log(1-n) \right] - \frac{\lambda}{1+\Delta} \log(1-x) + \frac{1+\Delta+\lambda}{1+\Delta} \log(1+\Delta x),$$

which is a constant of motion because the following holds true:

$$\dot{H} = \frac{\partial H}{\partial x}\dot{x} + \frac{\partial H}{\partial n}\dot{n} = 0$$

Therefore, the system with initial condition (x_0, n_0) in the interior of the square 0 < x, n < 1 and not at a fixed point will exhibit closed, periodic orbits. An analogous result is obtained when studying the second model of system (11); for the sake of brevity, it is omitted. This completes the proof.

Remark 1. By comparing the above formulation of the PD with the one in Weitz *et al.*⁵, we obtain a model of degree 2 whose fixed points share the same stability properties with the one resulting from the replicator dynamics. Two interesting differences emerge from comparing the two models. The first one is that our model does not directly include the fixed points corresponding to all defectors in a depleted/replete environment, unless P = S. The second one can be found by looking at the degree of our system, which is one lower than the one by Weitz *et al.* This can be explained by looking at the rate of changing strategy in the pairwise difference comparison: the value obtained by the proportional rule $\phi_{ij} = [a_j - a_i]_+$ considers the probability of a payoff increase only, thus assigning a different weighting factor to different events. This aspect is one of the core elements in prospect theory and is the motivation that underpins our approach³¹.

Example 3. Given the payoff matrix in (10), for the sake of clarity we now consider system (11) with the following parameters:

$$\epsilon = 0.1, \quad \lambda = 2,$$

 $R = 3, S = 0, \quad T = 5, \quad P = 1$

The model resulting from the pairwise comparison dynamics is

$$0.1\dot{x} = (1-x)[(1-2n)(1+x)]_{+} - x[-(1-2n)(1+x)]_{+},$$

$$n = n(1-n)[3x-1].$$

This model has the following fixed points: $(x^*, n^*) = (1, 0)$, $(x^*, n^*) = (0, 1)$, $(x^*, n^*) = (-1/2, 0)$, $(x^*, n^*) = (-1/2, 1)$ and $(x^*, n^*) = (1/3, 1/2)$. The third and the fourth are outside the domain [0, 1], and thus are not considered. The first two fixed points are unstable, whereas the interior fixed point is neutrally stable, since the corresponding Jacobian matrix has both eigenvalues with purely imaginary components. In accordance with Theorem 1, we can see that a stable limit cycle exists and that the trajectories converge to this attractive limit cycle. The time evolution and phase plane dynamics for this example are depicted in Fig. 3.

3 | OPTIONAL PRISONER'S DILEMMA WITH GAME-ENVIRONMENT FEEDBACK

A crucial aspect that is not captured by the standard PD is the possibility that players can choose neither option. The optional prisoner's dilemma (OPD) game is an extension of the PD where players can choose to abstain, and therefore neither cooperate nor defect ³⁶. This translates to a game with three possible strategies: cooperate, defect and abstain. The implications of this additional strategy are crucial in many applications, whose most notable examples are opinion dynamics during an election and duopolistic competition in marketing ^{28,29}.

To describe the evolution of the strategy profile in the population under game-environment feedback, let the environmentdependent payoff matrix be:

$$A(n) = (1-n) \begin{bmatrix} T & P & L \\ R & S & L \\ L & L & L \end{bmatrix} + n \begin{bmatrix} R & S & L \\ T & P & L \\ L & L & L \end{bmatrix} = \begin{bmatrix} T - n\delta_{TR} & P - n\delta_{PS} & L \\ R + n\delta_{TR} & S + n\delta_{PS} & L \\ L & L & L \end{bmatrix},$$
(14)

where the parameters have the usual meaning, and *L* is the loner's payoff. This payoff is given to both players if at least one chooses to abstain. As it is common in the literature, we assume T > R > L > P > S.

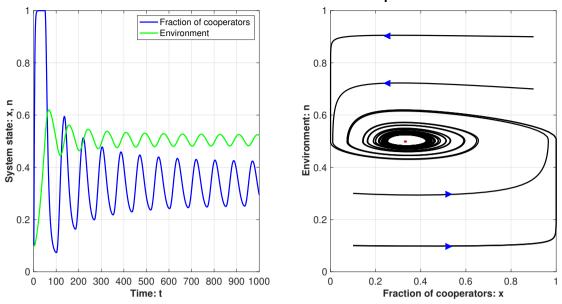
In the following, we discuss the feedback-evolving OPD game model via replicator dynamics and pairwise comparison dynamics. First, we provide a general formulation of the OPD via replicator dynamics as in the following:

$$\epsilon \dot{x}_i = x_i (1 - x_i) [r_i(x, A(n))] - x_i x_j [r_j(x, A(n))] - x_i L (1 - x_i - x_j),$$

$$\dot{n} = n(1 - n) [(1 + \lambda)x_1 - 1],$$
(15)

where i = 1, 2 and j = 2, 1. The specific model resulting from the payoff matrix (14) where $x_3 = 1 - x_1 - x_2$ is the following:

$$\begin{aligned} & \varepsilon \dot{x}_1 = x_1 (1 - x_1) [r_1(x, A(n))] - x_1 x_2 [r_2(x, A(n))] - x_1 L (1 - x_1 - x_2), \\ & \varepsilon \dot{x}_2 = x_2 (1 - x_2) [r_2(x, A(n))] - x_1 x_2 [r_1(x, A(n))] - x_2 L (1 - x_1 - x_2), \\ & \dot{n} = n(1 - n) [(1 + \lambda) x_1 - 1]. \end{aligned}$$
(16)



Game-Environment Feedback: Example 3

FIGURE 3 Feedback-evolving game model resulting from the pairwise comparison dynamics for the PD (*Example 3*). The first plot (left) shows the evolution of the fraction of cooperators and the environment over time. The second plot (right) shows the phase plane dynamics in the *x*-*n* plane for system (10): the blue arrows indicate the direction of dynamics while the red dot denotes the interior fixed point at (1/3, 1/2). Finally, the different trajectories correspond to the following initial conditions: (0.9, 0.9), (0.9, 0.7), (0.1, 0.3), (0.1, 0.1).

In the above model, the evolution of the environment is subject to the influence of the players choosing to cooperate, similarly to previous works^{5,6}. To derive the corresponding model via pairwise comparison dynamics, recall that the rate ϕ_{ij} is given by the proportional rule $\phi_{ij} = [a_j - a_i]_+ = \sum_k [a_{jk} - a_{ik}]_+ x_j$. Therefore we have:

$$\epsilon \dot{x}_i = x_j [\phi_{ji}]_+ + (1 - x_i - x_j) [\phi_{3i}]_+ - x_i ([\phi_{ij}]_+ + [\phi_{i3}]_+),$$

$$\dot{n} = n(1 - n)[(1 + \lambda)x_1 - 1],$$

(17)

where i = 1, 2 and j = 2, 1 as before. By substituting the values from the payoff matrix (14), the resulting model is the following:

$$\begin{aligned} \epsilon \dot{x}_1 &= (x_2 - 3nx_1)(\delta_{TR}x_1 + \delta_{PS}x_2) + \delta_{TL}x_1(1 - x_1 - x_2) + \delta_{PL}x_1x_2, \\ \epsilon \dot{x}_2 &= (x_1 - 2nx_2)(\delta_{TR}x_1 + \delta_{PS}x_2) + (1 - x_1 - x_2)((\delta_{RL} + \delta_{TR}n)x_1 + \delta_{PS}nx_2) + \delta_{TL}x_1x_2, \\ \dot{n} &= n(1 - n)[(1 + \lambda)x_1 - 1], \end{aligned}$$
(18)

where $\delta_{TL} = T - L$, $\delta_{PL} = P - L$ and $\delta_{RL} = R - L$, while the other parameters have the usual meaning.

Results – *Stability Analysis*. System (16) has a total of eleven fixed points, as reported in Table 1. The first one (0, 0, 0), namely all players abstain, is marginally stable as it can be seen by the Jacobian linearised about it:

$$J(0,0,0) = \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & -1 \end{bmatrix},$$

Depending on the initial conditions, the trajectories can converge to this point or be attracted to the interior fixed points 9 and 10 from Table 1, similarly to the PD with game-environment feedback. On a preliminary analysis, this second behaviour can be seen when no players choose to abstain at the start of the game, namely $x_1(0) + x_2(0) = 1$.

On the other hand, system (18) has ten fixed points, but the analytical expression for each of them is too large to fit in a table, albeit similar to the one for the replicator dynamics. The important element in this case is that, regardless of the initial

#	x_1	x_2	n
1	0	0	0
2	1	0	0
3	0	1	0
4	0	0	1
5	1	0	1
6	0	1	1
7	$\delta_{PS}/(\delta_{PS}-\delta_{TR})$	$-\delta_{TR}/(\delta_{PS}-\delta_{TR})$	0
8	$\delta_{PS}/(\delta_{PS}-\delta_{TR})$	$-\delta_{TR}/(\delta_{PS}-\delta_{TR})$	1
9	$1/(1+\lambda)$	$\lambda/(1+\lambda)$	1/2
10	$1/(1+\lambda)$	$-(R-2L+T)/((P-2L+S)(1+\lambda))$	1/2
11	$1/(1+\lambda)$	0	(L-T)/(R-T)

TABLE 1 List of all 11 fixed points for system (16).

conditions, all trajectories converge to the interior fixed point at which the number of cooperators is equal to $1/(1 + \lambda)$, which turns out to be asymptotically stable.

Remark 2. It is worth noting that by unilaterally choosing to assign weight zero to the probability of unfavourable events and thus by considering only the probability of a payoff increase via pairwise comparison dynamics, the population converges to a mixed strategy equilibrium, where cooperation is achieved by one part of the population. This formulation is in accordance to the main elements that constitute the prospect theory³¹. Finally, by considering a situation where the degrading effect is stronger, namely $\lambda < 1$, the population will converge to a strategy profile where the dominant strategy is cooperation.

Example 4. Let the payoff matrix be (14) with the following parameters:

$$\epsilon = 0.5, \quad \lambda = 2,$$

 $R = 3, \quad S = 0, \quad L = 2, \quad T = 5, \quad P = 1.$

The models resulting from the replicator dynamics and pairwise difference dynamics share many fixed points as before, but the stability behaviour of these points changes in relation to the dynamics used and the initial condition. For the replicator dynamics, we observe oscillations when $x_1 + x_2 = 1$, namely when no players abstain. The trajectories have an oscillating behaviour about the internal fixed point, which can be calculated as (0.33, 0.44, 0.5). The only stable fixed point is (0, 0, 0), namely when all players abstain. In the case of pairwise comparison dynamics, we observe a completely different behaviour: all trajectories converge to the internal fixed point, i.e. (0.33, 0.37, 0.51), regardless of the initial condition. This internal point is asymptotically stable. The behavior of the system in both cases and the calculation of the corresponding fixed points have been carried out through numerical simulations as the analytical expression for such system is very difficult to obtain. These behaviours can be seen in Figg. 4-5.

4 | APPLICATIONS IN THE LIFE SCIENCES

In this section, we highlight potential applications of our contribution in the life sciences and in particular we present two main examples: collective decision-making in honeybee swarms and opinion dynamics in the context of elections.

Honeybee Swarms

The system describing the optional prisoner's dilemma under game-environment feedback, namely system (16), can be interpreted in the context of the collective decision-making problem in honeybees when the entries of the payoff matrix are such that $L = 0^{34}$. The model takes inspiration from the process in which honeybees choose the nest for the future season: in particular, the values in the diagonal describe strength of the so-called "waggle dance" that is used to attract bees to choosing one option, whereas the parameters in the off-diagonal describe the cross-inhibitory stop signals sent by scout bees to other bees committed

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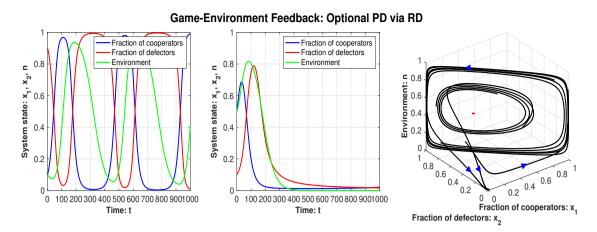


FIGURE 4 Feedback-evolving game model resulting from the replicator dynamics for the OPD (*Example 4*). The first two plots (left and centre) show the evolution of the fraction of cooperators and defectors and the environment over time for initial conditions (0.9, 0.1, 0.1) and (0.1, 0.9, 0.9), respectively. The last plot (right) shows the phase plane dynamics in the x_1 - x_2 -n space: the blue arrows indicate the direction of the dynamics while the red dot denotes the interior fixed point at (0.33, 0.44, 0.5). For different initial conditions, the trajectories are either trapped in a limit cycle or converge to (0, 0, 0).

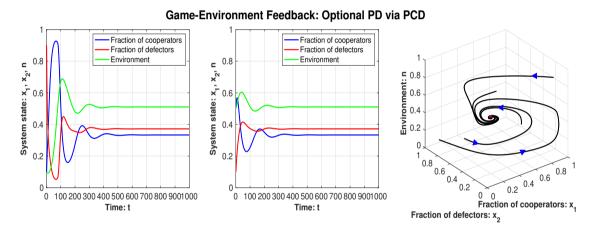


FIGURE 5 Feedback-evolving game model resulting from the pairwise comparison dynamics for the OPD (*Example 4*). The first two plots (left and centre) show the evolution of the fraction of cooperators and defectors and the environment over time for initial conditions (0.9, 0.1, 0.1) and (0.1, 0.9, 0.9), respectively. The last plot (right) shows the phase plane dynamics in the x_1 - x_2 -n space: the blue arrows indicate the direction of the dynamics while the red dot denotes the interior fixed point at (0.33, 0.37, 0.51). Regardless of the initial conditions, all trajectories converge to the interior fixed point.

to an option different from their own^{37} . An interpretation of the environmental feedback in this context can be given by considering the biological studies described in *Honeybee Democracy*. Given a number of next-boxes, the swarm quickly comes to a consensus even in the case of equally good nests; however, when a new next-box, better in quality, is introduced towards the end of the decision-making process, the swarm fails to select it as the environmental resource, namely time and food, has slowly degraded over time ³⁸.

Opinion Dynamics

In the context of an election, the system describes the campaign of two political parties³⁹. Individuals can choose to vote for either party or to abstain, thus the need for a third option. Individuals choose to vote one party is the value of one of the two entries in the main diagonal of the payoff matrix is larger than the other (L = 0 for simplicity as in the previous example).

Similarly, the entries in the off-diagonal represent the effort by each party to dissuade voters from voting for the opposite party. In this context the environmental feedback can be thought of the general resources that have an impact in the voters' lives, such as the availability of new jobs or the redevelopment of a neighborhood.

5 | CONCLUSIONS

Motivated by the emerging interest towards a game theoretic modeling framework that can capture player's irrational behaviours and the possibility to abstain in a feedback-evolving game context, in this paper we have proposed a unified framework to capture these three main aspects. The resulting feedback-evolving optional prisoner's dilemma under irrational behaviour is obtained via pairwise comparison dynamics. We have discussed the differences between our model and the prior works on the topic of gameenvironment feedback within evolutionary game theory. Driven by the need for capturing optional games, we have extended our analysis to the optional prisoner's dilemma by deriving the model corresponding to the replicator dynamics and the pairwise comparison dynamics. Interestingly, the behaviour of these two systems under game-environment feedback is notably different, despite the presence of oscillations in both models. The latter model gives rise to an interesting setting for partial cooperation, which provides an explanation for the reasons underpinning the presence of cooperation in many biological systems. Future work includes: i) the extension of this model to a structured setting where a network topology is used to capture the interactions in the population, ii) the study of different time scales for the population dynamics and the evolution of the environment, and iii) the impact of time-varying parameters on the population dynamics.

Author contributions

L.S. and D.B. designed the research, L.S. performed the research and wrote the paper.

Financial disclosure

None reported.

Conflict of interest

The authors declare no potential conflict of interests.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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