

Multiple strategies in structured populations

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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 , or 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 and 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 the following: What is the average frequency of a strategy in the stationary distribution? Which strategies are more abundant than others?

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 $w \rightarrow 0$. Weak selection is not an unnatural situation; it can arise in different ways: *i*) Payoff differences are small, *ii*) strategies are similar, and *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 $> 1/n$. Otherwise it is opposed by selection. Our main result is the following: Given some mild assumptions (specified in *SI Text*), strategy k is favored by selection if

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

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 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 that need to be calculated for the specific evolutionary process that is investigated. These parameters depend on the population structure, the update rule, and the mutation rate, but they do not depend on the number of strategies or 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 (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, $1/n$ (Fig. 1B).

Therefore, the surprising implication of our main result (Eq. 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 as follows: Strategy i is risk dominant over strategy j if $a_{ii} + a_{ij} > a_{ji} + a_{jj}$.

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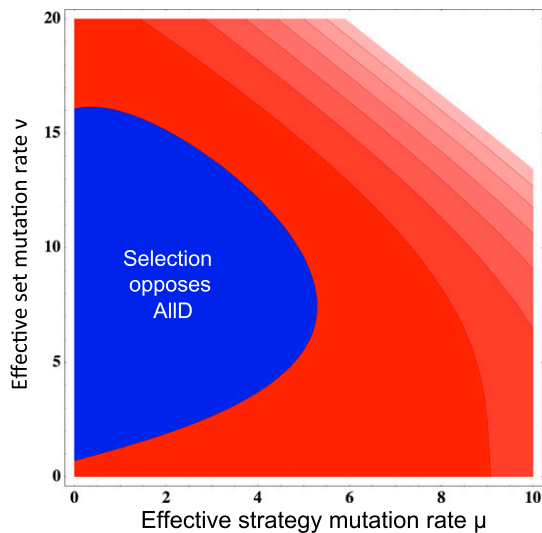


Fig. 3. The effect of strategy and set mutations on the condition to select against AIID. Selection opposes AIID for small strategy mutation rates and intermediate set mutation rates. For high strategy mutation rate and for low and high set mutation rate the structure behaves like a well-mixed population. There is an optimum set mutation rate. Parameters: $b = 2$, $c = 1$, $m = 7$, and $M = 8$.

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, ν . We use rescaled mutation rates $\mu = Nu$ and $\nu = N\nu$. In *SI Text* 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 $\sigma_1 \sim M(1 + \nu)/(M + \nu)$ and $\sigma_2 \sim \mu$. Note that large strategy mutation rate, μ , destroys the effect of population structure, as expected.

In Fig. 2, we show the dependence of σ_1 and σ_2 on the strategy mutation rate, μ . We choose $M = 100$ sets and show different values of the set mutation rate, ν . For $\nu \rightarrow 0$ and $\nu \rightarrow \infty$ we obtain the same behavior, because both cases correspond to a well-mixed population. A particular strategy mutation rate, μ^* , exists 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 $\mu^* \sim 1 + \nu$.

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; and 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:

$$\begin{array}{ccc}
 & \text{AllC} & \text{AllD} & \text{TFT} \\
 \text{AllC} & (b-c) & -c & (b-c) \\
 \text{AllD} & b & 0 & b/m \\
 \text{TFT} & (b-c) & -c/m & (b-c)
 \end{array} \quad [2]$$

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 $< 1/3$ in the stationary distribution. We observe that selection opposes AllD for

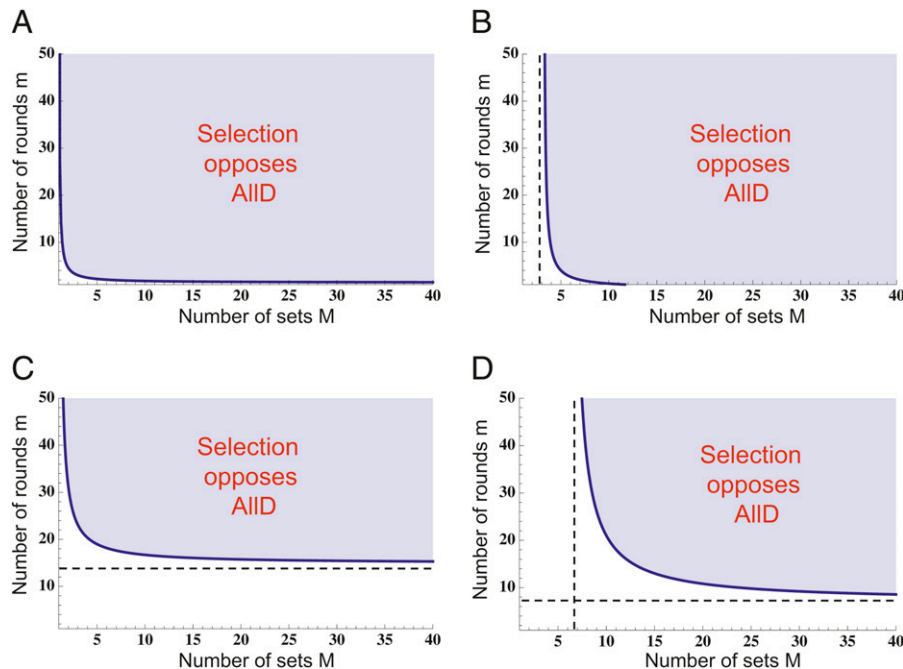


Fig. 4. The synergistic interaction of direct reciprocity and spatial selection. For certain parameter choices neither repetition nor structure alone can select against AIID. (A) $c = 1$, $b = 3$, $\mu = 0$, and $\nu = 0.5$. Either repetition or structure is sufficient. (B) $c = 1$, $b = 2$, $\mu = 0$, and $\nu = 5$. A minimum number of sets is needed. (C) $c = 1$, $b = 3$, $\mu = 0$, and $\nu = 0.05$. A minimum number of rounds is needed. (D) $c = 1$, $b = 2$, $\mu = 0$, and $\nu = 0.5$. Both a minimum number of rounds and a minimum number of sets are needed to select against AIID.

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 that maximally supports evolution of cooperation (32).

Next we study how the condition for selecting against AIID depends on repetition and structure (Fig. 4). We make the following observations. For $b/c < 3$, even if the game is infinitely repeated, $m \rightarrow \infty$, we still need population structure to oppose AIID. 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 ($M \rightarrow \infty$), we still need repetition to oppose AIID. 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 AIID.

In summary, we have derived a simple, general condition that 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, the update rule, and mutation rates, but do not depend on the number of strategies or 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 describes that 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, and *iii*) extending our theory from pairwise interactions to multiplayer games. Finally our general result can be used to guide the exploration of many specific evolutionary processes.

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Supporting Information

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SI Text

Model and Results. We consider stochastic evolutionary dynamics (with mutation and selection) in a structured population of finite size N . Individuals adopt one of n strategies, and they obtain a payoff by interacting with other individuals according to the underlying population structure. For example, the population structure could imply that interactions occur only between neighbors on a graph (1), inhabitants of the same island, or individuals that share certain phenotypic properties (2). On the basis of these interactions, an average (or total) payoff is calculated according to the payoff matrix $A = (a_{ij})$. We assume that the payoff is linear in the payoff values a_{ij} , with no constant terms. For instance, the total payoff of an individual using strategy k is $\sum_i [a_{ki} \times (\text{number of } i\text{-interactants})]$. The effective payoff of an individual is given by $1 + w$ payoff, where by payoff we mean the player's total payoff. The parameter w denotes the intensity of selection. The limit of weak selection is given by $w \rightarrow 0$.

Reproduction is subject to symmetric mutation. With probability u the offspring adopts one of the n strategies at random. With probability $1 - u$ the offspring adopts the parent's strategy. For $u = 0$ there is no mutation, only selection. For $u = 1$ there is no selection, only mutation. If $0 < u < 1$, then there is mutation and selection.

We say that a strategy is selected for (or is favored by selection) if it is more abundant than the average, $1/n$, in the stationary distribution of the mutation–selection process:

$$\langle x_k \rangle > 1/n. \quad [\text{S1}]$$

We call this concept “strategy selection.” Here x_k is the frequency of strategy k . The angular brackets denote the average taken over all states of the system, weighted by the probability of finding the system in each state.

A state S of the population assigns to each player a strategy (k , with $k = 1, \dots, n$) and a “location” (in space, phenotype space, etc.). A state must include all information that can affect the payoffs of players. For our proof, we assume a finite state space. We study a Markov process on this state space. Because the state space is finite and because we have symmetric mutation, the process will have a unique stationary distribution. We denote by P_{ij} the transition probability from state S_i to state S_j . These transition probabilities depend on the update rule and on the effective payoffs of individuals. Because the effective payoff is of the form $1 + w$ payoff and the payoff is linear in the entries of A , it follows that the transition probabilities are functions $P_{ij}(wA)$. Now we can state our main result.

Theorem 1. Consider a population structure and an update rule (as described above) such that i) the transition probabilities are infinitely differentiable at $w = 0$ and ii) the update rule is symmetric for the n strategies. Then, in the limit of weak selection, the condition that strategy k is selected for is a two-parameter condition either of the form

$$\sigma_1(a_{kk} - \bar{a}_{**}) + (\bar{a}_{k*} - \bar{a}_{*k}) + \sigma_2(\bar{a}_{k*} - \bar{a}) > 0 \quad [\text{S2}]$$

or of the form

$$\sigma_1(a_{kk} - \bar{a}_{**}) + \sigma_2(\bar{a}_{k*} - \bar{a}) > 0 \quad [\text{S3}]$$

where σ_1 and σ_2 are unique and depend on the model and the dynamics (population structure, update rule, and the mutation rates) but not on the entries of the payoff matrix, a_{ij} . Moreover, the

parameters σ_1 and σ_2 do not depend on the number of strategies. They are intrinsic to the model and the dynamics and they are the same for any number of strategies $n \geq 3$.

Because σ_1 and σ_2 do not depend on the number of strategies, it follows that for calculating them it suffices to study $n = 0$ strategies. That is already the most general case. The case $n = 2$ is special because then the expressions $a_{kk} - \bar{a}_{**}$, $\bar{a}_{k*} - \bar{a}_{*k}$, and $\bar{a}_{k*} - \bar{a}$ are not linearly independent.

Let us now discuss the two assumptions.

Assumption i. The transition probabilities are differentiable at $w = 0$.

We require the transition probabilities $p_{ij}(wA)$ to have first-order Taylor expansions at $w = 0$. Examples of update rules that satisfy Assumption i include the death–birth (DB) and birth–death (BD) updating on graphs (1), the synchronous updating on the basis of the Wright–Fisher process (2, 3), and the pairwise comparison (PC) process (4). If a game does not satisfy this property, then its solutions near $w = 0$ are not well behaved, and it becomes difficult to even define the game's action in the limit of weak selection.

Assumption ii. The update rule is symmetric for the n strategies. The update rule differentiates between the n strategies only on the basis of payoff. Arbitrarily relabeling the n strategies and correspondingly swapping the entries of the payoff matrix must yield symmetric dynamics. This statement says that the difference between the n strategies is fully captured by the payoff matrix, whereas the population structure and the update rule do not introduce any additional differences.

Proof of Theorem 1. Consider an evolutionary game with n competing strategies, whose interactions are given by the matrix $A = (a_{ij})$. The dynamics describe a Markov process, which, by assumption, has transition probabilities differentiable at $w = 0$. We want to study the stationary distribution of this Markov process. As above, we let x_k be the frequency of strategy k . The average frequency over the stationary distribution is denoted by $\langle x_k \rangle$. We say that strategy k is selected for if its abundance (average frequency) is greater than the average, $1/n$, as described by ref. 2. Using the same argument as in ref. 5, we know that the abundances are differentiable at $w = 0$ and thus we can write their first-order Taylor expansions:

$$\langle x_k \rangle = \langle x_k \rangle_0 + w \frac{\partial \langle x_k \rangle}{\partial w} \Big|_{w=0}. \quad [\text{S4}]$$

Here $\langle x_k \rangle_0$ denotes the average abundance of strategy k at neutrality. When $w = 0$, all strategies have equal payoffs and using the second assumption of our theorem, we conclude that all strategies must have equal abundances $\langle x_k \rangle_0 = 1/n$ for all k . Because every strategy has the same abundance at $w = 0$, the relative success of the strategies in the limit as w tends to 0 is determined by the first derivative of their abundances. Hence, strategy k is selected for if

$$\mathcal{R}_k := \frac{\partial \langle x_k \rangle}{\partial w} \Big|_{w=0} > 0. \quad [\text{S5}]$$

Here

$$\langle x_k \rangle = \sum_S x_{k,S} \pi_S, \quad [\text{S6}]$$

where π_S is the probability that the system is in a given state S and $x_{k,S}$ is the frequency of strategy k in state S . For our types of processes, these probabilities were shown in ref. 5 to be continuous and differentiable at $w = 0$. Moreover, the same paper shows that the the first-order derivative of these probabilities

with respect to w evaluated at $w = 0$ depends linearly on a_{ij} and has no constant terms. Hence we conclude that \mathcal{R}_k depends linearly with no constant terms on a_{ij} . Then strategy k is selected for if and only if

$$\sum_{i=1}^n \sum_{j=1}^n c_{kij} a_{ij} > 0, \quad [\text{S7}]$$

where each c_{kij} is a constant.

Next we use our assumption that the type labeling is immaterial, to reduce the total number of constants we must consider. Because we know that permuting the labeling system with any bijection $\pi, \{1, \dots, n\} \rightarrow \{1, \dots, n\}$ does not change the operation of the game, we must have that $c_{\pi(kij)} = c_{kij}$ for any such permutation π . 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 five different equivalence classes: $k = i = j$, $k = i \neq j$, $k = j \neq i$, $i = j \neq k$, and $i \neq j \neq k \neq i$. Each ordered triple belongs to one of these five equivalence classes. Thus, the game depends on only the five constants associated to each of these possibilities. That is, we can write

$$\mathcal{R}_k = \alpha a_{kk} + \beta \bar{a}_{k*} + \gamma \bar{a}_{*k} + \delta \bar{a}_{**} + \varepsilon \bar{a} \quad [\text{S8}]$$

for some constants $\alpha, \beta, \gamma, \delta$, and ε . However, because x_k are frequencies, they must sum up to 1. Hence the sum of the \mathcal{R}_k must be 0:

$$0 = \sum_{k=1}^n \mathcal{R}_k = n(\alpha + \delta) \bar{a}_{**} + n(\beta + \gamma + \varepsilon) \bar{a}. \quad [\text{S9}]$$

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

$$\mathcal{R}_k = \lambda_1 (a_{kk} - \bar{a}_{**}) + \lambda_2 (\bar{a}_{k*} - \bar{a}_{*k}) + \lambda_3 (\bar{a}_{k*} - \bar{a}) > 0, \quad [\text{S10}]$$

for $\lambda_1 := \alpha$, $\lambda_2 := -\gamma$, and $\lambda_3 := -\varepsilon$. These parameters depend on the structure and the dynamics, as well as on the number of strategies, n . However, next we show that this condition can be further simplified.

Next we show that the condition can be put in the form given by either Eq. S2 or Eq. S3, where σ_1 and σ_2 do not depend on the number of strategies.

Instead of playing the game with n strategies, let us play it with mn strategies, where each one of the previous n strategies is replaced by m copies of itself. Due to the fact that we mutate to any other strategy equally likely, this change will not affect the relative ranking of strategies. Its only effect will be that now the abundance of strategy k from the initial game is m times larger than any one of the abundances of its m copies. Let $x_k^{(s)}$ and $\mathcal{R}_k^{(s)}$ be, respectively, the frequency and the derivative evaluated at 0 of the frequency of strategy k in the game with s strategies. So we can write

$$x_k^{(n)} = \frac{1}{n} + w \mathcal{R}_k^{(n)}, \quad x_k^{(mn)} = \frac{1}{mn} + w \mathcal{R}_k^{(mn)}, \quad \text{and} \quad x_k^{(mn)} = \frac{1}{m} x_k^{(n)}. \quad [\text{S11}]$$

Thus, $\mathcal{R}_k^{(n)} = m \mathcal{R}_k^{(mn)}$. Noting that the pairwise comparisons $a_{kk} - \bar{a}_{**}$, $\bar{a}_{k*} - \bar{a}_{*k}$, and $\bar{a}_{k*} - \bar{a}$ are the same for both games, we conclude that $\lambda_i(n) = m \lambda_i(mn)$ for all integers $n, m \geq 1$. Switching the roles of m and n we obtain the symmetric relationship so that $\lambda_i(m) = n \lambda_i(mn)$ for all $n, m \geq 1$. Combining these two equations one can write $n \lambda_i(n) = nm \lambda_i(nm) = m \lambda_i(m)$

$\forall m, n \geq 1$. Thus, setting $m = 3$, we obtain $n \lambda_i(n) = 3 \lambda_i(3)$. Hence the condition (Eq. S10) that strategy k is selected for becomes

$$\frac{3}{n} [\lambda_1(3)(a_{kk} - \bar{a}_{**}) + \lambda_2(3)(\bar{a}_{k*} - \bar{a}_{*k}) + \lambda_3(3)(\bar{a}_{k*} - \bar{a})] > 0. \quad [\text{S12}]$$

Denoting by $\sigma_1 = \lambda_1(3)/\lambda_2(3)$ and by $\sigma_1 = \lambda_3(3)/\lambda_2(3)$ and dividing by $3/n \lambda_2(3)$ we can write the final condition that strategy k is selected for,

$$\sigma_1 (a_{kk} - \bar{a}_{**}) + (\bar{a}_{k*} - \bar{a}_{*k}) + \sigma_2 (\bar{a}_{k*} - \bar{a}) > 0, \quad [\text{S13}]$$

where the σ_i do not depend on the number of strategies n . This is condition [S2].

If, for certain processes, $\lambda_2(3) = 0$, then we simply divide by $3/n$ above and let $\sigma_1 = \lambda_1(3)$ and $\sigma_2 = \lambda_3(3)$ and write the condition for strategy k to be selected for as

$$\sigma_1 (a_{kk} - \bar{a}_{**}) + \sigma_2 (\bar{a}_{k*} - \bar{a}) > 0. \quad [\text{S14}]$$

This is condition [S3]. This concludes our proof.

Low Mutation. In the limit of low mutation, the population spends most of the time in a homogeneous state. When a mutant arises, it rapidly either goes to fixation or dies out. In both cases, we return to a homogeneous population. Because we assume that all mutants are equally likely to arise, the steady-state frequency distribution of strategies is given by the eigenvector with eigenvalue 1 of the transition matrix P . In the limit of low mutation, the transition probabilities P_{ij} are given by the fixation probabilities. Thus, $P_{ij} = \rho_{ij}$, which is the fixation probability of a strategy i mutant into a population of j players. Similarly, $P_{ii} = 1 - 1/(n-1) \sum_{j \neq i} \rho_{ji}$.

In the limit of weak selection, we can write the first-order Taylor expansion of the fixation probability ρ_{ij} as

$$\rho_{ij} = \frac{1}{N} + w \gamma_{ij}. \quad [\text{S15}]$$

This holds because at neutrality, all mutants in a population of size N have the same probability to fixate, $1/N$. Using this together with the Taylor expansion [S4] of the frequencies x_k , the solving for the eigenvector of P of eigenvalue 1 becomes

$$\left(\dots, \frac{1}{n} + w \mathcal{R}_k, \dots \right)^t = \left(\frac{1}{N} + w \gamma_{ij} \right) \left(\dots, \frac{1}{n} + w \mathcal{R}_k, \dots \right)^t. \quad [\text{S16}]$$

It immediately follows that

$$\mathcal{R}_k \sim \sum_i (\gamma_{ki} - \gamma_{ik}) = \sum_i (\rho_{ki} - \rho_{ik}). \quad [\text{S17}]$$

Thus, in low mutation, only the pairwise comparisons between the fixation probabilities of strategies matter. Ref. 5 shows that in the limit of low mutation

$$\rho_{ki} - \rho_{ik} \sim \sigma_0 a_{kk} + a_{ki} - a_{ik} - \sigma_0 a_{ii}, \quad [\text{S18}]$$

where σ_0 is the low mutation limit of the structure coefficient σ that characterizes games between two strategies. Thus, to study games on structured populations with several strategies, in the limit of low mutation and weak selection, it suffices to know the structure coefficient for games with two strategies. The condition for several strategies then becomes

$$\sigma_0(a_{kk} - \bar{a}_{**}) + (\bar{a}_{k*} - \bar{a}_{*k}) > 0. \quad [\text{S19}]$$

Connection to Previous Results. Games with two strategies in structured populations. Suppose we restrict ourselves to the case where there are only $n = 2$ distinct strategies. In this case the term \bar{a} becomes

$$\bar{a} = \frac{1}{4}(a_{11} + a_{12} + a_{21} + a_{22}) = \frac{1}{2}(\bar{a}_{k*} + \bar{a}_{*k} + \bar{a}_{**} - a_{kk}) \quad [\text{S20}]$$

for $k = 1, 2$. A quick check also confirms that

$$\bar{a}_{k*} - \bar{a} = \frac{1}{2}(a_{kk} - \bar{a}_{**}) + \frac{1}{2}(\bar{a}_{k*} - \bar{a}_{*k}), \quad [\text{S21}]$$

which means that we may equivalently rewrite the equation in Theorem 1 as

$$(\sigma_1 + \sigma_2/2)(a_{kk} - \bar{a}_{**}) + (1 + \sigma_2/2)(\bar{a}_{k*} - \bar{a}_{*k}) > 0. \quad [\text{S22}]$$

Supposing $1 + \sigma_2/2$ is positive, we may divide by it to yield

$$\frac{\sigma_1 + \sigma_2/2}{1 + \sigma_2/2}(a_{kk} - \bar{a}_{**}) + \bar{a}_{k*} - \bar{a}_{*k} > 0. \quad [\text{S23}]$$

[This occurs only if strategy 1 is favored under the matrix $\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}$. This condition essentially requires just that strategies with higher payoffs do better; see Tarnita et al. (5) for further discussion.]

Defining $\sigma := \frac{\sigma_1 + \sigma_2/2}{1 + \sigma_2/2}$ and rearranging, we get that strategy 1 is favored if

$$\sigma a_{11} + a_{12} > a_{21} + \sigma a_{22}, \quad [\text{S24}]$$

which is the result for two strategies proved in ref. 5.

Games with multiple strategies in well-mixed populations. Consider a well mixed population with N individuals playing n strategies. Ref. 6 showed that if we fix $\mu := Nu$ but let N tend to infinity, then in the limit of weak selection the strategy k is favored if

$$a_{kk} - \bar{a}_{**} + \bar{a}_{k*} - \bar{a}_{*k} + \mu(\bar{a}_{k*} - \bar{a}) > 0. \quad [\text{S25}]$$

Checking, we see that this is a special case of Theorem 1 with $\sigma_1 = \sigma_2 = 1$ and $\sigma_3 = \mu$.

To derive this result, the authors of ref. 6 explicitly computed the probabilities with which individual strategies interact and how these interactions affect the abundance of each strategy. Theorem 1 predicts the form of the general condition; however, the specific values must still be calculated explicitly. Theorem 1 also predicts extensions and generalizations of this result. For example, whereas the result in ref. 6 is only for the limit of large N , we now know that for any fixed, finite N we must have a similar result, although the values of σ_1 and σ_2 may be more complex.

Global Updating Formula. Here we derive formulas for the sigma coefficients that hold for all processes satisfying two conditions: *i*) *global updating*, which means individuals compete uniformly with all others for reproduction, and *ii*) *constant birth or death rate*, which means the payoff from the game can affect either the birth rate or the death rate but not both.

These assumptions are fulfilled, for example, by games in phenotype space (2) and by games on sets (3). They do not hold, however, for games on graphs (1). The first assumption is necessary because our calculation requires that the update rule depends only on fitness and not on locality. Local update rules are less well behaved. The second assumption ensures that the change in the frequency of players is due only to a change in

selection. Without this second assumption the conditions would be more complicated.

Such a dynamic is very special: Payoff is obtained through local interactions, according to the structure, but reproduction is global, like in a well-mixed population. Thus, if condition *ii* also holds, the dynamics can be described by a replicator equation, where the change in the frequency of type k is given as $\dot{x}_k = x_k(f_k - f^{\text{tot}})$. Here f_k is the effective payoff of an individual using strategy k and $f^{\text{tot}} = \sum_i f_i$ is the total effective payoff in the population. Using the fact that $f_i = 1 + wp_i$ where p_i is the payoff of an individual playing strategy i , we can rewrite the replicator equation as $\dot{x}_k = wx_k(p_k - p^{\text{tot}})$. Here p^{tot} is the total payoff in the population. Because p_k is the payoff of an individual of strategy k , then $x_k p_k = p_k^{\text{tot}}$ is the total payoff of strategy k and we can write $\dot{x}_k = w(p_k^{\text{tot}} - p^{\text{tot}})$. The condition that strategy k is favored by selection is that on average, over the stationary distribution of the mutation–selection process, there is a positive change in its frequency $\langle \dot{x}_k \rangle > 0$. In the limit of weak selection, one can write the first-order Taylor expansion of this inequality to obtain $\langle \dot{x}_k \rangle = \langle \dot{x}_k \rangle_0 + w \left\langle \frac{\partial}{\partial w} \dot{x}_k \right\rangle_0 > 0$. Now the averages are taken at neutrality, $\delta = 0$. Because at neutrality all strategies have equal frequency, the condition for strategy k to be favored in the limit of weak selection becomes $\left\langle \frac{\partial}{\partial w} \dot{x}_k \right\rangle_0 > 0$. This result is equivalent to

$$\langle p_k^{\text{tot}} - p^{\text{tot}} \rangle_0 > 0. \quad [\text{S26}]$$

The only difference between this replicator equation and the typical one used for well-mixed populations is that the interactions are given by the underlying structure (sets, phenotype, and dynamical networks). To describe the payoff under these circumstances, let us introduce the following notation. For each state of the system, let N_k be the number of individuals using strategy k . Furthermore, let I_{ij} denote the total (weighted) number of interactions that i individuals have with j individuals. Note that every $i - i$ pair is counted twice because each i individual in the pair has an encounter with another i individual. Then the payoff of strategy k in the population is given by $p_k^{\text{tot}} = \sum_j a_{kj} I_{kj}$ and the total payoff in the population is given by $p^{\text{tot}} = \sum_{k,j} a_{kj} I_{kj}$. Plugging these into Eq. S6 and collecting terms, we find that up to the same constant factor, the λ_i are proportional to

$$\begin{aligned} \lambda_1 &\propto \langle x_k I_{ij} \rangle_0 - \langle x_k I_{ij} \rangle_0 \\ \lambda_2 &\propto \langle x_k I_{jk} \rangle_0 - \langle x_k I_{ij} \rangle_0 \\ \lambda_3 &\propto n \langle x_k I_{ij} \rangle_0 \end{aligned} \quad [\text{S27}]$$

with $i \neq j \neq k \neq i$. This result then yields the values for σ_1 and σ_2 .

A different, more rigorous derivation of these results can be given along the lines of ref. 7.

Games on sets. Consider a population of N individuals distributed over M islands. The sets could be geographical islands but they could also be phenotypic traits or tags. Two individuals interact only if they are on the same island (have the same tag).

The system evolves according to global updating. At each time step, one individual is picked to die and an individual is picked proportional to payoff to reproduce. The offspring inherits the strategy of the parent with probability $1 - u$ and picks a random one with probability u . Moreover, the offspring inherits the tag or the location of the parent with probability $1 - v$ or chooses a random tag with probability v . Thus, there is a strategy mutation rate u and a set mutation rate (or migration rate) v . This system has been studied for only two strategies by refs. 2 and 3. Here we show what happens when the N individuals can choose to play one of n strategies.

Let x_{i*} be the fraction of individuals using strategy i ; let x_{il} be the fraction of individuals using strategy i and belonging to island l ; and finally, let x_{*l} be the total number of individuals in set l . Here i can take values from 1 through n and l can take values from 1 through M . Then, we can use our global updating formula where the total number of interactions between individuals having strategy i and individuals having strategy j is given by

$$I_{ij} = \sum_{l=1}^M x_{il}x_{jl}. \quad [\text{S28}]$$

Then it immediately follows that

$$\begin{aligned} \lambda_1 &\propto \langle x_{k*}x_{jl}^2 \rangle_0 - \langle x_{k*}x_{il}x_{jl} \rangle_0 \\ \lambda_2 &\propto \langle x_{k*}x_{kl}x_{jl} \rangle_0 - \langle x_{k*}x_{il}x_{jl} \rangle_0 \\ \lambda_3 &\propto \langle x_{k*}x_{il}x_{jl} \rangle_0, \end{aligned} \quad [\text{S29}]$$

One can interpret these quantities as follows. Pick three individuals at random. Then $\langle x_{k*}x_{jl}^2 \rangle_0$ is the probability that two of them are on the same island and have the same strategy, different from the third's; $\langle x_{k*}x_{il}x_{jl} \rangle_0$ is the probability that two of them are on the same island and all three have different strategies; and finally, $\langle x_{k*}x_{kl}x_{jl} \rangle_0$ is the probability that two have the same strategy, different from the third's, and the other two are on the same island.

To calculate these quantities we use the same method of the coalescent described in refs. 2, 3, 6, and 8. We fix the time τ to the most recent common ancestor and account for what could have happened since then. We perform the calculations in the limit of large population size N . The three important quantities are the probability $s_2(\tau)$ that two individuals have the same strategy, the probability $z_2(\tau)$ that two individuals are on the same island, and the probability $s_3(\tau)$ that three individuals have the same strategy at time τ after their most recent common ancestor. Following the trajectory of individuals back in time, we see that strategy mutations happen at rate $\mu/2 = N\mu/2$ and island migrations happen at rate $\nu/2 = N\nu/2$ to each trajectory.

The coalescence time is described by the density function $p_2(\tau) = e^{-\tau}$. Immediately after the coalescence of two players, they are identical with respect to both island and strategy. To find out what is the probability that they still have the same strategy at time τ afterward, we proceed as follows: With probability $e^{-\mu\tau}$ neither one mutated and hence they have the same strategy; otherwise at least one of them mutated and hence they have the same strategy with probability $1/n$. A similar derivation occurs for the island migration. Thus, we can write

$$s_2(\tau) = e^{-\mu\tau} + \frac{1 - e^{-\mu\tau}}{n} z_2(\tau) = e^{-\nu\tau} + \frac{1 - e^{-\nu\tau}}{M}. \quad [\text{S30}]$$

To find the probability that three individuals have the same strategy requires a little more but similar work. This calculation has already been done in Antal et al. (2) and we can write

$$s_3(\tau_2, \tau_3) = \frac{1}{n^2} [s_2(\tau_2)(1 + 3(n-1)e^{-\mu\tau_3} + (n-1)(n-2)e^{-3/2\mu\tau_3}) + (1 - s_2(\tau_2))(1 + (n-3)e^{-\mu\tau_3} - (n-2)e^{-3/2\mu\tau_3})]. \quad [\text{S31}]$$

Here τ_3 is the time to the first coalescence event and τ_2 is the time from between the first and the last coalescence events. The probability density function that describes this coalescence event is $p_3(\tau_2, \tau_3) = 3e^{-\tau_2 - 3\tau_3}$. Having derived these quantities, one can immediately calculate some quantities of interest as follows:

$$\begin{aligned} \langle x_{kl}^2 \rangle_0 &= \int_0^\infty p_2(\tau) s_2(\tau) z_2(\tau) d\tau \\ \langle x_{k*}x_{jl}^2 \rangle_0 &= \frac{1}{3} \int_0^\infty \int_0^\infty p_3(\tau_2, \tau_3) s_3(\tau_2, \tau_3) [z_2(\tau_3) + z_2(\tau_2 + \tau_3) + z_2(\tau_2 + \tau_3)] d\tau_2 d\tau_3 \\ \langle x_{k*}x_{kl}x_{*l} \rangle_0 &= \frac{1}{3} \int_0^\infty \int_0^\infty p_3(\tau_2, \tau_3) [s_2(\tau_3) z_2(\tau_2 + \tau_3) + s_2(\tau_2 + \tau_3) z_2(\tau_3) + s_2(\tau_2 + \tau_3) z_2(\tau_2 + \tau_3)] d\tau_2 d\tau_3. \end{aligned} \quad [\text{S32}]$$

The other quantities can be easily found by symmetry as

$$\begin{aligned} \langle x_{k*}x_{kl}x_{il} \rangle_0 &= \frac{1}{n-1} (\langle x_{k*}x_{kl}x_{*l} \rangle_0 - \langle x_{k*}x_{kl}^2 \rangle_0) \\ \langle x_{k*}x_{il}x_{jl} \rangle_0 &= \frac{1}{n-2} (\langle x_{kl}x_{il} \rangle_0 - 2\langle x_{k*}x_{kl}x_{il} \rangle_0), \end{aligned} \quad [\text{S33}]$$

where for the first equality we used the fact that $x_{il} = x_{*l} - \sum_{j \neq i} x_{jl}$ and for the second one we used the fact that $x_{k*} = \sum_j x_{kj}$. Finally, we obtain

$$\begin{aligned} \lambda_1 &\propto (1 + \nu)(3 + \mu + \nu)(M(2 + \mu)(3 + 3\mu + 2\nu) + \nu(4 + 3\mu + 2\nu)) \\ \lambda_2 &\propto M(2 + \mu)(9 + 3\mu(4 + \mu) + 6\nu + 5\mu\nu + \nu^2) + \nu(3\mu^3 + 2(2 + \nu)(3 + \nu)^2 + \mu^2(21 + 8\nu) + \mu(49 + \nu(38 + 7\nu))) \\ \lambda_3 &\propto \mu [M(2 + \mu)(9 + 3\mu(4 + \mu) + 7\nu + 5\mu\nu + 2\nu^2) + \nu(34 + 3\mu^3 + 40\nu + 2\nu^2(8 + \nu) + \mu(3 + \nu)(16 + 7\nu) + \mu^2(21 + 8\nu))]. \end{aligned} \quad [\text{S34}]$$

Because $\lambda_2 \neq 0$, one immediately finds $\sigma_1 = \lambda_1/\lambda_2$ and $\sigma_2 = \lambda_3/\lambda_2$. **Repetition and structure.** We now use these results to study a particular game on sets. Our game is meant to capture the essential problem of evolution of cooperation based on direct reciprocity. We consider three strategies: always cooperate (AllC), always defect (AllD), and tit-for-tat (TFT). We assume there is a repeated interaction between any two players subject to a certain continuation probability; the average number of rounds is given by m . We have the following payoff matrix:

	AllC	AllD	TFT
AllC	$m(b-c)$	$-mc$	$m(b-c)$
AllD	mb	0	b
TFT	$m(b-c)$	$-c$	$m(b-c)$

We find the condition for AllD to be selected against and note that there are parameter regions where one needs both structure and repetition to select against defection. Neither one can do it on its own. We can solve for the asymptotes; for simplicity, here we give only the low strategy mutation limit. Let $m_{M \rightarrow \infty}$ be the horizontal asymptote (the required number of repetitions) and let $M_{m \rightarrow \infty}$ be the vertical asymptote (the required number of sets). Then, for low mutation

$$\begin{aligned} m_{M \rightarrow \infty} &= \frac{(\frac{b}{c} + 1)(3 + \nu)}{\frac{b}{c}(3 + 9\nu + 4\nu^2) - 9 - 11\nu - 4\nu^2} \\ M_{m \rightarrow \infty} &= \frac{\nu(2 + \nu)(-\frac{b}{c}(-1 + \nu) + 5 + 3\nu)}{\frac{b}{c}(3 + 9\nu + 4\nu^2) - 9 - 11\nu - 4\nu^2}. \end{aligned} \quad [\text{S35}]$$

The condition for repetition to be needed is $m_{M \rightarrow \infty} > 1$, which yields

$$\frac{b}{c} < 1 + \frac{\nu + 3}{\nu(\nu + 2)}. \quad \text{[S36]}$$

The condition for structure to be needed is $M_{m \rightarrow \infty} > 1$, which yields

$$\frac{b}{c} < 3. \quad \text{[S37]}$$

Thus, the condition for both structure and repetition to be needed is

$$\frac{b}{c} < \min \left\{ 3, 1 + \frac{\nu + 3}{\nu(\nu + 2)} \right\}. \quad \text{[S38]}$$

This parameter region captures a very realistic situation because most games are played for small values of benefit relative to cost.

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