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Dynamic Properties of Evolutionary Multi-player Games in Finite Populations

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Abstract: William D. Hamilton famously stated that “human life is a many person game and not just a disjointed collection of two person games”. However, most of the theoretical results in evolutionary game theory have been developed for two player games. In spite of a multitude of examples ranging from humans to bacteria, multi-player games have received less attention than pairwise games due to their inherent complexity. Such complexities arise from the fact that group interactions cannot always be considered as a sum of multiple pairwise interactions. Mathematically, multi-player games provide a natural way to introduce non-linear, polynomial fitness functions into evolutionary game theory, whereas pairwise games lead to linear fitness functions. Similarly, studying finite populations is a natural way of introducing intrinsic stochasticity into population dynamics. While these topics have been dealt with individually, few have addressed the combination of finite populations and multi-player games so far. We are investigating the dynamical properties of evolutionary multi-player games in finite populations. Properties of the fixation probability and fixation time, which are relevant for rare mutations, are addressed in well mixed populations. For more frequent mutations, the average abundance is investigated in well mixed as well as in structured populations. While the fixation properties are generalizations of the results from two player scenarios, addressing the average abundance in multi-player games gives rise to novel outcomes not possible in pairwise games.

Keywords: multi-player games; finite population; fixation probability; fixation time; average abundance

1. Introduction

The analysis of stochastic evolutionary game dynamics has rapidly developed in the past decade [1–10]. Here, we are interested in two particular aspects: intrinsic stochastic effects induced by finite population size and nonlinearities in payoff induced by multi-player interaction. Finite population analysis in evolutionary game dynamics has the potential to challenge and extend the traditional predictions based on infinitely large populations [1,11]. For a game in an infinite large population, evolutionary outcomes are characterized by the equilibrium states of the system and their stability [12]. However, when we consider the evolutionary process in a finite population, it is important to investigate the stochastic properties of the system, such as fixation probability, fixation time and average abundance in mutation-selection equilibrium. In a multi-player game, an individual obtains its payoff from interactions with more than one co-player. Compared with pairwise games (or matrix games), this generalization depicts more complex scenarios relevant to biological and social situations [13–18]. For example, in the yeast *Saccharomyces cerevisiae*, strains with gene *SUC2* secrete an enzyme called invertase, which catalyses the hydrolysis of sucrose into glucose and fructose. These can then be transported inside the cells of yeast [19]. The strains with gene *suc2*, however, do not secrete invertase. Instead, they just take in the products hydrolysed by the *SUC2* strain. In this case, the *SUC2* gene has been referred to as a cooperator, and the *suc2* has been referred to as a defector. Due to the viscosity or the limited dispersal of the nutrients, the interactions often involve more than two cells, thus it can be referred as a multiple player game. While some authors have argued that the dynamics of the interaction of these two strains can then be captured by a snow drift game [20,21], it is not clear if this situation is a social dilemma at all, since the maximum population payoff occurs for a mixture of the two types [22]. In general, for multiple player games, the payoff is determined by the probability of a specific configuration of the players. This probability is a nonlinear function of the population composition and thus makes the fitness nonlinear. Therefore, multi-player games provide a natural framework for exploring nonlinear effects. For example, when there are only two strategies *A* and *B* in a *d*-player game where orderings of players do not matter, the payoff structure in a multi-player game is a simple table,

$$\begin{array}{c}
 \hline \hline
 \text{Opposing A players } d-1 \quad d-2 \quad \dots \quad k \quad \dots \quad 0 \\
 \hline
 \begin{array}{cccccc}
 A & a_{d-1} & a_{d-2} & \dots & a_k & \dots & a_0 \\
 B & b_{d-1} & b_{d-2} & \dots & b_k & \dots & b_0
 \end{array} \\
 \hline \hline
 \end{array}
 , \tag{1}$$

where a_k and b_k refer to the payoffs for a strategy *A* and *B* individual. If we are interested in calculating the average payoff of a focal individual with a certain strategy, then we need to choose $d - 1$ other co-players to make up a *d*-player game. Out of the $d - 1$ other players, some can have strategy *A* while others have strategy *B*. The index *k* refers to the number of *A* co-players in the group. In a finite population of size *N* with *i* individuals of type *A*, the probability for a focal individual of type *A* to

choose a co-player group that consists of k A players and $d-1-k$ B players is given by a hypergeometric distribution. The probability that an A player interacts with k other A players is given by

$$H(k, d; i, N) = \frac{\binom{i-1}{k} \binom{N-i}{d-1-k}}{\binom{N-1}{d-1}}, \tag{2}$$

which can be approximated by a binomial distribution when the population size N is large. The hypergeometric sampling leads to the average payoffs,

$$\begin{aligned} \pi_A &= \sum_{k=0}^{d-1} H(k, d; i, N) a_k \\ \pi_B &= \sum_{k=0}^{d-1} H(k, d; i+1, N) b_k. \end{aligned} \tag{3}$$

Since this is valid for the average payoffs, the relation between d and N is not an issue, as long as $d \leq N$. If we would consider only a single interaction instead, one has to ensure that every individual is taking part in an interaction [23]. Note that $H(k, d; i, N)$ is a polynomial of degree $d-1$ in i . The average payoff of each strategy is thus also a polynomial of degree $d-1$. For $d = 2$, that is a pairwise interaction, the payoffs are linear in the number of strategy A players in the population. For a multi-player game, *i.e.*, $d > 2$, the payoffs are nonlinear, but remain polynomials. Such nonlinearities mimic the interaction pattern among individuals, like the public goods, for example, the invertase produced by the cooperator yeast in the above example is a saturating function of cooperators' concentration. Dynamical properties of such multi-player games in infinitely large populations have been previously addressed [24–26] and we focus on their finite population version.

Both mutation and selection are fundamental in evolutionary theory. Mutations have the potential to generate distinct genotypes and phenotypes while selection acts upon those diverse phenotypes. The Moran process with mutations is employed to mimic this evolutionary process. In addition, intrinsic random drift is present in this process [1,27]. An individual is chosen with a probability proportional to its fitness for birth and another randomly selected individual is chosen for death. Mutations can occur during birth with probability μ . For two strategies A and B , this is a one-dimensional birth–death process with the transition probabilities T_i^\pm from i A individuals to $i \pm 1$ A individuals,

$$\begin{aligned} T_i^+ &= \frac{if_A}{if_A + (N-i)f_B} \frac{N-i}{N} (1-\mu) + \frac{N-i}{N} \mu \\ T_i^- &= \frac{(N-i)f_B}{if_A + (N-i)f_B} \frac{i}{N} (1-\mu) + \frac{i}{N} \mu. \end{aligned} \tag{4}$$

The probability to remain in the same state is $1 - T_j^+ - T_j^-$. Fitness has to be an increasing function of payoff [28]. We define the fitness of a strategy S as $f_S = \exp[w\pi_S]$ [29]. We follow the usual assumption that mutations only switch between the pre-existing strategies but do not generate an entirely novel strategy; for such a model we refer to [30–32]. The non-negative parameter w measures the intensity of selection [33]. For $w \ll 1$, selection is weak and the game has a very small effect on the fitness of the strategies, whereas for $w \gg 1$, selection is strong and only the fitter type reproduces and survives. The choice of $f_S = \exp[w\pi_S]$ has the convenient property to recover the usual results valid for

weak selection, and to allow for arbitrary limit. Besides, such an exponential fitness can sometimes also be biologically relevant [34,35].

When the probability of mutation is sufficiently small [4], the waiting time for a mutation to occur is much longer than the time required for the mutant type to fixate or go extinct [7,10]. To quantify the evolutionary fate of the mutant type, it is thus important to address the probability of fixation of a single mutant. Furthermore, if this happens, then how long does it take, *i.e.* what is the conditional fixation time?

The fixation probability has been used to define evolutionary stability in finite population [1,36,37]. It has been proposed that a strategy is evolutionary stable in a finite population if in addition to the usual requirements of evolutionary stability, the fixation probability of an invading mutant is smaller than the neutral fixation probability. One of the most interesting results arising from this definition is the one-third rule. For a coordination game, a 2×2 game with an unstable internal equilibrium, the fixation probability of a mutant strategy is larger than that in the neutral case ($1/N$) if the attraction basin of the wild type strategy in replicator dynamics is smaller than one third. This result has been proved to be robust for a wide class of evolutionary processes [28,36–38]. The one third rule has also been extended to multi-player games [39,40] and has been proven to be valid for all processes in the domain of Kingman's coalescence even in its generalized, multi-player form [41]. Yet, the one third rule as well as its extensions are only based on weak selection. It is not yet clear how the fixation probability changes with increasing selection intensity.

Fixation times can be interesting to analyse, *e.g.*, the fixation probability can tell us that a strategy can fix with a probability greater than neutral, but it can take longer for fixation to occur. This seemingly unintuitive property of the conditional fixation time has been termed as stochastic slowdown [42,43]. It was shown that a mutant with a slight frequency dependent advantage can take longer to fixation than a neutral mutant. How does the fixation time change with the number of players under weak selection? Do we observe stochastic slowdown for multi-player games as well? If so, is this effect enhanced or inhibited with the increase of the number of players involved in the game? While multi-player games naturally convey nonlinearity to the evolutionary dynamics, weak selection reduces the differences in the fitnesses of the strategies bringing the dynamics close to neutrality. What is the interplay between these two effects?

For intermediate mutation probabilities, mutations can occur while the previous mutant still has an intermediate abundance in the population. In this case, considering extinction or fixation does not make sense as mutations keep the population polymorphic. The system can be characterized by the abundances of the strategies in the long run. These average abundances can give a measure of how favored a strategy is in the selection mutation equilibrium. For 2×2 games, for a given population structure and evolutionary dynamics with mutation, a single parameter condition is obtained to determine which strategy is more abundant than in the neutral case under weak selection [44]. For general $n \times n$ games, a two-parameter condition is obtained [45]. These parameters do not depend on the number of strategies or the payoff matrix, but only on the particular process under study. But how many such parameters are necessary for multi-player games?

Motivated by these questions, we investigate the fixation probability, the conditional fixation time and average abundance in multi-player games. For the fixation probability, we concentrate on how the

fixation probability changes with increasing selection intensity. For the conditional fixation time, we address the so-called stochastic slowdown effect [42,43]. For the average abundance, we generalize the so-called σ rule [45].

2. Fixation

For sufficiently small mutation probabilities, the time of fixation or extinction is much shorter than the average time between two consecutive mutants. In this case, the transition probabilities are given by Equation (4) with zero mutation probability, $\mu = 0$.

2.1. Fixation Probability

If there are i individuals of type A in a population of size N initially, the probability that the whole population will eventually consist only of A individuals is given by [46,47],

$$\rho_i^A = \frac{1 + \sum_{k=1}^{i-1} \prod_{l=1}^k \frac{T_l^-}{T_l^+}}{1 + \sum_{k=1}^{N-1} \prod_{l=1}^k \frac{T_l^-}{T_l^+}}, \tag{5}$$

where in our case the ratio of transition probabilities is

$$\frac{T_l^-}{T_l^+} = \frac{f_B}{f_A} = e^{-w\Delta\pi(l)}, \tag{6}$$

with $\Delta\pi(l) = \pi_A - \pi_B$.

The concept of evolutionary stability in finite populations by using the fixation probability was proposed in [1]. A condition for evaluating the stability of strategy A in a finite population is $\rho_1^B(w) < 1/N$. For small selection intensity, this condition leads to the one third rule, which has been derived to capture evolutionary stability. For strong selection intensity, this concept is consistent with the conventional evolutionary stability [37]. Yet, few authors have considered intermediate selection intensity. Here we are addressing the shape of the fixation probability through the whole range of the selection intensity ($w > 0$). In particular, we are addressing how many maxima and minima there are at most for a d -player game.

Theorem 1. *For a d -player, two strategy game and for the Moran process with the exponential fitness mapping, the fixation probability as a function of the selection intensity can only be monotonically increasing or decreasing, or have a single maximum.*

Proof. By Equation (5), the fixation probability of a mutant taking over the whole population is

$$\rho_1^A(w) = \frac{1}{1 + \sum_{k=1}^{N-1} e^{-w(\sum_{i=1}^k \Delta\pi_i)}}. \tag{7}$$

Thus, the number of the maxima and minima of $\rho_1^A(w)$ is determined by the number of the positive roots of the equation $\rho_1^A(w) = 0$. This derivative can be written as

$$\rho_1^A(w) = (\rho_1^A(w))^2 \underbrace{\sum_{k=1}^{N-1} \left(\sum_{i=1}^k \Delta\pi_i \right)}_{P(w)} e^{-w(\sum_{i=1}^k \Delta\pi_i)}. \tag{8}$$

Now, $\rho_1^A(w) = 0$ is equivalent to $P(w) = 0$ due to the fact that $\rho_1^A(w) > 0$ for all $w < \infty$. We take the derivative of $P(w)$ with respect to w ,

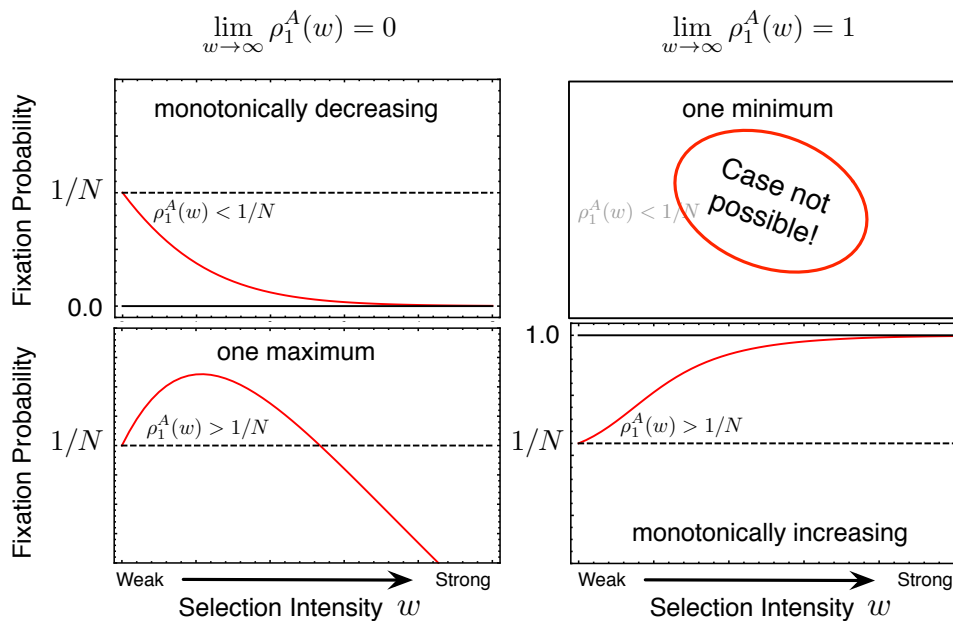
$$P'(w) = - \sum_{k=1}^{N-1} \left(\sum_{i=1}^k \Delta\pi_i \right)^2 e^{-w(\sum_{i=1}^k \Delta\pi_i)}. \tag{9}$$

$P'(w)$ is never positive. It is zero if the payoff difference fulfills $\sum_{i=1}^k \Delta\pi_i = 0$ for all $1 \leq k \leq N - 1$ and negative in all other cases. In other words, $P(w)$ is always non-increasing. Hence the equation $P(w) = 0$, or, equivalently, $\rho_1^A(w) = 0$, has at most one solution. This implies that the fixation probability as a function of selection intensity can be either monotonically increasing or decreasing or have a single extremum. However, it turns out that $\rho_1^A(w)$ cannot have a minimum, since this assumption leads to a contradiction: If there exists a two player game such that $\rho_1^A(w)$ has a minimum, then it is necessary that both $\rho_1^A(0) < 0$ and $\lim_{w \rightarrow \infty} \rho_1^A(w) = 1$ hold (Figure 1 top right). Yet, if $\lim_{w \rightarrow \infty} \rho_1^A(w) = 1$, by Equation (7), we have $\sum_{i=1}^k \Delta\pi_i > 0$ for all $1 \leq k \leq N - 1$. Then, from Equation (8), we have at $w = 0$, $\rho_1^A(0) = (\rho_1^A(0))^2 \sum_{k=1}^{N-1} \left(\sum_{i=1}^k \Delta\pi_i \right) > 0$. This is a contradiction to $\rho_1^A(0) < 0$. Thus, the fixation probability as a function of selection intensity can only increase or decrease monotonically or have a single maximum. Note that this result holds also for any two player games and proves that the extremum discussed in [1] can only be a maximum. \square

Corollary. For a two strategy d -player game, if there is $w^* > 0$ such that $\rho_1^A(w^*) > 1/N$, then the set of the selection intensities that makes $\rho_1(w) > 1/N$ is an interval.

Employing the corollary, given two selection intensities w_1 and w_2 ($w_1 > w_2$), if $\rho_1^A(w_1) > \rho_1^A(w_2) > 1/N$, then $\rho_1^A(w) > 1/N$ for all intensities of selection w fulfilling $w_1 < w < w_2$. For frequency independent fitness, the fixation probability of a mutant is $\phi(r) = (1 - (1/r))/(1 - (1/r)^{N-1})$, where $r > 0$ is the relative fitness of the mutant strategy compared with the wild strategy. In population genetics, $s = r - 1$ is often termed as selection intensity [48]. Notice that $\phi(r)$ is an increasing function of r , the set such that $\phi(r) > 1/N$ is $(1, +\infty)$, an interval. Therefore in terms of the selection intensity s , it is still an interval. For the frequency dependent case, such as the most simple 2×2 games, it has been shown that there can be one hump in the fixation probability with the selection intensity via numerical methods [1]. This also suggests that the set $\{w > 0 | \rho_1^A(w) > 1/N\}$ is also an interval. This corollary shows that this is universal for general multi-player games.

Figure 1. Illustrations of possible shapes of the fixation probability as a function of the selection intensity. Based on Theorem 1, we illustrate the qualitative shape of the fixation probability as a function of the selection intensity, given that the strong and weak selection scenarios are known. Under weak selection, the fixation probability of strategy A can be less than neutral (top row) or greater than neutral (bottom row). Simultaneously, in the limit of strong selection, the fixation probability can approach zero (left column) or unity (right column). We show that the top right case, *i.e.*, the fixation probability being less than neutrality under weak selection and approaching unity for strong selection, is not possible (Theorem 1). This means that an unfavorable strategy under strong selection can be selected for under weak selection (bottom left), but a favorable strategy under strong selection will never be unfavorable for any intensity of selection (top right).



2.2. Fixation Time

Under the assumption of small mutation probabilities, the time until a single mutant A reaches fixation (conditional fixation time) can be written as [7,47,49],

$$\tau_1^A = \sum_{p=1}^{N-1} \sum_{l=1}^p \frac{\rho_l^A}{T_l^+} \prod_{m=l+1}^p \frac{T_m^-}{T_m^+}. \tag{10}$$

For the conditional fixation time in the neutral case, $\tau_1^A|_{w=0}$, we have $\rho_l^A = l/N$, $T_l^+ = l(N-l)/N^2$, and $T_m^-/T_m^+ = 1$. Inserting these expressions into Equation (10) results in $\tau_1^A|_{w=0} = \sum_{p=1}^{N-1} \sum_{l=1}^p N/(N-l)$. With the identity $\sum_{p=1}^{N-1} \sum_{l=1}^p = \sum_{l=1}^{N-1} \sum_{p=l}^{N-1}$ [50], we obtain $\tau_1^A|_{w=0} = N(N-1)$ [51,52].

For weak selection, we can formally write down the series expansion of the conditional fixation time to the first order,

$$\tau_1^A \approx [\tau_1^A]_{w=0} + w \left[\frac{\partial}{\partial w} \tau_1^A \right]_{w=0}, \tag{11}$$

where the constant term is the neutral term calculated above. It has been shown that the conditional fixation time of a single mutant of either type is the same, $\tau_1^A = \tau_{N-1}^B$ [7,53,54]. This identity holds for any birth–death process, and is thus valid for any two strategy games and for any selection intensity. Since τ_1^A and τ_{N-1}^B are identical up to any order in w , we obtain

$$\left[\frac{\partial}{\partial w} \tau_1^A \right]_{w=0} = \left[\frac{\partial}{\partial w} \tau_{N-1}^B \right]_{w=0}. \tag{12}$$

By Equation (10), the first order term in Equation (11) reads

$$\frac{\partial}{\partial w} \tau_1^A = \sum_{|\alpha|=1} \sum_{p=1}^{N-1} \sum_{l=1}^p h_\alpha, \tag{13}$$

$$h_\alpha = \left(\frac{\partial^{\alpha_1}}{\partial w^{\alpha_1}} \frac{1}{T_1^+} \right) \left(\frac{\partial^{\alpha_2}}{\partial w^{\alpha_2}} \phi_l \right) \left(\frac{\partial^{\alpha_3}}{\partial w^{\alpha_3}} \prod_{m=l+1}^p \frac{T_m^-}{T_m^+} \right), \tag{14}$$

with the multi-index $\alpha = (\alpha_1, \alpha_2, \alpha_3)$, $|\alpha| = \alpha_1 + \alpha_2 + \alpha_3$ with $\alpha_i \geq 0$. For each above α , h_α is linear in the payoff entries. In other words, h_α is in the form of $\sum_{k=0}^{d-1} G_k^\alpha a_k + \sum_{k=0}^{d-1} F_k^\alpha b_k$, where G_k^α and F_k^α do not depend on the payoff entries. Therefore, by Equation (13), the first order expansion of the conditional fixation time is of the form $\sum_{k=0}^{d-1} G_k a_k + \sum_{k=0}^{d-1} F_k b_k$, where G_k and F_k are only dependent on the population size N and the group size of the game d , while they have no relationship with the payoff entries. By the symmetry property, Equation (12), the first order expansion of the fixation time is invariant under the payoff matrix transformation $A \leftrightarrow B$. In other words, the conditional fixation time of a single strategy A individual in the game given by Equation (1) is identical with that of a single strategy B individual in a game with the transformed payoff matrix

Opposing B players	$d - 1$	$d - 2$	\dots	k	\dots	0
B	b_0	b_1	\dots	b_k	\dots	b_{d-1}
A	a_0	a_1	\dots	a_k	\dots	a_{d-1}

Thus, we have

$$\sum_{k=0}^{d-1} G_k a_k + \sum_{k=0}^{d-1} F_k b_k = \sum_{k=0}^{d-1} G_k b_{d-1-k} + \sum_{k=0}^{d-1} F_k a_{d-1-k} \tag{16}$$

for arbitrary a_k and b_k . This expression holds for any game, but the G_k and F_k are independent of the game. Thus, we can calculate them for an arbitrary special case. In particular, for the game with payoffs $a_i = \delta_{i0}$ and $b_i = 0$, where δ_{ij} is the Kronecker delta, Equation (16) yields $G_0 = F_{d-1}$. Similarly, we obtain

$$G_k = F_{d-1-k}, \quad 0 \leq k \leq d - 1. \tag{17}$$

Thus, the first order expansion of the conditional fixation time is in the form

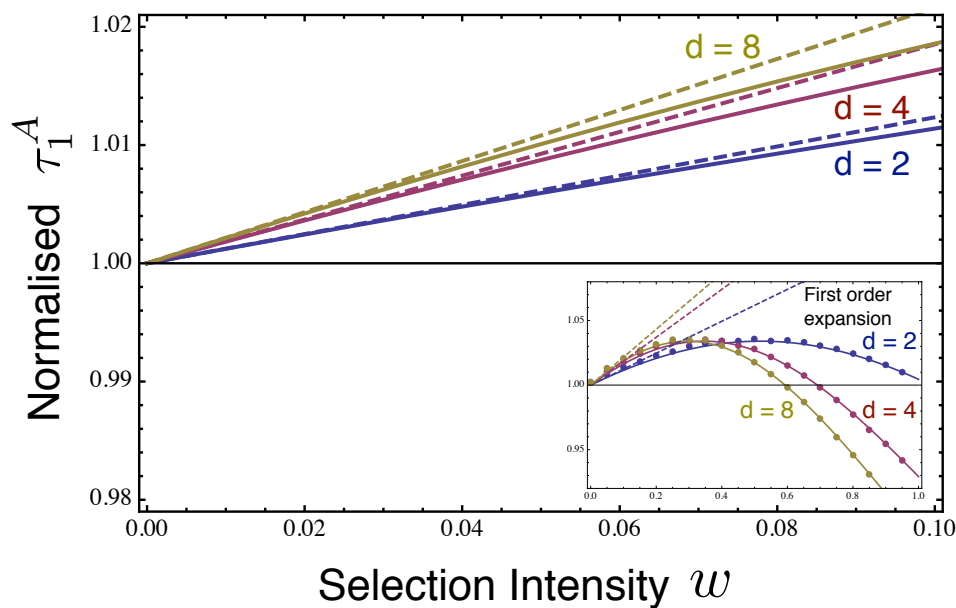
$$\left[\frac{\partial}{\partial w} \tau_1^A \right]_{w=0} = \sum_{k=0}^{d-1} G_k a_k + \sum_{k=0}^{d-1} G_{d-1-k} b_k. \tag{18}$$

G_k , as mentioned before, can be obtained via calculating the conditional fixation time for the game with matrix $a_i = \delta_{ik}$ and $b_i = 0$ (see the Appendix)

$$G_k = N \sum_{i=1}^{N-1} H(k, d; i, N) [i(H_{N-1} - H_{i-1} - H_{N-i}) + NH_{N-i}] - (2 + NH_{N-1}) \frac{N^2(d-k) - N(k+1)}{d(d+1)}, \tag{19}$$

where $H_N = \sum_{i=1}^N (1/i)$ represents the Harmonic number. In other words, the weak selection expansion for an arbitrary d -player game is fully determined by d special games, where for each k , G_k has the form above.

Figure 2. Stochastic slowdown is enhanced in multi-player games. The figure shows the fixation time conditioned on fixation for a game in which strategy A never has a selective disadvantage, $a_k = 2 - (k + 1)/d$ and $b_k = 1$. The main figure shows the normalized conditional fixation times (solid lines) and the first order approximations (dashed lines) for games with $d = 2$, $d = 4$, and $d = 8$ player games. The inset shows the same for higher intensities of selection elucidating the hump shape of the function that becomes more pronounced as the number of players increases (population size $N = 10$).



An interesting property of conditional fixation time that has been observed for finite populations with biased transition probabilities is that of stochastic slowdown. Consider that a strategy has a selective advantage over another, which is negatively proportional to the frequency of the strategy, but always

present. In such a case the conditional fixation time of one such mutant is actually greater than neutral, despite its selective advantage [42,43]. This phenomenon can be quantified by the slope of the first order expansion of the conditional fixation time. For multi-player games we see that stochastic slowdown is even more pronounced (Figure 2).

3. Average Abundance

For frequent mutations, the concept of fixation is meaningless [10]. The average abundances of the two strategies are usually different. Under neutrality where both strategies perform equally well, the average abundance of the two strategies will be just one half. It is therefore of interest to investigate the conditions under which strategy *A* is favored, *i.e.*, the expected frequency of the strategy is over one half. This issue was addressed for a large class of evolutionary dynamics under weak selection in structured populations [44,55]. For 2×2 games a single parameter condition, the so-called σ rule, was derived under mild constraints. Most interestingly, this single parameter σ does not depend on the payoff entries but is intrinsic to the population structure, update rule and mutation probabilities. This parameter can be obtained from any special non-zero game. Once it is known, we can make use of this parameter to determine which strategy is more abundant for all 2×2 games. Here, we extend this so-called σ rule to a two strategy *d*-player evolutionary game.

3.1. σ Rule for *d*-player Games

Theorem 2. Consider a population structure and an update rule such that

- (i) the transition probabilities are infinitely differentiable at $w = 0$
- (ii) the update rule is symmetric for the two strategies and
- (iii) there is at least one $i^* \in \{0, 1, 2, \dots, d - 1\}$ such that for the game given by the matrix $a_i = \delta_{i,i^*}$ and $b_i = 0$ for all $0 \leq i \leq d - 1$, the frequency of strategy *A* is over one half.

Then in the limit of weak selection, the condition that strategy *A* is favored is a $(d - 1)$ -parameter condition:

$$\sum_{\substack{0 \leq i \leq d-1 \\ i \neq i^*}} \sigma_i a_i + a_{i^*} > \sum_{\substack{0 \leq i \leq d-1 \\ i \neq i^*}} \sigma_i b_{d-1-i} + b_{d-1-i^*}, \tag{20}$$

where σ_i , $0 \leq i \leq d - 1$ and $i \neq i^*$, depends on the model and the dynamics (population structure, mutation probabilities, update rules) yet not on the entries of the payoff matrix, a_i and b_i .

Proof. By assumption (i), based on the Appendix B in [44], we have that strategy *A* is more abundant than strategy *B* if and only if

$$\sum_{0 \leq i \leq d-1} k_i a_i > \sum_{0 \leq i \leq d-1} h_i b_i, \tag{21}$$

where k_i and h_i are not dependent on the payoff entries a_i and b_i . By switching the name of *A* and *B* (Matrix (15)) and since the update rule is symmetric for both strategies (assumption (ii)), strategy *B* is favored, provided

$$\sum_{0 \leq i \leq d-1} k_i b_{d-1-i} > \sum_{0 \leq i \leq d-1} h_i a_{d-1-i}. \tag{22}$$

Since strategy A and strategy B cannot both have an abundance over one half, strategy A is favored if and only if

$$\sum_{0 \leq i \leq d-1} h_i a_{d-1-i} > \sum_{0 \leq i \leq d-1} k_i b_{d-1-i}. \tag{23}$$

Both condition (21) and (23) are necessary and sufficient conditions. These two inequalities can be mapped to each other by a positive rescaling factor λ . Thus $k_i = \lambda h_{d-1-i}$ and $h_i = \lambda k_{d-1-i}$. This leads to $\lambda = 1$ resulting in $h_i = k_{d-1-i}$. This turns condition (21) into

$$\sum_{0 \leq i \leq d-1} k_i a_i > \sum_{0 \leq i \leq d-1} k_{d-1-i} b_i. \tag{24}$$

By assumption (iii), we have $k_{i^*} > 0$. Multiplying by $1/k_{i^*} > 0$ on both sides of condition (24) leads to

$$\sum_{\substack{0 \leq i \leq d-1 \\ i \neq i^*}} \sigma_i a_i + a_{i^*} > \sum_{\substack{0 \leq i \leq d-1 \\ i \neq i^*}} \sigma_i b_{d-1-i} + b_{d-1-i^*}, \tag{25}$$

where $\sigma_i = k_i/k_{i^*}$, $0 \leq i \leq d - 1$ and $i \neq i^*$. Since k_i is independent of the payoff entries, σ_i is also independent of the payoff entries. □

In particular, for $d = 2$ and $i^* = 1$, this degenerates to the main Theorem in [44]. In addition, our result is also valid for general fitness mapping $f(w\pi)$, whose first order derivative does not vanish at $w = 0$. For general $n \times n$ games, only two parameters are required to capture the condition [45], under which a strategy is more abundant than the neutral case. Here, however, even for two strategy games, the number of parameters is increasing linearly with the number of the players (d). This implies that a multi-player game is far more complex than any pairwise game, even under weak selection.

For 2×2 games, the population structure coefficient σ reflects the interaction rate ratio between two patterns of interaction, the interaction of two individuals with the same strategy and that with different strategies [56]. Similarly, σ_i depicts the relative interaction rate of the group, in which i co-players have the same strategy as the focal individual [57,58].

3.2. Calculating the Structure Parameters σ_i : Three Examples

While the σ rule is valid for well mixed as well as structured populations, what changes is the interpretation of the parameter σ . In this part, we calculate the σ_i 's for three different processes. We begin with a case of a standard Moran process in a well mixed population, then interpret the results of [59] where the death–birth dynamics takes place on a cycle, and finally we again consider well mixed populations but with aspiration dynamics [60,61].

3.2.1. The Moran Process with Mutations in Well Mixed Population

For a 3-player game for the Moran process with mutations in well mixed population, it has been shown based on coalescence theory that for any mutation probability μ , the abundance of strategy A is greater than one half if and only if (Equation (B.20) in Appendix B in [58])

$$a_0 (\mu^3 + 6\mu^2 + 8\mu) + a_1 (2\mu^3 + 8\mu^2 + 8\mu) + a_2 (\mu^3 + 6\mu^2 + 8\mu) > b_2 (\mu^3 + 6\mu^2 + 8\mu) + b_1 (2\mu^3 + 8\mu^2 + 8\mu) + b_0 (\mu^3 + 6\mu^2 + 8\mu). \tag{26}$$

Based on this equation, for the game $a_i = \delta_{i1}$ and $b_i = 0$, we have $(2\mu^3 + 8\mu^2 + 8\mu) > 0$ for any non-zero mutation probability. Let $i^* = 1$, such that σ_1 does not exist. Condition (iii) in Theorem 2 is satisfied, provided the mutation probability μ does not vanish. Dividing Equation (26) by $2\mu^3 + 8\mu^2 + 8\mu$ results in $\sigma_0 a_0 + a_1 + \sigma_2 a_2 > \sigma_2 b_0 + b_1 + \sigma_0 b_2$, where

$$\sigma_0 = \sigma_2 = \frac{\mu^3 + 6\mu^2 + 8\mu}{2\mu^3 + 8\mu^2 + 8\mu}. \tag{27}$$

In 2×2 games, it has been shown that the σ is independent of mutation probabilities [62]. In contrast, our result implies that for multiple player games, the σ_i s depend on the mutation probabilities. Therefore, the strategy order for multiple player game can change with the increase of the mutation probabilities [58], which cannot occur for two player games with two strategies [62].

3.2.2. The Death Birth Process on the Cycle

For death–birth process on the cycle with small mutations, strategy A is more abundant than strategy B if and only if $\rho_A > \rho_B$ [63]. It has been shown in [59] that this is equivalent to

$$a_0 + 2 \sum_{i=2}^{d-1} a_{i-1} + 3a_{d-1} > 3b_0 + 2 \sum_{i=2}^{d-1} b_{d-i} + b_{d-1}. \tag{28}$$

For $a_i = \delta_{i0}$ and $b_i = 0$, this reduces to $1 > 0$. With $i^* = 0$, Condition (iii) in Theorem 2 is satisfied. Thus we have

$$\begin{aligned} \sigma_i &= 2, \quad 1 \leq i \leq d - 2 \\ \sigma_{d-1} &= 3. \end{aligned} \tag{29}$$

3.2.3. The Aspiration Dynamics in the Well Mixed Population.

For aspiration dynamics, one random individual s is selected, it switches its current strategy to the other with probability $1/[1 + \exp(-w(\pi_s - a))]$, where a and w represent the aspiration rate and selection intensity [61].

For weak selection in a well mixed population, it has been found that the average abundance of strategy A is over one half if and only if $\sum_{k=0}^{d-1} \binom{d-1}{k} a_k > \sum_{k=0}^{d-1} \binom{d-1}{k} b_k$ [64]. Since $\binom{d-1}{k} = \binom{d-1}{d-1-k}$, this is equivalent with

$$\sum_{k=0}^{d-1} \binom{d-1}{k} a_k > \sum_{k=0}^{d-1} \binom{d-1}{d-1-k} b_k. \tag{30}$$

Let $a_i = \delta_{i,0}$ and $b_i = 0$, then by Equation (30) we have $1 > 0$. By letting $i^* = 0$, Condition (iii) in Theorem 2 is satisfied. Then we have

$$\sigma_i = \binom{d-1}{i}, \quad 1 \leq i \leq d-1. \quad (31)$$

4. Summary and Discussion

Multi-player games characterize more complex interactions compared with pairwise games. It is also a natural way to introduce non-linear fitness effects into evolutionary game theory [65,66]. This non-linearity mimics more realistic biological situations such as saturating effect of public goods. Thus, multi-player games have great applications in both biology and social dilemmas [67–69]. Shifting from infinite to finite in the size of population leads to the intrinsic stochastic properties of game dynamics. Compared with previous infinite large population models described in the replicator dynamics, the fixation probability and the fixation time become relevant properties for rare mutations. For more frequent mutations, where fixation becomes impossible, the average abundance or the stationary distribution is taken into account [10,70]. Previous studies focus on how mutation, selection and population structure affect these properties of stochastic evolutionary games. However, relatively little work has been done on this issue in the context of multi-player games [26,39,40,71–73]. Motivated by these, we have investigated how the multi-player interaction pattern influences those dynamical properties. Here, we have concentrated on the two strategy case and addressed the fixation probability, the fixation time and the average abundance.

The conditional fixation time and the generalized σ rule are both derived under weak selection. This is why the results are both in the form of a linear combination of payoff entries (conditional fixation time for Equations (11) and (18) and the generalized σ rule given in Equation (20)). Intuitively, the number of coefficients required for the generalizations should be equal to the dimension of the payoff matrix, *i.e.*, $2d$. However, due to the symmetry conditions (Equation (12) and Assumption (ii) in Theorem 2), the number of the coefficients of the conditional fixation time reduces to d and that of the σ rule degenerates to $d - 1$. The linear increase of the number of coefficients required with increasing d reveals that the complexity of the multiple player interaction is increasing with the number of players d . If we take the number of the maxima or minima of the fixation probability as a function of the intensity of selection as an indicator for complexity, then multi-player interactions do not increase the complexity.

Our considerations illustrate that multi-player games can lead to substantial additional complications that do not appear in two-player games and that are also absent in linear public goods games, probably the best studied examples of multiplayer games. However, it turns out that there is still a lot to be done to understand the full complexity of such multi-player interaction.

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References

1. Nowak, M.A.; Sasaki, A.; Taylor, C.; Fudenberg, D. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **2004**, *428*, 646-650.
2. Traulsen, A.; Claussen, J.C.; Hauert, C. Coevolutionary dynamics: From finite to infinite populations. *Phys. Rev. Lett.* **2005**, *95*, 238701.
3. Imhof, L.A.; Fudenberg, D.; Nowak, M.A. Evolutionary cycles of cooperation and defection. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 10797-10800.
4. Fudenberg, D.; Imhof, L.A. Imitation processes with small mutations. *J. Econ. Theor.* **2006**, *131*, 251-262.
5. Hauert, C.; Traulsen, A.; Brandt, H.; Nowak, M.A.; Sigmund, K. Via freedom to coercion: The emergence of costly punishment. *Science* **2007**, *316*, 1905-1907.
6. Ohtsuki, H.; Bordalo, P.; Nowak, M.A. The one-third law of evolutionary dynamics. *J. Theor. Biol.* **2007**, *249*, 289-295.
7. Antal, T.; Scheuring, I. Fixation of strategies for an evolutionary game in finite populations. *B. Math. Biol.* **2006**, *68*, 1923-1944.
8. Imhof, L.A.; Nowak, M.A. Stochastic evolutionary dynamics of direct reciprocity. *Proc. R. Soc. B* **2010**, *277*, 463-468.
9. Zhou, D.; Qian, H. Fixation, transient landscape, and diffusion dilemma in stochastic evolutionary game dynamics. *Phys. Rev. E* **2011**, *84*, 031907.
10. Wu, B.; Gokhale, C.S.; Wang, L.; Traulsen, A. How small are small mutation rates? *J. Math. Biol.* **2012**, *64*, 803-827.
11. Nowak, M.A.; Sigmund, K. Evolutionary Dynamics of Biological Games. *Science* **2004**, *303*, 793-799.
12. Hofbauer, J.; Sigmund, K. *Evolutionary Games and Population Dynamics*; Cambridge University Press: Cambridge, UK, 1998.
13. Gintis, H. Costly signaling and cooperation. *J. Theor. Biol.* **2001**, *213*, 103-119.
14. Broom, M. The use of multiplayer game theory in the modeling of biological populations. *Comments. Theor. Biol.* **2003**, *8*, 103-123.
15. Connor, R.C. Cooperation beyond the dyad: On simple models and a complex society. *Phil. Trans. R. Soc. B* **2010**, *365*, 2687-2697.
16. Archetti, M.; Scheuring, I. Review: Evolution of cooperation in one-shot social dilemmas without assortment. *J. Theor. Biol.* **2012**, *299*, 9-20.
17. Taylor, M. *The Possibility of Cooperation*; Cambridge University Press: Cambridge, UK, 1987.
18. Schelling, T.C. *Micromotives and Macrobehavior*; W. W. Norton & Company: New York, NY, USA, 2006.
19. Greig, D.; Travisano, M. The Prisoner's Dilemma and polymorphism in yeast SUC genes. *Biol. Lett.* **2004**, *271*, S25-S26.
20. Doebeli, M.; Hauert, C. Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. *Ecol. Lett.* **2005**, *8*, 748-766.

21. Gore, J.; Youk, H.; van Oudenaarden, A. Snowdrift game dynamics and facultative cheating in yeast. *Nature* **2009**, *459*, 253-256.
22. MacLean, G.; Fuentes-Hernandez, A.; Greig, D.; Hurst, L.D.; Gudelj, I. A mixture of “cheats” and “co-operators” can enable maximal group benefit. *PLoS Biology* **2010**, *8*, e1000486.
23. Woelfing, B.; Traulsen, A. Stochastic sampling of interaction partners *versus* deterministic payoff assignment. *J. Theor. Biol.* **2009**, *257*, 689-695.
24. Broom, M.; Cannings, C.; Vickers, G. Multi-player matrix games. *B. Math. Biol.* **1997**, *59*, 931-952.
25. Bukowski, M.; Miekisz, J. Evolutionary and asymptotic stability in symmetric multi-player games. *Int. J. Game Theory* **2004**, *33*, 41-54.
26. Han, T.A.; Traulsen, A.; Gokhale, C.S. On equilibrium properties of evolutionary multi-player games with random payoff matrices. *Theor. Popul. Biol.* **2012**, *81*, 264-72.
27. Moran, P.A.P. Random processes in genetics. *Proc. Cambridge Philos. Soc.* **1958**, *54*, 60-71.
28. Wu, B.; Altrock, P.M.; Wang, L.; Traulsen, A. Universality of weak selection. *Phys. Rev. E* **2010**, *82*, 046106.
29. Traulsen, A.; Shores, N.; Nowak, M.A. Analytical results for individual and group selection of any intensity. *B. Math. Biol.* **2008**, *70*, 1410-1424.
30. Huang, W.; Traulsen, A. Fixation probabilities of random mutants under frequency dependent selection. *J. Theor. Biol.* **2010**, *263*, 262-268.
31. Huang, W.; Haubold, B.; Hauert, C.; Traulsen, A. Emergence of stable polymorphism driven by evolutionary games between mutants. *Nature Commun.* **2012**, *3*, 919.
32. Huang, W.; Werner, B.; Traulsen, A. The impact of random frequency-dependent mutations on the average population fitness. *BMC Evol. Biol.* **2012**, *12*, 160.
33. Traulsen, A.; Pacheco, J.M.; Nowak, M.A. Pairwise comparison and selection temperature in evolutionary game dynamics. *J. Theor. Biol.* **2007**, *246*, 522-529.
34. Bürger, R. *The Mathematical Theory of Selection, Recombination, and Mutation*; John Wiley and Sons: Chichester, UK, 2000.
35. Wu, B.; Gokhale, C.S.; Van Veelen, M.; Wang, L.; Traulsen, A. Interpretations arising from Wrightian and Malthusian fitness under strong frequency dependent selection. *Ecol. Evol.* **2013**, doi: 10.1002/ece3.500.
36. Imhof, L.A.; Nowak, M.A. Evolutionary game dynamics in a Wright-Fisher process. *J. Math. Biol.* **2006**, *52*, 667-681.
37. Traulsen, A.; Pacheco, J.M.; Imhof, L.A. Stochasticity and evolutionary stability. *Phys. Rev. E* **2006**, *74*, 021905.
38. Lessard, S.; Ladret, V. The probability of fixation of a single mutant in an exchangeable selection model. *J. Math. Biol.* **2007**, *54*, 721-744.
39. Kurokawa, S.; Ihara, Y. Emergence of cooperation in public goods games. *Proc. R. Soc. B* **2009**, *276*, 1379-1384.
40. Gokhale, C.S.; Traulsen, A. Evolutionary games in the multiverse. *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 5500-5504.

41. Lessard, S. On the robustness of the extension of the one-third law of evolution to the multi-player game. *Dynam. Games Appl.* **2011**, *1*, 408-418.
42. Altrock, P.M.; Gokhale, C.S.; Traulsen, A. Stochastic slowdown in evolutionary processes. *Phys. Rev. E* **2010**, *82*, 011925.
43. Altrock, P.M.; Traulsen, A.; Galla, T. The mechanics of stochastic slowdown in evolutionary games. *J. Theor. Biol.* **2012**, *311*, 94-106.
44. Tarnita, C.E.; Ohtsuki, H.; Antal, T.; Fu, F.; Nowak, M.A. Strategy selection in structured populations. *J. Theor. Biol.* **2009**, *259*, 570-581.
45. Tarnita, C.E.; Wage, N.; Nowak, M.A. Multiple strategies in structured populations. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 2334-2337.
46. Karlin, S.; Taylor, H.M.A. *A First Course in Stochastic Processes*, 2nd edition ed.; Academic: London, UK, 1975.
47. Traulsen, A.; Hauert, C. Stochastic evolutionary game dynamics. In *Reviews of Nonlinear Dynamics and Complexity*; Schuster, H.G., Ed.; Wiley-VCH: Weinheim, Germany, 2009; Vol. II, pp. 25-61.
48. Kimura, M. On the probability of fixation of mutant genes in a population. *Genetics* **1962**, *47*, 713-719.
49. Kampen, N.G.v. *Stochastic Processes in Physics and Chemistry*, 2nd ed.; Elsevier: Amsterdam, Netherlands, 1997.
50. Graham, R.L.; Knuth, D.E.; Patashnik, O. *Concrete Mathematics*, 2nd ed.; Addison-Wesley: Reading, MA, USA, 1994.
51. Ewens, W.J. *Mathematical Population Genetics. I. Theoretical Introduction*; Springer: New York, NY, USA, 2004.
52. Altrock, P.M.; Traulsen, A. Fixation times in evolutionary games under weak selection. *New J. Phys.* **2009**, *11*, 013012.
53. Maruyama, T.; Kimura, M. A note on the speed of gene frequency changes in reverse direction in a finite population. *Evolution* **1974**, *28*, 161-163.
54. Taylor, C.; Iwasa, Y.; Nowak, M.A. A symmetry of fixation times in evolutionary dynamics. *J. Theor. Biol.* **2006**, *243*, 245-251.
55. Nathanson, C.G.; Tarnita, C.E.; Nowak, M.A. Calculating evolutionary dynamics in structured populations. *PLoS Comput. Biol.* **2009**, *5*, e1000615.
56. Tang, C.; Li, X.; Cao, L.; Zhan, J. The σ law of evolutionary dynamics in community-structured population. *J. Theor. Biol.* **2012**, *306*, 1-6.
57. Antal, T.; Traulsen, A.; Ohtsuki, H.; Tarnita, C.E.; Nowak, M.A. Mutation-selection equilibrium in games with multiple strategies. *J. Theor. Biol.* **2009**, *258*, 614-622.
58. Gokhale, C.S.; Traulsen, A. Strategy abundance in evolutionary many-player games with multiple strategies. *J. Theor. Biol.* **2011**, *238*, 180-191.
59. Van Veelen, M.; Nowak, M.A. Multi-player games on the cycle. *J. Theor. Biol.* **2012**, *292*, 116-128.
60. Szabó, G.; Hauert, C. Phase transitions and volunteering in spatial public goods games. *Phys. Rev. Lett.* **2002**, *89*, 118101.

61. Szabó, G.; Fáth, G. Evolutionary games on graphs. *Phys. Rep.* **2007**, *446*, 97-216.
62. Antal, T.; Nowak, M.A.; Traulsen, A. Strategy abundance in 2×2 games for arbitrary mutation rates. *J. Theor. Biol.* **2009**, *257*, 340-344.
63. Allen, B.; Tarnita, C.E. Measures of success in a class of evolutionary models with fixed population size and structure. *J. Math. Biol.* **2012**.
64. Du, J.; Wu, B.; Wang, L. Evolutionary dynamics of multi-player games driven by aspiration. submitted **2013**.
65. Eshel, I.; Motro, U. The three brothers' problem: Kin selection with more than one potential helper. 1. The case of immediate help. *Amer. Nat.* **1988**, *132*, 550-566.
66. Hauert, C.; Michor, F.; Nowak, M.A.; Doebeli, M. Synergy and discounting of cooperation in social dilemmas. *J. Theor. Biol.* **2006**, *239*, 195-202.
67. Dionisio, F.; Gordo, I. The tragedy of the commons, the public goods dilemma, and the meaning of rivalry and excludability in evolutionary biology. *Evol. Ecol. Res.* **2006**, *8*, 321-332.
68. Sigmund, K.; De Silva, H.; Traulsen, A.; Hauert, C. Social learning promotes institutions for governing the commons. *Nature* **2010**, *466*, 861-863.
69. Gokhale, C.S.; Traulsen, A. Mutualism and evolutionary multiplayer games: revisiting the Red King. *Proc. R. Soc. B* **2012**, *279*, 4611-4616.
70. Claussen, J.C.; Traulsen, A. Non-Gaussian fluctuations arising from finite populations: Exact results for the evolutionary Moran process. *Phys. Rev. E* **2005**, *71*, 025101(R).
71. Kurokawa, S.S.; Ihara, Y. Evolution of social behavior in finite populations: A payoff transformation in general n-player games and its implications. *Theor. Popul. Biol.* **2013**, *84*.
72. Wang, J.; Wu, B.; Ho, A.D.; Wang, L. Evolution of cooperation in multilevel public goods games with community structures. *Eur. Phys. Lett.* **2011**, *93*, 58001.
73. Du, J.; Wu, B.; Wang, L. Evolution of global cooperation driven by risks. *Phys. Rev. E* **2012**, *85*.

Appendix

For the conditional fixation time given in Equation (11), the linear term in the weak selection expansion is given by

$$\left[\frac{\partial}{\partial w} \tau_1^A \right]_{w=0} = \sum_{j=1}^{N-1} \sum_{l=1}^j \left[\frac{1}{T_l^+} \frac{\partial \rho_l^A}{\partial w} + \rho_l^A \frac{\partial}{\partial w} \frac{1}{T_l^+} \right]_{w=0} - \sum_{j=1}^{N-1} \sum_{l=1}^j \left[\frac{\rho_l^A}{T_l^+} \sum_{m=l+1}^j \Delta\pi(m) \right]_{w=0}. \quad (32)$$

The weak selection expansion of the fixation probability and the inverse of the positive transition probability read as,

$$\left[\frac{\partial}{\partial w} \rho_l^A \right]_{w=0} = \frac{l}{N^2} \sum_{p=1}^{N-1} \sum_{i=1}^p \Delta\pi(i) - \frac{1}{N} \sum_{p=1}^{l-1} \sum_{i=1}^p \Delta\pi(i), \quad (33)$$

$$\left[\frac{\partial}{\partial w} \frac{1}{T_l^+} \right]_{w=0} = -\frac{N}{l} \Delta\pi(l). \quad (34)$$

Using these two expressions, we can rewrite the conditional fixation time as,

$$\begin{aligned} \left[\frac{\partial}{\partial w} \tau_1^A \right]_{w=0} &= \underbrace{\sum_{j=1}^{N-1} \sum_{l=1}^j \frac{N^2}{l(N-l)} \left(\frac{l}{N^2} \sum_{p=1}^{N-1} \sum_{i=1}^p \Delta\pi(i) \right)}_{\xi_1} - \sum_{j=1}^{N-1} \sum_{l=1}^j \frac{N^2}{l(N-l)} \frac{1}{N} \sum_{p=1}^{l-1} \sum_{i=1}^p \Delta\pi(i) \\ &\quad - \underbrace{\sum_{j=1}^{N-1} \sum_{l=1}^j \frac{l}{N} \frac{N}{l} \Delta\pi(l)}_{\xi_2} - \underbrace{\sum_{j=1}^{N-1} \sum_{l=1}^j \frac{l}{N} \frac{N^2}{l(N-l)} \sum_{m=l+1}^j \Delta\pi(m)}_{\xi_3}. \end{aligned} \tag{35}$$

Based on the arguments and calculations provided previously in [28,52] we can simplify ξ_1 and ξ_3 for the special payoff structure comprising of $a_i = \delta_{ik}$ and $b_i = 0$, such that $\Delta\pi(l) = H(k, d; k, N)$. The term ξ_2 has previously been calculated in [40]. For our special matrix it reads

$$\xi_2 = \sum_{j=1}^{N-1} \sum_{l=1}^j \frac{\binom{l-1}{k} \binom{N-l}{d-1-k}}{\binom{N-1}{d-1}} = \frac{N^2(d-k) - N(k+1)}{d(d+1)}. \tag{36}$$

Using the expression for the conditional fixation time as shown in Equation (18), for the above matrix we have, $G_k = \left[\frac{\partial}{\partial w} \tau_1^A \right]_{w=0}$. Thus, putting together the simplified terms ξ_1 , ξ_2 and ξ_3 leads us to the complete expression for G_k ,

$$\begin{aligned} G_k &= N \sum_{i=1}^{N-1} H(k, d; i, N) [i(H_{N-1} - H_{i-1} - H_{N-i}) + NH_{N-i}] \\ &\quad - (2 + NH_{N-1}) \frac{N^2(d-k) - N(k+1)}{d(d+1)}. \end{aligned} \tag{37}$$