Multiple Strategies in Structured Populations

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Abstract

Many specific models have been proposed to study evolutionary game dynamics in structured populations, but most analytical results so far describe the competition of only two strategies. Here we derive a general result that holds for any number of strategies, for a large class of population structures under weak selection. We show that for the purpose of strategy selection any evolutionary process can be characterized by two key parameters that are coefficients in a linear inequality containing the payoff values. These structural coefficients, σ_1 and σ_2, depend on the particular process that is being studied, but not on the number of strategies, n, nor on the payoff matrix. For calculating these structural coefficients one has to investigate games with three strategies, but more are not needed. Therefore, $n = 3$ is the general case. Our main result has a geometric interpretation: strategy selection is determined by the sum of two terms, the first one describing competition on the edges of the simplex, the second one in the center. Our formula includes all known weak selection criteria of evolutionary games as special cases. As a specific example we calculate games on sets and explore the synergistic interaction between direct reciprocity and spatial selection. We show that for certain parameter values both repetition and space are needed to promote evolution of cooperation.

Evolutionary games arise whenever the fitness of individuals is not constant, but depends on the relative abundance of strategies in the population [1-7]. Evolutionary game theory is a general

theoretical framework that can be used to study many biological problems including host-parasite interactions, ecosystems, animal behavior, social evolution and human language [8-18]. The traditional approach of evolutionary game theory uses deterministic dynamics describing infinitely large, well-mixed populations. More recently the framework was expanded to deal with stochastic dynamics, finite population size and structured populations [19-32].

Here we consider a mutation-selection process acting in a population of finite size. The population structure determines who interacts with whom to accumulate payoff and who competes with whom for reproduction. Individuals adopt one of n strategies. The payoff for an interaction between any two strategies is given by the $n \times n$ payoff matrix $A = [a_{ij}]$. The rate of reproduction is proportional to payoff: individuals that accumulate higher payoff are more likely to reproduce. Reproduction is subject to symmetric mutation: with probability $1 - u$ the offspring inherits the strategy of the parent, but with probability u a random strategy is chosen. Our process leads to a stationary distribution characterizing the mutation-selection equilibrium. Important questions are: what is the average frequency of a strategy in the stationary distribution? which strategies are more abundant than others?

In order to make progress, we consider the limit of weak selection. One way to obtain this limit is as follows: the rate of reproduction of each individual is proportional to $1 + w$Payoff, where w is a constant that measures the intensity of selection; the limit of weak selection is then given by $w \to 0$. Weak selection is not an unnatural situation; it can arise in different ways: (i) payoff differences are small; (ii) strategies are similar; (iii) individuals are confused about payoffs when updating their strategies; in such situations, the particular game makes only a small contribution to the overall reproductive success of an individual.

For weak selection, all strategies have roughly the same average frequency, $1/n$, in the stationary distribution. A strategy is favored by selection, if its average frequency is greater than $1/n$. Otherwise it is opposed by selection. Our main result is the following: given some mild assumptions (specified in the Supporting Information, SI) strategy k is favored by selection if

$$(\sigma_1 a_{kk} + \bar{a}_{k*} - \bar{a}_{*k} - \sigma_1 \bar{a}_{**}) + \sigma_2(\bar{a}_{k*} - \bar{a}) > 0 \tag{1}$$

Here $\bar{a}_{**} = (1/n)\sum_{i=1}^{n} a_{ii}$ is the average payoff when both individuals use the same strategy; $\bar{a}_{k*} = (1/n)\sum_{i=1}^{n} a_{ki}$ is the average payoff of strategy k; $\bar{a}_{*k} = (1/n)\sum_{i=1}^{n} a_{ik}$ is the average

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payoff when playing against strategy k; and $\bar{a} = (1/n^2) \sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij}$ is the average payoff in the population. The parameters σ_1 and σ_2 are structural coefficients which need to be calculated for the specific evolutionary process that is investigated. These parameters depend on the population structure, the update rule, the mutation rate, but they do not depend on the number of strategies nor on the entries of the payoff matrix.

How can we interpret this result? Let x_i denote the frequency of strategy i. The configuration of the population (just in terms of frequencies of strategies) is given by a point in the simplex S_n, which is defined by $\sum_{i=1}^{n} x_i = 1$. The vertices of the simplex correspond to population states where only one strategy is present. The edges of the simplex correspond to states where two strategies are present. In the interior of the simplex all strategies are present. Inequality (1) is the sum of two terms, both of which are linear in the payoff values. The first term, $\sigma_1 a_{kk} + \bar{a}_{k*} - \bar{a}_{*k} - \sigma_1 \bar{a}_{**}$, describes competition on the edges of the simplex that include strategy k (see Fig 1a). In particular, it is an average over all pairwise comparisons between strategy k and each other strategy, weighted by the structural coefficient, σ_1. The second term, $\sigma_2(\bar{a}_{k*} - \bar{a})$, evaluates the competition between strategy k and all other strategies in the center of the simplex, where all strategies have the same frequency, $1/n$ (see Fig 1b).

Therefore, the surprising implication of our main result (1) is that strategy selection (in a mutation-selection process in a structured population) is simply the sum of two competition terms, one that is evaluated on the edges of the simplex and the other one in the center of the simplex. The simplicity of this result is surprising because an evolutionary process in a structured population has a very large number of possible states; to describe a particular state it is not enough to list the frequencies of strategies but one also has to specify the population structure.

Further intuition for our main result is provided by the concept of risk-dominance. The classical notion of risk-dominance for a game with two strategies in a well-mixed population is: strategy i is risk-dominant over strategy j if $a_{ii} + a_{ij} > a_{ji} + a_{jj}$. If i and j are engaged in a coordination game, given by $a_{ii} > a_{ji}$ and $a_{jj} > a_{ij}$, then the risk-dominant strategy has the bigger basin of attraction. In a structured population the risk-dominance condition is modified to $\sigma a_{ii} + a_{ij} > a_{ji} + \sigma a_{jj}$, where σ is the structural coefficient [31]. Therefore, the first term in inequality (1) represents the average over all pairwise risk-dominance comparisons between strategy k and each other strategy (taking into account population structure). The second term in inequality (1) measures the risk-dominance

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of strategy k when simultaneously compared to all other strategies in a well-mixed population; it is the generalization of the concept of risk-dominance to multiple strategies, $\bar{a}_{k*} > \bar{a}$.

In the Supporting Information we show that the structural coefficients, σ_1 and σ_2, do not depend on the number of strategies. In order to calculate σ_1 and σ_2 for any particular evolutionary process, we need to consider games with $n = 3$ strategies. More than three strategies are not needed. Therefore, $n = 3$ is the general case. An important practical implication of our result is the following: if we want to calculate the competition of multiple strategies in a structured population for weak selection but any mutation rate, then all we have to do is to calculate two parameters, σ_1 and σ_2. This can be done for a very simple payoff matrix and $n = 3$ strategies. Once σ_1 and σ_2 are known they can be applied to any payoff matrix and any number of strategies.

For $n = 2$ strategies, inequality (1) leads to $(a_{11} - a_{22})(2\sigma_1 + \sigma_2) + (a_{12} - a_{21})(2 + \sigma_2) > 0$. If $2 + \sigma_2 \neq 0$, we obtain the well known condition $\sigma a_{11} + a_{12} > a_{21} + \sigma a_{22}$ with $\sigma = (2\sigma_1 + \sigma_2)/(2 + \sigma_2)$. Many σ values have been calculated characterizing evolutionary games with two strategies in structured populations [31].

For a large, well-mixed population we know that $\sigma_1 = 1$ and $\sigma_2 = \mu$ where $\mu = Nu$ is the product of population size and mutation rate [30]. Therefore, if the mutation rate is low, $\mu \to 0$, then the evolutionary success of a strategy is determined by average pair-wise risk dominance, $a_{kk} + \bar{a}_{k*} - \bar{a}_{*k} - \bar{a}_{**}$. If the mutation rate is high, $\mu \to \infty$, then the evolutionary success depends on risk dominance, $\bar{a}_{k*} - \bar{a}$.

For any population structure, we can show that low mutation, $\mu \to 0$, implies $\sigma_2 \to 0$. Therefore, in the limit of low mutation, the condition for strategy k to be selected becomes $\sigma_0 a_{kk} + \bar{a}_{k*} > \bar{a}_{*k} + \sigma_0 \bar{a}_{**}$ where σ_0 is the low mutation limit of the structure coefficient $\sigma = (2\sigma_1 + \sigma_2)/(2 + \sigma_2)$. Hence, for low mutation it suffices to study 2-strategy games, and all known σ results [31] carry over to the multiple strategy case.

In the limit of high mutation, $\mu \to \infty$, we conjecture (but can not prove) that, for a large class of processes, σ_2 becomes much larger than σ_1 and much larger than 1. In that case the selection condition is simply risk dominance, $\bar{a}_{k*} - \bar{a}$, which is also the high mutation limit for a well-mixed population. Thus, if the mutation rate is large enough then the effect of population structure on strategy selection is destroyed.

In the Supporting Information we give a computational formula for how to calculate σ_1 and σ_2

for any process with global updating (which means all individuals compete globally for reproduction).

Let us now study a specific evolutionary process, where the individuals of a population of size N are distributed over M sets [32]. These sets can be geographic islands, social institutions or tags [32-35]. At any one time each individual belongs to one set and adopts one of n strategies. Individuals interact with others in the same set and thereby obtain payoff. Individuals reproduce proportional to payoff. Offspring inherit their parent's strategy, subject to a strategy mutation rate, u, and their parent's set, subject to a set mutation rate, v. We use rescaled mutation rates $\mu = Nu$ and $\nu = Nv$. In the Supporting Information we calculate σ_1 and σ_2 for this process and provide analytic results for large population size, N, but for any number of sets, M, and for any mutation rates. For large μ we obtain $\sigma_1 \approx M(1+\nu)/(M+\nu)$ and $\sigma_2 \approx \mu$. Note that large strategy mutation rate, μ, destroys the effect of population structure, as expected.

In Figure 2, we show the dependency of σ_1 and σ_2 on the strategy mutation rate, μ. We choose $M = 100$ sets and show panels for different values of the set mutation rate, ν. For $\nu \to 0$ and $\nu \to \infty$ we obtain the same figure, because both cases correspond to a well-mixed population. There exists a particular strategy mutation rate, μ^*, for which $\sigma_1 = \sigma_2$. For $\mu < \mu^*$ structural effects prevail over mutation, because $\sigma_1 > \sigma_2$. For $\mu > \mu^*$ mutation destroys the effect of population structure, because $\sigma_1 < \sigma_2$. For large M, the critical mutation rate is given by $\mu^* \approx 1 + \nu$.

We now use these results to study a particular game on sets. Our game has three strategies, always cooperate (AllC), always defect (AllD) and tit-for-tat (TFT), and is meant to describe the essential problem of evolution of cooperation under direct reciprocity. We assume there are repeated interactions between any two players subject to a certain continuation probability; the average number of rounds is given by m. In any one round, cooperation has a cost, c, and yields benefit, b, for the other player, where $b > c > 0$. Defection has no cost and yields no benefit. We use average payoff per round to denote the entries of the payoff matrix:

$$
\begin{array}{c}
\begin{array}{ccc} \text{AllC} & \text{AllD} & \text{TFT} \end{array} \\
\begin{array}{c} \text{AllC} \\ \text{AllD} \\ \text{TFT} \end{array}
\begin{pmatrix}
b-c & -c & b-c \\
b & 0 & b/m \\
b-c & -c/m & b-c
\end{pmatrix}
\end{array}
\tag{2}
$$

AllD is the only strict Nash equilibrium. If $b - c \geq b/m$ then TFT is a Nash equilibrium, but not an evolutionarily stable strategy.

We are interested in calculating the condition for natural selection to oppose AllD, which means that its frequency is less than $1/3$ in the stationary distribution. We observe that selection opposes AllD for small strategy mutation rates and intermediate set mutation rates (Fig 3). For high strategy mutation rate and for low or high set mutation rate the structure behaves like a well-mixed population, which is detrimental to cooperation. There is an optimum set mutation rate which maximally supports evolution of cooperation [32].

Next we study how the condition for selecting against AllD depends on repetition and structure (Fig 4). We make the following observations. For $b/c < 3$, even if the game is infinitely repeated, $m \to \infty$, we still need population structure to oppose AllD. In this parameter region repetition alone is not enough. For $b/c < 1 + (\nu+3)/(\nu(\nu+2))$, even if there are infinitely many sets ($M \to \infty$), we still need repetition to oppose AllD. Hence, for certain parameter choices both repetition and spatial structure must work together to promote evolution of cooperation [36,37]. This example demonstrates the need for synergistic interactions between various mechanisms for the evolution of cooperation [38]. In particular it is of interest that unless the benefit-to-cost ratio is substantial, $b/c > 3$, repetition alone does not provide enough selection pressure to oppose AllD.

In summary, we have derived a simple, general condition which characterizes strategy selection, if multiple strategies compete in a structured population under weak selection. The condition is linear in the payoff values and includes two structural coefficients, σ_1 and σ_2, which depend on the population structure, update rule, mutation rates, but do not depend on the number of strategies nor on the entries of the payoff matrix. The condition is a simple sum of two terms: one describes competition on the edges of the simplex and the other one in the center. Future research directions suggested by this result include: (i) a classification of population structures and update rules based on the two structural parameters; (ii) numerical and analytic explorations of how the weak selection result carries over to stronger selection intensities in specific cases; (iii) extending our theory from pairwise interactions to multi-player games. Finally our general result can be used to guide the exploration of many specific evolutionary processes.

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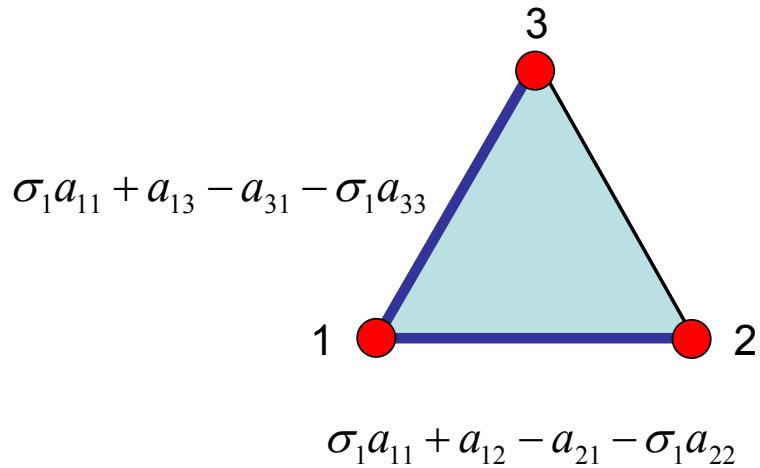38. Nowak MA (2006) Five rules for the evolution of cooperation. *Science* 314:1560-1563.

Figure legends

Figure 1. Our main result has a simple geometric interpretation, which is illustrated here for the case of $n = 3$ strategies. (a) The first term of inequality (1) describes competition on the edges of the simplex. (b) The second term of inequality (1) describes competition in the center of the simplex. In general, the selective criterion for strategy 1 is the sum of the two terms.

Figure 2. The dependency of σ_1 and σ_2 on the strategy mutation rate, μ. We choose $M = 100$ sets and show panels for different values of the set mutation rate: (a) $\nu = 0$; (b) $\nu = 3$; (c) $\nu = 10$; (d) $\nu = 100$; (e) $\nu = 1000$. We observe that $\sigma_2 \approx \mu$. For $\nu \to 0$ and $\nu \to \infty$ we obtain the same figure, because both cases correspond to a well-mixed population. For a particular strategy mutation rate, μ^*, we have $\sigma_1 = \sigma_2$. For $\mu < \mu^*$ structural effects prevail over mutation, because $\sigma_1 > \sigma_2$. For $\mu > \mu^*$ mutation destroys the effect of population structure, because $\sigma_1 < \sigma_2$.

Figure 3. The effect of strategy and set mutations on the condition to select against AllD. Selection opposes AllD for small strategy mutation rates and intermediate set mutation rates. For high strategy mutation rate and for low and high set mutation rate the structure behaves like a well-mixed population. There is an optimum set mutation rate. Parameters: $b = 2$, $c = 1$, $m = 7$, $M = 8$.
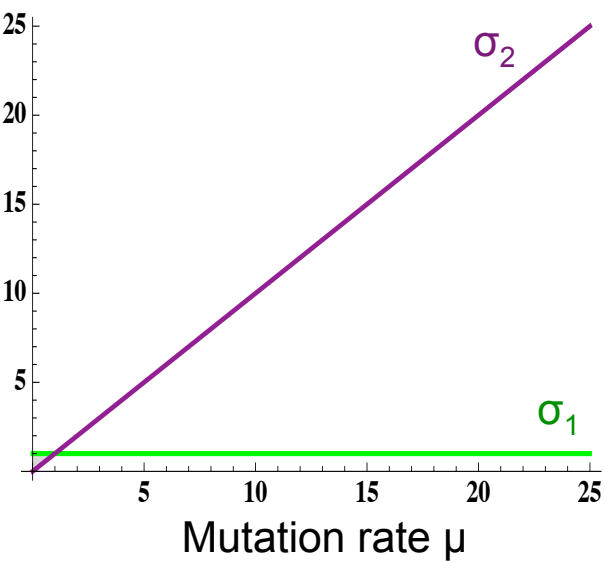
Figure 4. The synergistic interaction of direct reciprocity and spatial selection. For certain parameter choices neither repetition nor structure alone can select against AllD. (a) $c = 1$, $b = 3$, $\mu = 0$, $\nu = 0.5$. Either repetition or structure are sufficient. (b) $c = 1$, $b = 2$, $\mu = 0$, $\nu = 5$. A minimum number of sets is needed. (c) $c = 1$, $b = 3$, $\mu = 0$, $\nu = 0.05$. A minimum number of rounds is needed. (d) $c = 1$, $b = 2$, $\mu = 0$, $\nu = 0.5$. Both a minimum number of rounds and a minimum number of sets are needed to select against AllD.

$$\sigma_1 a_{11} + a_{13} - a_{31} - \sigma_1 a_{33}$$

$$\sigma_1 a_{11} + a_{12} - a_{21} - \sigma_1 a_{22}$$

(a)

$$\sigma_2 (\overline{a}_{1*} - \overline{a})$$

(b)

(a) (b) (c)

(d) (e) (f)

(a)

(b)

(c)

(d)