Replicator Dynamics with Feedback-Evolving Games: Towards a Co-Evolutionary Game Theory

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A tragedy of the commons occurs when individuals take actions to maximize their payoffs even as their combined payoff is less than the global maximum had the players coordinated. The originating example is that of over-grazing of common pasture lands. In game theoretic treatments of this example there is rarely consideration of how individual behavior subsequently modifies the commons and associated payoffs. Here, we generalize evolutionary game theory by proposing a class of replicator dynamics with feedback-evolving games in which environment-dependent payoffs and strategies coevolve. We apply our formulation to a system in which the payoffs favor unilateral defection and cooperation, given replete and depleted environments respectively. Using this approach we identify a new class of dynamics: an oscillatory tragedy of the commons in which the system cycles between deplete and replete environmental states and cooperation and defection behavior states. Further, we utilize fast-slow dynamical systems theory to provide an intuitive explanation for the observed changes. In closing, we propose new directions for the study of control and influence in games in which individual actions exert a substantive effect on the environmental state.

Game theory is based on the principle that individuals make rational decisions regarding their choice of actions given suitable incentives [1, 2]. In practice, the incentives are represented as strategy-dependent payoffs. Evolutionary game theory extends game theoretic principles to model dynamic changes in the frequency of strategists [3]. Replicator dynamics is one commonly used framework for such models. In replicator dynamics, the frequencies of strategies change as a function of the social makeup of the community [4–6]. For example in a snowdrift game (also known as a hawk-dove game), individuals defect when cooperators are common but cooperate when cooperators are rare [2]. As a result, cooperation is predicted to be maintained amongst a fraction of the community [4, 6]. Whereas, in the prisoner's dilemma individuals are incentivized to defect irrespective of the fraction of cooperators. This leads to domination by defectors [6, 7].

Here, we are interested in a different kind of evolutionary game in which individual action modifies both the social makeup and environmental context for subsequent actions. Strategy-dependent feedback occurs across scales from microbes to humans in public good games and in commons' dilemmas [8–11]. Amongst microbes, feedback may arise due to fixation of inorganic nutrients given depleted organic nutrient availability [12, 13], the production of extracellular nutrient-scavenging enzymes like siderophores [14–16] or enzymes like invertase that hydrolyze diffusible products [17], and the release of extracellular antibiotic compounds [18]. The incentive for public good production changes as the production influences the environmental state. Such joint influence occurs in human systems, e.g., when individuals decide to vaccinate or not [19–21]. Decisions not to vaccinate have been linked most recently to outbreaks of otherwise preventable childhood infectious diseases in Northern California [22]. These outbreaks modify the subsequent incentives for vaccination. Such coupled feedback also arises in public goods dilemmas involving water or other resource use [23]. In a period of replete resources there is less incentive for restraint [24]. Yet, over-use in times of replete resource availability can lead to depletion of the resource and changes in incentives.

In this manuscript we propose a unified approach to analyze and understand feedback-evolving games (Figure 1). We term this approach "co-evolutionary game theory", denoting the coupled evolution of the strategies and the environment. The key conceptual innovation is to extend replicator dynamic within evolutionary game theory [4] to include dynamical changes in the environment. In that sense, our approach is complementary to recent efforts to consider the evolvability of payoffs in a fixed environment [25]. Here, changes in the environment modulate the payoffs. In so doing, we are able to address problems in which individual behavior constitutes a non-negligible component of the system. As a case study, we revisit the originating tragedy of the commons example [24] and ask: what happens if over-exploitation of a resource changes incentives for future action? As we show, when decisions affect the environment they can subsequently alter incentives leading to new dynamical phenomena and new challenges for control.

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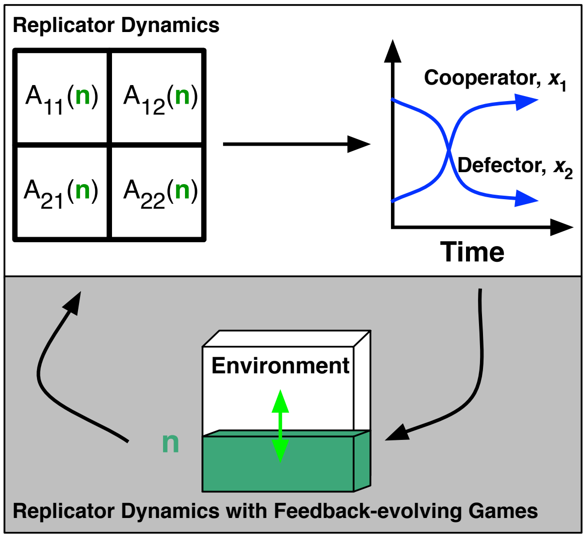

FIG. 1: Schematic of replicator dynamics in feedback-evolving games. (Top) In replicator dynamics, the payoff matrix A determines frequency-dependent changes in strategies, x_i. (Top and bottom) In replicator dynamics with feedback-evolving games, the frequencies of strategies influences the environment, which, in term modifies the payoffs, $A(n)$. The coupled system includes dynamics of both the payoff matrix and the strategies.

Methods and Results

The context – evolutionary game theory as modeled via replicator dynamics

Here we introduce evolutionary game theory in the context of the prisoner's dilemma as a means to motivate our co-evolutionary game theory formalism. Consider a two player game each of which can take one of two strategies C and D, denoting cooperation and defection respectively. A standard instance of the payoff matrix is the prisoner's dilemma (PD) in which the payoffs can be written as:

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

In this game, the player C receives a payoff of 3 and 0 when playing against player C and D, respectively. Similarly, the player D receives a payoff of 5 and 1 when playing against player C and D, respectively. In this game, the D strategy is the Nash equilibrium.

In evolutionary game theory, such payoffs can be coupled to the changes in population or strategy frequencies, x_1 and x_2, e.g., where x_1 and x_2 denote the frequency of cooperators and defectors such that $x_1 + x_2 = 1$. The coupling is expressed via replicator dynamics. The standard replicator dynamics for two-players games can be written as

$$\dot{x_1} = r_1(\mathbf{x}, A)x_1 - \langle r\rangle(\mathbf{x}, A)x_1, \tag{2}$$

$$\dot{x_2} = r_2(\mathbf{x}, A)x_2 - \langle r\rangle(\mathbf{x}, A)x_2. \tag{3}$$

where r_1, r_2 and $\langle r\rangle$ denote the fitness of player 1, the fitness of player 2, and the average fitness respectively, all of which depend on the frequency of players and the game theoretic payoffs. We interpret the payoffs in Eq. (1) as contributions to an effective per-capita growth rate, weighted by the relative proportion of interactions. In this convention then

$$r_1 = 3x_1 + 0x_2 = 3x_1, \tag{4}$$

$$r_2 = 5x_1 + x_2 = 5x_1 + x_2, \tag{5}$$

and the average fitness is:

$$\langle r\rangle = r_1x_1 + r_2x_2 = 3x_1^2 + (5x_1 + x_2)x_2. \tag{6}$$

Note that this system remains on the simplex $x_1+x_2 = 1$ (that is $\dot{x}_1 + \dot{x}_2 = 0$). Hence, we can focus on a single variable and rewrite the dynamics of $x \equiv x_1$ after some algebraic simplification as:

$$\dot{x} = -x(1 - x)(1 + x). \tag{7}$$

The replicator dynamics for the PD in Eq. (7) has 3 equilibria, but only two in the domain $[0, 1]$, i.e., $x^* = 0$ and $x^* = 1$. The stability can be identified from the sign of the cubic, i.e., $x^* = 0$ is stable and $x^* = 1$ is unstable. Therefore, any initial condition not on a fixed point will converge to $x^* = 0$. The convergence of the system to $x^* = 0$ means that the relative proportion of cooperators is 0 and, correspondingly, that the relative proportion of defectors is 1. This corresponds to domination by defectors. In the PD game, a population with a minority of D players will, over time, change to one with a minority of C players, and the elimination of C players altogether.

In general, replicator dynamics for games in which two populations select amongst two strategies with a fixed payoff matrix can be written as:

$$\dot{x} = x(1 - x)(r_1(x) - r_2(x)) \tag{8}$$

where the convention is again that $x \equiv x_1$ and that $x_1 + x_2 = 1$. This formulation implies that the frequency of strategy 1 in the population will increase if the frequency-dependent payoff of strategy 1 exceeds that of strategy 2, and vice-versa. We can leverage this simple representation to consider the replicator dynamics given an alternative game:

$$A = \begin{bmatrix} 5 & 1 \\ 3 & 0 \end{bmatrix}. \tag{9}$$

Here $r_1 = 4x + 1$ and $r_2 = 3x$ such that

$$\dot{x} = x(1 - x)(1 + x). \tag{10}$$

Again, the stability can be identified from the sign of the cubic, i.e., $x^* = 1$ is stable and $x^* = 0$ is unstable. The payoffs have changed such that cooperation is now a Nash equilibrium and a population with a minority of C players will, over time, change to one with a majority of C players, and eventually the elimination of D players.

A model of replicator dynamics with feedback-evolving games

We consider a modified version of the standard replicator dynamics in which:

$$\begin{aligned} \epsilon\dot{x} &= x(1-x)\left[r_1(x, A(n)) - r_2(x, A(n))\right], \\ \dot{n} &= n(1-n)f(x), \end{aligned} \tag{11}$$

where $f(x)$ denotes the feedback of strategists with the environment and the term $n(1-n)$ in Eq.(11) ensures that the environmental state is confined to the domain $[0,1]$. The value of ϵ is a property of the agents and denotes the relative speed by which individual actions modify the environmental state. What distinguishes the model is that the payoff matrix $A(n)$ is *environment-dependent* and that strategy and environmental dynamics are coupled (see Figure 1). The state of the environment is characterized by the scalar value, n. The environmental state changes as a result of the actions of strategists, such that the sign of $f(x)$ denotes whether n will increase or decrease, corresponding to environmental degradation or enhancement when $f < 0$ or $f > 0$ respectively. Finally, the rate of environmental dynamics is set, in part, by the dimensionless quantity ϵ, such that when $0 < \epsilon \ll 1$ then environmental change is relatively slow when compared to the change in the frequency of strategists.

We evaluate this class of feedback-evolving games via the use of the following environment-dependent payoff matrix:

$$A(n) = (1-n)\begin{bmatrix} 5 & 1 \\ 3 & 0 \end{bmatrix} + n\begin{bmatrix} 3 & 0 \\ 5 & 1 \end{bmatrix} \tag{12}$$

or, alternatively

$$A(n) = \begin{bmatrix} 5-2n & 1-n \\ 3+2n & n \end{bmatrix} \tag{13}$$

This payoff matrix interpolates between the two scenarios described in Section , such that cooperation or defection are favored in the limits of $n \to 0$ or $n \to 1$, respectively. In addition, we assume that the environmental state is modified by actions of the population:

$$f(x) = \theta x - (1-x) \tag{14}$$

in which $\theta > 0$ is the ratio of the enhancement rates to degradation rates of cooperators and defectors, respectively. The model of replicator dynamics with feedback-evolving games can be written as:

$$\begin{aligned} \epsilon\dot{x} &= x(1-x)\left[r_1(x,n) - r_2(x,n)\right], \\ \dot{n} &= n(1-n)\left[-1 + (1+\theta)x\right], \end{aligned} \tag{15}$$

where

$$r_1(x,n) = 1 + 4x - n(x+1), \tag{16}$$

$$r_2(x,n) = 3x + n(x+1). \tag{17}$$

Finally, the complete model can be written as:

$$\begin{aligned} \epsilon\dot{x} &= x(1-x)(1+x)(1-2n), \\ \dot{n} &= n(1-n)\left[-1 + (1+\theta)x\right]. \end{aligned} \tag{18}$$

There are five fixed points of this system. Of these, four represent "boundary" fixed points, that is (i) $(x^* = 0, n^* = 0)$ - defectors in a degraded environment; (ii) $(x^* = 0, n^* = 1)$ - defectors in a replete environment; (iii) $(x^* = 1, n^* = 0)$ - cooperators in a degraded environment; and (iv) $(x^* = 1, n^* = 1)$ - cooperators in a replete environment. There is also an interior fixed point, $(x^* = \frac{1}{1+\theta}, n^* = \frac{1}{2})$, representing a mixed population of cooperators and defectors in an intermediate environment. The local stability of each point will be helpful in understanding the dynamics of the full system. The eigenvalues of the Jacobian of the system evaluated at each of the boundary are $\lambda_{boundary} = \pm 1$. Hence, each of the four "boundary" points are unstable with respect to perturbations to the interior. For the interior fixed point, the Jacobian is:

$$J = \begin{bmatrix} 0 & -2x^*(1-x^*)(1+x^*) \\ \theta/4 & 0 \end{bmatrix} \tag{19}$$

where $0 < x^* = 1/(1+\theta) < 1$ for the interior fixed point Therefore, the eigenvalues for the interior fixed point are: $\lambda_{interior} = \pm i\sqrt{\frac{\theta x^*(1-x^*)(1+x^*)}{2}}$. The interior point is neutrally stable such that small deviations from it will oscillate.

The orientation of cycles in the phase plane defined by (x, n) should be counter-clockwise. The intuition is as follows. Consider initial conditions in the interior but near to $(x = 0, n = 0)$. In that case, then cooperator is favored as a Nash equilibrium, and the system will rapidly move to one near $(x = 1, n = 0)$ due to the relatively fast change in population frequencies compared to environmental state. Then, given an environment dominated by cooperators, the environmental state will be enhanced and the system will be drive closer to $(x = 1, n = 1)$. In an environmentally enhanced state, then defection is favored as a Nash equilibrium, and the system will rapidly move to one near $(x = 0, n = 1)$. Finally, in an environment dominated by defectors, the environmental state will be degraded and the system will be driven closer to $(x = 0, n = 0)$. The system should display periodic orbits for the entire domain. There are a family of such orbits, each neutrally stable due to the separability of the system dynamics. In this initial example the oscillations are not true limit cycles, i.e., the dynamics depend on the initial condition.

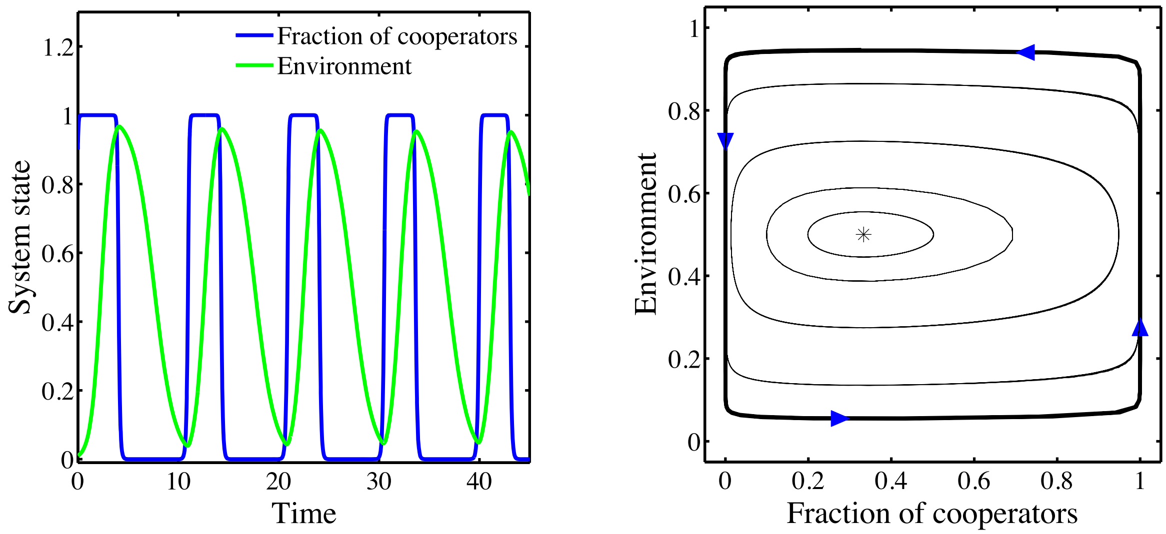

FIG. 2: Persistent oscillations of strategies and the environment. (Left) Time series of the fraction of cooperators x (blue) and the environmental state n (green), correspond to dynamics arising from Eq. (15) with $\epsilon = 0.1$, $\theta = 0.2$. (Right) Phase plane dynamics of $x - n$ system. The arrows denote the direction of dynamics with time. The distinct curves correspond to initial conditions $(0.9, 0.01)$, $(0.8, 0.15)$, $(0.7, 0.3)$, $(0.5, 0.4)$, $(0.4, 0.45)$. The asterisk denotes the predicted neutrally-stable equilibrium point at $(1/3, 1/2)$.

Identifying an Oscillating Tragedy of the Commons

The prior section extends replicator dynamics to include feedback-evolving games retaining symmetries in the payoffs at the extremal values of the environmental state. However, there are likely to be payoff differences between cooperation given a depleted state and defection given a replete state. We address this by breaking the symmetry of the prior game such that the total magnitude and distribution of payoffs are different in the $n = 0$ and $n = 1$ states, i.e., $A(n) = (1 - n)A_0 + nA_1$ where A_0 and A_1 represent fixed payoff matrices in the environmental deplete and replete states. As an example, consider the case that A_0 has a single Nash equilibrium corresponding to domination by cooperators and that A_1 has a single Nash equilibrium corresponding to domination by defectors:

$$A(n) = (1-n)\begin{bmatrix} 3.5 & 1 \\ 2 & 0.75 \end{bmatrix} + n\begin{bmatrix} 4 & 1 \\ 7 & 2 \end{bmatrix}. \tag{20}$$

From a technical perspective, the dynamics of the system can be predicted by solving for the conditions of stability near the interior equilibrium, when it exists. Algebraic conditions for (in)stability do not always yield intuitive conditions. Hence, as a first step we leverage the fact that when $0 < \epsilon \ll 1$ the dynamics correspond to that of fast-slow systems where x is the "fast" variable and n is the "slow" variable [26]. Later we will show that insights gained in the limit case hold irrespective of the relative rate change of environment and strategies.

Consider a rescaling of time such that $\tau = t/\epsilon$, such that we rewrite Eq. (15) as:

$$\begin{aligned} x' &= x(1-x)\left[r_1(x,n) - r_2(x,n)\right], \\ n' &= \epsilon n(1-n)\left[-1 + (1+\theta)x\right], \end{aligned} \tag{21}$$

where the $'$ denotes a derivative with respect to τ. For $0 < \epsilon \ll 1$, this rescaling identifies n as the slow variable. Let S_0 denote the critical manifold of the system [26], i.e., the set of values of (x, n) for which $x' = 0$. So long as the system is not close to this critical manifold, then the dynamics of x are much faster than that of n, i.e., by a factor of order $1/\epsilon$. The critical manifolds of this system in the bounded domain $0 \le x \le 1$ and $0 \le n \le 1$ are: (i) $x = 0$; (ii) $x = 1$; and (iii) the set of points (x_c, n_c) that satisfy $r_1(x_c, n_c) = r_2(x_c, n_c)$. The last of these critical manifolds can be interpreted as the interior nullcline of x. We assume that n parameterizes the dynamics of x far from the critical manifold.

Given the payoff matrix in Eq. (20), the one-dimensional fast-subsystem can can be written as:

$$x' = x(1-x)(1.25x + 0.25 - n(3.25x + 1.25)). \tag{22}$$

In this case, the interior critical manifold satisfies $n = \frac{5x+1}{13x+5}$. For $n > 1/3$, there are two fixed points, $x = 0$ and $x = 1$, which are stable and unstable respectively. For $n < 1/5$, there are are also two fixed points, $x = 0$ and $x = 1$, which are unstable and stable respectively. This system undergoes two saddle-node bifurcations at the values $n = 1/5$ and $n = 1/3$. For values of the slow variable $1/5 < n < 1/3$, the system has three fixed points, such that $x = 0$ and $x = 1$ are stable and x_c is unstable where

$$x_c(n) = \frac{5n-1}{5-13n}. \tag{23}$$

System dynamics can be understood in terms of a series of fast and slow changes. Consider initializing the system at values (x_0, n_0) with $n_0 < 1/5$, i.e., in the region where there are only two fixed points of the fast-dynamics. The system will behave akin to a one-dimensional system and increase rapidly in x, parameterized by the value $n = n_0$. As the system approaches the attracting critical manifold, $x = 1$, then the system dynamics will be governed by the slow variable dynamics, n'. Cooperators will enhance the environmental state, given that $n' > 0$ for $x \to 1$. The system will then *slowly* approach the fixed point $(1, 1)$. This fixed point is unstable in the fast direction, such that the system will *rapidly* approach the attracting critical manifold of $x = 0$, i.e., the point $(0, 1)$. Again, the system will then *slowly* change in environmental state towards the point $(0, 0)$, given that $n' < 0$ for $x \to 0$. Now that $n < 1/5$, the system will be dominated by the fast subsystem dynamics, *rapidly* increasing x - completing the cycle. The resulting dynamics will appear as relaxation oscillations with slow changes in environment alternating with rapid changes in the fraction of cooperators. The dynamics overlaid with the critical manifolds for this system are shown in Figure 3a.

The key to the emergence of relaxation oscillations is that the interior critical manifold is a repeller. This is not universally the case. A counter-example is the state-dependent payoff matrix:

$$A(n) = (1-n)\begin{bmatrix} 3.5 & 1 \\ 2 & 0.05 \end{bmatrix} + n\begin{bmatrix} 4 & 1 \\ 7 & 2 \end{bmatrix}. \tag{24}$$

Rather than oscillating, the overall dynamics converge to a stable state – such that there is a mixed population of cooperator and defectors at the point (x^*, n^*). Figure 3 illustrates such a case, again using the fast-slow systems framework. The key difference is that the critical interior manifold is an attractor. Hence dynamics on the fast subsystem is attracted to a point in the slow variable closer to that of n^*. The overall dynamics is again characterized by a mix of fast and slow changes, however they spiral in to the interior fixed point rather than away from it. The dynamics overlaid with the critical manifolds for this system are shown in Figure 3b. Of note, the feedback-evolving game analyzed here is closest in intent to a prior analysis of coupled strategy and environmental change in the context of durable public goods games [27]. That model assumed that fitness differences between producers and non-producers had no frequency-dependence and the environmental dynamics had at most a single fixed point. Unlike the present case, the model in [27] did not exhibit persistent oscillations.

We can generalize these findings with the help of two definitions. Let $n_c(0)$ and $n_c(1)$ denote the intersection of the interior critical manifold with the boundary critical manifold of the fast-system at $x = 0$ and $x = 1$, respectively. For example, in the left panel of Figure 3, $n_c(0) = 1/5$ and $n_c(1) = 1/3$. We propose the following conjecture: the system will converge to a stable limit cycle via relaxation oscillations if and only if $n_c(0) < n_c(1)$. In the event that $n_c(0) > n_c(1)$ then the system will converge to a fixed point via relaxation oscillations. The system will exhibit neutrally stable orbits exhibiting relaxation oscillations in the marginal case of $n_c(0) = n_c(1)$. The critical value $n_c(0)$ corresponds to the value of the environmental state for which $r_1(x = 0, n) = r_2(x = 0, n)$.

Generalized conditions for an oscillating tragedy of the commons

Here we formally evaluate the conjecture of a general set of conditions for which feedback-evolving games will exhibit an oscillating tragedy of the commons. To do so, consider the environment-dependent payoff matrix

$$A(n) = (1-n)\begin{bmatrix} a_1 & a_2 \\ a_3 & a_4 \end{bmatrix} + n\begin{bmatrix} b_1 & b_2 \\ b_3 & b_4 \end{bmatrix}, \tag{25}$$

where $0 \le n \le 1$. We assume that when $n = 0$ then the payoff matrix has a unique Nash equilibrium corresponding to cooperative dominance. For this to be the case, then $a_1 > a_3$ and $a_2 > a_4$. We further assume that $a_1 > a_4$. Similarly, we assume that when $n = 1$ then the payoff matrix has a unique Nash equilibrium corresponding to defector dominance. For this to be the case, then $b_1 < b_3$ and $b_2 < b_4$. Dominance by defectors is termed a tragedy of the commons if $b_1 > b_4$.

In Appendix A we derive the conditions for relaxation oscillations around an unstable fixed point:

$$\boxed{\frac{b_4 - b_2}{b_3 - b_1} > \frac{a_2 - a_4}{a_1 - a_3}}. \tag{26}$$

This derivation utilizes local stability analysis to evaluate the condition in which the internal equilibrium is present and is unstable. We also confirm that the boxed condition coincides to that in the conjecture, that is if and only if $n_c(0) < n_c(1)$ then there are persistent relaxation oscillations in the system that converge to a limit cycle. When this condition is satisfied we say that the system exhibits an *Oscillating Tragedy of the Commons*. We term the lhs of this equation the "defector advantage asymmetry" and the rhs of this equation the "cooperator advantage asymmetry". All of these differences are positive given the conditions of the payoff matrices in the limits of $n = 0$ and $n = 1$. Here the qualitative outcomes depend on both the *sign* and *magnitude* of differences between payoffs, unlike in evolutionary game theory modeled via replicator dynamics in which qualitative outcomes depend only on the sign differences. We also find that the qualitative outcomes do not depend on the speed of the feedback (see Figure 4). This ϵ-invariance of

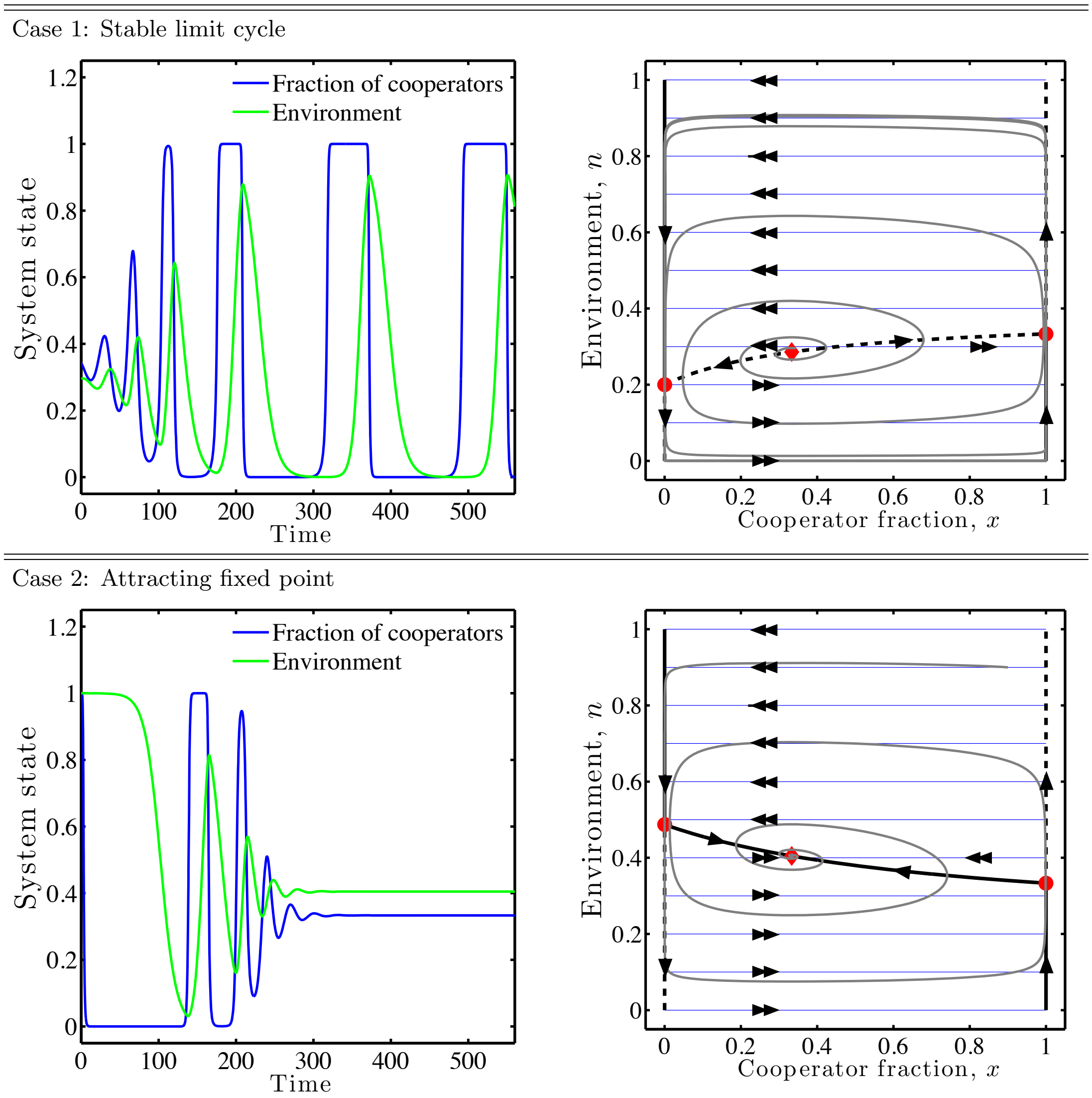

FIG. 3: Fast-slow dynamics of feedback-evolving games, where x and n are the fast and slow variables respectively - including critical manifolds and realized dynamics. In both panels, the black lines denote the critical manifolds with solid denoting attractors and dashed denoting repellers. The blue lines and double arrows denote expected fast dynamics in the limit $\epsilon \to 0$. The red circles denote the bifurcation points of the fast subsystem parameterized by n. The single arrows denote expected slow dynamics. The gray curve denotes the realized orbit. In both cases, $\epsilon = 0.1$ and $\theta = 2$. (Top) Relaxation oscillations converging to a limit cycle arising due to a saddle-node bifurcation in the fast-subsystem parameterized by n in which the critical manifold is a repeller. The payoff matrix $A(n)$ is that defined in Eq. (20). (Bottom) Relaxation oscillations converging to a fixed point arising due to a saddle-node bifurcation in the fast-subsystem parameterized by n in which the critical manifold is an attractor. The payoff matrix $A(n)$ is that defined in Eq. (24).

qualitative outcomes is not universally the case for fast-slow systems [26].

Discussion

We proposed a co-evolutionary game theory that incorporates the feedback between game and environment and between environment and game. In so doing, we extended replicator dynamics to include feedback-evolving games. This extension is facilitated by assuming the environmental state can be represented as a linear combination of two different payoff matrices. Motivated by the study of the tragedy of the commons in evolutionary biology [28] we demonstrated how new kinds of dynamics can arise when cooperators dominate in deplete environments and when defectors dominate in replete environments. In essence, cooperators improve the environment, leading to a change in incentives that shift the game theoretic strategy towards defection. Repeated defections degrade the environment which re-incentives the emergence of cooperators. In this way there is the potential for a sustained cycle in strategy and environmental state, i.e., an oscillating tragedy of the commons. Whether or not the cycle dies out or is persistent depends on the *magnitude* of payoffs. This result is in contrast to the results of evolutionary game theory in which the relative *sign* of payoffs determines qualitative system behavior.

Our proposed replicator model with feedback-evolving games considers the consequences of repetition in which the repeated actions of the game influences the environment in which the game is played. Thus, the model is complementary to long-standing interest in a different kind of repeated games, most famously the iterated prisoner's dilemma [7, 29–32]. In such iterated games, winning cooperative strategies emerge that are otherwise losing strategies in singly-played versions of the game. Here, individuals do not play against another repeatedly or, posed alternatively, do not "recall" playing against another repeatedly. Instead, a feedback-evolving game changes with time as a direct result of the accumulated actions of the populations. The motivating example of a feedback-evolving game has two fixed payoff matrices at its extremes one of which has a tragedy of the commons structure given a replete environmental state. Nonetheless, investigation of other linear combinations of fixed payoff matrices are warranted. For example, if defection and cooperation are favored in depleted and replete environments, respectively, then the current model can exhibit alternative stable states in the dual environment-strategy space – rather than oscillations or convergence to a fixed point.

Thus far, we have assumed that the environment can recover from a nearly deplete state. The rate of renewal was assumed to be proportional to the cooperator fraction. In that sense, our work also points to new opportunities for control - whether for renewable or finite resources. Is it more effective to influence the strategists, the state, and/or the feedback between strategists and state? Analysis of feedback-evolving games could also have implications for theories of human population growth [33], ecological niche construction [34], and the evolution of strategies in public good games [25]. The extension of the current model to microbial and human social systems may deepen understanding of the short- and long-term consequences of individual actions in a changing and changeable environment [35]. We are hopeful that recognition and analysis of the feedback between game and environment can help to more effectively manage and restore endangered commons.

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Appendix A: Stability analysis of replicator dynamics with feedback-evolving games

Derivation of the instability of the interior nullcline

The interior equilibrium (x^*, n^*) has an associated Jacobian:

$$J = \begin{bmatrix} x(1-x)\frac{\partial g}{\partial x} & x(1-x)\frac{\partial g}{\partial n} \\ \epsilon n(1-n)(1+\theta) & 0 \end{bmatrix}_{(x^*,n^*)} \tag{A1}$$

Here $\partial g/\partial n < 0$ for all cases of concern here because the replicator dynamics favor decreases in cooperation as an increasing function of the environmental state n. As such, the determinant is always positive. The stability of the fixed point depends on the sign of the trace of J. Because $0 < x^* < 1$, then the sign of the trace is equivalent to the sign of $\partial g/\partial x$. This result can also be anticipated by a fast-slow systems analysis in which the stability of any point on the nullcline depends strictly on $\partial g/\partial x$. Another consequence is that the trace does not depend on ϵ. Therefore, the qualitative dynamics will be the same for all values of ϵ, i.e., irrespective of the relative speed of the fast and slow variables (see Figure 4). Such an ϵ-invariance of qualitative phenomena is not universally the case in fast-slow dynamics.

Formally, $\partial g/\partial x$ can be written as:

$$\frac{\partial g}{\partial x} = \frac{\partial r_1}{\partial x} - \frac{\partial r_2}{\partial x} \tag{A2}$$

$$= A(n)[1,1] - A(n)[2,1] - A(n)[1,2] + A(n)[2,2] \tag{A3}$$

given the condition at equilibrium $r_1 = r_2$. We must solve for n^* as a function of the payoff coefficients. As such,

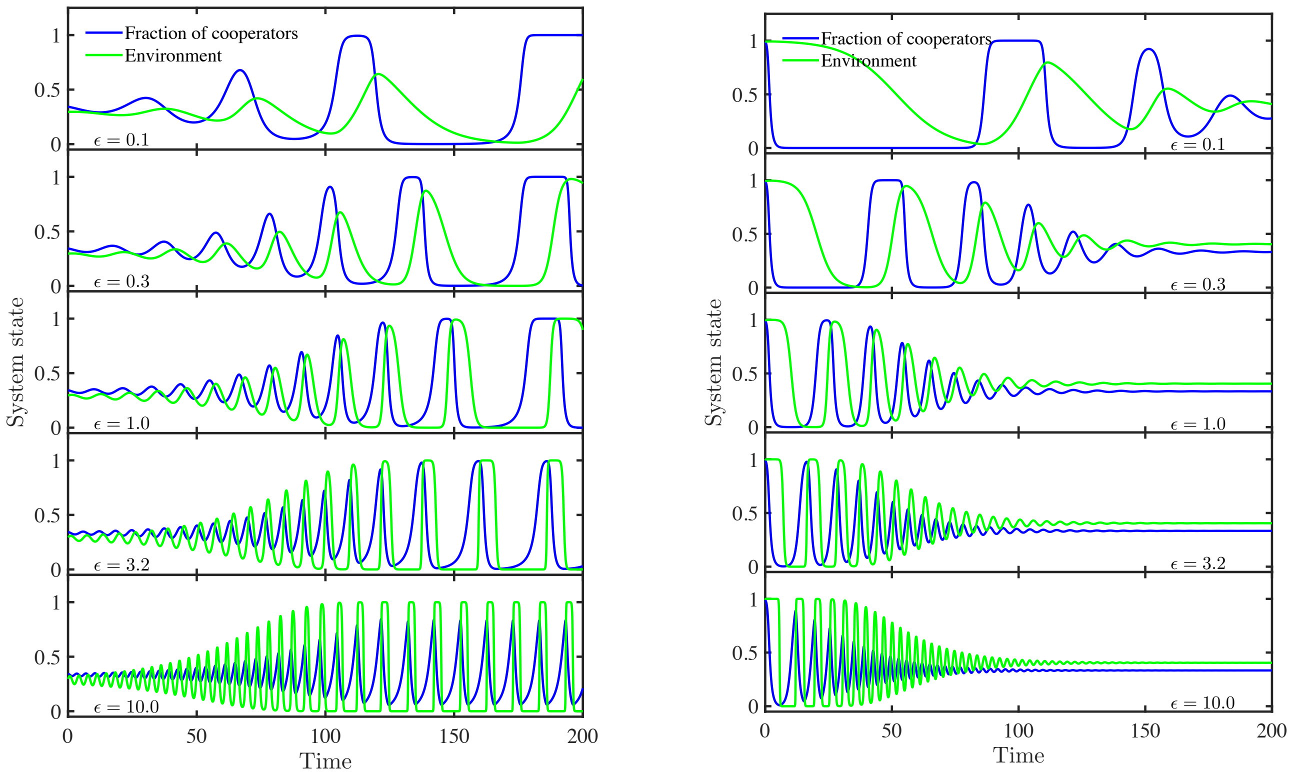

FIG. 4: Invariance of system dynamics given change in the relative speed of strategy and environmental dynamics. The parameter ϵ is varied from 0.1 to 10 given cases where dynamics are expected to lead to stable limit cycles (left) and to a fixed point (right). Other parameters are the same as in Figure 3. Although the transient dynamics differ, the qualitative dynamics remain invariant with respect to changes in ϵ.

when $r_1 = r_2$ given $x = x^* = 1/(1+\theta)$, the following condition must be satisfied:

$$A(n)[1,1]x^* + A(n)[1,2](1-x^*) = A(n)[2,1]x^* + A(n)[2,2](1-x^*) \tag{A4}$$

$$A(n)[1,1] - A(n)[2,1] + A(n)[2,2] - A(n)[1,2] = (1+\theta)\left(A(n)[2,2] - A(n)[1,2]\right) \tag{A5}$$

Recall that

$$A(n)[1,1] = (1-n)a_1 + nb_1, \tag{A6}$$

$$A(n)[1,2] = (1-n)a_2 + nb_2, \tag{A7}$$

$$A(n)[2,1] = (1-n)a_3 + nb_3, \tag{A8}$$

$$A(n)[2,2] = (1-n)a_4 + nb_4. \tag{A9}$$

so that the equilibrium condition for n^* is

$$n^*\left[(b_1-b_3)+(b_4-b_2)+(a_2-a_4)+(a_3-a_1)\right]+(a_1-a_3)+(a_4-a_2) = \left[(a_4-a_2)+n^*\left((b_4-b_2)+(a_2-a_4)\right)\right](1+\theta) \tag{A10}$$

or equivalently,

$$n^*\left[(b_1-b_3)-\theta(b_4-b_2)-\theta(a_2-a_4)+(a_3-a_1)\right] = (a_3-a_1)+\theta(a_4-a_2) \tag{A11}$$

$$n^* = \frac{(a_1-a_3)+\theta(a_2-a_4)}{(b_3-b_1)+\theta(b_4-b_2)+\theta(a_4-a_2)+(a_1-a_3)} \tag{A12}$$

The point of interest n^* satisfies $r_1 = r_2$. Hence, from (B5) an (B3) above, then

$$\text{Sign}\left(\frac{\partial g}{\partial x}\right) = (1-n^*)(a_4-a_2)+n^*(b_4-b_2) \tag{A13}$$

In other words the interior fixed point is unstable when $\partial g/\partial x > 0$, equivalently:

$$n^* > \frac{a_2 - a_4}{(a_2 - a_4) + (b_4 - b_2)} \tag{A14}$$

Recall that $a_2 > a_4$ and $b_4 > b_2$ in the games we consider and further that the r.h.s. of Eq. (A14) is equivalent to $n_c(0)$ in the main text, i.e., the intersection of the nullcline of $\dot{x}$ with the $(x = 0, n)$ boundary. We can then write the condition on instability as

$$\frac{(a_3 - a_1) + \theta(a_4 - a_2)}{(b_1 - b_3) + \theta(b_2 - b_4) + \theta(a_2 - a_4) + (a_3 - a_1)} > \frac{a_2 - a_4}{(a_2 - a_4) + (b_4 - b_2)} \tag{A15}$$

We denote the strictly positive dummy variables $C_1 = a_3 - a_1$, $C_2 = b_1 - b_3$, $D_1 = a_4 - a_2$ and $D_2 = b_2 - b_4$ and rewrite Eq. (A15) as:

$$\frac{C_1 + \theta D_1}{C_1 + C_2 + \theta D_1 + \theta D_2} > \frac{D_1}{D_1 + D_2} \tag{A16}$$

which after some algebraic re-arrangement yields

$$\frac{C_1}{C_1 + C_2} > \frac{D_1}{D_1 + D_2} \tag{A17}$$

where we recognize the l.h.s. as

$$\frac{a_1 - a_3}{(a_1 - a_3) + (b_3 - b_1)} \tag{A18}$$

or equivalent to $n_c(1)$ in the main text, i.e., the intersection of the nullcline of $\dot{x}$ with the $(x = 1, n)$ boundary. To summarize, the interior fixed point is unstable when

$$\frac{a_1 - a_3}{(a_1 - a_3) + (b_3 - b_1)} > \frac{a_2 - a_4}{(a_2 - a_4) + (b_4 - b_2)} \tag{A19}$$

This can be further reduced to the boxed equation in the main text:

$$\boxed{\frac{b_4 - b_2}{b_3 - b_1} > \frac{a_2 - a_4}{a_1 - a_3}.} \tag{A20}$$

Deriving the conditions for the intersection of the interior critical manifold with the boundary critical manifold

Consider the generalized payoff matrix

$$A(n) = (1 - n)\begin{bmatrix} a_1 & a_2 \\ a_3 & a_4 \end{bmatrix} + n\begin{bmatrix} b_1 & b_2 \\ b_3 & b_4 \end{bmatrix} \tag{A21}$$

where $0 \le n \le 1$, $a_1 > a_3$, $a_2 > a_4$, $a_1 > a_4$, $b_1 < b_3$, $b_2 < b_4$ and $b_1 > b_4$. Further, let $n_c(0)$ and $n_c(1)$ denote the intersection of the interior critical manifold with the boundary critical manifold of the fast-system at $x = 0$ and $x = 1$, respectively. We find these points by setting $r_1(0, n) = r_2(0, n)$ and $r_1(1, n) = r_2(1, n)$, respectively:

$$r_1 = A(n)[1, 1]x + A(n)[1, 2](1 - x) \tag{A22}$$
$$r_2 = A(n)[2, 1]x + A(n)[2, 2](1 - x) \tag{A23}$$

where the notation $[i, j]$ denotes the i-th row and j-th column of the matrix. We find

$$n_c(0) = \frac{a_2 - a_4}{(b_4 - b_2) + (a_2 - a_4)} \tag{A24}$$
$$n_c(1) = \frac{a_1 - a_3}{(b_3 - b_1) + (a_1 - a_3)} \tag{A25}$$

Therefore $n_c(0) < n_c(1)$ when

$$\frac{b_4 - b_2}{b_3 - b_1} > \frac{a_2 - a_4}{a_1 - a_3} \tag{A26}$$

which is Eq. (A20) in this Appendix and Eq. (26) in the main text.

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