Evolutionary Games on Structured Populations under Weak Selection

Author: Nicholas Wage, wage@fas.harvard.edu, (920)-450-4293

Advisor: Martin Nowak

Abstract

All biological systems are, at some level, guided by the laws of natural selection and evolutionary dynamics. Adaptations with increased fitness tend to proliferate and fixate within populations. Those situations in which an individual's fitness depends not only upon a static environment, but upon the fluctuating phenotypes of the surrounding population, fall within the domain of evolutionary game theory. In a beautiful paper, Tarnita et al. (2009c) proved that for a large class of evolutionary games on structured populations with $n = 2$ strategies, the conditions for a strategy to be selected for in the limit of weak selection could be described entirely by one, real-valued structure coefficient σ. This paper explores a generalization of this result to an arbitrary number of strategies n, and finds that to describe selection conditions for any n we need only three such real-valued structure coefficients $\sigma_1, \sigma_2, \sigma_3$. In an attempt to describe exactly which games this theorem applies to, we define a new, general class of evolutionary games which may be of independent interest. We also demonstrate a specific application of our results to the evolution of cooperation, a popular research topic.

1 Introduction

Since the publication of *The Origin of Species* [Darwin 1859], evolution has grown to be an integral part of how people view biology and the world. The theory of evolution is, at its mot basic, a nearly tautological principle: things which more successfully replicate will become more common. Yet in the complex and seemingly arbitrary world of living systems, this basic fact is often the only tool we have to answer the question "Why?" The reason any species or population has any specific behavior or characteristic is simply that, evolutionarily speaking, it is successful. When attempting to explain the existence of a known trait or to predict adaptations we cannot directly observe, our only recourse is to examine how they function under the forces of natural selection.

How creatures evolve in response to a fixed fitness landscape is often straight-forward: polar bears with warmer coats or gazelles that run faster tend to survive and procreate. The most interesting situations, from an evolutionary standpoint, instead tend to be those which involve frequency-dependent selection, where the success of a specific survival strategy within a population is influenced not only by the static properties of its surrounding environment but by the evolving properties of the population itself. These are the situations where the structure of the evolutionary system itself becomes important and interesting. The tools used to study such situations fall within the realm of evolutionary game theory [Maynard Smith 1982, Hofbauer & Sigmund 1988].

The general model used by evolutionary game theory to study the interaction of n competing survival strategies employs a $n \times n$ payoff matrix A with entries $a_{i,j}$. A player utilizing strategy i receives payoff $a_{i,j}$ from an interaction with a player utilizing strategy j. This leaves a wide range of flexibility as to specifically how interactions occur and how their payoffs influence the resulting evolutionary dynamics. When we assume the population is infinitely large and well mixed, the resulting dynamics can be studied through differential equations and specifically the "replicator equation" [Taylor & Jonker 1978, Hofbauer *et al.* 1979, Zeeman 1980]. However, real populations are rarely well-mixed and always finite, which has lead to substantial research into evolutionary games on structured populations.

1.1 Evolutionary Games on Structured Populations

These models tend to involve a Markov chain[1]in which a population of individuals evolves through different states according to the dynamics of the system. A state consists of a set of individuals, each of which is assigned one of the n strategies, and a structure of the relationships between these individuals. An individual interacts with each of the other members of the population with a weight given by the population structure. The total payoff Π to the individual is then the weighted sum of the payoffs from matrix A which are associated to each of these interactions. That is, if $P = \{1, \ldots, N\}$ is the (finite) set of individuals in the population and $C : \{1, \ldots, N\} \to \{1, \ldots, n\}$ is the function assigning each individual a strategy, then individual $x \in P$ will receive total payoff

$$\Pi_x := \sum_{y=1}^{N} \omega_{x,y} a_{C(x),C(y)}, \tag{1}$$

where the coefficients $\omega_{x,y}$ are parameters of the population structure. From this payoff, the player's fitness is calculated by

$$F_x := 1 + w\Pi_x, \tag{2}$$

where w is a parameter denoting the strength of selection. Large w makes the game a very important aspect of an individual's fitness, while a low one keeps all fitnesses closer together despite the outcome of the game. These fitnesses are then used to determine the probability with which the system transitions to each of the possible next states. These probabilities, along with the values of the interaction weights $\omega_{x,y}$, are additional factors which go into defining an evolutionary game and there are many ways in which these aspects may be implemented.

The most basic model is known as the Moran process [Moran 1962, Nowak *et al.* 2004, Nowak 2006a], and it involves a "well-mixed" population of fixed size N. In each state, any given player interacts with each of the other $N - 1$ players with equal weight to determine its payoff and fitness. To transition to the next state one player is randomly chosen to replicate and another to be replaced (these two players are not necessarily distinct). Players are chosen for replication with probability proportional to their fitness, while all players have equal likelihood of being replaced. In any such replacement event, the replaced player takes on the the strategy of the replicating player with probability $1 - u$, while a mutation occurs with probability $0 < u < 1$, in which case the player being replaced is equally likely to take on each one of the n possible strategies.

The Moran process, however, still does not allow us to change the structure of the population. This lead to the introduction of evolutionary graph theory, where individuals in the population are viewed as nodes on a graph with the connections of the graph determining the payoff and replacement interactions [Lieberman *et al.* 2005]. In such a game, the values $\omega_{x,y}$ (for each pair $x, y \in P$) from above are fixed properties of the game, and denote the weight of the directed edge from player x to player y. These values essentially denotes how closely a player x interacts with a player y. At each time step a player x is randomly selected to procreate, with probability proportional to fitness, and this player produces an offspring which replaces one of its neighbors y with probability proportional to the weight of directed edge $\omega_{x,y}$. As in the Moran process, a

---

[1] Those unfamiliar with Markov chains should refer to Appendix A, for a rigorous definition and a review of the basic theory.

mutation occurs with some probability $0 < u < 1$. This update rule is known as the *birth-death* process, but many others exist [Ohtsuki & Nowak 2006b].

In the *death-birth* process, a player x is randomly selected to die with uniform probability, and one of its neighbors y is randomly selected to replace it, with probability proportional to both its fitness and the value of $\omega_{y,x}$, its proximity to player x . The *Wright-Fisher* process is the same as the death-birth process, but instead of choosing just one individual x for replacement during each time step, we simultaneously choose a replacement individual y for each $x \in P$, so that the entire population is replaced during each time step. Other update rules such as "pairwise-comparison" or "imitation" processes have also studied [Ohtsuki & Nowak 2006b], and one could also utilize an entirely novel update rule. In another variation which has been studied, separate graphs are used to determine interaction and replacement likelihoods [Ohtsuki *et al.* 2007a, Ohtsuki *et al.* 2007b].

Such a game defines a Markov chain, and if it is sufficiently nice, over time the process tends to a unique stationary distribution where it takes on each state S with some fixed probability π_S [Markov 1906, Meyn & Tweedie 1993]. The success of any particular strategy k in this game can then be measured by its *abundance* x_k, which we define to be the average frequency with which the strategy occurs in this stationary distribution [Antal *et al.* 2009c]. We say that strategy k is selected for if its abundance is above average so that $x_k > 1/n$.

Though evolutionary graph theory allows the study of a huge diversity of structured games, there are still interesting games which do not fit within its confines. Specifically, games in which the population structure is constantly shifting cannot be defined by a single interaction graph. Researchers have investigated games where interactions are determined by player's shifting memberships in different "sets" [Tarnita *et al.* 2009b] or by a player's location in "phenotype space" [Antal *et al.* 2009b]. Variable structures have also been used to study the viability of group selection [Traulsen *et al.* 2008, Traulsen & Nowak 2006].

1.2 Weak Selection

Much research has been done investigating specific such models and the selection criteria they result in. While a few basic results have been obtained for general values of the selection strength w [Traulsen *et al.* 2008, Antal *et al.* 2009a, Fudenberg *et al.* 2006], a majority published results hold only in *the limit of weak selection*, meaning w is assumed to be arbitrarily small [Nowak *et al.* 2004, Antal *et al.* 2009c, Taylor *et al.* 2004, Ohtsuki & Nowak 2006a, Ohtsuki *et al.* 2006, Taylor *et al.* 2007a, Fu *et al.* 2009, Tarnita *et al.* 2009a, Tarnita *et al.* 2009b, Traulsen *et al.* 2009].

The weak selection assumption is heavily used not only because it leads to much cleaner results, but also because it seems to be a reasonable approximation of the biological world being modeled. An organism is an unfathomably complicated entity and its successful survival and reproduction is a function of countless traits, each of which is experiencing selective pressure. Any one adaptation or attribute we choose to study with our game is just a small part of this greater whole, and as such should have only a minor impact on the overall fitness of the organism. As such, throughout this paper, we concern ourselves only with analyzing models in the limit of weak selection.

In a beautiful paper, Tarnita *et al.* examine the case of $n = 2$ strategies in order to prove a general result about the effect of weak selection upon a general class of evolutionary games on structured populations [Tarnita *et al.* 2009c]. The paper proves the remarkable fact that, under weak selection, the evolutionary dynamics implied by any such structure boil down to *a single, real-valued parameter* σ. They prove that a value of σ exists such that when any 2×2 payoff matrix

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \tag{3}$$

is plugged into the game, the condition that strategy 1 be selected for is equivalent to the simple inequality

$$\sigma a + b > c + \sigma d. \tag{4}$$

Nowak *et al.* build upon this result and claim that this σ can fully describe the weak selection dynamics for *any* number of strategies n for processes which take place in the limit of low mutation $\mu := Nu \to 0$ [Nowak *et al.* 2010]. Specifically they state that for such processes, strategy k is selected for if

$$\sum_{j=1}^{n} \sigma a_{k,k} + a_{k,j} - a_{j,k} - \sigma a_{j,j} > 0. \tag{5}$$

However, this statement cannot hold for general mutation rates u due to the following result. Antal *et al.* [2009] show that if we study the standard Moran process in the limit of large population size N while fixing $\mu := Nu$, the condition that strategy k is favored under weak selection is

$$\sum_{i=1}^{n} \sum_{j=1}^{n} a_{k,k} + a_{k,i} - a_{i,k} - a_{i,i} + \mu(a_{k,j} - a_{i,j}) > 0 \tag{6}$$

for any $n \times n$ payoff matrix A.

The goal of this paper is to present and prove a generalization of the result of [Tarnita *et al.* 2009c] which holds for any number of strategies n and any mutation rate μ, and of which both (5) and (6) are specific examples. It turns out that while the outcome for $n = 2$ can described with just one degree of freedom (the value of the structure coefficient σ), to generalize the result to arbitrary n we require one additional degree of freedom in the description.

The paper is organized as follows. In Section 2, we rigorously define the class of games on which this theorem holds and present the precise statements of the theorems outlined above. Then in Section 3 we present the proof of our main result. Section 4 provides an alternate description of a large class of games to which our result applies. The class of games, called *evolutionary game Markov chains*, may also be of independent interest. In Section 5 we demonstrate a specific application of our results to the hot-button topic of the evolution of cooperation. The final section, Section 6, summarizes our findings and catalogs several possible future research directions opened up by the results within.

2 Model and Results

The evolutionary games described in the previous section all share a similar feel, yet it is difficult to define this notion precisely. Attempting a bottom-up description of all the possible rules which could govern a general evolutionary game Markov chain gets very messy and makes it hard to reach the level generality we would desire. Instead, in this section we start with a very basic definition of such a game and impose several higher-level conditions on its operation.

2.1 Evolutionary Game Selection Criteria

Scraping away all but the bare essentials from the games we have described, we ultimately have that an evolutionary game takes as an input an $n \times n$ payoff matrix A, and returns for each strategy a *selection condition* by which we may measure its relative effectiveness against the other strategies in A. That is, an evolutionary game is just a class of selection conditions $x_1, \ldots, x_n$ which map from the space of $n \times n$ real matrices to the real numbers.

Definition. *An* ***evolutionary game selection criterion*** $[x_{k,n}]_{1\leq k\leq n}$ *is a class of functions*

$$x_{k,n} : \mathbb{R}^{n^2} \to \mathbb{R}, \tag{7}$$

with the property that

$$1 = \sum_{k=1}^{n} x_{k,n}(A) \tag{8}$$

for each $n \in \mathbb{N}$ *and* $A \in \mathbb{R}^{n^2}$.

The condition in equation (8) simply normalizes the value of the selection conditions, so that the sum over all strategies in any game is one, and any specific selection condition $x_{k,n}$ essentially represents the fraction of the population controlled by strategy k, which we call its *abundance*. Again, we say that a strategy k is selected for under payoff matrix A if this abundance is above average so that $x_{k,n}(A) > 1/n$.

This definition of an evolutionary game as just a set of functions is a bit too general. Thus, to prove our main theorem, we will require an evolutionary game selection criteria to have the following three properties.

(i) Differentiability: For each $1 \leq k \leq n$, the function $x_{k,n} : \mathbb{R}^{n^2} \to \mathbb{R}$ is differentiable at the zero matrix $\mathbf{0}$.

   Our theorem is a statement about the dynamics of the game in the limit of weak selection. With selection equal to 0 there should be no advantages and each strategy should have abundance $1/n$, so for such a "limit" to make sense our function must be well-behaved in this region, making this assumption essential. Just about any naturally defined $x_{k,n}$ should have this property, and all the games considered in Section 1.1 do.

(ii) Permutability: Let $\pi : \{1, \ldots, n\} \to \{1, \ldots, n\}$ be a bijection or *permutation* of the positive integers less than or equal to n. Then, for any $n \times n$ matrix A with entries $a_{i,j}$, we can define an action of π upon A by the rule $\pi(A) = A'$ with entries $[a'_{i,j}]_{1\leq i,j\leq n}$ where $a_{i,j} = a'_{\pi(i),\pi(j)}$ or equivalently $a'_{i,j} = a_{\pi^{-1}(i),\pi^{-1}(j)}$. With this notation, we require for all $1 \leq k \leq n$, all permutations π of the set $\{1, \ldots, n\}$, and all real-valued $n \times n$ matrices A, that $x_{k,n}(A) = x_{\pi(k),n}(\pi(A))$.

   This rule requires that the labeling of the strategies $1, \ldots, n$ be immaterial. The point of examining evolutionary games on population structures is to determine how different payoff matrices are affected differently. If (ii) does not hold, then the game is somehow biased towards strategies with specific labels over others, and the outcome of the game is no longer just a result of the effectiveness of the competing strategy payoffs. The payoff matrix itself should capture the only differences between strategies in an evolutionary game, and this is essentially what the permutability condition requires. As such, any true evolutionary game should satisfy this condition, and again all the games considered in Section 1.1 do.

(iii) Divisibility: For an $n \times n$ payoff matrix A and a positive integer m, define $D_m(A)$ to be the $mn \times mn$ payoff matrix which contains m identical copies $(k,1), \ldots, (k,m)$ of each original strategy k. Then $x_{k,n}(A) = mx_{(k,i),nm}(D_m(A))$ for all $1 \leq k \leq n$, $1 \leq i \leq m$, and payoff matrices A.

   This condition states that if we take n strategies and split each one into m identical copies, then this should not cause any change in the dynamics because everything has been done uniformly. If we are to examine the operation of an evolutionary game over different size strategy sets, we must have a condition ensuring the game has some sort of consistency between the different values of n. Without this condition, there would be nothing preventing silly games which, for example, employed completely different dynamics for odd and even values of n. Though this condition, like the previous two, is satisfied by all of the evolutionary games presented in Section 1.1, it is perhaps the most restrictive in that reasonable examples do exist which do not satisfy it. Take, for example, the ordinary Moran process on a well-mixed population, but with the slight change that when an offspring mutates, it randomly takes on one of the $n-1$ strategies which are *different* from the strategy of its parent. Then, when we divide strategies into multiple copies of themselves, players can then mutate to one of the other copies of their strategy when previously they couldn't, altering the dynamics.

2.2 Generalized Weak Selection

One remaining issue with our general characterization of evolutionary games is the concept of weak selection, which is an integral assumption used by our theorem. Our initial definition of the strength of selection involved computing the payoff to an individual, and then weighting it by a selection strength parameter w before adding it to fitness. Since our present definition does not require any of these steps to be taken, we need to generalize our definition in order for it to still apply. Recalling equations (1) and (2), we have that in the games for which selection strength was originally defined, a player x in a state S has fitness

$$F_x = 1 + w \sum_{y=1}^{N} \omega_{x,y} a_{C(x),C(y)}, \tag{9}$$

where N, $\omega_{x,y}$, and $C : \{1, \ldots, N\} \to \{1, \ldots, n\}$ are properties of the state of the system. This equation assumes fixed payoff matrix A and variable strength of selection given by w. However, if we instead fix the strength of selection at 1 and utilize payoff matrix wA, we get the exact same formula. Since the payoff matrix only determines the player fitnesses, and then these values are what determine the dynamics of the game, these two games are really equivalent. Thus, a game with selection strength w and payoff matrix A is equivalent to a game with selection strength 1 and payoff matrix wA.

Then we may redefine, for general evolutionary games, the strength of selection parameter rule so that playing a game using payoff matrix A and strength of selection w is equivalent playing the ordinary game utilizing the payoff matrix wA, leading to a general notion of selection strength and a rigorous definition of the limit of weak selection.

Definition. *For any evolutionary game selection criteria $[x_{k,n}]_{1\leq k\leq n}$ and an $n \times n$ payoff matrix A, the strategy k is selected for in the* ***limit of weak selection*** *if $x_{k,n}(wA) > 1/n$ for arbitrarily small values of $w > 0$.*

This definition of weak selection can be applied to any evolutionary game selection criteria, and most importantly, aligns with our original definition on the subset of games for which the notion was originally. In fact, multiplying the strength of selection directly into the payoff matrix seems to be conceptually a more direct method of modulating the impact of the game on selection, and it additionally allows the omission of the complicating payoff/fitness distinction.

2.3 Presentation of the Main Result

With these preliminaries out of the way, we now have all the tools to present rigorous statements of the theorems discussed in Section 1.2. The following theorem of [Tarnita *et al.* 2009c] essentially states that for $n = 2$, the effect of the game structure upon the evolutionary dynamics can be summarized by a single *structure coefficient* σ.

Theorem 1 ([Tarnita *et al.* 2009c]). *Consider a game whose evolutionary game selection criterion* $[x_{k,n}]_{1\leq k\leq n}$ *satisfies properties (i) and (ii), and additionally is such that with payoff matrix* $\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}$, *strategy* 1 *is selected for in the limit of weak selection, meaning that*

$$x_{1,2}\left(w\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}\right) > 1/n \tag{10}$$

for sufficiently small $w > 0$. *To such a game we may associate a* ***structure coefficient*** $\sigma \in \mathbb{R}$ *with the property that for any payoff matrix*

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix} \tag{11}$$

describing the interactions between the two strategies, the game favors strategy 1 *in the limit of weak selection if*

$$\sigma a + b > c + \sigma d. \tag{12}$$

It is important to stress that σ *depends only on the structure of the game itself, and not upon the payoff values* a, b, c, *and* d.

The inequality (10) essentially imposes the reasonable condition that increasing a strategies payoff against opponents increases its abundance. If this is not the case, then a higher payoff value b hurts strategy 1, so the equation (12) would need a negative coefficient on b. Many results previous to this one calculated σ values for specific games, without knowing that such a general theorem held [Nowak *et al.* 2004, Antal *et al.* 2009c, Taylor *et al.* 2004, Ohtsuki & Nowak 2006a, Ohtsuki *et al.* 2006, Taylor *et al.* 2007a, Fu *et al.* 2009, Tarnita *et al.* 2009a, Tarnita *et al.* 2009b, Traulsen *et al.* 2009]. This theorem unifies these previous results under one umbrella, and allows us to summarize the entire effect of a population structure upon two-strategy game dynamics by the single structure coefficient σ.

Before we present our generalized version of this theorem, it will be useful to introduce a bit of notation. For an $n \times n$ matrix A with entries $[a_{i,j}]_{1\leq i,j\leq n}$, we define the following quantities. Define $\overline{a_{k,\bullet}} := n^{-1}\sum_{i=1}^{n} a_{k,i}$ as the average payoff strategy k gets from other strategies, $\overline{a_{\bullet,k}} := n^{-1}\sum_{i=1}^{n} a_{i,k}$ as the average payoff other strategies get from strategy k, $\overline{a_{\bullet,\bullet}} := n^{-1}\sum_{i=1}^{n} a_{i,i}$ as the average payoff a strategy gets from itself, and $\overline{a_{\bullet,\circ}} := n^{-2}\sum_{i=1}^{n}\sum_{j=1}^{n} a_{i,j}$ as the average payoff in the population. Under this notation, we can restate equation (5) can be equivalently written as

$$\sigma a_{k,k} + \overline{a_{k,\bullet}} - \overline{a_{\bullet,k}} - \sigma\overline{a_{\bullet,\bullet}} > 0 \tag{13}$$

and equation (6) simplifies to

$$a_{k,k} + \overline{a_{k,\bullet}} - \overline{a_{\bullet,k}} - \overline{a_{\bullet,\bullet}} + \mu(\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}}). \tag{14}$$

With this notation established, we present the central result of this paper.

Theorem 2. *For any evolutionary game selection criterion satisfying properties (i), (ii), and (iii), there exist choices of three structure coefficients* $\sigma_1, \sigma_2, \sigma_3 \in \mathbb{R}$ *with the following characteristic. For any number of strategies* n *and any* $n \times n$ *payoff matrix* A, *the game favors strategy* k *in the limit of weak selection if*

$$\sigma_1(a_{k,k} - \overline{a_{\bullet,\bullet}}) + \sigma_2(\overline{a_{k,\bullet}} - \overline{a_{\bullet,k}}) + \sigma_3(\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}}) > 0. \tag{15}$$

The theorem essentially states that the dynamics generated by any game in the limit of weak selection can be completely described by the relative weights the structure of the game places upon the three expressions $a_{k,k} - \overline{a_{\bullet,\bullet}}$, $\overline{a_{k,\bullet}} - \overline{a_{\bullet,k}}$, and $\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}}$. This means that the set of possible dynamics imposed by games under weak selection is much more restricted than one might initially imagine, and allows us to conclude much more than we otherwise could have.

Note that while we require three structure coefficients σ_1, σ_2, and σ_3, equation (15) is homogeneous in these values and thus replacing them with scalar multiples of each other does not affect the theorem. In Theorem 1, this fact is exploited in order to fix the coefficient on b and c to 1, leaving only the single variable σ. The natural condition (10) allows this normalization by insuring the initial coefficient on b and c terms is positive, so they can be divided out without altering the inequality. In the general case of Theorem 2, there is no natural condition by which we can guarantee that any one structure coefficient is positive, so such a scaling is difficult. Still, though we use three variables to describe the structure, this scalability means that there are really only two degrees of freedom in a games structure, not three.

The results we have discussed so far are all closely related to Theorem 2. Note that when $n = 2$ we have that $(\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}}) = \frac{1}{2}(a_{k,k} - \overline{a_{\bullet,\bullet}}) + \frac{1}{2}(\overline{a_{k,\bullet}} - \overline{a_{\bullet,k}})$. and thus because Theorem 2 holds for $n = 2$ we may conclude that the structure coefficients of any such evolutionary game selection criteria are related by the expression $\sigma = \frac{2\sigma_1+\sigma_3}{2\sigma_2+\sigma_3}$. Additionally, in light of Theorem 2, the claim made in [Nowak *et al.* 2010] is equivalent to the statement that $\sigma_3 = 0$ for games which takes place in the limit of low mutation[2] Finally, we can view equation (6) as a calculation of these structure coefficients $\sigma_1 = 1$, $\sigma_2 = 1$, and $\sigma_3 = \mu$ for a specific evolutionary game, the standard Moran process.

3 Proof of Theorem 2

Let $[x_{k,n}]_{1\leq k\leq n}$ be an evolutionary game selection criterion satisfying properties (i), (ii), and (iii). To prove the theorem, we will begin by showing that for each number of strategies $n \in \mathbb{N}$ there are constants σ_1^n, σ_2^n, and σ_3^n with the desired properties (these are superscripts, not exponents), and then show that these values may be replaced with one triple σ_1, σ_2, σ_3 which works for all n.

Fix a number of strategies n. When $w = 0$, all strategies have equal payoffs and by property (ii), permutability, all strategies are identical at neutrality. Thus, they must have equal abundances $x_{k,n}(0) = 1/n$ for all k. Since each strategy has equal abundance at $w = 0$, the relative success of the strategies in the limit as w tends to 0 is determined by the derivative of their abundances. Hence, for any $A = [a_{i,j}]_{1\leq i,j\leq n}$, strategy k is selected for if

$$\mathcal{R}_{k,n}(A) := \frac{\partial}{\partial w} x_{k,n}(wA)\bigg|_{w=0} > 0. \tag{16}$$

From property (i), differentiability, we know that the partial derivatives of $x_{k,n}$ exist at the zero matrix $\mathbf{0}$. This implies that the derivative in (16) exists, and that in fact we may evaluating this using the chain rule. This simplifies dramatically to an expression of the form

$$\mathcal{R}_{k,n}(A) = \sum_{i=1}^{n}\sum_{j=1}^{n} c_{k,i,j}a_{i,j} > 0, \tag{17}$$

where each $c_{k,i,j}$ is a constant given by taking the partial derivative of $x_{k,n}$ with respect to the i,jth matrix entry and then evaluating this partial at $A = \mathbf{0}$.

---

[2] A rigorous definition of the limit of low mutation and the claim of [Nowak *et al.* 2010] would require a substantial amount of additional machinery. Since we present the claim only to provide general context for Theorem 2 from the literature, and this goal is accomplished by the loose description provided thus far, we omit a rigorous definition in the interest of brevity.

Next we make use of property (ii), permutability, in order to reduce the total number of constants we must consider. We know that permuting the labeling system with any bijection $\pi : \{1, \ldots, n\} \to \{1, \ldots, n\}$ does not change the operation of the game, and specifically that $x_{k,n}(A) = x_{\pi(k),n}(\pi(A))$. From the definition of $\mathcal{R}_{k,n}$, this implies that $\mathcal{R}_{k,n}(A) = \mathcal{R}_{\pi(k),n}(\pi(A))$ for any $n \times n$ payoff matrix $A = [a_{i,j}]_{1 \leq i,j \leq n}$ and thus

$$\sum_{i=1}^{n}\sum_{j=1}^{n} c_{k,i,j}a_{i,j} = \sum_{i=1}^{n}\sum_{j=1}^{n} c_{\pi(k),i,j}a_{\pi^{-1}(i),\pi^{-1}(j)} \tag{18}$$

$$= \sum_{i=1}^{n}\sum_{j=1}^{n} c_{\pi(k),\pi(i),\pi(j)}a_{i,j}. \tag{19}$$

By choosing A to be zero in every entry except $a_{i,j}$ for any $1 \leq i,j \leq n$, we conclude that $c_{\pi(k),\pi(i),\pi(j)} = c_{k,i,j}$ for any such permutation π and any $1 \leq k,i,j \leq n$.

We say that the ordered triples (k,i,j) and (k',i',j') lie within the same equivalence class if a permutation exists with $\pi((k,i,j)) = (k',i',j')$. In fact, the only things that matter are the equality relations between the indexes; this analysis leads to 5 different equivalence classes: $k = i = j$, $k = i \neq j$, $k = j \neq i$, $i = j \neq k$, or $i \neq j \neq k \neq i$. Each ordered triple belongs to one of these five equivalence classes. Thus the game depends on only the 5 constants associated to each of these possibilities. In fact, with a bit of massaging we can write

$$\mathcal{R}_{k,n}(A) = \alpha a_{k,k} + \beta\overline{a_{k,\bullet}} + \gamma\overline{a_{\bullet,k}} + \delta\overline{a_{\bullet,\bullet}} + \epsilon\overline{a_{\bullet,\circ}}, \tag{20}$$

for real numbers α, β, γ, δ, and ϵ which we may calculate in the following manner. Some $a_{i,j}$ with $k \neq i \neq j \neq k$ shows up only in the expression $\overline{a_{\bullet,\circ}}$ and with coefficient $\frac{\epsilon}{n^2}$, so we must take $\epsilon := n^2 c_{k,i,j} = n^2 c_{1,2,3}$. The term $a_{i,i}$ with $k \neq i$ shows up in the last two terms and has total coefficient $\frac{\delta}{n} + \frac{\epsilon}{n^2} = c_{k,i,i} = c_{1,2,2}$ so we define $\delta := n(c_{1,2,2} - c_{1,2,3})$. In this same fashion we may calculate the values $\gamma := n(c_{1,2,1} - c_{1,2,3})$, $\beta := n(c_{1,1,2} - c_{1,2,3})$, and then $\alpha := c_{1,1,1} - c_{1,1,2} - c_{1,2,1} - c_{1,2,2} + 2c_{1,2,3}$ which make equation (20) equivalent to equation (17).

However, from equation (8), we know that the sum of the $\mathcal{R}_k$ must be 0, and thus

$$0 = \sum_{k=1}^{n} \mathcal{R}_{k,n}(A) = n(\alpha + \delta)\overline{a_{\bullet,\bullet}} + n(\beta + \gamma + \epsilon)\overline{a_{\bullet,\circ}}, \tag{21}$$

and since this equation holds for any matrix A, we must have that $0 = \alpha + \delta = \beta + \gamma + \epsilon$. Thus, the condition that strategy k is selected for is

$$\mathcal{R}_{k,n}(A) = \sigma_1^n(a_{k,k} - \overline{a_{\bullet,\bullet}}) + \sigma_2^n(\overline{a_{k,\bullet}} - \overline{a_{\bullet,k}}) + \sigma_3^n(\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}}) > 0, \tag{22}$$

for $\sigma_1^n := \alpha$, $\sigma_2^n := -\gamma$, and $\sigma_3^n := -\epsilon$. These parameters depend on the structure and the dynamics, as well as on the number of strategies, n. Now we need only show that the σ_i^n can be replaced by σ_i which do not depend on n.

Let n and m be positive integers and $A = [a_{i,j}]_{1 \leq i,j \leq n}$ be an $n \times n$ payoff matrix, and consider the $nm \times nm$ matrix $D_m(A) = [d_{i,j}]_{1 \leq i,j \leq nm}$ defined in the statement of property (iii). From property (iii), we have that $x_{k,n}(A) = m x_{(k,i),nm}(D_m(A))$ for all $1 \leq k \leq n$ and $1 \leq i \leq m$, and because $wD_m(A) = D_m(wA)$, we obtain immediately from the definition that $\mathcal{R}_{k,n}(A) = m\mathcal{R}_{(k,i),nm}(D_m(A))$. Note that $a_{k,k} - \overline{a_{\bullet,\bullet}} = d_{k,k} - \overline{d_{\bullet,\bullet}}$, $\overline{a_{k,\bullet}} - \overline{a_{\bullet,k}} = \overline{d_{(k,i),\bullet}} - \overline{d_{\bullet,(k,i)}}$, and $\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}} = \overline{d_{(k,i),\bullet}} - \overline{d_{\bullet,\circ}}$, so we have that

$$0 = \mathcal{R}_{k,n}(A) - m\mathcal{R}_{(k,i),nm}(D) \tag{23}$$

$$= (\sigma_1^n - m\sigma_1^{nm})(a_{k,k} - \overline{a_{\bullet,\bullet}}) + (\sigma_2^n - m\sigma_2^{nm})(\overline{a_{k,\bullet}} - \overline{a_{\bullet,k}}) + (\sigma_3^n - m\sigma_3^{nm})(\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}}). \tag{24}$$

This holds for any $n \times n$ matrix A, so by choosing a few judicious special cases, we may conclude that $\sigma_i^n = m\sigma_i^{nm}$ for $i = 1, 2, 3$. Since this works for any positive integers n and m, switching their positions we also have that $\sigma_i^m = n\sigma_i^{nm}$ and thus $\sigma_i^m = \frac{n}{m}\sigma_i^n$. If we define $\sigma_i := \frac{1}{3}\sigma_i^3$ for each $i = 1, 2, 3$, then we have that

$$n\mathcal{R}_{k,n}(A) = \sigma_1(a_{k,k} - \overline{a_{\bullet,\bullet}}) + \sigma_2(\overline{a_{k,\bullet}} - \overline{a_{\bullet,k}}) + \sigma_3(\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}}). \tag{25}$$

From this it is clear that the inequality (16), which is the condition for strategy k to be selected for, is equivalent to

$$\sigma_1(a_{k,k} - \overline{a_{\bullet,\bullet}}) + \sigma_2(\overline{a_{k,\bullet}} - \overline{a_{\bullet,k}}) + \sigma_3(\overline{a_{k,\bullet}} - \overline{a_{\bullet,\circ}}) > 0. \tag{26}$$

Thus $\sigma_1, \sigma_2, \sigma_3$ with the desired properties do exist, completing the proof.

4 Evolutionary Game Markov chains

The introduction discussed a large number of evolutionary games which have been studied. All these games have a similar feel, but it is very difficult to rigorously define this notion. Evolutionary graph theory is a step in the correct direction, but it does not admit a changing population structure. Even more troublesome is dealing with the multitude of possible update rules which have been previously studied or may be invented in the future. Many papers which prove general statements about evolutionary games assume a single update rule, such as the birth-death process, but note that an analogous proof results in analogous results for other update rules [Fu *et al.* 2009, Taylor *et al.* 2007a, Taylor *et al.* 2007b, Ohtsuki *et al.* 2006, Ohtsuki & Nowak 2006b, Ohtsuki & Nowak 2008, Ohtsuki *et al.* 2007]. Here we rigorously define a class of games known as evolutionary game Markov chains, which contains a large portion of the classical evolutionary games, and show that these games satisfy the conditions necessary in order to apply Theorem 2.

An evolutionary game is a Markov chain, with populations transitioning through different structures and strategies. As we attempt rigorously define this idea, we will make use of the following two guiding concepts.

(1) The effectiveness of a strategy should be determined only by the payoff matrix A. That is, player strategy choices should *only* affect the game through the payoffs they receive from interactions (and only those interactions which actually occur in the game).

(2) As we transition from one state to a new one, individuals are assigned new strategies. These strategies should only come from one of two sources: they should either be inherited from an individual in the old state or be the result of a random mutation which assigns each of the n strategies with equal probability.

The first guideline leads us to clarify exactly what a state of an evolutionary game consists of. Each state S of a Markov chain which is an evolutionary game has two components: (a) a *population structure* s and (b) a *strategy choice function* C assigning each member of the population structure to one of the n possible strategies. It is important to distinguish between these two aspects in order to "protect the privacy" of the each individual's strategy choice. That is, if we want make sure condition (1) is satisfied, then we must be sure to restrict how the game can utilize the information contained in part (b) of a state. As such, for any finite population set $P = \{1, \ldots, N\}$ and positive integer n, we define the set of strategy of functions $\mathbf{C}_{P,n}$ to be the set of all functions $C : \{1, \ldots, N\} \to \{1, \ldots, n\}$. Then, to determine how an $n \times n$ matrix A affects the dynamics of a state with strategy choice function C, we should not use A directly but instead employ the $N \times N$ with entries $a_{C(x),C(y)}$.

From the second guideline we can begin to define how the transition function must be operate. Towards this end, for any finite population $\{1, \ldots, N\}$, we define an *inheritance rule* from the population to itself to be any function $I : \{1, \ldots, N\} \to \{1, \ldots, N, \mu\}$. Such a function associates each member of the new population to the source of its strategy: either inherited from one of the members of the old population or a result of the special mutation event μ. For any finite population set $\{1, \ldots, N\}$, we define $\mathbf{I}_N$ to be the set of all such inheritance functions. When an evolutionary game transitions from one state to the next, the population structure may change freely change, but the strategy choice function C' of the new state must be related to the previous strategy choice function C by such an inheritance function I. Specifically, it must be the case that $C'(x) = C(I(x))$ for all $1 \leq x \leq N$ such that $I(x) \neq \mu$. For any two such $C, C' \in \mathbf{C}_{N,n}$, we define

$$\mathbf{I}_{C,C'} := \{I \in \mathbf{I}_N : I(x) \in C^{-1}(C'(k)) \cup \{\mu\}\}, \tag{27}$$

to be this set of all inheritance functions which could possibly lead from strategy choice function C to strategy choice C'.

Putting these ideas together, we present a rigorous definition of an *evolutionary game Markov chain*, after which we further describe the intuition behind the process.

Definition. *For a* ***population size*** $N \in \mathbb{N}$*, a* ***population structure set*** $\mathcal{S}$*, and an* ***update likelihood function***

$$L : \mathcal{S} \times \mathcal{S} \times \mathbf{I}_N \times \mathbb{R}^{N^2} \to \mathbb{R} \tag{28}$$

such that

$$1 = \sum_{s' \in \mathcal{S}} \sum_{I \in \mathbf{I}_P} L(s, s', I, M) \tag{29}$$

for all $M \in \mathbb{R}^{N^2}$ *and* $s \in \mathcal{S}$*, the triple* $\langle N, \mathcal{S}, L \rangle$ *defines an* ***evolutionary game Markov chain****.*

These parameters then determine the Markov chain by which the game operates for any $n \times n$ *payoff matrix* A *(with entries* $a_{i,j}$*). For any such* A *of dimension* n*, the game is a Markov chain on state space* $\mathbf{S} := \mathcal{S} \times C_{N,n}$*, where the probability of transitioning from state* $S = (s, C) \in \mathbf{S}$ *to state* $S' = (s', C') \in \mathbf{S}$ *is given by*

$$T_{S,S'}(A) := \sum_{I \in \mathbf{I}_{C,C'}} n^{-|I^{-1}(\mu)|} L_s\left(s', I, \bigoplus_{x,y=1}^{N} a_{C(x),C(y)}\right). \tag{30}$$

Though the ultimate transition probability values given by (30) is a bit daunting, the idea behind how one transitions from one state to the next is much simpler. Starting in state S, one chooses a new population structure s' and an inheritance rule I based only on the current population structure s and the payoffs from interactions occurring within the current the population. Equation (29) simply requires that these probabilities sum to 1. The new state then has structure s' and population choice function C' given by $C'(x) = C(I(x))$ unless $I(x) = \mu$ in which case the new strategy is chosen randomly.

Note that a large class of such games, including any example from evolutionary graph theory, have a fixed structure and thus can be defined with only a single element in their population structure set $\mathcal{S}$. In such cases, the definition simplifies dramatically and transitions rely on a single inheritance likelihood function $L : I_N \times \mathbb{R}^{N^2} \to \mathbb{R}$.

As an example, we explicitly define the function L for the standard Moran process on a population of size N with mutation rate u. For $x \in \{1, \ldots, N, \mu\}, y \in \{1, \ldots, N\}$, define the inheritance rule $I_{x,y} \in \mathbf{I}_N$ by $I(y) := x$ and $I(z) := z$ for all $z \neq y$. Note that because there is only one replacement in any time step, inheritance rules of this form are the only ones which occur for the standard Moran process. Then for any $x, y \in \{1, \ldots, N\}$ we have that

$$L\left(I_{x,y}, \bigoplus_{w,z=1}^{N} b_{w,z}\right) := (1-u) \cdot \frac{1}{N} \cdot \frac{1 + \sum_{z=1}^{N} b_{x,z}}{N + \sum_{w,z=1}^{N} b_{w,z}}, \tag{31}$$

and

$$L\left(I_{\mu,y}, \bigoplus_{w,z=1}^{N} b_{w,z}\right) := \frac{u}{N}, \tag{32}$$

with L taking on the value 0 for any $I \in \mathbf{I}_N$ not of this form. For more complicated evolutionary graphs the function L is more complex, and for games with a changing population structure things become even more convoluted. However, it is fairly easy to check that all the specific games presented thus far do fit into this structure in some manner or another.

Note that while in our definition we assume a fixed population size N, there is no particular reason this should be a requirement of such a game. In fact, one could generalize the definition above so that each structure $s \in \mathcal{S}$ had its own associated population size N_s. Transitions would require generalized inheritance functions $I : \{1, \ldots, N_{s'}\} \to \{1, \ldots, N_s, \mu\}$, but only certain inheritance functions would be compatible with certain population structure changes. With enough care, such a generalized definition can be created, but it is substantially more convoluted. Since few, if any, examples of games with variable population size exist within the literature, we restrict ourselves to fixed population size in order to prevent the definition from becoming any more convoluted.

The definition of strategy abundance for an evolutionary game Markov chain is clear when the process has a unique stationary distribution.

Definition. *If an evolutionary game Markov chain $\langle N, \mathcal{S}, L\rangle$ has a unique stationary distribution $[\pi_S(A)]_{S\in\mathbf{S}}$ for each $n \times n$ payoff matrix A, then we may define $x_{k,n}(A)$, the abundance of strategy k, by*

$$x_{k,n}(A) := \frac{1}{N} \sum_{s\in\mathcal{S}} \sum_{C \in \mathbf{C}_{N,n}} \pi_{s,C}(A) |C^{-1}(\{k\})|. \tag{33}$$

With this definition in mind, we may characterize which evolutionary game Markov chains yield abundance functions which satisfy the conditions (i), (ii), and (iii).

Theorem 3. *Let $\langle N, \mathcal{S}, L\rangle$ be an evolutionary game Markov chain with a unique stationary distribution. Then the abundance functions $[x_{k,n}]_{1\le k\le n}$ satisfy property (ii), permutability, and property (iii), divisibility. Further, if the population structure set $\mathcal{S}$ is finite and if the function $L_{s,s',I} : \mathbb{R}^{N^2} \to \mathbb{R}$ defined*

$$L_{s,s',I}(M) = L(s, s', I, M), \tag{34}$$

is differentiable at the zero matrix $M = \mathbf{0} \in \mathbb{R}^{N^2}$ for any fixed values of $s, s' \in \mathcal{S}$ and $I \in \mathbf{I}_N$, then property (i), divisibility, is also satisfied.

As a corollary, we have that Theorem 2 applies to any evolutionary game Markov chain with a unique stationary distribution, finite population structure set $\mathcal{S}$, and differentiable function L. This is convienient, because this is generally more straight-forward to show for any given game than each the three properties seperately. Note that an infinite population structure set $\mathcal{S}$ does not necessarily imply that the game does not satisfy property (i), but simply means that one must be more careful in proving this.

Proof of Theorem 3. The transition functions $T_{(s,C),(s',C')}$ are clearly differentiable functions of the update likelihood functions $L_{s,s',I}$, and because these are differentiable at the zero matrix, the transition functions must be as well. Note also that if $\mathcal{S}$ is finite then so is the state space $\mathbf{S} := \mathcal{S} \times C_{N,n}$. In proving Theorem 1, the paper [Tarnita *et al.* 2009c] proves, in an appendix, that if the transition functions of a Markov process are differentiable functions at a point then the unique stationary distribution probabilities π_S are differentiable functions there as well. Finally, the actual abundance functions are linear combinations of the π_S, and thus they two must be differentiable, proving that such games satisfy property (i).

The fact that property (ii) is satisfied by evolutionary game Markov processes is essentially obvious from the fact that such a process can in no way access the strategy indexes. Specifically we want to show that $x_{k,n}(A) = x_{\pi(k),n}(\pi(A))$ for any $1 \leq k \leq n$, any permutation $\pi : \{1, \ldots, n\} \to \{1, \ldots, n\}$, and $n \times n$ payoff matrix $A = [a_{i,j}]_{1 \leq i,j \leq n}$, where $\pi(A) = [a'_{i,j}]_{1 \leq i,j \leq n}$ with $a'_{i,j} := a_{\pi^{-1}(i),\pi^{-1}(j)}$. Essentially, the state (s, C) of the game under matrix A is equivalent to the state $(s, \pi \circ C)$ under the matrix $\pi(A)$. Specifically, noting that $I_{C,C'} = I_{\pi\circ C,\pi\circ C'}$, it follows from definitions that

$$T_{(s,C),(s',C')}(A) = T_{(s,\pi\circ C),(s',\pi\circ C')}(\pi(A)) \tag{35}$$

for any $(s, C), (s', C') \in \mathbf{S}$ and payoff matrix A. This equivalence between the transition functions of the two Markov processes implies a corresponding equivalence

$$\pi_{(s,C)}(A) = \pi_{(s,\pi\circ C)}(\pi(A)) \tag{36}$$

in the stationary probability distributions. Then, note that if $C' = \pi^{-1} \circ C$ then $C = \pi \circ C'$ and

$$C^{-1}(\{\pi(k)\}) = \{x : C(x) = \pi(k)\} = \{x : \pi(C'(x)) = \pi(x)\} = C'^{-1}(\{k\}), \tag{37}$$

and thus

$$\begin{aligned} x_{\pi(k),n}(\pi(A)) &= \frac{1}{N} \sum_{s\in\mathcal{S}} \sum_{C\in\mathbf{C}_{N,n}} \pi_{(s,C)}(\pi(A))|C^{-1}(\{\pi(k)\})| &(38)\\ &= \frac{1}{N} \sum_{s\in\mathcal{S}} \sum_{C'\in\mathbf{C}_{N,n}} \pi_{(s,\pi\circ C')}|C^{-1}(\{\pi(k)\})| &(39)\\ &= \frac{1}{N} \sum_{s\in\mathcal{S}} \sum_{C'\in\mathbf{C}_{N,n}} \pi_{(s,\pi\circ C')}|C'^{-1}(\{k\})| &(40)\\ &= x_{k,n}(A), &(41) \end{aligned}$$

which completes the proof.

The fact that any evolutionary game Markov process satisfies property (iii), divisibility is almost as intuitive as the fact that it satisfiies property (ii), but the details are a bit messy. Intuitively, if we watch the Markov process as it runs under the operation of payoff matrix $D_m(A)$, but ignore the irrelevant tags $1 \leq i \leq m$ each strategy carries and instead view each strategy as its root strategy from the matrix A, we see that the operation of the Markov process is exactly the same as it would be if running under the payoff matrix A. Thus the abundances of the duplicates of any one strategy should sum to the abundance of that strategy, meaning

$$x_{k,n}(A) = \sum_{i=1}^{m} x_{(k,i),n}(D_m(A)). \tag{42}$$

The fact that $x_{k,n}(A) = mx_{(k,i),n}(D_m(A))$ then follows easily from the fact that the game satisfies property (ii) and thus all of the identitical strategies $\{(k,i) : 1 \leq i \leq m\}$ must have the same abundances.

The rigorous proof in terms of transition probabilities is a bit messy. Essentially, the intuitive idea that larger groups of states of the Markov process on $D_m(A)$ correspond to individual states in the process on A is summarized by the following straight-forward lemma about general Markov processes.

Lemma. *Let $\langle \mathbf{S}, T\rangle$ and $\langle \mathbf{S}', T'\rangle$ be two Markov chains, each with a unique stationary distribution. Let π_S and π'_S, respectively, denote the equilibrium probability distributions for these processes. If $f : \mathbf{S}' \to \mathbf{S}$ is a surjective function such that for all $S_1, S_2 \in \mathbf{S}$ and $S_1' \in f^{-1}(\{S_1\}) \subseteq \mathbf{S}$, we have that*

$$T_{S_1,S_2} = \sum_{S_2' \in f^{-1}(\{S_2\})} T_{S_1',S_2'}, \tag{43}$$

then

$$\pi_S = \sum_{S' \in f^{-1}(\{S\})} \pi'_{S'}, \tag{44}$$

for all $S \in \mathbf{S}$.

Define the function $R : \mathbf{C}_{N,nm} \to \mathbf{C}_{N,n}$ which maps the function $C \in \mathbf{C}_{N,nm}$ to the function $C' := R(C) \in \mathbf{C}_{N,n}$, where $C' \in \mathbf{C}_{N,n}$ is defined so that for whatever values $1 \leq k \leq n$ and $1 \leq i \leq m$ are such that $C(x) = (k,i)$, we have that $C'(x) = k$. Then, in applying our lemma, we wish to use the function $f : \mathcal{S} \times \mathbf{C}_{N,nm} \to \mathcal{S} \times \mathbf{C}_{N,n}$ such that $f((s,C)) := (s, R(C))$. Note that with these definitions we have for any $S = (s,C) \in \mathcal{S} \times \mathbf{C}_{N,n}$, we have that $f^{-1}(S) = \{s\} \times R^{-1}(C) \subseteq \mathcal{S} \times \mathbf{C}_{N,nm}$.

With these definitions, to apply our lemma we need to show that

$$T_{S_1,S_2}(A) = \sum_{S_2' \in f^{-1}(S_2)} T_{S_1',S_2'}(D_m(A)) \tag{45}$$

for all $S_1 = (s_1, C_1), S_2 = (s_2, c_2) \in \mathcal{S} \times \mathbf{C}_{N,n}$ and $S_1' = (s_1, C_1') \in f^{-1}(S_1) \subseteq \{s_1\} \times \mathbf{C}_{N,nm} \subseteq \mathcal{S} \times \mathbf{C}_{N,nm}$. Expanding the right side of this equation yields the expression

$$\sum_{S_2' = (s_2, C_2') \in f^{-1}(S_2')} \sum_{I \in \mathbf{I}_{C_1',C_2'}} (nm)^{-|I^{-1}(\{\mu\})|} L_{s_1}\left(s_2, I, \bigoplus_{x,y=1}^{N} d_{C_1'(x),C_1'(y)}\right). \tag{46}$$

Note that the interior of this summation does not depend on the value of of S_2', and as such, things should simplify if we manage to switch the order of summation. First note that

$$\bigcup_{S_2' \in f^{-1}(S_2)} \mathbf{I}_{C_1',C_2'} \subseteq \mathbf{I}_{C_1,C_2}. \tag{47}$$

Thus, in switching the order of summation our first sum can be over all $I \in \mathbf{I}_{C_1,C_2}$, with the second summation over the set $\{(s_2, C_2') \in f^{-1}(S_2) : I \in I_{C_1',C_2'}\}$. Note that if $I \in I_{C_1',C_2'}$ then we must have that $C_2'(x) = C_1'(I(x))$ for all $x \in \{1, \ldots, N\}$ for which $I(x) \neq \mu$. For $x \in \{1, \ldots, N\}$ for which $I(x) = \mu$, we must have $C_2' \in f^{-1}(S_2)$, so $R(C_2'(x)) = C_2(x)$, meaning that C_2' can assign to

x any one of the m duplicate strategies equivalent to the strategy assigned to x by C_2. Thus we have that

$$|(s, C_2) \in f^{-1}(S_2) : I \in I_{C_1', C_2'}\}| = m^{|I^{-1}(\{\mu\})|}. \tag{48}$$

Since the interior of the summation does not depend upon the specific choice of $S_2' = (s, C_2')$, equation (46) simplifies to

$$\sum_{I \in I_{C_1,C_2}} n^{-|I^{-1}(\{\mu\})|} L_{s_1} \left(s_2, I, \bigoplus_{x,y=1}^{N} d_{C_1'(x),C_1'(y)} \right). \tag{49}$$

By the definition of $D_m(A)$ and the fact that $(s_1, C_1') \in f^{-1}(\{(s_1, C_1)\})$, we have that $d_{C_1'(x),C_1'(y)} = a_{C_1(x),C_1(y)}$. Making this replacement in the equation above yields exactly the definition of $T_{S_1,S_2}(A)$, which proves equation (45). This allows us to apply our lemma and conclude that

$$\pi_{s,C}(A) = \sum_{(s,C') \in f^{-1}(\{(s,C)\})} \pi_{(s,C')}(D_m(A)) = \sum_{C' \in R^{-1}(\{C\})} \pi_{(s,C')}(D_m(A)). \tag{50}$$

for all $(s, C) \in \mathcal{S} \times C_{N,n}$. Since for every $C' \in R^{-1}(C)$ we have that $C'(x) = (C(x), i)$ for some $1 \leq i \leq m$, we have that the abundance of a strategy k in specific state (s, C) is equivalent to the the sum of the abundances of (k, i) over all $1 \leq i \leq m$ for *any* state $(s, C') \in f^{-1}((s, C))$. Thus when we take

$$\sum_{i=1}^{m} \sum_{(s,C') \in f^{-1}((s,C)) = \{s\} \times R^{-1}(C)} \pi_{s,C'}(D_m(A)) |C'^{-1}(\{(k, i)\})| \tag{51}$$

and swith the order of summation, the multiplier on $\pi_{s,C'}(D_m(A)$ is becomes constant and equal to $|C^{-1}(\{k\})|$, so from equation (50) we may conclude that

$$x_{k,n}(A) = \sum_{i=1}^{m} x_{(k,i),n}(D_m(A)). \tag{52}$$

This is equation (42), and we already know that the desired result follows easily from it using property (ii). □

5 Cooperation

One of the most intruiging topics in evolutionary biology is the evolution of cooperation [Trivers 1971, Axelrod & Hamilton 1981, May 1987, Milinski 1987, Nowak & Sigmund 1990, Doebeli & Knowlton 1998, Frank 1988, Bshary *et al.* 2008]. It seems counter-intuitive that competing individuals would evolve altruistic tendencies, yet cooperation pervades biology at every level. Cooperation is most commonly viewed as occurring between organisms, but is it is also essential for life to reach any new level of organization. Cooperation was most likely essential in the formation of now-basic elements of life, such as cells and chromosomes, from even more basic replicators such as proteins or nucleic acids [Maynard Smith & Szathmáry 1997, Jain & Krishna 2001]. The evolution of multicellular organisms from individual cells is also an instance of cooperation [Michod & Roze 2001, Blackstone & Green 1999], and when this cooperation breaks down, with individual cells replicating at the expense of the organism as a whole, the resulting disease is known as cancer. Each time a new level of organization arises through evolution, it is the result of cooperation between lower levels of organization which were formerly competing against each other. In light of this, cooperation has been referred to as the third fundamental principle of evolution, along with mutation and selection [Nowak 2006b].

Evolutionary game theory provides a unique forum in which to study how population structure affects the viability of cooperative strategies. The prototypical cooperative game is known as the prisoner's dilemma, and in its most basic form is given by the payoff matrix

$$\begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \tag{53}$$

with the assumption that $b > c > 0$. The first strategy is known as cooperation C and the second as defection D. The value c represents the cost paid by a player choosing to cooperate, and b is the benefit received by the player who is on the receiving end of this cooperation. Defection strictly dominates cooperation as a strategy, making mutual defection the only Nash equilibrium of the game, yet both players would benefit more from mutual cooperation. Many population structures, such as a well-mixed one, cannot ever select for cooperators under this payoff matrix, regardless of the choices of b and c. As such, the cataloging of different population structures and their capacity to support such cooperative strategies is a subject of much active research [Nowak *et al.* 2004, Ohtsuki *et al.* 2006, Traulsen & Nowak 2006, Ohtsuki & Nowak 2007, Langer *et al.* 2008, Traulsen *et al.* 2009, Antal *et al.* 2009b, Tarnita *et al.* 2009b, Nowak *et al.* 2010]. In this section, we demonstrate some interesting results along these lines which follow naturally from our main result.

One known mechanism for increasing cooperation is called tag-based cooperation or the "green beard effect" [Hamilton 1964a, Hamilton 1964b, Dawkins 1976]. The name derives from imagining a single gene (or multiple, linked genes) simultaneously caused its owner to have a green beard and to show altruistic behavior towards all individuals with green beards. Green beards are so strange that any individual with one would be sure to be a carrier of this gene, and thus all acts of altruism would work to further the survival and spread of the gene itself. More generally, the idea is that by using an arbitrary phenotypic symbol or "tag" in deciding between cooperation and defection, individuals may be able to choose to cooperate more judiciously and profitably. This general concept has been analyzed and proven to be effective in promoting cooperation under numerous implementations and population structures [Riolo *et al.* 2001, Masuda & Ohtsuki 2007, Traulsen & Nowak 2007]. There are many different implementations of this general concept, one of which we described below. Using it we will show that, provided sufficiently specific tags are used, tag-based cooperation can be supported by *any* mutation-selection process on a structured population *with a positive* σ_1 *structure coefficient.* Note that a structure has a positive σ_1 if and only if strategy 1 is favored under weak selection with the payoff matrix

$$\begin{pmatrix} 1 & 0 & 0 \\ 0 & 0 & 1 \\ 0 & 1 & 0, \end{pmatrix} \tag{54}$$

which essentially means that payoffs from self-interactions are more important than those from opponent-interactions.

Imagine that each player, in addition to being either a cooperator C or defector D, has an integer tag valued between 1 and m. This would give us $n := 2m$ strategies $C_1, D_1, \ldots, C_m, D_m$. The idea is that a player can only "see" the opponents tag when deciding which action to take. As such, cooperators cooperate if and only if their opponent shares their tag, and otherwise defect. Defectors still defect at all times. Thus the payoff to strategy X_i in its interaction with strategy

Y_j is

$$a_{X_i,Y_j} := \begin{cases} 0 \text{ if } i \neq j \text{ or } X = Y = D; \\ b - c \text{ if } i = j, X = Y = C; \\ -c \text{ if } i = j, X = C, Y = D; \\ b \text{ if } i = j, X = D, Y = C. \end{cases} \tag{55}$$

Imagine some evolutionary game with structure coefficients σ_1, σ_2, and σ_3. Under the ordinary two-strategy prisoners dilemma given by (53), we have that $a_{C,C} - \overline{a_{\bullet,\bullet}} = \frac{1}{2}(b-c)$, $a_{C,\bullet} - a_{\bullet,C} = -\frac{1}{2}(b+c)$, and $a_{C,\bullet} - \overline{a_{\bullet,\circ}} = -\frac{1}{2}c$. As such, cooperation is favored only if

$$\sigma_1(b-c) - \sigma_2(b+c) - \sigma_3 c > 0. \tag{56}$$

However, the fact that the σ_i are fixed over varying numbers of strategies n allows us to compare this result to the one which uses m tags and the payoffs given by (55). In this case we have that $a_{C_k,C_k} - \overline{a_{\bullet,\bullet}} = \frac{1}{2}(b-c)$, $a_{C_k,\bullet} - a_{\bullet,C} = -\frac{1}{2m}(b+c)$, and $a_{C_k,\bullet} = -\frac{c}{2m}$, so cooperation is selected for if

$$\sigma_1(b-c) - \frac{\sigma_2}{m}(b+c) - \frac{\sigma_3}{m}c > 0. \tag{57}$$

As claimed, for a sufficient number of tags m, the first term dominates the equation and cooperators are selected for as long as $\sigma_1 > 0$.

6 Discussion

6.1 Summary

In Sections 2 and 3 we presented and proved our main result, Theorem 2. This theorem states that for a large class of evolutionary games satisfying certain natural properties, the condition which determines if any strategy k within payoff matrix A is favored in the limit of weak selection can be written as a simple inequality which depends on just three structure coeficients $\sigma_1, \sigma_2, \sigma_3 \in \mathbb{R}$. This generalizes a previous result of [Tarnita *et al.* 2009c] which held for $n = 2$ strategy matrices, and is closely related to several other results within the literature.

Section 4 defines the notion of an *evolutionary game Markov process*, a class into which most ordinary evolutionary games fall within. This rigorously defines a novel and more general class of evolutionary games than currently exists in the literature. We then show that, given certain differentiability requirements, such games satisfy the necessary conditions and fall within the scope of Theorem 2, providing a large, concrete class of examples for this theorem. Finally, in Section 5 we discuss implications Theorem 2 has in the particularly case of the evolution of cooperation.

6.2 Future Directions

The ideas presented thus far provide numerous, specific ideas for future research. The structure coefficient of Theorem 1 has been calculated for many specific evolutionary games. However, the structure coefficients $\sigma_1, \sigma_2, \sigma_3$ are currently only known for the standard Moran process [Antal *et al.* 2009c]. Now that such values are known to exist for all evolutionary games, they should be calculated as well.

In general, for any two-strategy theorems relating to Theorem 1, we should seek generalized n-strategy theorems associated to Theorem 2. One intruiging example of this is in using computer simulations to calculate approximate structure coefficients. Two insightful papers have been published which are concerned with achieving efficient approximations of the structure coefficient σ for specific update rules [Fu *et al.* 2009, Nathanson *et al.* 2009]. Not only should these methods also lead to ways of calculating all three structure coefficients, but we may also be able to use the rigorous definition of evolutionary game Markov chains to increase the number of evolutionary games to which they apply.

In fact, the definition of evolutionary game Markov chains presented in Section 4, may be this papers best jumping off point for future research. The definition is novel in that it is general enough to support diverse population structures and update rules, but rigorous and restrictive enough to retain the intuitive properties desired in such an evolutionary game. Specifically, the idea of an inheritance rule allows us to unify diverse update rules, such as birth-death, death-birth, and Wright-Fisher processes, under one umbrella. Many general results currently in the literature are proven for just one specific update rule, such as the birth-death process, but with a footnote that for other processes an analogous proof works just as well [Fu *et al.* 2009, Taylor *et al.* 2007a, Taylor *et al.* 2007b, Ohtsuki *et al.* 2006, Ohtsuki & Nowak 2006b, Ohtsuki & Nowak 2008, Ohtsuki *et al.* 2007]. In the past, the generality of such results may have been limited more by the lack of a general description capturing the unifying characteristics of such update rules. With this definition in hand, we may may be able to generalize the results provided within these papers to large classes of Evolutionary game Markov chains.

Acknowledgments

The results achieved within this text would not have been possible without the years of advice and guidance provided by my thesis advisor, Martin Nowak, and by many other members of the Program for Evolutionary Dynamics (PED) at Harvard University. Of particular note are Corina Tarnita and Tibor Antal, as many of the results within this manuscript come from work done in conjunction with these individuals. Also, none of these relationships would exist without Erez Lieberman and the Research Opportunities in Mathematical Evolution (ROME) program, through which I got my introduction to the Program for Evolutionary Dynamics. Last, but certainly not least, this research was supported, financially and otherwise, by my loving parents Michael Wage and Kathy Vogel.

Appendix - Markov Chains

A stochastic process is a sequence of random variables $X_0, X_1, \dots$ indexed by the natural numbers and taking values in some *state space* $\mathbf{S}$, which is a finite or countable set. Such a process is a *Markov chain* if it is memoryless, meaning the probability it takes on future states is conditional only upon the present state. More formally we require that

$$\mathbb{P}[X_t = x_t | X_{t-1} = x_{t-1}] = \mathbb{P}[X_t = x_t | X_{t-1} = x_{t-1}, X_{t-2} = x_{t-2}, \dots, X_1 = x_1] \tag{58}$$

for any $t \in \mathbb{N}$ and $x_1, \dots, x_t \in \mathbf{S}$. In this paper we are concerned only with time-homogeneous Markov chains, which have the additional property that the specific time t is irrelevant to the transition probabilities, meaning

$$\mathbb{P}[X_{t+2} = x | X_{t+1} = y] = \mathbb{P}[X_{t+1} = x | X_t = y] \tag{59}$$

for any $t \in \mathbb{N}$ and $x, y \in S$. Such a process is completely described by transition probabilities

$$T_{S,S'} := \mathbb{P}[X_1 = S' : X_0 = S] \tag{60}$$

defined for all $S, S' \in \mathbf{S}$. We can further define the values

$$T^{(n)}_{S,S'} := \mathbb{P}[X_n = S' : X_0 = S], \tag{61}$$

denoting the probability that S' is the state of the system n time steps after being in state S.

State S' is said to be *accessible* from state S if there exists an integer $n \in \mathbb{N}$ such that $T^{(n)}_{S,S'} > 0$, meaning that there is positive probability a system in state S will eventually reach state S'. A Markov chain is called *irreducible* if every state is accessible from every other.

For any state S we can define a random variable, known as the *hitting time*, H_S by

$$H_S := \inf\{n \geq 1 : X_n = S | X_0 = S\}. \tag{62}$$

This represents the first time the process returns to state n. If the expected hitting time $M_S := \mathbf{E}[H_S]$ is finite, then the state S is called *positive recurrent.*

A vector of probabilities $[\pi_S]_{S \in \mathbf{S}}$ is called a *stationary distribution* of the Markov chain if

$$\pi_S = \sum_{S' \in \mathbf{S}} \pi_{S'} T_{S',S} \tag{63}$$

for all $S \in \mathbf{S}$. An irreducible Markov chain has a stationary distribution if and only if all of its states are positive recurrent, and in this case the distribution is unique and given by $\pi_S = M_S^{-1}$.

References

[Antal *et al.* 2009a] Antal T, MA Nowak, A Traulsen (2009a). Strategy abundance in 2x2 games for arbitrary mutation rates. *J Theor Biol* 257: 340-344.

[Antal *et al.* 2009b] Antal T, H Ohtsuki, J Wakeley, PD Taylor, MA Nowak (2009b). Evolution of cooperation by phenotypic similarity. *P Natl Acad Sci USA* 106: 8597-8600.

[Antal *et al.* 2009c] Antal T, A Traulsen, H Ohtsuki, CE Tarnita, MA Nowak (2009c). Mutationselection equilibrium in games with multiple strategies. *J Theor Biol* 258: 614-622.

[Axelrod & Hamilton 1981] Axelrod R, WD Hamilton (1981). The evolution of cooperation. *Science* 211: 13901396.

[Blackstone & Green 1999] Blackstone NW, DR Green (1999). The evolution of a mechanism of cell suicide. *Bioessays* 21: 84-88.

[Bshary *et al.* 2008] Bshary R, A Grutter, A Willener, O Leimar (2008). Pairs of cooperating cleaner fish provide better service quality than singletons. *Nature* 455: 964967.

[Darwin 1859] Darwin C (1859). *On the origin of species.* London: J Murray.

[Dawkins 1976] Dawkins R (1976). *The Selfish Gene.* Oxford University Press, Oxford.

[Doebeli & Knowlton 1998] Doebeli M, N Knowlton (1998). The evolution of interspecific mutualisms. *P Natl Acad Sci USA* 95: 86768680.

[Frank 1988] Frank SA (1998). *Foundations of social evolution.* Princeton, NJ: Princeton University Press.

[Fu *et al.* 2009] Fu F, L Wang, MA Nowak, C Hauert (2009). Evolutionary dynamics on graphs: Efficient method for weak selection. *Phys Rev E* 79: 046707.

[Fudenberg *et al.* 2006] Fudenberg D, MA Nowak, C Taylor, LA Imhof (2006). Evolutionary game dynamics in finite populations with strong selection and weak mutation. *Theor Popul Biol* 70: 352-363.

[Hamilton 1964a] Hamilton WD (1964a). The genetical evolution of social behaviour I. *J Theor Biol* 7(1): 116.

[Hamilton 1964b] Hamilton WD (1964b). The genetical evolution of social behaviour II. *J Theor Biol* 7(1): 1752.

[Hauert *et al.* 2002] Hauert C, S De Monte, J Hofbauer, K Sigmund (2002). Volunteering as Red Queen Mechanism for Cooperation in Public Goods Games. *Science* 296: 1129-1132.

[Hofbauer *et al.* 1979] Hofbauer J, P Schuster, K Sigmund (1979). A note on evolutionary stable strategies and game dynamics. *J Theor Biol* 81: 609-612.

[Hofbauer & Sigmund 1988] Hofbauer J, K Sigmund (1988). *The theory of evolution and dynamical systems.* Cambridge, UK: Cambridge University Press.

[Jain & Krishna 2001] Jain S, S Krishna (2001). A model for the emergence of cooperation, interdependence, and structure in evolving networks. *P Natl Acad Sci USA* 98: 543-547.

[Langer *et al.* 2008] Langer P, MA Nowak, C Hauert (2008). Spatial invasion of cooperation. *J Theor Biol* 250: 634-641.

[Lieberman *et al.* 2005] Lieberman E, C Hauert, MA Nowak (2005). Evolutionary dynamics on graphs. *Nature* 433: 312-316.

[Markov 1906] Markov AA (1906). Rasprostranenie zakona bol'shih chisel na velichiny, zavisyaschie drug ot druga. *Izvestiya Fiziko-matematicheskogo obschestva pri Kazanskom universitete, 2-ya seriya* 1: 135156.

[Masuda & Ohtsuki 2007] Masuda N, H Ohtsuki (2007). Tag-based indirect reciprocity by incomplete social information. *Proc R Soc B* 274: 689-695.

[May 1987] May RM (1987). More evolution of cooperation. *Nature* 327: 1517.

[Maynard Smith 1982] Maynard Smith J (1982). *Evolution and the theory of games.* Cambridge: Cambridge University Press.

[Maynard Smith & Szathmáry 1997] Maynard Smith J, E Szathmáry (1997). *The major transitions in evolution.* New York: Oxford University Press.

[Meyn & Tweedie 1993] Meyn SP, RL Tweedie (1993). *Markov Chains and Stochastic Stability.* London: Springer-Verlag.

[Michod & Roze 2001] Michod RE, D Roze (2001). Cooperation and conflict in the evolution of multicellularity *Heredity* 86: 1-7.

[Milinski 1987] Milinski M (1987). Tit for tat in sticklebacks and the evolution of cooperation. *Nature* 325: 433435.

[Moran 1962] Moran PAP (1962). *The Statistical Processes of Evolutionary Theory.* Oxford: Clarendon Press.

[Nathanson *et al.* 2009] Nathanson CG, CE Tarnita, MA Nowak (2009). Calculating evolutionary dynamics in structured populations. *PLoS Comput Biol* 5: e1000615.

[Nowak 2006a] Nowak MA (2006a). *Evolutionary Dynamics.* Cambridge, MA: Harvard University Press.

[Nowak 2006b] Nowak MA (2006b). Five rules for the evolution of cooperation. *Science* 314: 1560-1563.

[Nowak *et al.* 2004] Nowak MA, A Sasaki, C Taylor, D Fudenberg (2004). Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428: 646-650.

[Nowak & Sigmund 1990] Nowak MA, K Sigmund (1990). The evolution of stochastic strategies in the prisoner's dilemma. *Acta Appl Math* 20: 247-265.

[Nowak *et al.* 2010] Nowak MA, CE Tarnita, T Antal (2010). Evolutionary dynamics in structured populations. *Phil Trans R Soc B* 365: 19-30.

[Ohtsuki *et al.* 2007] Ohtsuki H, P Bordalo, MA Nowak (2007). The one third law of evolutionary dynamics. *J Theor Biol* 249: 289-295.

[Ohtsuki *et al.* 2006] Ohtsuki H, C Hauert, E Lieberman, MA Nowak (2006). A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441: 502-505.

[Ohtsuki & Nowak 2006a] Ohtsuki H, MA Nowak (2006a). Evolutionary games on cycles. *Proc R Soc B* 273: 2249-2256.

[Ohtsuki & Nowak 2006b] Ohtsuki H, MA Nowak (2006b). The replicator equation on graphs. *J Theor Biol* 243: 86-97.

[Ohtsuki & Nowak 2007] Ohtsuki H, MA Nowak (2007). Direct reciprocity on graphs. *J Theor Biol* 247: 462-470.

[Ohtsuki & Nowak 2008] Ohtsuki H, MA Nowak (2008). Evolutionary stability on graphs. *J Theor Biol* 251: 698-707.

[Ohtsuki *et al.* 2007a] Ohtsuki H, MA Nowak, JM Pacheco (2007a). Breaking the symmetry between interaction and replacement in evolutionary dynamics on graphs. *Phys Rev Lett* 98: 108106.

[Ohtsuki *et al.* 2007b] Ohtsuki H, JM Pacheco, MA Nowak (2007b). Evolutionary graph theory: Breaking the symmetry between interaction and replacement. *J Theor Biol* 246: 681-694.

[Riolo *et al.* 2001] Riolo R, M Cohen, R Axelrod (2001). Evolution of cooperation without reciprocity. *Nature* 414: 441-443.

[Tarnita *et al.* 2009a] Tarnita CE, T Antal, MA Nowak (2009a). Mutation-selection equilibrium in games with mixed strategies. *J Theor Biol* 261: 50-57.

[Tarnita *et al.* 2009b] Tarnita CE, T Antal, H Ohtsuki, MA Nowak (2009b). Evolutionary dynamics in set structured populations. *P Natl Acad Sci USA* 106: 8601-8604.

[Tarnita *et al.* 2009c] Tarnita CE, H Ohtsuki,T Antal, F Fu, MA Nowak (2009c). Strategy selection in structured populations. *J Theor Biol* 259: 570-581.

[Taylor *et al.* 2004] Taylor C, D Fudenberg, A Sasaki, MA Nowak (2004). Evolutionary game dynamics in finite populations. *B Math Biol* 66: 1621-1644.

[Taylor *et al.* 2007a] Taylor PD, T Day, G Wild (2007a). Evolution of cooperation in a finite homogeneous graph. *Nature* 447: 469-472.

[Taylor *et al.* 2007b] Taylor PD, T Day, G Wild (2007b). From inclusive fitness to fixation probability in homogeneous structured populations. *J Theor Biol* 249: 101-110.

[Taylor & Jonker 1978] Taylor PD, LB Jonker (1978). Evolutionary stable strategies and game dynamics. *Math Biosci* 40: 145-156.

[Traulsen *et al.* 2009] Traulsen A, C Hauert, H Brandt De Silva, MA Nowak, K Sigmund (2009). Exploration dynamics in evolutionary games. *P Natl Acad Sci USA* 106: 709-712.

[Traulsen & Nowak 2006] Traulsen A, MA Nowak (2006). Evolution of cooperation by multilevel selection. *P Natl Acad Sci USA* 103: 10952-10955.

[Traulsen & Nowak 2007] Traulsen A, MA Nowak (2007). Chromodynamics of cooperation in finite populations. *PLoS ONE* 2: e270.

[Traulsen *et al.* 2008] Traulsen A, N Shoresh, MA Nowak (2008). Analytical results for individual and group selection of any intensity. *B Math Biol* 70: 1410-1424.

[Trivers 1971] Trivers RL (1971). The evolution of reciprocal altruism. *Q Rev Biol* 46: 3557.

[Zeeman 1980] Zeeman EC (1980). Population dynamics from game theory. In ZH Nitecki and RC Robinson, eds., *Global theory of dynamical systems: Proceedings of an international conference held at Northwestern University, Evanston, Illinois, June 18-22, 1979*, Lecture Notes in Mathematics, vol. 819. Berlin: Springer-Verlag.