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Evolutionary dynamics of two communities under environmental feedback

Yu Kawano, *Member*, Lulu Gong, *Student Member*, Brian D. O. Anderson, *Life Fellow*, and Ming Cao, *Senior Member*

Abstract—In this paper, we study the evolutionary dynamics of two different types of communities in an evolving environment. We model the dynamics using an evolutionary differential game consisting of two sub-games: 1) a game between two different communities and 2) a game between communities and the environment. Our interest is to clarify when the two communities and environment can coexist dynamically under the feedback from the changing environment. Mathematically speaking, we show that for specific game payoffs, the corresponding three-dimensional replicator dynamics induced by the evolutionary game have an infinite number of periodic orbits.

Index Terms—Biological systems, game theory

I. INTRODUCTION

INTERACTIONS among communities and their surrounding environments have been studied from various aspects, see e.g., [1], [2] for ecosystems and [3], [4] for epidemic processes. Especially in evolutionary game theory, interactions among two communities (without environments), e.g. two competing species [5] or males and females [6], have been intensively studied in order to understand the mechanisms for their evolution. Such games with two types of players [7] have been generalized to games within a networked population [8] or interacting communities [9]. More importantly, the results in [8], [9] with the help of the classical tools from evolutionary game theory [10], [11] have built up extended replicator dynamics models [11], [12].

In contrast to the development of analysis of interacting communities, the interactions between communities and their environments have not been well studied in the evolutionary game framework even though for a dynamic game evolving over a long period, the surrounding environment can dynamically change and affect the strategies of each community. For instance, if two competing species prey on the same species, their strategy can vary depending on the amount of the prey, since if the species of prey were to die out, this would lead to extinction of either or both species of predators. Recently, to

study interaction between the environment and a single community, the paper [13] introduced the concept of environmental feedback and accordingly modified the replicator dynamics into the so-called *replicator dynamics with feedback-evolving games*. Based on this model, dynamical coexistence or non-coexistence of an environment and the single community has been studied.

By extending the concept of an environment, in this paper, we clarify under what conditions two competing communities and a surrounding environment can all coexist dynamically, which is a first but necessary step toward analyzing interaction among multiple communities and environments. Such conditions can be easily understood in pedagogical examples: In the two competing predators and a single prey example, if both species of predators stop preying on the prey when its amount becomes small, then the prey does not die out, and eventually its amount increases. After sufficient increase, the predators start to prey again. Our goal is then to mathematically prove that for specific payoffs, the modified replicator dynamics of two communities with feedback-evolving games have an infinite number of periodic orbits. Note that studying oscillating coexistence is mathematically more challenging than studying non-coexistence because non-coexistence analysis usually reduces to stability analysis of an equilibrium point, and then linearization very often works for such a problem.

If the dimension of a system is higher than two, as is the system we study, which has dimension 3, analysis of periodic orbits (including establishing their existence) is technically more involved, since the Poincaré-Bendixson theorem [14] is not directly applicable. Nevertheless, perhaps surprisingly, the evolutionary game considered in this paper can be decomposed into two sub-games: 1) a game between two-different communities which turns out to be very straightforward to analyze, and 2) a game between the communities and environment. The periodic behavior arises in the latter game and to demonstrate this, our main idea is to somehow integrate the two communities into a single community. Then, the problem reduces to an evolutionary game with the integrated single community and environment, and the obtained new dynamics, which are second order, can be viewed as replicator dynamics of the reduced game. For the reduced replicator dynamics, one can apply the Poincaré-Bendixson theorem.

Besides the contribution of providing a more comprehensive model for evolutionary dynamics for two communities under environmental feedback, there are also several notable technical contributions compared to the existing literature. First, our replicator dynamics are parameter-varying systems,

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and we provide detailed analysis and a formal proof for the existence of an infinite number of periodic orbits. Furthermore, we provide a new interpretation of environmental feedback in terms of a game and then establish the connection between environmental feedback and an evolutionary game on a networked population (or interacting communities). We clarify that in fact the existing model and ours are specific games on a networked population, i.e., replicator dynamics with feedback-evolving games are equivalent to replicator dynamics on a networked population. Note however that the work in [8], [9] on networked population focuses on analysis of the Nash equilibria by restricting payoff matrix structures to different structures from ours; for this reason, results in these papers cannot be applied to our problem.

We emphasize that our evolutionary game models with environmental feedback can be interpreted using predator-prey interactions. In fact, the standard predator-prey dynamics are typically represented by the Lotka-Volterra equation, which is equivalent to replicator dynamics of a single-community without an environment [15]. Therefore, our modified replicator dynamics can also be viewed as an extension of the Lotka-Volterra equation to represent interaction among two different species of predators and a single species of prey.

The remainder of this paper is organized as follows. Section II introduces two evolutionary games: 1) a game between two different communities and 2) a game between the communities and the environment. Then, the corresponding three-dimensional replicator dynamics are presented. In Section III, the payoff matrix structures for coexistence of two communities and the environment are given. Then, for these payoff matrix structures, it is shown that the replicator dynamics have an infinite number of periodic orbits. Section IV considers a special case when one community fixes its strategy irrespective of the state of the environment, and Section V makes concluding remarks.

II. EVOLUTIONARY DYNAMICS OF TWO COMMUNITIES UNDER ENVIRONMENTAL FEEDBACK

A. Games between Two Different Types of Community

Consider an evolutionary game with two different types of community $i = I, II$. Here, each community consists of two types of populations, i_1 and i_2 , where each community does not have a game within the community. Let s_{i,i_1} and s_{i,i_2} be the proportions (frequencies) of cooperators and defectors in community i , respectively. Then, $[s_{i,i_1}, s_{i,i_2}]$ is the vector of distribution in community i , which describes the state of the community. Without loss of generality, assume each member of the community is either a cooperator or defector, namely $s_{i,i_1} + s_{i,i_2} = 1$, and define $x_i := s_{i,i_1}$.

Suppose that the payoffs (fitness) of every population i_j linearly depends on both $[s_{I,I_1}, s_{I,I_2}] = [x_I, 1 - x_I]$ and $[s_{II,I_1}, s_{II,I_2}] = [x_{II}, 1 - x_{II}]$. Let $A^I = (a_{I_j, II_k}^I)$ and $A^{II} = (a_{I_j, II_k}^{II})$, $j, k = 1, 2$ be the two differing payoff matrices of communities I and II , respectively, e.g., population I_j receives a payoff a_{I_j, II_k}^I when it interacts with population II_k . Since there is no game within each community, there is no interaction between i_1 and i_2 , $i = I, II$. In this situation, the expected

payoffs of populations I_j and II_k are respectively given by

$$\begin{aligned} U_I(I_j, x_{II}) &= a_{I_j, II_1}^I x_{II} + a_{I_j, II_2}^I (1 - x_{II}), \\ U_{II}(II_k, x_I) &= a_{I_1, II_k}^{II} x_I + a_{I_2, II_k}^{II} (1 - x_I). \end{aligned} \quad (1)$$

Then, the average expected payoffs of communities I and II are respectively given by

$$\bar{U}_i(x) = x_i U_i(i_1, x_j) + (1 - x_i) U_i(i_2, x_j), \quad i \neq j. \quad (2)$$

B. Environmental Feedback

In this subsection, we extend the concept of environmental feedback [13] to the two-community scenario and investigate under what conditions two different types of communities and the environment coexist dynamically. Accordingly, payoffs of communities are modified as functions of the environment, where by abuse of notation, the same symbols are used to describe payoff functions depending on the environment. Note that, differently from [13], we introduce environmental dynamics from the perspective of a game with communities and the environment. Building on this, we establish the connection between environmental feedback and a game on an interacting communities [8], [9].

Consider a single environment consisting of two types of populations, III_1 and III_2 , and there is no game within the environment. Let r_j , $j = 1, 2$ be the proportion of population j of environment, and then $r_1 + r_2 = 1$. Define $n := r_1$, and consequently $r_2 = 1 - n$. Then, the modified payoff matrices are defined as functions of n , $A^I(n) = (a_{I_j, II_k}^I(n))$ and $A^{II}(n) = (a_{I_j, II_k}^{II}(n))$.

Suppose that the payoffs of populations III_1 and III_2 linearly depend on the populations of communities, $s_{i_1} = x_i$ and $s_{i_2} = 1 - x_i$, $i = I, II$. Let $B^i = (b_{j,i_k})$, $i = I, II$, $j, k = 1, 2$ be the payoff matrices of environment III when it interacts with community i , i.e., population III_j receives b_{j,i_k} when it interacts with population i_k . Then, the expected payoff of population III_j is

$$V(III_j, x) = \sum_{i=I}^{II} (b_{j,i_1} x_i + b_{j,i_2} (1 - x_i)), \quad (3)$$

and the average expected payoff of the environment is

$$\bar{V}(x, n) = nV(III_1, x) + (1 - n)V(III_2, x). \quad (4)$$

In summary, we obtain modified replicator dynamics with environmental feedback:

$$\begin{cases} \varepsilon \dot{x}_I = x_I (U_I(I_1, x_{II}, n) - \bar{U}_I(x, n)), \\ \varepsilon \dot{x}_{II} = x_{II} (U_{II}(II_1, x_I, n) - \bar{U}_{II}(x, n)), \\ \dot{n} = n(V(III_1, x) - \bar{V}(x, n)). \end{cases} \quad (5)$$

where from the modified versions of (1) and (2),

$$\begin{aligned} U_i(i_1, x_j, n) - \bar{U}_i(x, n) &= (1 - x_i) (a_{I_1, II_2}^i(n) - a_{I_2, II_2}^i(n)) \\ &\times \left(1 + \left(\frac{a_{I_1, II_1}^i(n) - a_{I_2, II_1}^i(n)}{a_{I_1, II_2}^i(n) - a_{I_2, II_2}^i(n)} - 1 \right) x_j \right), \quad i \neq j \end{aligned}$$

and from (3) and (4),

$$V(III_1, x) - \bar{V}(x, n)$$

$$= (1-n) \left(\sum_{i=I}^{II} (b_{1,i_1} - b_{2,i_1})x_i + (b_{1,i_2} - b_{2,i_2})(1-x_i) \right).$$

In the first and second equations of (5), $\varepsilon > 0$ represents the difference of time-scales between communities and environment. The last equation describes the dynamics of the environment. Notice that the system (5) is specific replicator dynamics for a networked population [8] or interacting communities [9], where one component, environment, has a different type of payoff from the others. This kind of situation has not been studied in [8], [9]. Finally, the difference from a situation describing replicator dynamics for six populations in one community is that $s_{i,i_1} + s_{i,i_2} = 1$, $i = I, II$ and $r_1 + r_2 = 1$ hold instead of $\sum_{j=1}^2 s_{I,I_j} + s_{II,I_j} + r_j = 1$.

III. COEXISTENCE OF TWO DIFFERENT TYPES OF COMMUNITIES AND ENVIRONMENT

In this section, for a specific choice of payoff matrices, we show that the modified replicator dynamics (5) have an infinite number of periodic orbits.

A. Studied Replicator Dynamics

In a similar manner with the single community case [13], we consider the following asymmetric payoff matrices for communities:

$$A^i(n) := n \begin{bmatrix} a_i & b_i \\ c_i & d_i \end{bmatrix} + (1-n) \begin{bmatrix} c_i & d_i \\ a_i & b_i \end{bmatrix}, \quad (6)$$

where $a_i > c_i$ and $b_i > d_i$, $i = I, II$. Each matrix has an embedded symmetry to ensure that mutual cooperation is a Nash equilibrium when $n = 1$ and mutual defection is a Nash equilibrium when $n = 0$ [13].

For the environment, we choose payoff matrices so that if two communities are relatively cooperative (resp. defective), then environment tends to defective (resp. cooperative), i.e., snowdrift types of payoff, $b_{1,i_1} < b_{2,i_1}$ and $b_{1,i_2} > b_{2,i_2}$, $i = I, II$.

In summary, we use the following model:

$$\Sigma : \begin{cases} \varepsilon \dot{x}_I = -\sigma_I x_I(1-x_I)(1+\Delta_I x_{II})(1-2n), \\ \varepsilon \dot{x}_{II} = -\sigma_{II} x_{II}(1-x_{II})(1+\Delta_{II} x_I)(1-2n), \\ \dot{n} = -n(1-n) \sum_{i=I}^{II} ((\theta_i + \lambda_i)x_i - \lambda_i), \end{cases} \quad (7)$$

where $\sigma_i := b_i - d_i > 0$, $\Delta_i := (a_i - c_i)/(b_i - d_i) - 1 > -1$, $\theta_i := b_{2,i_1} - b_{1,i_1} > 0$, and $\lambda_i := b_{1,i_2} - b_{2,i_2} > 0$, $i = I, II$. For the dynamics (7), the boundary of the cube $[0, 1]^3$ is positively invariant. Therefore, the cube itself is positively invariant. Our interest is dynamics in this cube. To avoid the confusion with a point in \mathbb{R}^2 , denote open and closed intervals by $I_{(a,b)} := (a, b)$ and $I_{[a,b]} := [a, b]$ for $a < b$, respectively, e.g. $I_{[0,1]}^3 = [0, 1]^3$.

The model Σ has the following properties.

- (a) If $n > 1/2$ ($n < 1/2$) then $\dot{x}_i > 0$ (< 0), $i = I, II$;
- (b) if $\sum_{i=I}^{II} (\theta_i + \lambda_i)x_i - \lambda_i > 0$ (< 0) then $\dot{n} < 0$ (> 0).

Therefore, one might reasonably expect that there are limiting orbits in which none of x_I , x_{II} or n converges to zero (we note also that there is an equilibrium point for the equations in which no variable is 0 or 1, defined by $x_i = \lambda_i(\theta_i + \lambda_i)^{-1}$

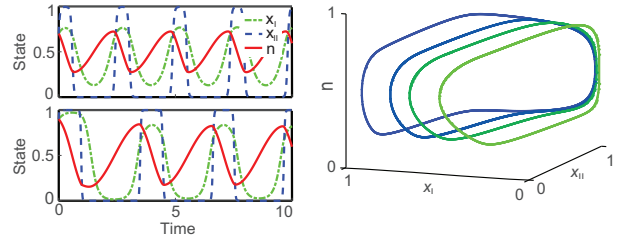


Fig. 1. Trajectories of system Σ , where $\varepsilon = 0.1$, $\sigma_I = 1$, $\sigma_{II} = 3$, $\Delta_I = -1/2$, $\Delta_{II} = 2$, $\lambda_1 = \lambda_2 = 1$ and $\theta_1 = \theta_2 = 2$. (Left) Time series of the state (x_I, x_{II}, n) . (Right) Four trajectories of x_I - x_{II} - n system.

and $n = 1/2$, the stability of which needs closer examination). In the predator-prey example of the Introduction, none of two competing predators and single prey dies out. Figures 1 shows some trajectories of system Σ . For different choices of payoff matrices, one might observe periodic behaviors. However, even in our intuitively reasonable problem setting, it is a mathematically nontrivial fact that these trajectories are actually periodic orbits. The difference of behaviors between x_I and x_{II} actually corresponds to the game between two communities. Studying this difference is another goal of the research.

Our goal is to prove that the system Σ has an infinite number of periodic orbits. The periodic behavior occurs due to the interaction between communities and the environment. To focus on this interaction, we examine how to integrate two communities into a single community, i.e., reduce the first two equations of the system Σ into a single equation. Then, we study the reduced order two-dimensional system.

B. Integration of Two Communities

The main idea of our analysis is applying the change of variables $a = \varphi_{II}(x_{II}) - \varphi_I(x_I)$, where

$$\varphi_i(x_i) = (\ln(x_i) - (1 + \Delta_j) \ln(1 - x_i)) / \sigma_i, \quad j \neq i. \quad (8)$$

This $\varphi_i(x_i)$ exists and is analytic on $I_{(0,1)}$, and its range is \mathbb{R} . From $\sigma_i > 0$ and $\Delta_j > -1$, its derivative

$$\frac{d\varphi_i(x_i)}{dx_i} = \frac{1 + \Delta_j x_i}{\sigma_i x_i (1 - x_i)} \quad (9)$$

is positive on $I_{(0,1)}$, i.e., φ_i is strictly increasing on $I_{(0,1)}$. Thus, φ_i has the (global) inverse function $\varphi_i^{-1} : \mathbb{R} \rightarrow I_{(0,1)}$, which is analytic on \mathbb{R}^1 .

Now, we apply globally real-analytic diffeomorphism $\psi : I_{(0,1)}^3 \ni (x_I, x_{II}, n) \mapsto (z, n, a) \in I_{(0,1)}^2 \times \mathbb{R}$, where

$$\psi(x_I, x_{II}, n) = [x_I \quad n \quad \varphi_{II}(x_{II}) - \varphi_I(x_I)]^T. \quad (10)$$

From the first two equations of (7) and (9), the system Σ in the (z, n, a) -coordinates is

$$\Sigma_a : \begin{cases} \varepsilon \dot{z} = -\sigma_I z(1-z)(1 + \Delta_I \varphi_{II}^{-1}(a + \varphi_I(z)))(1-2n), \\ \dot{n} = -n(1-n)f(z), \\ \dot{a} = 0, \\ f(z) := (\theta_I + \lambda_I)z + (\theta_{II} + \lambda_{II})\varphi_{II}^{-1}(a + \varphi_I(z)) \\ \quad - (\lambda_I + \lambda_{II}). \end{cases}$$

¹This conclusion depends critically on the assumption of use of prisoner's dilemma payoff matrices $A^{i,j}(n)$, i.e., $\sigma_i > 0$ and $\Delta_i < -1$, $i = I, II$.

Since $a(t) = a(0)$ for any $t \geq 0$, the first two subsystems of Σ in the new coordinates denoted by Σ_a constitute a two-dimensional system with a constant parameter $a \in \mathbb{R}$. The new variable z can be viewed as the integrated proportion of communities I and II . Therefore, the system Σ_a describes the interaction between the integrated community and environment. In the following subsections, we analyze this two-dimensional system Σ_a with a constant parameter, and then go back to the original coordinates.

Although the range of ψ in (10) does not contain $I_{[0,1]}^2 \times \mathbb{R}$, the system Σ_a itself is defined on $I_{[0,1]}^2$ at each fixed $a \in \mathbb{R}$. Actually, at each $a \in \mathbb{R}$, we have $\varphi_{II}^{-1}(a + \varphi_I(0)) = 0$ and $\varphi_{II}^{-1}(a + \varphi_I(1)) = 1$, with $\varphi_{II}^{-1}(a + \varphi_I(z)) \in I_{(0,1)}$ for $z \in I_{(0,1)}$. Then one sees easily that $I_{[0,1]}^2$ is a positively invariant set of the system Σ_a for any $a \in \mathbb{R}$.

To study orbits and their periodicity, one needs to take several steps. We first compute equilibria. Then, we construct an energy function whose time derivative along the trajectory of the system Σ_a is identically zero, which is effectively a constant of motion. Finally we show that almost each level set corresponds to a periodic orbit, based on the Poincaré-Bendixson theorem [14].

C. Equilibrium Points

We compute the equilibria of the system Σ_a . First, at each $a \in \mathbb{R}$, each corner in $\{0,1\}^2 = \{(0,0), (0,1), (1,0), (1,1)\}$ is an equilibrium. By checking the system Σ_a , there is a heteroclinic cycle [14] $(0,0) \rightarrow (0,1) \rightarrow (1,1) \rightarrow (1,0) \rightarrow (0,0)$ on the boundary $I_{[0,1]}^2 \setminus I_{(0,1)}^2$. Also, at each corner, one can check that the Jacobian matrix has one positive and one negative real eigenvalue. This implies that there is no trajectory converging to a corner without touching the boundary $I_{[0,1]}^2 \setminus (I_{(0,1)}^2 \cup \{0,1\}^2)$. Otherwise, the dimension of the unstable manifold around each corner would be two, contradicting the eigenvalue sign property.

Next, we consider the interior $I_{(0,1)}^2$. In the right hand side of the first equation for \dot{z} , the range of φ_{II}^{-1} is $I_{(0,1)}$ and $\Delta_I > -1$. Thus, $\dot{z} = 0$ if and only if $n = 1/2$. When $n = 1/2$, $\dot{n} = 0$ if and only if $f(z) = 0$. We now show that just one such possibility exists:

Proposition 3.1: For any $a \in \mathbb{R}$, $f(z) = 0$ has a unique solution \bar{z}_a in $I_{(0,1)}$.

Proof: First, we show that $f(z)$ is strictly increasing on $I_{(0,1)}$. Since $\theta_i + \lambda_i > 0$, $i = I, II$, it suffices to show that $\varphi_{II}^{-1}(a + \varphi_I(z))$ is strictly increasing. As mentioned after (9), $\varphi_i(z)$, $i = I, II$ are strictly increasing, and so are their inverses φ_i^{-1} , as is the composition $\varphi_{II}^{-1}(a + \varphi_I(z))$.

Next, we show that $f(z) = 0$ has a solution in $I_{(0,1)}$. For any $a \in \mathbb{R}$, the ranges of both z and $\varphi_{II}^{-1}(a + \varphi_I(z))$ are $I_{(0,1)}$, and consequently the range of $f(z)$ is $I_{(-\lambda_I - \lambda_{II}, \theta_I + \theta_{II})}$ that contains 0. Finally, we consider the uniqueness. In the original coordinates, $f(z) = 0$ is

$$(\theta_I + \lambda_I)x_I + (\theta_{II} + \lambda_{II})x_{II} - (\lambda_I + \lambda_{II}) = 0.$$

For any fixed x_{II} , x_I is a unique solution, which implies that for any $a \in \mathbb{R}$, $f(z) = 0$ has a unique solution. ■

It is worth mentioning that the two eigenvalues of the Jacobian matrix at $(\bar{z}_a, 1/2)$ lie on the imaginary axis, and thus the Hartman-Grobman theorem [14] is not applicable to identify the stability of Σ_a . In fact, as shown in Section III-E, $(\bar{z}_a, 1/2)$ is neutrally stable, a fact which follows from the existence of an infinite number of periodic orbits.

D. Constant of Motion

In this subsection, we construct a constant of motion for the system Σ_a and then show that it takes a unique maximum at $(\bar{z}_a, 1/2)$, a fact to be used for analysis of its level sets.

A constant of motion is obtained as follows.

Theorem 3.2: Define the following scalar valued function H_a on $I_{(0,1)}^2$:

$$H_a(z, n) := H_{z,a}(z) + H_n(n), \quad (11)$$

$$H_n(n) := (\sigma_I/\varepsilon)(\ln(n) + \ln(1-n)), \quad (12)$$

$$H_{z,a}(z) := \int_{1/2}^z h_{z,a}(y) dy, \quad \forall z \in I_{(0,1)}, \quad (13)$$

$$h_{z,a}(y) := \frac{-f(y)}{y(1-y)(1 + \Delta_I \varphi_{II}^{-1}(a + \varphi_I(y)))}.$$

Then, H_a is analytic on $I_{(0,1)}^2$, and its time derivative along the trajectory of system Σ_a is identical to zero on $I_{(0,1)}^2$.

Remark 3.3: From the system equation of Σ_a , we have $-h_{z,a}(z)dz = (\sigma_I(1-2n)/\varepsilon n(1-n))dn$. By performing the integrations, one can construct the constant of motion H_a . In [13], a constant of motion for two-dimensional replicator dynamics are constructed in a similar way, but without analysis on a maximum point or level sets as is done in this paper.

Proof: First, we show that H_a is analytic. Since H_n is analytic on $I_{(0,1)}$, we focus on $H_{z,a}$. For any fixed $a \in \mathbb{R}$, $\varphi_{II}^{-1}(a + \varphi_I(\cdot))$ is analytic on $I_{(0,1)}$, and its range is $I_{(0,1)}$. From $\Delta_I > -1$, the denominator of $h_{z,a}$ is positive on $I_{(0,1)}$, and thus $h_{z,a}$ is defined and analytic on $I_{(0,1)}$. Therefore, $h_{z,a}$ is integrable on any compact interval in $I_{(0,1)}$, i.e., its primitive function $H_{z,a}$ exists on $I_{(0,1)}$. Since $h_{z,a}$ is analytic on the simply connected interval $I_{(0,1)}$, $H_{z,a}$ is analytic on $I_{(0,1)}$. Finally, one can confirm $dH_a(z, n)/dt = 0$. ■

Next, we investigate the existence of a maximum point.

Lemma 3.4: The function $H_a(z, n)$ in (11) takes a unique maximum value over $I_{(0,1)}^2$, denoted by $c_a \in \mathbb{R}$, at $(\bar{z}_a, 1/2)$.

Proof: It can be confirmed that $H_n(n)$ takes a unique maximum at $n = 1/2$. Then, we show that $H_{z,a}(z)$ takes a unique maximum at \bar{z}_a . The derivative of $H_{z,a}(z)$ with respect to z is $h_{z,a}(z)$. According to the proof of Theorem 3.2, the denominator of $h_{z,a}(z)$ is positive for any $z \in I_{(0,1)}$. Since $z = \bar{z}_a$ is a unique solution to $f(z) = 0$, $\partial H_{z,a}(z)/\partial z = h_{z,a}(z) = 0$ if and only if $z = \bar{z}_a$. That is, \bar{z}_a is a unique stationary point of $H_{z,a}(z)$.

To demonstrate the stationary point is a maximum, it suffices to show that the Hessian

$$\frac{d^2 H_{z,a}(z)}{dz^2} = \frac{d}{dz} \left(\frac{-f(z)}{z(1-z)(1 + \Delta_I \varphi_{II}^{-1}(a + \varphi_I(z)))} \right)$$

²Existence of H_a requires the denominator of $h_{z,a}$ to be nonzero, and the prisoner's dilemma property helps assure this.

is negative at \bar{z}_a . Using the usual derivative formula for a quotient, the denominator is positive for any $z \in I_{(0,1)}$, and the numerator is

$$-\frac{df(z)}{dz}z(1-z)(1+\Delta_I\varphi_{II}^{-1}(a+\varphi_I(z))) \\ + f(z)\frac{d(z(1-z)(1+\Delta_I\varphi_{II}^{-1}(a+\varphi_I(z))))}{dz}.$$

Because $f(\bar{z}_a) = 0$, the second term vanishes at \bar{z}_a . Next, in the first term, the proof of Proposition 3.1 implies $df(z)/dz$ is positive on $I_{(0,1)}$, and $z(1-z)(1+\Delta_I\varphi_{II}^{-1}(a+\varphi_I(z)))$ is positive on $I_{(0,1)}$. Thus, the Hessian is negative at \bar{z}_a . ■

E. Level Sets and Closed Orbits

In this subsection, we first show that each level set of the constant of motion is a periodic orbit except for the unique maximum. Then, we conclude the property of the original three dimensional system.

First, we analyze the level sets.

Lemma 3.5: Let B_a be the range of H_a in (11), i.e., $B_a := H_a(I_{(0,1)}^2) \subset \mathbb{R}$. For any $b \in B_a$, define

$$\Omega_{a,b} := \{(z, n) \in I_{(0,1)}^2 : H_a(z, n) = b\}. \quad (14)$$

Then, each $\Omega_{a,b}$ is a positively invariant set of the system Σ_a . Moreover, denote $L_{a,b}^+$ as the set of positive limit points of its trajectories starting from $\Omega_{a,b}$. Then, $L_{a,b}^+$ is a non-empty, compact, and positively invariant subset of $\Omega_{a,b}$.

Proof: First, we show positive invariance of $\Omega_{a,b} \subset I_{(0,1)}^2$, where we recall that $I_{[0,1]}^2$ is positively invariant as mentioned in Section III-B. Note that H_a is not finite on $I_{[0,1]}^2 \setminus (I_{(0,1)}^2 \cup \{0, 1\}^2)$. Thus, any trajectory starting from the interior $I_{(0,1)}^2$ does not converge into $I_{[0,1]}^2 \setminus (I_{(0,1)}^2 \cup \{0, 1\}^2)$. Then, the discussion of the trajectories near each corner $\{0, 1\}^2$ in Section III-C allows the conclusion that the interior $I_{(0,1)}^2$ is positively invariant.

Let $(z(t), n(t))$ be the solution to the system Σ_a starting from $(z(0), n(0)) \in I_{(0,1)}^2$. According to Theorem 3.2, $\dot{H}_a = 0$ on $I_{(0,1)}^2$. Consequently if $H_a(z(0), n(0)) = b$ then

$$H_a(z(t), n(t)) = H_a(z(0), n(0)) = b \quad (15)$$

for any $t \geq 0$ and $(z(0), n(0)) \in I_{(0,1)}^2$. Since $I_{(0,1)}^2$ is positively invariant, $\Omega_{a,b}$ is positively invariant. Finally, the statement for $L_{a,b}^+$ follows from [16, Lemma 4.1]. ■

In the above lemma, the set of sets $\Omega_{a,b}$ obtained by varying a and b can be regarded as comprising two subsets. From Lemma 3.4, H_a takes a unique maximum c_a at $(\bar{z}_a, 1/2)$, i.e., $\Omega_{a,c_a} = \{(\bar{z}_a, 1/2)\} = L_{a,c_a}^+$. This is the first subset. The second is $\Omega_{a,b}$, $b \neq c_a$, and almost all $\Omega_{a,b}$ are in this second subset, for which we have the following.

Theorem 3.6: Each $L_{a,b}^+$, $b \neq c_a$ in Lemma 3.5 is a periodic orbit and $\Omega_{a,b} = L_{a,b}^+$.

Proof: Since $L_{a,b}^+$, $b \neq c_a$, does not contain any equilibrium, the Poincaré-Bendixson theorem implies that this is a periodic orbit. Next, we show $\Omega_{a,b} = L_{a,b}^+$. From index theory [16, Corollary 2.1], any periodic orbit $L_{a,b}^+$, $b \neq c_a$ contains at least one equilibrium point in its interior. In our case, from Proposition 3.1, an equilibrium point uniquely exists and

is $L_{a,c_a}^+ = \{(\bar{z}_a, 1/2)\}$. From the proof of Lemma 3.4, $H_z(z)$ decreases as z increases above \bar{z}_a or decreases below \bar{z}_a . Also $H_n(n)$ decreases as n increases above $1/2$ or decreases below $1/2$. This means that if we pick an arbitrary point other than $(\bar{z}_a, 1/2)$, denoted by (z_0, n_0) and then move on the straight line joining (z_0, n_0) to $(\bar{z}_a, 1/2)$ in a direction away from $(\bar{z}_a, 1/2)$, both H_z and H_n must decrease, and consequently H_a decreases. Hence, on any straight ray emanating from $(\bar{z}_a, 1/2)$, any value taken by H_a on the ray is taken at only one point on the ray. Now suppose that there exists $(z_0, n_0) \neq (\bar{z}_a, 1/2)$, which is in $\Omega_{a,b} \setminus L_{a,b}^+$. Consider the ray starting at $(\bar{z}_a, 1/2)$ and passing (z_0, n_0) . There is a limiting trajectory in $L_{a,b}^+$ intersecting this ray, and the value of H_a at the intersection point must be the same as that determined by $\Omega_{a,b}$, i.e. the same as the value of H_a at the point (z_0, n_0) . By the uniqueness of the point on this ray with this value of H_a , the point on $L_{a,b}^+$ must be the same as (z_0, n_0) . That is, $(z_0, n_0) \in L_{a,b}^+$. ■

Corollary 3.7: A unique equilibrium point $(\bar{z}_a, 1/2)$ of the system Σ_a is neutrally stable.

Proof: First, the stability of $(\bar{z}_a, 1/2)$ can be shown with a Lyapunov function $-H(z, n) + c_a \geq 0$ on $I_{(0,1)}^2$, where $-H(z, n) + c_a = 0$ if and only if $(z, n) = (\bar{z}_a, 1/2)$. From Theorem 3.6, $(\bar{z}_a, 1/2)$ is not asymptotically stable and thus it is neutrally stable. ■

Now, we go back to the original coordinates. Since ψ is a globally real-analytic diffeomorphism from $I_{(0,1)}^3$ to $I_{(0,1)}^2 \times \mathbb{R}$, Theorem 3.6 and Corollary 3.7 are applicable to conclude the property in the original coordinates as follows. This is the main theorem of this paper.

Theorem 3.8: The system Σ has the following properties.

- 1) Each equilibrium point in E is neutrally stable, where

$$E := \{(x_I, x_{II}, n) \in I_{(0,1)}^3 : n = 1/2, \\ (\theta_I + \lambda_I)x_I + (\theta_{II} + \lambda_{II})x_{II} = \lambda_I + \lambda_{II}\};$$

- 2) Each trajectory starting from $I_{(0,1)}^3 \setminus E$ is a periodic orbit³.

IV. ON BOUNDARIES

In this section, we consider trajectories of the system in the original coordinates on boundaries $I_{[0,1]}^3 \setminus I_{(0,1)}^3$ that are six squares. When $n = 0$ or $n = 1$, the problem reduces to a game between two different types of community. As mentioned in Section III-A, mutual cooperation $x_I = x_{II} = 0$ (mutual defection $x_I = x_{II} = 1$) is a Nash equilibrium when $n = 1$ ($n = 0$).

Therefore, we focus on the case $x_I = 0$ or $x_I = 1$ noting the cases $x_{II} = 0$ or $x_{II} = 1$ are essentially the same. The motivation corresponds to a situation that one community takes defection or cooperation irrespective of the state of environment; this scenario cannot be studied when one studies a single community. Actually, if community I is always defective, i.e., its payoff matrix is $A^{I,II}(0)$, then $\dot{x}_I < 0$ for any $(x_I, x_{II}, n) \in I_{[0,1]}^3$ such that $x_I \neq 0$ and $x_I \neq 1$.

³Note the distinction between having a one-parameter family of closed orbits, as opposed to a single limit cycle.

Therefore, $x_I \rightarrow 0$ as $t \rightarrow \infty$ for any $(x_I, x_{II}, n) \in I_{[0,1]}^3$, $x_I \neq 1$. The transient dynamics can be analyzed by studying the case $x_I = 0$.

By substituting $x_I = 0$ into Σ , we have

$$\begin{cases} \varepsilon \dot{x}_{II} = -\sigma_{II} x_{II} (1 - x_{II}) (1 - 2n), \\ \dot{n} = -n(1 - n) ((\theta_{II} + \lambda_{II}) x_{II} - (\lambda_I + \lambda_{II})) \end{cases}$$

This system has a constant of motion on $I_{(0,1)}^2$.

$$\begin{aligned} H_{x_I=0}(x_{II}, n) &:= (\sigma_{II}/\varepsilon)(\ln(n) + \ln(1 - n)) \\ &+ (\lambda_I + \lambda_{II}) \ln(x_{II}) + (\theta_{II} - \lambda_I) \ln(1 - x_{II}). \end{aligned}$$

If $\theta_{II} - \lambda_I > 0$, then $H_{x_I=0} < 0$ on $I_{(0,1)}^2$, and $H_{x_I=0} \rightarrow -\infty$ as (x_{II}, n) tends to a corner in $\{0, 1\}^2$. Also, there is a heteroclinic cycle $(0, 0) \rightarrow (0, 1) \rightarrow (1, 1) \rightarrow (1, 0) \rightarrow (0, 0)$ on the boundary $I_{[0,1]}^2 \setminus I_{(0,1)}^2$, and at each corner, the Jacobian matrix has one positive and one negative real eigenvalue. In a similar manner with the previous section, one can conclude that the interior $I_{(0,1)}^2$ is positively invariant. Furthermore, there is an infinite number of periodic orbits in $I_{(0,1)}^2$.

If $\theta_{II} - \lambda_I < 0$, there are heteroclinic orbits $(1, 0) \rightarrow (0, 0) \rightarrow (0, 1) \rightarrow (1, 1)$ on the boundary $I_{[0,1]}^2 \setminus I_{(0,1)}^2$. At an equilibrium $(1, 0)$ ($(1, 1)$), the Jacobian matrix has two positive real (two negative real) eigenvalues. At each equilibrium $(0, 0)$ and $(0, 1)$, the Jacobian matrix has one positive and one negative eigenvalue. Thus, any trajectory starting from the interior $I_{(0,1)}^2$ converges to $(1, 1)$ or stays in the interior $I_{(0,1)}^2$, i.e. converges to a periodic orbit.

The case $\theta_{II} - \lambda_I = 0$ is complicated, since the behaviour of the system varies depending on the sign of $\theta_{II} - \lambda_I$. In this case, there are heteroclinic orbits $(1, 0) \rightarrow (0, 0) \rightarrow (0, 1) \rightarrow (1, 1)$ on the boundary $I_{[0,1]}^2 \setminus I_{(0,1)}^2$. At the equilibria $(0, 0)$ or $(0, 1)$, the Jacobian matrix has one positive and one negative eigenvalue. Therefore, any trajectory starting from the interior $I_{(0,1)}^2$ does not converge to a line $\{0\} \times I_{[0,1]}$. On the other hand, the line $\{1\} \times I_{[0,1]}$ is a set of equilibria. A constant energy function $H_{x_I=0}(x_{II}, n)$ is negative and finite on this line $\{1\} \times I_{[0,1]}$ and the interior $I_{(0,1)}^2$, and it takes a unique maximum at $(1, 1/2)$. Except for the level set (point) corresponding to $(1, 1/2)$, each level set contains a pair of points on the line, $(1, n)$, $n = \bar{n} < 1/2$ and $n = 1 - \bar{n}$, where in a similar manner of the previous section, one can show that each level set is positively invariant. Next, at equilibrium $(1, n)$, the eigenvalues of the Jacobian matrix are $\sigma_{II}(1 - 2n)/\varepsilon$ and 0, and the first eigenvalue is positive (zero or negative) when $n < 1/2$ ($n = 1/2$ or $n > 1/2$). Therefore, the Poincaré-Bendixson theorem implies that there exists an infinite number of heteroclinic orbits starting from $(1, n)$, $n = \bar{n} < 1/2$ and approaching $(1, n)$, $n = 1 - \bar{n}$. Moreover, $(1, 1/2)$ is neutrally stable.

In the case $x_I = 1$, we have similar conclusions depending on the sign of $\lambda_{II} - \theta_I$. Especially when $\lambda_{II} - \theta_I$ is negative, community II and environment coexist. In summary, depending on λ_i and θ_i , the behavior of replicator dynamics varies when one community fixes its strategy irrespective of the state of the environment. However, the other community and environment still can coexist depending on ratios of λ_i and θ_i , i.e. effects on the environment from the two communities.

V. CONCLUSION

In this paper, we have studied an evolutionary differential game consisting of two different types of communities (both evolving according to a prisoner's dilemma game) and an evolving environment. Our main result shows that the corresponding replicator dynamics have an infinite number of periodic orbits, i.e., none of the communities and environment dies out if the communities are mutual cooperative (defective) when environment is repleted (depleted), and if the environment is defective (cooperative) when the communities are mutually profligate (frugal).

This paper is the first step toward clarifying when multiple communities and environments can coexist periodically. There are a number of interesting future work such as studying higher dimensional systems⁴ and different choices of payoff matrices⁵. Moreover, we have focused on proving the coexistence, and to understand more detailed behavior of each community, the game between two communities is needed to be studied. We are currently working on these directions.

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⁴Some specialized higher dimensional situations can be reduced to two-dimensional situations, as in this paper, but not in general.

⁵Simulations show that if two species have different types of game, periodic behavior does not result.