# Transition matrix model for evolutionary game dynamics 

G. Bard Ermentrout<br>Department of Mathematics, University of Pittsburgh, Pittsburgh, Pennsylvania 15260, USA<br>Christopher Griffin<br>Mathematics Department, United States Naval Academy, Annapolis, Maryland 21402, USA

Andrew Belmonte<br>Department of Mathematics, Pennsylvania State University, University Park, Pennsylvania 16802, USA<br>(Received 16 October 2015; published 21 March 2016)


#### Abstract

We study an evolutionary game model based on a transition matrix approach, in which the total change in the proportion of a population playing a given strategy is summed directly over contributions from all other strategies. This general approach combines aspects of the traditional replicator model, such as preserving unpopulated strategies, with mutation-type dynamics, which allow for nonzero switching to unpopulated strategies, in terms of a single transition function. Under certain conditions, this model yields an endemic population playing non-Nash-equilibrium strategies. In addition, a Hopf bifurcation with a limit cycle may occur in the generalized rock-scissors-paper game, unlike the replicator equation. Nonetheless, many of the Folk Theorem results are shown to hold for this model.


DOI: 10.1103/PhysRevE. 93.032138

## I. INTRODUCTION

The central idea of evolutionary game theory is to specify mathematically a process by which strategies develop temporally, in response to some quantitative measure of the interaction of those strategies in playing the game. Depending upon the way the equations are posed, and their interpretation, this can be used to describe a player's decision-making process, or the evolution of relative species populations, traits, or genetic materials. A standard approach to the continuous time evolution of game strategies, represented by the vector $\mathbf{x}$ for a given payoff matrix $\mathbf{A}$, is the replicator equation

$$
\begin{equation*}
\frac{d x_{i}}{d t}=x_{i}\left(\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}-\mathbf{x}^{T} \mathbf{A} \mathbf{x}\right)=x_{i}\left(f_{i}-\bar{f}\right) \tag{1}
\end{equation*}
$$

for the $i$ th strategy, where $\mathbf{e}_{i}$ is a standard basis vector; this equation is proportional to $x_{i}$, and thus has the character of a modified birth-rate or growth kinetics. The replicator is also linear in the difference between the expected payoff for the $i$ th strategy, $\mathbf{e}_{i}^{T} \mathbf{A x}=(\mathbf{A x})_{i}$, and the average payoff over all strategies, $\mathbf{x}^{T} \mathbf{A x}$. To put this in a biological context one identifies the fitness of the $i$ th strategy as $f_{i}=\mathbf{e}_{i}^{T} \mathbf{A x}$, and the average fitness as $\bar{f}=\sum x_{i} f_{i}$; see Eq. (1). The replicator equation was originally proposed by Taylor and Jonker in 1978 [1], and has been studied extensively [2-6]. Variations, including imitation dynamics [3,5] and others (discussed in detail below), have also been studied [2,4,7,8]. These dynamics lead to largely the same class of behaviors as the replicator [5].

Because of the important role that random mutations can play in evolution, the replicator equation is often supplemented by the addition of noise, or other terms that allow for the emergence of new strategies; a brief review is included below. The model we present here originates from a more unified approach, not based on a superposition of birth or growth kinetics with mutation terms; our evolutionary game model is governed instead by a transition matrix between strategies, in which both aspects depend on a single analytic function. The
resulting dynamics are shown to admit a Hopf bifurcation and thus a limit cycle for generalized rock-scissors-paper game, rather than a simple center. Thus convergence to a stationary population mixture is not the only possible outcome, as also is seen for models with mutation [9,10] (see [11] for comparison). Additionally, we show, as expected, that a majority of the Folk theorem of evolutionary game theory [12] hold in these dynamics with a few modifications. We illustrate that for certain assumptions on the function governing the transition matrix, the spontaneous emergence of dominated strategies is possible. We also find that strictly dominating pure strategy equilibria (e.g., defect in prisoner's dilemma) need not be fixed points of the system. Instead, our model enables a form of continuous mutation that allows the dominated population to maintain a finite representation.

## II. PRIOR ALTERNATIVES TO THE REPLICATOR EQUATION

We first give a brief review of some of the alternatives to the replicator, Eq. (1); more thorough presentations reviewing the varieties and dynamics of these models have been provided by Sandholm [6], and more recently by Cressman and Tao [13]. A unifying approach based on the covariance between traits and fitness was given by Page and Nowak [14], while the inclusion of non-mean-field effects was studied by Roca, Cuesta, and Sánchez [15]. The replicator has often been generalized in the form

$$
\begin{equation*}
\frac{d x_{i}}{d t}=H(\mathbf{x}) x_{i} \tag{2}
\end{equation*}
$$

as studied in $[2-5,7,8]$, where the primary consideration is $H(\mathbf{x})$ being convex and monotone. Because $d x_{i} / d t$ is proportional to $x_{i}$ in this equation, the "extinct" solution $x_{i}=0$ is always a fixed point. Thus the replicator dynamic does not admit spontaneous generation of species, which is not surprising as it was constructed as a reproductive model; as

Taylor and Jonker state, "the simplest hypothesis is that of exponential growth or decay" [1].

Several authors have distinguished between two different classes of such equations: imitative dynamics versus pairwise comparison dynamics $[6,13,16]$. To clarify our classification of the various strategy evolution equations, we distinguish between two types, along similar lines to Sandholm's classification of revision protocols [6]: (1) reproductive or birth process models, for which $\dot{x}_{i}=0$ whenever $x_{i}=0$, and (2) innovation process models, for which $\dot{x_{i}}>0$ is possible when $x_{i}=0$ (due possibly to mutation).

What we call birth process models are almost identical to the class imitative dynamics, while innovation process models are approximately the same as pairwise comparison models. The model we propose here is easily adjusted to follow either a birth or innovation process, depending on the properties of the transition function discussed below; however, it does follow the rule that a flux can only originate from a state that is populated-thus it is a pairwise comparison model $[6,13]$. It also shares common aspects with several other models, as we discuss next.

A very general approach to the evolution of multispecies communities was posed by May in his 1973 model of interacting populations near equilibrium [17]. He proposed the following first order equation:

$$
\begin{equation*}
\frac{d x_{i}}{d t}=\sum_{j} a_{i j} x_{j} \tag{3}
\end{equation*}
$$

where the $x_{i}$ are perturbations around the time-independent populations for each species, and the $a_{i j}$ are elements of an interaction matrix which determine the evolutionary dynamics. More recently, a modified version of this model was used by Sneppen and co-workers

$$
\begin{equation*}
\frac{d x_{i}}{d t}=\sum_{j} \Gamma_{i j} x_{i} x_{j}-\sum_{j} \Gamma_{j i} x_{i} x_{j} \tag{4}
\end{equation*}
$$

where the $\Gamma_{i j}$ are constants [18].
The classical imitation dynamic is similarly based on a matrix element $f_{i j}(\mathbf{x})$ which represents the rate at which players of type $i$ adopt the strategy of players of type $j$ [3], discussed in general terms by Hofbauer and Sigmund [cf. Eq. (46) in [5], and Chap. 8 in [19]]. They start with the "input-output model"

$$
\begin{equation*}
\frac{d x_{i}}{d t}=x_{i} \sum_{j} x_{j}\left(f_{i j}(\mathbf{x})-f_{j i}(\mathbf{x})\right) \tag{5}
\end{equation*}
$$

which describes the "flow" between pure strategies, such that the flow between $i$ and $j$ is proportional to $x_{i} x_{j} f_{i j}(\mathbf{x})$. For a given payoff matrix $\mathbf{A}$, they assume that

$$
f_{i j}=f\left(\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}, \mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}\right)
$$

where we use our notation instead of theirs to emphasize similarities. They refer to $f$ as the "imitation rule" (universal to all players), and further define two cases: (1) imitate the better, where $f(u, v)=0$ for $u<v$, and $f(u, v)=1$ for $u>v$, and (2) switching depends on payoff difference, where $f(u, v)=F(u-v)$. With a few more assumptions including linearity $F$, this leads to the replicator equation. Note that (4)
and (5) are birth process models, whereas (3) is an innovation process model.

The generation of new strategies has often been added to a birth process model by the inclusion of mutation terms, which account for the probability of randomly switching from one strategy to another. Nowak presents the quasispecies equation, which he credits to Eigen and Schuster [20], for replication of a genome "with mistakes"

$$
\begin{equation*}
\frac{d x_{i}}{d t}=\sum_{j=1}^{N} x_{j} f_{j} Q_{j i}-\phi x_{i} \tag{6}
\end{equation*}
$$

Here $Q_{j i}$ is the probability that the process of replicating sequence $j$ also generates sequence $i, f_{j}$ is the replication rate ( $i=j$ is possible), and $\phi$ is the removal rate of sequence $i$ which keeps the total population size constant; errors are represented by off-diagonal elements of $Q$. Nowak also presents another equation of the same form, which he calls the replicator-mutator equation [20]. In this case $f_{i}$ is the fitness for species $i$ (or grammar, in his model for language learning), and $\phi=\sum x_{i} f_{i}$ is the average fitness. This equation appears elsewhere, for instance in a study of mixing times in evolutionary games with mutation [11]. By adding a mutation term to a pairwise comparison dynamic, these models allow for the intrinsic seeding of an unrepresented strategy independent of the population of other strategies.

Another pairwise comparison approach is known as Best Reply dynamics, which in a continuous approximation is known as Logit Dynamics [16]. The structure of this model is

$$
\frac{d x_{i}}{d t}=\frac{\exp \left[\beta(A \mathbf{x})_{i}\right]}{\sum_{j} \exp \left[\beta(A \mathbf{x})_{j}\right]}-x_{i}
$$

where $\beta$ controls the sharpness of the switching transition. In addition to bearing several similarities to our model, Logit dynamics was recently shown to produce a Hopf bifurcation in rock-scissors-paper games [16].

In a different applied context, the mathematical modeling of opinion dynamics and the convergence towards consensus among individuals [21,22], as well as other related social dynamics [20,23], share certain aspects with evolutionary games-opinions are represented by continuous variable, and are updated as the result of social interactions [24,25]. For instance, the DeGroot model [21] assigns evolving belief (trust) scores to interacting agents through a process governed by an (ergodic) Markov chain.

## III. FORMULATION OF THE TRANSITION MATRIX MODEL AND RESULTS

In this section we present our derivation of the model, and then derive several analytic results, before illustrating its behavior numerically in the next section.

We first recall a few definitions and preliminary results used in the proofs of subsequent theorems. Let $\mathbf{x} \in \Delta_{n}$ be the vector containing the proportions of the population playing each strategy, where $\Delta_{n}$ is the simplex defined as

$$
\begin{equation*}
\Delta_{n}=\left\{\mathbf{x} \in \mathbb{R}^{n}: x_{1}+\cdots+x_{n}=1, x_{1}, \ldots, x_{n} \geqslant 0\right\} \tag{7}
\end{equation*}
$$

Let $\mathbf{A} \in \mathbb{R}^{n \times n}$ be a game matrix in a symmetric bimatrix game $(\mathbf{A}, \mathbf{B})$ with $\mathbf{B}=\mathbf{A}^{T}$. Assume that $\mathbf{A}$ has a symmetric Nash
equilibrium $\mathbf{x}^{*} \in \Delta_{n}$, being a Nash equilibrium for both row and column player, is any strategy satisfying the condition

$$
\begin{equation*}
\left(\mathbf{x}^{*}\right)^{T} \mathbf{A} \mathbf{x}^{*} \geqslant(\mathbf{y})^{T} \mathbf{A} \mathbf{x}^{*} \quad \forall \mathbf{y} \in \Delta_{n} \tag{8}
\end{equation*}
$$

We next review several important properties of $\mathbf{x}^{*}$ and its elements $x_{i}=\mathbf{e}_{i}^{T} \mathbf{x}$, where $\mathbf{e}_{i}$ is a standard basis vector.

Lemma 1. If $\mathbf{x}$ is a Nash equilibrium and $\mathbf{x}_{i}, \mathbf{x}_{j}>0$, then $\mathbf{e}_{i}^{T} \mathbf{A x}=\mathbf{e}_{j}^{T} \mathbf{A x}$.

Corollary 2. If $\mathbf{x}$ is a Nash equilibrium, then $\mathbf{e}_{i}^{T} \mathbf{A x}=\mathbf{x}^{T} \mathbf{A x}$ for any $\mathbf{x}_{i} \neq 0$.

In other words, the expected payoffs for all the nonzero strategies are equal, and they are also equal to the average payoff.

Lemma 3. Suppose $\mathbf{x} \in \Delta$ and let $S \subseteq\{1, \ldots, n\}$ be the set of indices so that $\mathbf{x}_{i} \neq 0$ if and only if $i \in S$. Denote the complement of $S$ in $\{1, \ldots, n\}$ by $\bar{S}$. If $\mathbf{e}_{i}^{T} \mathbf{A x}=\mathbf{e}_{j}^{T} \mathbf{A x}$ for all pairs $i, j$ in $S$, and if for every $k \in \bar{S}$ and $i \in S$, we have $\mathbf{e}_{i}^{T} \mathbf{A x} \geqslant \mathbf{e}_{k}^{T} \mathbf{A x}$, then $\mathbf{x}$ is a Nash equilibrium.

Corollary 4. If $\mathbf{x}$ is not a Nash equilibrium, then there is at least one pair of indices $i, j \in\{1, \ldots, n\}$ such that $\mathbf{e}_{i}^{T} \mathbf{A x}-$ $\mathbf{e}_{j}^{T} \mathbf{A x}>0$.

## A. Transition matrix approach

Our model is based on three basic assumptions. In common with the other models described above, we are concerned with the change in time of the distribution of strategies $\mathbf{x}$. Our first assumption is that any increase in population (frequency) of a given strategy $i$ is due to a net inflow from all other strategies (what Sandholm calls a mean dynamics [6]). We write this inflow for the $i$ th strategy as

$$
\begin{equation*}
I_{i}(\mathbf{x})=\sum_{j} G_{j i} x_{j} \tag{9}
\end{equation*}
$$

where the sum is over all other strategies. In analogy with similar concepts in quantum mechanics and optical processes (see, e.g., [26]), we identify the strength of the coupling with a matrix element for the transition between two strategies (two energy eigenstates); the coefficients $G_{j i}$ are the elements of this transition matrix, to be defined later. We similarly define the total outflow from strategy $i$ to the other strategies as

$$
\begin{equation*}
O_{i}(\mathbf{x})=\sum_{j} G_{i j} x_{i} \tag{10}
\end{equation*}
$$

Combining these, we write the rate equations (first order in time) for the total change of the number of players for a given strategy:

$$
\begin{equation*}
\frac{d x_{i}}{d t}=I_{i}(\mathbf{x})-O_{i}(\mathbf{x})=\sum_{j} G_{j i}(\mathbf{x}) x_{j}-\sum_{j} G_{i j}(\mathbf{x}) x_{i} \tag{11}
\end{equation*}
$$

The form of these equations is similar to "migration dynamics" [13], or the Smith dynamic [6].

Secondly, we assume that the expected payoffs for the strategies, written as $(A \mathbf{x})_{i}=\mathbf{e}_{i}^{T} \mathbf{A x}$, define the dynamics. The difference in payoff levels between strategies $i$ and $j$ (between two states) is used to determine the flux between populations playing those strategies. Thus if

$$
\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}-\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x} \geqslant 0
$$

there is non-negative outflow from strategy $i$ to strategy $j$, since the expected payoff to (pure) strategy $j$ against the population is at least as great as the expected payoff to (pure) strategy $i$ against the population. By the same argument, if $\mathbf{e}_{j}^{T} \mathbf{A x}-$ $\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x} \leqslant 0$, then there should be a zero or nearly zero outflow from strategy $i$ to strategy $j$.

The third aspect of our model is the function $g(z)$, which universally characterizes the dependence of the transition matrix elements $G_{i j}$ on the expected payoffs:

$$
\begin{equation*}
G_{i j}=g\left(\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}-\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}\right) \tag{12}
\end{equation*}
$$

Here $g: \mathbb{R} \rightarrow \mathbb{R}$ is a non-negative monotone increasing transition function, defining quantitatively the character of switching between strategies. In its simplest form, $g(z)>0$ for $z>0$ (the switch is ON ) and $g(z)=0$ for $z<0$ (the switch is OFF). The value of $g(0)$ represents the equilibrium when the inflow and outflow are equal. It is natural to expect fluctuation-type phenomena to be represented by this value, and we think of the smoothness of a less sharp transition around $z=0$ to represent a "higher temperature." When $g$ is a sigmoid, then the population drifts toward better performing strategies. Several forms of $g$ are natural:

$$
\begin{aligned}
& g(z)=\max (\tanh (\beta z), 0) \quad \text { TANH } \\
& g(z)=1 /(1+\exp (-\beta z)) \quad \text { LOGIST, } \\
& g(z)=\exp (\beta z) \quad \text { EXP. }
\end{aligned}
$$

The first one is zero when $z \leqslant 0$ and has a discontinuous derivative at zero. Both TANH and LOGIST approach the Heaviside step function as $\beta \rightarrow \infty$. Both EXP and LOGIST allow for the possibility transitions even when $z \leqslant 0$ (see below). EXP is like a Boltzmann function with $\beta$ playing the role of inverse temperature.

We study the same equilibrium shaping and control questions in these dynamics as for the ordinary replicator. In some sense, these dynamics are simpler because they do not exhibit exponential growth of successful strategies. On the other hand, the dynamics admit more complex behaviors in our archetypal example (RSP), as shown below.

In summary, the transition matrix model is defined by the following equations:

$$
\begin{equation*}
\frac{d x_{i}}{d t}=\sum_{j} x_{j} g\left(\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}-\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}\right)-\sum_{j} x_{i} g\left(\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}-\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}\right), \tag{13}
\end{equation*}
$$

along with the definition of the transition function $g(\cdot)$. As we shall see, the salient features of this model include its inclusion of the mutation and innovation (nonbirth) process property in a general way, since $x_{i}=0$ is not necessarily a fixed point for $g(0) \neq 0$. We also allow for general and possibly nonlinear forms of $g$. Interestingly, there does not appear to be a choice of $g(\cdot)$ which would lead directly to the replicator equation, which points out an important difference with the input-output model [5,19] shown in Eq. (5); there is no overall proportionality to $x_{i}$ in (13). This also indicates that the presence of $g$ in both sums in our model is a strongly imposed symmetry on the inflows and outflows between strategies.

Note that a recent social dynamics model takes a mapping approach with some similarity to our model, in which the
updating of continuous opinion variables is proportional to pairwise differences with other opinions [24].

## B. Nash equilibria and fixed points

We now state some analytic results for the transition matrix model, the so-called Folk Theorems of evolutionary game theory [12]. Note that these results tend to distinguish between "interior" (mixed) strategies and "exterior" (pure) ones.

Proposition 5. Suppose that $g(0)=0$ and $\mathbf{x}$ is an interior point Nash equilibrium (i.e., $\mathbf{x}>\mathbf{0}$ ). Then $\mathbf{x}$ is a fixed point for system (13).

Proof. From Lemma 1, we know there is a $c \in \mathbb{R}$ such that $c=\mathbf{e}_{i}^{T} \mathbf{A x}$ for all $i \in\{1, \ldots, n\}$. Then $G_{i j}(\mathbf{x})=g(0)$ for all ( $i, j$ ) pairs. Consequently, Eq. (13) becomes

$$
\begin{equation*}
\frac{d x_{i}}{d t}=g(0)\left(\sum_{j}\left(x_{j}-x_{i}\right)\right) \tag{14}
\end{equation*}
$$

The proposition follows immediately from the preceding expression.

Corollary 6. Suppose $g(0)>0$ and $\mathbf{x}$ is an interior Nash equilibrium. If $x_{1}=x_{2}=\cdots=x_{n}$, then $\mathbf{x}$ is a fixed point for system (13).

This special result for "equally distributed" mixed strategy Nash equilibria follows directly from Eq. (14); a classic example would be the rock-scissors-paper game, which has a Nash equilibrium at $\left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right)$. This example is discussed in detail in Sec. IV.

Proposition 7. If $g(0)=0$ and $\mathbf{x}^{*} \in \partial \Delta_{n}$ is a pure strategy (exterior) Nash equilibrium, then $\mathbf{x}^{*}$ is a fixed point of system (13).

Proof. First note that only one element of $\mathbf{x}^{*}$ is nonzero. Suppose that $x_{i}=0$. Then Eq. (13) reduces to

$$
\begin{equation*}
\frac{d x_{i}}{d t}=\sum_{j} g\left(\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}^{*}-\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}^{*}\right) x_{j} \tag{15}
\end{equation*}
$$

If $x_{j}>0$, then $\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}^{*} \geqslant \mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}^{*}$ and thus $g\left(\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}^{*}-\right.$ $\left.\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}^{*}\right)=0$; for all other terms $k \neq j, x_{k}=0$. Thus the righthand side of Eq. (15) is zero, and we have a fixed point.

Now suppose that $x_{i}>0$. In this case, the first sum in Eq. (13) has only the $j=i$ term, for which $g(0)=0$. In the second sum, if $j \neq i$ then $x_{j}=0$, and

$$
\begin{equation*}
g\left(\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}^{*}-\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}^{*}\right) x_{i}=0 \tag{16}
\end{equation*}
$$

because $\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}^{*}-\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}^{*}<0$. And also for the $i$ th term in this sum we have $g(0)=0$. Thus all terms on the right-hand side of Eq. (13) are zero, and again $\mathbf{x}^{*}$ is a fixed point.

Interestingly, the previous proposition, that a Nash equilibrium is also a fixed point of the dynamics, does not hold if $g$ is continuous and $g(0)>0$, which corresponds to allowing some flux to continue even to less favorable strategies. An example of this is presented in Sec. V.

## C. Nash equilibria and stability

Proposition 8. Suppose that $g(z)=0$ for $z<0$ and $g(z) \geqslant$ 0 for $z \geqslant 0$, and $g$ is continuous on its domain except possibly
at zero. If $\mathbf{x} \in \Delta_{n}$ is Lyapunov stable for system (13), then $\mathbf{x}$ is a Nash equilibrium.

Proof. Suppose that $\mathbf{x}$ is Lyapunov stable and not a Nash equilibrium. Then for at least one $i, j$ pair, we know that $\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}-\mathbf{e}_{j}^{T} \mathbf{A x}>0$ by Corollary 4. Moreover, we can order the values $\mathbf{e}_{k}^{T} \mathbf{A x}$ for $k=1, \ldots, n$ and see that there is some set $K=\left\{k_{1}, \ldots, k_{m}\right\}(m<n)$ so that if $k \in K$, then $\mathbf{e}_{k}^{T} \mathbf{A x} \geqslant$ $\mathbf{e}_{j}^{T} \mathbf{A x}$ for all $j \in\{1, \ldots, n\}$. Assume that $i \in K$; if not, select $i \in K$. By our choice of $g, G_{i j}=0$ for all $j \notin K$. If $k \in K$, then $G_{i k}(\mathbf{x})=g(0)$. Thus $O_{i}(\mathbf{x})=m g(0)$. On the other hand, for $j \notin K, G_{j i}(\mathbf{x})>0$, since $\mathbf{e}_{i}^{T} \mathbf{A x}-\mathbf{e}_{j}^{T} \mathbf{A x}>0$. Let $\bar{K}$ be those indices in $\{1, \ldots, n\}$ not in $K$. Define

$$
\begin{equation*}
r:=\min _{j \in \bar{K}}\left\{\mathbf{e}_{i}^{T} \mathbf{A} \mathbf{x}-\mathbf{e}_{j}^{T} \mathbf{A} \mathbf{x}\right\} . \tag{17}
\end{equation*}
$$

Then $G_{j i}(\mathbf{x})>g(r)$ for all $j \in \bar{K}$. If $k \in K$, then $G_{k i}(\mathbf{x})=$ $g(0)$. Thus $I_{i}(\mathbf{x})>(n-m) r+m g(0)$. It follows that

$$
\begin{equation*}
\dot{\mathbf{x}}_{i}(\mathbf{x})>(n-m) g(r) . \tag{18}
\end{equation*}
$$

By continuity of $g(\cdot)$ there is a neighborhood $U$ of $\mathbf{x}$ for which if $\mathbf{y} \in U$, then there is some $\delta>0$ so that $\dot{\mathbf{x}}_{i}(\mathbf{y})>\delta$. If $\varphi_{i}\left(t, \mathbf{x}^{(0)}\right)$ is a solution flow for strategy $i$, with initial point $\mathbf{x}^{(0)} \in U \cap \Delta_{n}$, we see that $\varphi_{i}(t, \mathbf{x})>\delta t$ so long as $\varphi_{i}(t, \mathbf{x}) \in U \cap \Delta_{n}$. But this implies that $\mathbf{x}$ is not Lyapunov stable.

The proof of the following proposition is almost identical to the proof of Proposition 8.

Proposition 9. Suppose that $g(z)=0$ for $z<0$ and $g(z) \geqslant$ 0 for $z \geqslant 0$, and $g$ is continuous on its domain, except possibly at zero. If $\mathbf{x} \in \Delta_{n}$ is the limit of an interior orbit of system (13), then $\mathbf{x}$ is a Nash equilibrium.

Proof. Suppose that $\mathbf{x}$ is the limit of an interior orbit, but $\mathbf{x}$ is not a Nash equilibrium. By a similar argument to the proof of Proposition 8, we know that $\dot{\mathbf{x}}_{i}(\mathbf{x})>(n-m) r$ for some $r>0$ and $m<n$. Denote the right-hand side of system (13) by $\mathbf{f}(\mathbf{x})$, so that

$$
\begin{equation*}
\frac{d x_{i}}{d t}=\sum_{j} G_{j i} x_{j}-\sum_{j} G_{i j} x_{i}=\mathbf{f}_{i}(\mathbf{x}) \tag{19}
\end{equation*}
$$

We know that $\mathbf{f}_{i}(\mathbf{x})$ is continuous almost everywhere by our assumption on $g$. Let $\varphi\left(t, \mathbf{x}^{(0)}\right)$ be a solution flow for strategy $i$. As $t$ approaches infinity, we know that $\varphi\left(t, \mathbf{x}^{(0)}\right)$ approaches $\mathbf{x}$. Thus for some time $s \in \mathbb{R}$ so that for all $t>s$, we know that $\mathbf{f}_{i}(\mathbf{x})>(n-m) r / 2$. We can say this only for index $i$ precisely because of our continuity assumptions on $g$. But then $\varphi_{i}\left(t, \mathbf{x}^{(0)}\right)$ approaches infinity for $t>s$, which contradicts our assumption that $\varphi\left(t, \mathbf{x}^{(0)}\right)$ approaches $\mathbf{x}$.

## IV. ROCK-SCISSORS-PAPER DYNAMICS IN THE TRANSITION MATRIX MODEL

Consider the generalized rock-scissors-paper (RSP) game, a cyclic dominance game defined by the matrix

$$
\mathbf{A}:=\left[\begin{array}{ccc}
0 & 1+a & -1  \tag{20}\\
-1 & 0 & 1+a \\
1+a & -1 & 0
\end{array}\right]
$$

Here $a$ is the shift parameter away from zero sum; when $a=0$, this is the standard zero-sum RSP game, with row and column player strategies in that order. Recall that for any value of $a$, this game has a symmetric interior Nash equilibrium strategy
$x_{1}=x_{2}=x_{3}=\frac{1}{3}$. Under the replicator dynamics, when $a>$ 0 , then $\mathbf{x}^{*}=\left(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}\right)$ is stable; for $a<0$, $\mathbf{x}^{*}$ is unstable, and when $a=0$, $\mathbf{x}^{*}$ is a nonlinear center [27]. Zeeman further classifies all three-strategy replicator phase portraits [27], and shows that there can be no isolated periodic orbits and hence no limit cycles (see also [5], p. 5). We use this to show that the dynamics we study cannot be diffeomorphically mapped to the replicator dynamics, by analyzing the RSP dynamics. We then study this model in a simple stochastic simulation, which allows us to explore the attraction properties of the different states.

## A. Analytic results

For the remainder of this section, we relax our assumption that $g(z)=0$ for $z<0$, and assume only that $g(z)$ is positive, monotonic, and differentiable (and hence continuous). From Corollary 6, any Nash equilibrium is a fixed point of the transition matrix model given in (13) for any non-negative monotonic increasing $g(z)$. The fixed point in this case represents a balance in transition matrix fluxes. What can we say about the dynamics of RSP in the transition matrix model? For the remainder of this section, we substitute $x_{3}=1-x_{1}-x_{2}$, for simplicity, and analyze the resulting two-dimensional system, with $x=x_{1}$ and $y=x_{2}$.

Proposition 10. Assume $g(z)$ is differentiable, $g^{\prime}(0)>0$, and $g(0) \geqslant 0$. Define

$$
\begin{equation*}
a_{\mathrm{crit}}=-\frac{3 g(0)}{g^{\prime}(0)} \tag{21}
\end{equation*}
$$

Then (1) when $a>a_{\text {crit }}$, the fixed point is stable; (2) when $a<a_{\text {crit }}$, the fixed point is unstable.

Proof. We evaluate the Jacobian of the two-dimensional dynamical system and then analyze its eigenvalues at the fixed point. The eigenvalues are

$$
\left[\begin{array}{l}
-g^{\prime}(0) a-3 g(0)+\sqrt{-3 g^{\prime}(0)^{2}(a+2)^{2}}  \tag{22}\\
-g^{\prime}(0) a-3 g(0)-\sqrt{-3 g^{\prime}(0)^{2}(a+2)^{2}}
\end{array}\right]
$$

The stability of the point is entirely decided by the real part of the eigenvalues. Applying Theorem 3.2 of [28] and inspection yields the result.

A specific function that satisfies these assumptions is

$$
\begin{equation*}
g(z ; \alpha)=\frac{1}{2}(\tanh (\alpha z)+1) \tag{23}
\end{equation*}
$$

For this function, $a_{\text {crit }}=-3 / \alpha$. When $a=a_{\text {crit }}$, the dynamics are entirely contained on the center manifold, and numerical simulations show that a nonlinear center emerges. This behavior is qualitatively similar to the behavior observed in the ordinary replicator dynamics in generalized rock-scissorspaper and other imitation dynamics (as $\alpha \rightarrow \infty$ ) (see relevant sections in [5] and [3] and their references). In Fig. 1 we show numerical evidence for a Hopf bifurcation, by plotting the stable limit cycle for $\alpha=10$ and $a=-1$ (for $a_{\text {crit }}=-0.3$ ).

Proposition 11. Assume $g(x) \geqslant 0$ and monotonically increasing for $x \in \mathbb{R}$. Further assume $g(x)$ is differentiable and that $g(x)>0$ for $x>0$. Suppose that $x=y=\frac{1}{3}$ is the unique unstable fixed point in $\Omega=\{(x, y): x+y \leqslant 1, x, y \geqslant$ $0\}, 3 g(0) / g^{\prime}(0)<2$, and $-2<a<-3 g(0) / g^{\prime}(0)$. Finally,


FIG. 1. Phase portrait for the two-dimensional variation of the generalized RSP dynamics with $g(x ; \alpha)=\frac{1}{2}(\tanh (\alpha x)+1), \alpha=10$, and $a=-1$ in Eq. (20), showing a limit cycle.
assume that for

$$
\begin{equation*}
\frac{1}{a+3}<\lambda<1, \tag{24}
\end{equation*}
$$

we have

$$
\begin{align*}
& g(a \lambda-a-1) \lambda-(1-\lambda) \\
& \quad \times[g(-a \lambda+a+1)+g(a \lambda+3 \lambda-1)]<0 . \tag{25}
\end{align*}
$$

Then system (13) admits a limit cycle.
Proof. The fixed point $x=\frac{1}{3}, y=\frac{1}{3}$ is unstable by Proposition 10, and thus there is a ball of radius $\epsilon>0$ about this point from which all flow leaves. This proof relies on there being only one unstable interior fixed point; we then show that the flow dynamics at the boundary of $\Omega$ is inward.

Consider now the flow in the $y$ direction, along the line segment $x=\lambda$, for $\lambda \in[0,1]$. The magnitude of this flow in the positive $y$ direction is given by

$$
\begin{align*}
& g(-2 \lambda+(1-\lambda)(1+a)+1) \lambda \\
& \quad+g(-\lambda+(1-\lambda)(1+a)-\lambda(1+a))(1-\lambda) \tag{26}
\end{align*}
$$

which is non-negative given our assumptions on $g$. If $g(x)>0$ for all $x$, then there is always flow into the interior of $\Omega=$ $\{(x, y): x+y \leqslant 1, x, y \geqslant 0\}$ along the given line segment. If $g(x)=0$, then $x \leqslant 0$. It suffices to show that for some value of $\lambda$ the flow in question is positive in the $y$ direction. This occurs when either

$$
\begin{aligned}
-2 \lambda+(1-\lambda)(1+a)+1 & >0 \text { or } \\
-\lambda+(1-\lambda)(1+a)-\lambda(1+a) & >0,
\end{aligned}
$$

which occurs when
$\left\{\frac{2+a}{a+3}<\lambda\right\}, \quad\left\{\frac{1+a}{3+2 a}<\lambda\right\}, \quad a<-3$,
$\{2 / 3<\lambda\}, \quad a=-3$,
$\left\{\lambda<\frac{2+a}{a+3}\right\}, \quad\left\{\frac{1+a}{3+2 a}<\lambda\right\}, \quad-3<a<-3 / 2$,
$\{\lambda<1 / 3\}, \quad a=-3 / 2$,
$\left\{\lambda<\frac{2+a}{a+3}\right\}, \quad\left\{\lambda<\frac{1+a}{3+2 a}\right\}, \quad-3 / 2<a$.
In each case, there is a subset of $[0,1]$ such that when $\lambda$ is in this subset all flow must be directed into $\Omega$.

We show that a similar statement holds on the other two line segments on $\partial \Omega$. From the fact that there are no stability points other than $x=y=\frac{1}{3}$, it follows that flow must leave the boundary and enter $\Omega$.

The flow in the positive $x$ direction on the line segment $y=\lambda, \lambda \in[0,1]$ is given by

$$
\begin{align*}
& g(\lambda(1+a)-1+\lambda-(1-\lambda)(1+a)) \lambda \\
& \quad+g(\lambda(1+a)-1+2 \lambda)(1-\lambda), \tag{28}
\end{align*}
$$

which also is non-negative for $\lambda \in[0,1]$. By a similar argument to the one above, we can show that for any choice of $a$ there is at least some subset of this line segment on which the flow enters $\Omega$.

Finally, the flow in the $y$ direction on the line segment $x+y=1$ is given by

$$
\begin{align*}
& \lambda g(a \lambda-a-1)-(1-\lambda)\{g(-a \lambda+a+1) \\
& \quad+g(a \lambda+3 \lambda-1)\} \tag{29}
\end{align*}
$$

for any point $x=\lambda$ and $y=1-\lambda$. Our final assumptions on $g$ tell us that when inequality (24) holds, the flow in the $y$ direction is negative. Thus our assumption ensures that there is a subset of the line segment from which flow leaves and enters $\Omega$. It then follows from the Poincare-Bendixson theorem that there must be a limit cycle.

The limit cycle shown in Fig. 1 is eventually destroyed as the value of $a$ increases, as illustrated in Fig. 2(b). When $\alpha=$ 10 , and $a=-3 / 10+0.001$, the limit cycle appears almost semistable as illustrated in the phase portrait in Fig. 2(a). This suggests a Hopf bifurcation caused by the real parts of the eigenvalues [see expression (22)] of the Jacobian matrix crossing over the real axis. Note the angular bends in the trajectories shown in Fig. 2 are not an artifact of the numerical solution. Such highly curved trajectories are reminiscent of the phase portrait for the Van der Pol oscillator (see, e.g., [28,29]). It is also worth noting that these dynamics persist when a variation of the Heaviside step function (defined as $1 / 2$ at zero) is used for $g(z)$. Thus the conditions given in Proposition 11 are sufficient, but not necessary.

We can get a fuller picture of the dynamics by first fixing $\alpha=10$ and tracking the dynamics as the parameter $a$ varies using the software package XPPAUT (which incorporates an interface to the continuation package, AUTO) [30]. Figure 3(a) shows the dynamics of RSP as the asymmetry parameter $a$ varies with fixed $\alpha$. Starting from the left (at the maximum asymmetry), we see that there is a stable equilibrium (red


FIG. 2. Phase portrait for the two-dimensional variation of the generalized RSP dynamics with $g(x ; \alpha)=\frac{1}{2}(\tanh (\alpha x)+1), \alpha=10$, and (a) $a=-3 / 10+0.001$, (b) $a=1$.
line) corresponding to $y$ (paper) dominating. There are corresponding stable equilibria with $x$ and $z$ as winners. As $a$ increases, this stable equilibrium coalesces with a saddle point at a saddle-node bifurcation and disappears. Starting from the right at $a=0$, there is a unique stable coexistent equilibrium $(1 / 3,1 / 3,1 / 3)$ that remains stable until $a=a_{\text {crit }}$ where there is a supercritical Hopf bifurcation leading to a stable periodic orbit (green curve). This branch of oscillations persists until it meets the saddle point at a heteroclinic orbit. At this point, there is a heteroclinic cycle going between each of the saddles (see the phase plane in Fig. 4). There is a small region of $a$ for which there is multistability. The stable oscillation exists and


FIG. 3. (a) Numerical bifurcations for Eq. (20), shown for the variable $y$, as the asymmetry parameter $a$ varies for fixed $\alpha=10$; (SN) labels a saddle-node bifurcation, and (He) a heteroclinic orbit. Thick green lines show the periodic orbit emerging from the Hopf bifurcation. Red lines are stable equilibria and black are unstable. (b) Two parameter diagram showing the curve of Hopf bifurcations, saddle nodes (SN), and heteroclinics (He).
in addition there are three stable equilibria that correspond to each of R, P, or S strategies dominating.

## B. Finite stochastic model

The formulation of a model in terms of a transition matrix between the different populations of RSP suggests a simple stochastic simulation, in which there are a finite number of agents $N$ divided between the three strategy populations $X, Y, Z$, non-negative integers representing rock, scissors, paper, respectively. We simulate this by using a Gillespie algorithm with transition rates that are given by Eq. (13). That is, for a given state $(X, Y, Z)$, we form the normalized quantities, $(x, y, z)=(X, Y, Z) / N$, compute the fitness from these numbers, from which we produce a transition rate from each of the three states to the others. For example, rock $(X)$ will transition to paper $(Z)$ at a rate $g\left(f_{z}-f_{x}\right)$ where the $f_{i}$ are the fitnesses of the two strategies. As $N \rightarrow \infty$, we expect the dynamics to follow the deterministic equation. When $N$ is small enough and there are multiple attractors such as near the heteroclinic cycle in Fig. 4, then the stochastic nature of the problem can introduce enough "noise" to allow transitions between the various stable states.

Figure 5 shows histograms of the stochastic trajectories for $N=90$ agents and $10^{6}$ iterations, as the parameter $a$


FIG. 4. Heteroclinic cycle (blue) for $\alpha=10$ and $a \approx-1.2595$ in RSP dynamics; the blue circles are the saddle points, and black squares are stable nodes. The cycle consists of three saddle-saddle connections. The red and green lines are the $x$ nullclines and $y$ nullclines, respectively. The red circle is the unstable coexistence equilibrium.
decreases. Each pixel is colored according to the log of the fraction of iterations that the state is reached during the simulation. In panel (a), the dominance attractors do not yet exist $(a=-1)$, and the probabilities are all centered around the deterministic limit cycle, shown in black. In panel (b), the dominance attractors coexist with the limit cycle ( $a=-1.12$ ), but have relatively small basins of attraction. Thus most of the time is spent near the limit cycle, especially along the center edges of the triangle. At the corners, however, probability density is lost from the limit cycle as the dynamics is pulled toward the dominance equilibria. Finally, in Fig. 5(c), where $a=-1.15$, the basins of the three dominance equilibria are large and deep enough such that most of the time is spent near the extremes ( $X=N, Y=0, Z=0$, and the other two analogous attractors). There are three red pixels at the corners corresponding to these points. The limit cycle is still evident, but has a low probability compared to the corners. For large $N$, the multiple attractors will be harder to see in the stochastic simulation, since the probability of making a jump is roughly proportional to $\exp (-K \sqrt{N})$ where $K$ is related to the basin of attraction (see, e.g., [31]).

## V. COOPERATOR PERSISTENCE IN THE PRISONER'S DILEMMA

As mentioned above, the transition matrix model does not necessarily have the property that a Nash equilibrium is also a fixed point of the dynamics; there are other possibilities, in the case where $g$ is continuous and $g(0)>0$. To see this, consider the canonical Prisoner's Dilemma matrix:

$$
\mathbf{B}:=\left[\begin{array}{ll}
R & S \\
T & P
\end{array}\right],
$$

with $S<P<R<T$. The Nash equilibrium is $\mathbf{e}_{2}$, the defect strategy. The evolution of population proportions $x$ and $y$ in


FIG. 5. Histograms for the stochastic RSP model with $N=90$ agents, for $a$ near the region of multistability between the limit cycle and the three dominant equilibria. Color scale shows log of the probability of finding $(X, Y)$ at that pixel; solid black curve is the deterministic limit cycle: (a) $a=-1.0$, in the deterministic system, there is only a stable limit cycle and the dominant equilibria do not exist; (b) $a=-1.12$, the limit cycle and the three dominance attractors co-exist; (c) $a=-1.15$, the basin of the dominance attractors is large enough so that most time is spent near them (three small red pixels in the corners of the triangle).
the transition matrix model is given by

$$
\begin{align*}
\dot{x}= & y g((R-T) x+(S-P) y), \\
& -x g(-(R-T) x-(S-P) y),  \tag{30}\\
\dot{y}= & x g(-(R-T) x-(S-P) y) \\
& -y g((R-T) x+(S-P) y)
\end{align*}
$$

Evaluating the right-hand side at the Nash equilibrium $(x, y)=$ $(0,1)$ yields

$$
\begin{aligned}
\left.\dot{x}\right|_{(0,1)} & =g(S-P), \\
\left.\dot{y}\right|_{(0,1)} & =-g(S-P) .
\end{aligned}
$$

Since $S-P<0$, if $g(z)=0$ for $z \leqslant 0$ then $(0,1)=\mathbf{e}_{2}$ is a fixed point. If $g(S-P)>0$, then $g(0)>0$ by the monotonic properties of $g$ and the fact that $g$ is continuous, which means that $\mathbf{e}_{2}$ is not a fixed point. Note that if $g(z)=0$ for $z<0$ and $g(0) \neq 0$ but $g$ is discontinuous, we still have a fixed point at $\mathbf{e}_{2}$.

One way to interpret this property is that $g(S-P)>0$ represents spontaneous mutations of the dominant (pure) strategy to a weaker strategy. The result is there will always be a small endemic element of the population playing the cooperate strategy. The details are highly dependent on the relative values in the Prisoner's Dilemma matrix. To analyze this further, we define the combined population variable ( $R-$ $T) x+(S-P) y \equiv \nu(x, y)$, which with $x+y=1$ becomes

$$
v(x)=(R-T) x+(S-P)(1-x)
$$

From system (30), the fixed point equation is

$$
\begin{equation*}
\dot{x}=0=(1-x) g(v(x))-x g(-v(x)) . \tag{31}
\end{equation*}
$$

If the function $g(\cdot)$ has the property

$$
\begin{equation*}
g(z)+g(-z)=C \tag{32}
\end{equation*}
$$

where $C$ is a constant, then Eq. (31) simplifies to

$$
\begin{equation*}
g(v)-x(g(v)+g(-v))=(g \circ v)(x)-C x=0 \tag{33}
\end{equation*}
$$

Thus if we define the function

$$
\begin{equation*}
\gamma(x) \equiv \frac{1}{C}(g \circ v)(x) \tag{34}
\end{equation*}
$$

then any fixed point cooperator population of system (30) is also a solution to $x=\gamma(x)$.

Unfortunately, there is no generalized closed form solution to (34). As mentioned before, one of the strengths of this approach is that it allows for the analytic derivation of dynamic properties based on given functions $g(z)$. The example defined by Eq. (23), with $g(z)=\frac{1}{2}(\tanh (\alpha z)+1)$, satisfies property (32) with $C=1$. We obtain the effect of $\alpha$ on the proportion of the endemic cooperator population, shown in Fig. 6 for a fixed Prisoner's Dilemma payoff matrix:

$$
\mathbf{B}=\left[\begin{array}{ll}
15 & 10  \tag{35}\\
17 & 11
\end{array}\right]
$$

We next derive a general analytic result for our model, starting with Eq. (34) for the Prisoner's Dilemma

$$
x=\frac{1}{2}(\tanh (\alpha[(S-P)+(P+R-S-T) x])+1)
$$



FIG. 6. Comparison of the effect of $\alpha$, which governs the sharpness of the function $g$ defined in (23), on the proportion of cooperators that remain endemic (in the stationary state) for the Prisoner's Dilemma defined by (35). We compare the precise value, computed from (34), to the first-order approximation characterizing the structure of the curve, given by (38).

If the matrix parameters are chosen such that $P+R-S-$ $T=0$, then the RHS of the fixed point condition becomes a constant (independent of $x$ ), and we have

$$
\begin{equation*}
x=\frac{1}{2}(\tanh (\alpha(S-P))+1) . \tag{36}
\end{equation*}
$$

It is somewhat surprising that, in this case, the endemic population of cooperators depend only on the values $S$ and $P$, i.e., on defect payoffs.

We expand around this by defining $\phi=P+R-S-T$ and $\theta=S-P$, so that the fixed point condition becomes

$$
x(\phi)=\frac{1}{2}(\tanh (\alpha[\theta+\phi x])+1)
$$

Using a linear approximation (for small values of $\phi$ ), we see that

$$
\begin{equation*}
\left.\frac{d x}{d \phi}\right|_{\phi=0}=\frac{1}{2} \alpha x(0) \operatorname{sech}^{2}(a \alpha) \tag{37}
\end{equation*}
$$

where $x(0)=\frac{1}{2}(\tanh (\alpha \theta)+1)$, as in (36). Thus the proportion of the population that remains cooperative in the Prisoner's Dilemma (as a function of $\alpha$ ) has first order approximation:

$$
\begin{equation*}
x^{*} \approx \frac{1}{2}(\tanh (\alpha \theta)+1)\left(1+\frac{\phi}{2} \alpha \operatorname{sech}^{2}(\alpha \theta)\right) \tag{38}
\end{equation*}
$$

The effectiveness of this approximation is illustrated for $x^{*}$ vs $\alpha$ in Fig. 6, for $\phi=1$. This approximation is not valid when $\phi$ is large, but for small values does capture the shape shown in the figure. It is also worth noting that as $\alpha$ approaches infinity [and the function $g(z)$ becomes discontinuous but with the property that $g(z)=0$ for $z<0$ ] the proportion of the endemic cooperator population goes to zero, as one would expect. Thus the approximation is well behaved.

## VI. DISCUSSION

In this paper, we have considered a general approach to evolutionary games, in which the changing distribution of strategies is determined by a transition matrix characterizing the strength of coupling between any two strategies. This
approach allows for a population flux to any strategy choice, without the requirement that it be previously populated. The populations move away from unsuccessful strategies and towards more successful ones, in a manner qualitatively consistent with evolution on a Markov chain, or the master equation approach to transition probabilities. The presence of the universal transition function $g(\cdot)$, on which our model is based, allows some flexibility-including the possibility of a (low probability) flux towards less successful strategies-in terms of the properties of $g$. We show that a majority of the Folk Theorem of evolutionary game theory (with slight modifications) holds for our model, suggesting that additional analytic results may be derived for this model.

We also show that the transition matrix model admits a Hopf bifurcation for the generalized rock-scissors-paper (RSP) game, and discuss conditions under which the limit cycle appears. A similar result is found for RSP with global mutations [9], and more recently with single mutations [10]. The specifics of our proof require that there be only one interior fixed point; however, the necessary and sufficient conditions for the actual existence of limit cycles for generalized RSP may be more general.

In our model, the occurrence of "mutation" arises directly from the value of the transition function $g(0)$, instead of being superposed as an additional term. The resultant possibility of flow to less fit strategies is similar to trembling hand equilibria [3]; the full implications of this feature on the dynamics remain to be explored. We have shown that for any $g(0)>0$, a strictly dominating boundary equilibrium (e.g., defect in prisoner's dilemma) need not be a fixed point of the system. Instead, the kind of continuous mutation included in this model allows the dominated population to maintain a finite representation; the spontaneous emergence of dominated strategies is also possible.

As a future extension of this work, it would be interesting to explore its relationship to the DeGroot model for social dynamics, and related phenomena [21,23]. In addition, we would like to identify an evolving trust-opinion data set to determine whether a game-theoretic model can capture the dynamic opinions, following the approach of [24]. In these social applications, the transition matrix model may provide a useful mathematical perspective.

We have studied the transition matrix model in the context of evolutionary games; however, this approach could be further generalized to biological contexts. In terms of the definition of the fitness for species $i$ in the replicator, our model is written

$$
\frac{d x_{i}}{d t}=\sum_{j} x_{j} g\left(f_{i}-f_{j}\right)-\sum_{j} x_{i} g\left(f_{j}-f_{i}\right)
$$

Although it is unclear that this unified approach, based on $g(\cdot)$, is more appropriate than the standard, additive approach to mutation in evolutionary dynamics, it is intriguing to consider the implications of treating both replication and mutation as being derived from a single function.

## ACKNOWLEDGMENTS

A.B. acknowledges support from Université Paris Diderot Paris 7, and R. deForest, G. Gunaratne, K. Sneppen, and S. Tian for helpful discussions. C.G. thanks E. Paulson for a critical
reading and suggestions on the manuscript. A.B. and C.G. were partially supported by the National Science Foundation, under

Grant No. CMMI-1463482. B.E. was partially supported by NSF Grant No. DMS-1219753.
[1] P. D. Taylor and L. B. Jonker, Math. Biosci. 40, 145 (1978).
[2] D. Friedman, Econometrica 59, 637 (1991).
[3] J. W. Weibull, Evolutionary Game Theory (MIT Press, Boston, 1997).
[4] J. Hofbauer and K. Sigmund, Evolutionary Games and Population Dynamics (Cambridge University Press, Cambridge, UK, 1998).
[5] J. Hofbauer and K. Sigmund, Bull. Am. Math. Soc. 40, 479 (2003).
[6] W. H. Sandholm, Population Games and Evolutionary Dynamics (MIT Press, Boston, 2010).
[7] K. H. Schlag, J. Econ. Theory 78, 130 (1997).
[8] D. Fudenberg and D. K. Levine, The Theory of Learning in Games (MIT Press, Boston, 1998).
[9] M. Mobilia, J. Theor. Biol. 264, 1 (2010).
[10] D. F. P. Toupo and S. H. Strogatz, Phys. Rev. E 91, 052907 (2015).
[11] A. J. Black, A. Traulsen, and T. Galla, Phys. Rev. Lett. 109, 028101 (2012).
[12] K. Sigmund, Proc. Symp. Appl. Math. 69, 1 (2011).
[13] R. Cressman and Y. Tao, Proc. Natl. Acad. Sci. (USA) 111, 10810 (2014).
[14] K. M. Page and M. A. Nowak, J. Theor. Biol. 219, 93 (2002).
[15] C. P. Roca, J. A. Cuesta, and A. Sánchez, Phys. Life Rev. 6, 208 (2009).
[16] C. H. Hommes and M. I. Ochea, Games Econ. Behav. 74, 434 (2012).
[17] R. M. May, Ecology 54, 638 (1973).
[18] J. Mathiesen, N. Mitarai, K. Sneppen, and A. Trusina, Phys. Rev. Lett. 107, 188101 (2011).
[19] J. Hofbauer and K. Sigmund, Evolutionary Games and Population Dynamics (Cambridge University Press, Cambridge, UK, 1998).
[20] M. A. Nowak, Evolutionary Dynamics: Exploring the Equations of Life (Belknap Press, Cambridge, MA, 2006).
[21] M. H. DeGroot, J. Am. Stat. Assoc. 69, 118 (1974).
[22] R. Hegselmann and U. Krause, J. Artific. Societ. Soc. Simul. 5, 1 (2002).
[23] C. Castellano, S. Fortunato, and V. Loreto, Rev. Mod. Phys. 81, 591 (2009).
[24] J. Török, G. Iñiguez, T. Yasseri, M. San Miguel, K. Kaski, and J. Kertész, Phys. Rev. Lett. 110, 088701 (2013).
[25] P. Jia, A. MirTabatabaei, N. E. Friedkin, and F. Bullo, SIAM Rev. 57, 367 (2015).
[26] E. Segrè, Nuclei and Particles, 2nd ed. (Benjamin Cummings Publishing, New York, 1977).
[27] E. C. Zeeman, Global Theory of Dynamical Systems, Springer Lecture Notes in Mathematics Vol. 819 (Springer, New York, 1980).
[28] F. Verhulst, Nonlinear Differential Equations and Dynamical Systems, 2nd ed. (Springer, New York, 2006).
[29] M. Desroches and M. R. Jeffrey, Proc. R. Soc. A 467, 2404 (2011).
[30] G. B. Ermentrout, Simulating, Analyzing, and Animating Dynamical Systems: A Guide to XPPAUT for Researchers and Students (SIAM, Philadelphia, PA, 2002), Vol. 14.
[31] C. W. Gardiner, Handbook of Stochastic Methods for Physics, Chemistry and the Natural Sciences (Springer-Verlag, Berlin, 2004).

