

Evolution of cooperation by multilevel selection

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We propose a minimalist stochastic model of multilevel (or group) selection. A population is subdivided into groups. Individuals interact with other members of the group in an evolutionary game that determines their fitness. Individuals reproduce, and offspring are added to the same group. If a group reaches a certain size, it can split into two. Faster reproducing individuals lead to larger groups that split more often. In our model, higher-level selection emerges as a byproduct of individual reproduction and population structure. We derive a fundamental condition for the evolution of cooperation by group selection: if $b/c > 1 + n/m$, then group selection favors cooperation. The parameters b and c denote the benefit and cost of the altruistic act, whereas n and m denote the maximum group size and the number of groups. The model can be extended to more than two levels of selection and to include migration.

finite populations | prisoner's dilemma | group selection | fixation probability | stochastic process

Competition between groups can lead to selection of cooperative behavior. This idea can be traced back to Charles Darwin, who wrote in 1871: "There can be no doubt that a tribe including many members who...were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over other tribes; and this would be natural selection" (1). The first mathematical model of group selection was proposed in 1945 by Sewall Wright (2). The enthusiastic attempt of early group selectionists to understand all of the evolution of altruism from this one perspective (3, 4) has led to vigorous criticism and a general denial of such ideas for decades (5–8). Only a small number of biologists continued to work in this area (9–19). Over many years, D. S. Wilson was the main proponent of the idea of group selection (20–22). Nowadays, there seems to be a renewed interest in the subject, as demonstrated by many empirical and theoretical studies (23–28). The current analysis of group selection is also closely related to the attempt at understanding the simultaneous effect of natural selection on multiple-levels (29–31). In our opinion, group selection is an important organizing principle that permeates evolutionary processes from the emergence of the first cells to eusociality and the economics of nations.

Consider a population that is subdivided into groups. The fitness of individuals is determined by the payoff from an evolutionary game. Interactions occur between members of the same group. We model stochastic evolutionary dynamics. In any one time step, a single individual from the entire population is chosen for reproduction with a probability proportional to its fitness. The offspring is added to the same group. If the group reaches a critical size, n , it will divide into two groups with probability q . The members of the group are randomly distributed over the two daughter groups, see Fig. 1. With probability $1 - q$, the group does not divide, but a random individual of the group is eliminated. Therefore, n resembles the maximum number of individuals in a single group. The total number of groups is constant and given by m ; whenever a group divides, another group is eliminated. These assumptions ensure that the total population size is constrained between a lower bound, m , and an upper bound, mn .

Our simple model has some interesting features. The entire evolutionary dynamics are driven by individual fitness. Only individuals are assigned payoff values. Only individuals reproduce. Groups can stay together or split (divide) when reaching a certain size. Groups that contain fitter individuals reach the critical size faster and, therefore, split more often. This concept leads to selection among groups, although only individuals reproduce. The higher-level selection emerges from lower-level reproduction. Remarkably, the two levels of selection can oppose each other.

Any evolutionary game can be analyzed in our framework, but here, we focus on the interaction between cooperators and defectors. Cooperators pay a cost, c , which ensures that other members of the same group receive a benefit, b . Defectors pay no cost and provide no benefit. Defectors benefit from cooperators that are present in the same group. In any mixed group, defectors have a higher payoff than cooperators. In homogeneous groups, however, cooperators have a higher payoff than defectors. This tension might allow for the evolution of cooperation. Our aim is to calculate the associated fixation probabilities. Therefore, we study the effect of population structure on pure selection dynamics.

Imagine that a single cooperator is added to a population of defectors. What is the probability, ρ_C , that this cooperator gives rise to a lineage that replaces all defectors and takes over the entire population? As long as the cooperators exist in mixed groups, the odds are against them, but, if by chance, a homogeneous cooperator group arises, then the emerging higher-level selection works for them. Conversely we can also calculate the fixation probability, ρ_D , of a single defector that is added to a population of cooperators. Here, the situation is reversed. The invading defectors are initially favored by individual selection in mixed groups but, later, opposed by the emerging higher-level selection among homogeneous groups. We argue that selection favors cooperation if the fixation probability ρ_C is greater than the inverse of the population size, which is greater than ρ_D .

In general, even our very simple model is too complicated to allow an exact calculation of the fixation probabilities. We can make progress, however, by assuming that splitting of groups occurs only very rarely (small q). Then, most groups are at their maximum carrying capacity and consist of only cooperators or only defectors when they split. Therefore, the fixation probability is simply the product of the fixation probability of a single individual in a group times the fixation probability of this group in the population. In this limit, the model becomes a hierarchy of two Moran processes, one for individuals and one for groups. A similar setup was studied by Paulsson (31) in the context of plasmid replication in bacteria.

For the fixation probability of one cooperator in a group of $n - 1$ defectors, we obtain $\phi_C = [1/n] \cdot [1 - (b + cn - c)w/2]$. For the fixation probability of one cooperator group in a population of $m - 1$ defector groups, we obtain $\Phi_C = [1/m] \cdot [1 + (b - c)(m - 1)w/2]$. The intensity of selection is given by the

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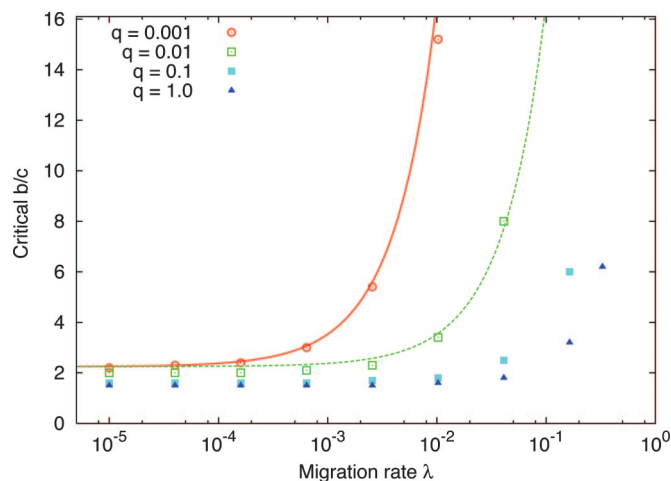


Fig. 3. The critical benefit-to-cost ratio, b/c , where cooperators and defectors have the same fixation probability, is shown as a function of the migration rate λ . After each reproductive event, the offspring can move to another group (with probability λ) or stay in the same group (with probability $1 - \lambda$). The simulations for $q = 10^{-3}$ (open circles) and $q = 10^{-2}$ (filled squares) agree well with the theory (shown as solid and dashed lines, respectively) for weak selection, $w \ll 1$, and small splitting probabilities, $q \ll 1$, given by $b/c > 1 + (n + m - z)/(m - 2 - z/n)$; see Eq. 34 in Supporting Text. Simulations for $q = 1$ show that cooperators can be favored even for higher migration rates if groups split rapidly (parameters: $m = 10$, $n = 10$, $w = 0.1$).

We can relax the assumption that groups represent perfect boundaries and allow for some migration of individuals between groups. Migration can be seen as “noise” of group selection. At any one time step, there is a (small) probability, λ , that a random individual moves to another group. Migration enables defectors to invade and take over groups of cooperators. The reverse is also possible but less likely. Including migration, cooperators are favored over defectors provided

$$\frac{b}{c} > 1 + z + \frac{n}{m}. \quad [2]$$

The benefit-to-cost ratio has to exceed the same term as before plus the average number of migrants $z = \lambda/q$ arising from one group during its lifetime. (The lifetime of a group is defined as the time between the foundation of the group and its elimination caused by the splitting of another group.) Again, Eq. 2 holds in the limit of weak selection, $w \ll 1$, and rare group splitting, $q \ll 1$. We have also assumed that $m \gg 1$; the condition for any m is shown in Supporting Text. For $m \gg n$, Eq. 2 means that the benefit-to-cost ratio must exceed one plus the average number of migrants arising from one group. Fig. 3 again illustrates the excellent agreement between our theory and numerical data from computer simulations.

We can extend our analysis to more than two levels of selection. On the lowest level, there is frequency-dependent selection between cooperators and defectors. On all higher levels, there is constant selection between groups, groups of groups (metagroups), and so on. If there are h levels of selection with population sizes m_1, \dots, m_h , then we find that a single cooperator is an advantageous mutant if

$$\frac{b}{c} > 1 + \frac{m_1}{-h + \sum_{i=2}^h m_i}. \quad [3]$$

This result holds for weak selection on all levels and ignoring migration. For $h = 2$, we recover our earlier finding. Note that Eq. 3 implies, for example, that $h = 2$ levels of selection with $m_2 = 6$ groups have the same effect as $h = 3$ levels of selection with $m_2 = 3$ groups and $m_3 = 4$ metagroups.

There is a long-standing tradition of comparing group selection with kin selection (7, 29, 30, 32–39), and, often, the distinction between these two approaches is blurred. Our present model can be interpreted as describing purely cultural evolution: Groups consist of genetically unrelated individuals, and successful groups attract new individuals, which learn the strategies of others in the same group. For this interpretation, kin selection seems to be inappropriate. But our model can also be interpreted as describing genetic evolution, in which case, the members of the same group could be said to be more related than members of different groups, and the machinery of kin selection might apply. It would be interesting to see how the mathematical methods of kin selection can be used to derive our central results given by Eqs. 1–3 and what assumptions are needed for such a derivation. The problem is that the typical methods of kin selection are based on traditional considerations of evolutionary stability, which are not decisive for games in finite populations (40).

In summary, we have presented a minimalist model of multilevel selection that allows the analytic calculation of a critical benefit-to-cost ratio of the altruistic act required for the evolution of cooperation. If $b/c > 1 + n/m$, then a single cooperator has a fixation probability that is greater than the inverse of the population size, and a single defector has a fixation probability that is less than the inverse of the population size. Hence, this simple condition ensures that selection favors cooperators and opposes defectors. The condition holds in the limit of weak selection and rare group splitting. The parameters n and m denote the maximum group size and the number of groups. If we include migration, the fundamental condition becomes $b/c > 1 + z + n/m$, where z is the average number of migrants arising from one group during its lifetime. These simple conditions have to hold for the group selection of altruistic behavior.

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Supporting Text

1. Frequency-Dependent Selection in a Single Group

Consider a Prisoner's Dilemma with the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array}. \quad [1]$$

We have $T > R > P > S$. Consider a group of size n with i cooperators and $n - i$ defectors. The fitness of cooperators and defectors are, respectively,

$$f(i) = 1 - w + w \frac{R(i - 1) + S(n - i)}{n - 1} \quad [2]$$

$$g(i) = 1 - w + w \frac{Ti + P(n - i - 1)}{n - 1}. \quad [3]$$

The parameter w measures the contribution of the game to the fitness (the intensity of selection). In each time step, an individual is chosen at random proportional to its fitness. It produces an identical offspring that replaces a randomly chosen individual. A single defector reaches fixation in a group of $n - 1$ cooperators with probability

$$\phi_D = \frac{1}{1 + \sum_{k=1}^{n-1} \prod_{i=1}^k \frac{f(n-i)}{g(n-i)}}, \quad [4]$$

see Refs. (1-3). The corresponding fixation probability of a single cooperator is

$$\phi_C = \frac{1}{1 + \sum_{k=1}^{n-1} \prod_{i=1}^k \frac{g(i)}{f(i)}}. \quad [5]$$

For weak selection, $w \ll 1$, the fixation probabilities within the group reduce to (4)

$$\phi_D \approx \frac{1}{n} \left[1 + \frac{w}{6} \delta_D \right] \quad [6]$$

$$\phi_C \approx \frac{1}{n} \left[1 - \frac{w}{6} \delta_C \right], \quad [7]$$

where

$$\delta_D = (2T - 2R + P - S)n - (T - 4R + 2P + S) \quad [8]$$

and

$$\delta_C = (T - R + 2P - 2S)n + (T + 2R - 4P + S). \quad [9]$$

2. Multiple Groups

Consider now a population with m different groups, which all have a maximum size n . Therefore, the maximum population size is $N = mn$. Because each group must contain at least one individual, the minimum population size is m . In each time step, an individual is chosen from the entire population with a probability proportional to its fitness. This individual produces an identical offspring that is added to the same group. If the group size is greater than n after this step, then either a randomly chosen individual from the group is eliminated (with probability $1 - q$) or the group splits into two groups (with probability q). Each individual of the splitting group has probability $1/2$ to end up in each of the daughter groups. One daughter group remains empty with probability 2^{1-n} . In this case, the splitting process is repeated to avoid empty groups. In order to keep the number of groups constant, a randomly chosen group is eliminated whenever a group splits into two.

In the limit of small splitting probabilities, $q \ll 1$, two approximations can be made: (i) most groups have size n and (ii) most groups are homogeneous when they split. Hence, for $q \ll 1$ the fixation probability of a single defector, ρ_D , is the product of the fixation probability within the group, ϕ_D , and the fixation probability of the defector group in the whole population, Φ_D :

$$\rho_D = \phi_D \Phi_D. \quad [10]$$

Similarly, the fixation probability of a single cooperator, ρ_C , is the product of the fixation probability within the group, ϕ_C , and the fixation probability of the cooperator group, Φ_C :

$$\rho_C = \phi_C \Phi_C. \quad [11]$$

In the following, the fixation probabilities ρ_D and ρ_C are calculated for two different scenarios for $q \ll 1$. First, we study the basic process without migration, then we add migration. In both cases, we can derive simple equations for weak selection, $w \ll 1$.

2.1. No Migration

In homogeneous defector groups, individuals have fitness $g(0)$. In homogeneous cooperator groups, individuals have fitness $f(n)$. New defector groups arise when an individual from a defector group is selected for reproduction, and the group splits, replacing a cooperator group. Hence, the probability to decrease the number of cooperator groups from j to $j - 1$ is the product of these probabilities given by

$$P_{j,j-1} = q \frac{g(0)(m-j)}{f(n)j + g(0)(m-j)} \frac{j}{m}. \quad [12]$$

The number of cooperator groups grows from j to $j + 1$ with probability

$$P_{j,j+1} = q \frac{f(n)j}{f(n)j + g(0)(m-j)} \frac{m-j}{m}. \quad [13]$$

Although $q \ll 1$ is necessary for these assumptions, the value of q cancels in the following, because the fixation probabilities depend solely on the ratio $\Omega_j = P_{j,j-1}/P_{j,j+1} = g(0)/f(n)$. The fixation probability of a single defector group in a population of cooperator groups is given by

$$\Phi_D = \frac{1}{1 + \sum_{k=1}^{m-1} \prod_{j=1}^k (\Omega_{m-j})^{-1}}. \quad [14]$$

Similarly, the fixation probability of a single cooperator group is

$$\Phi_C = \frac{1}{1 + \sum_{k=1}^{m-1} \prod_{j=1}^k \Omega_j} \quad [15]$$

For weak selection, $w \ll 1$, we have $\Omega_j \approx 1 - (R - P)w$, and, therefore, the probabilities that a single defector group or a single cooperator group takes over the population are, respectively,

$$\Phi_D \approx \frac{1}{m} \left[1 - \frac{w}{2}(m-1)(R-P) \right] \quad [16]$$

and

$$\Phi_C \approx \frac{1}{m} \left[1 + \frac{w}{2}(m-1)(R-P) \right]. \quad [17]$$

Combining Eqs. **6** and **16** as well as **7** and **17**, the fixation probabilities for single defector and cooperator individuals are

$$\rho_D = \frac{1}{N} \left[1 + w \left(+\frac{\delta_D}{6} - \frac{m-1}{2}(R-P) \right) \right] \quad [18]$$

and

$$\rho_C = \frac{1}{N} \left[1 + w \left(-\frac{\delta_C}{6} + \frac{m-1}{2}(R-P) \right) \right]. \quad [19]$$

For $m = 1$, the Eqs. **18** and **19** reduce to the equations for a single group given by Eqs. **6** and **7**. For $m \geq 2$, the population structure determines which kind of individuals are advantageous; i.e., whether their fixation probability is higher than the fixation probability of a neutral mutant, $1/N$. For weak selection, cooperators are advantageous if the condition $\rho_C > 1/N$ holds. This leads to

$$(T - R + 2P - 2S)n < 3m(R - P) - (T + 5R - 7P + S). \quad [20]$$

On the other hand, defectors are advantageous, if $\rho_D > 1/N$. This inequality leads to

$$(2T - 2R + P - S)n > 3m(R - P) + (T - 7R + 5P + S). \quad [21]$$

Note that cooperators and defectors can be advantageous simultaneously. For example, for the payoff matrix $T = 5$, $R = 3$, $P = 1$, and $S = 0$ with $m = n = 8$ from Eqs. **20** and **21** we have $\rho_C > 1/N$ and $\rho_D > 1/N$. Therefore, it is interesting to ask when cooperators fixate with higher probability than defectors, $\rho_C > \rho_D$. This inequality leads to

$$n(T - R + P - S) < 2(m - 2)(R - P). \quad [22]$$

For the interpretation of this condition, it is convenient to rewrite the payoff matrix as

$$\begin{pmatrix} R & S \\ T & P \end{pmatrix} = \begin{pmatrix} b - c & -c \\ b & 0 \end{pmatrix}, \quad [23]$$

which describes a subset of all Prisoner's Dilemmas. Here, c is the cost of cooperation and b the benefit from cooperation. From Eq. **22** we find that cooperators will dominate defectors if

$$\frac{b}{c} > 1 + \frac{n}{m - 2}. \quad [24]$$

Interestingly, we note that $m = 2$ groups are not enough to favor cooperators over defectors, which can also be seen in Eq. **22**. The intuitive reason is described in Figure 4. Observe that smaller group sizes, n , and larger group numbers, m , favor cooperation. For the limit of many groups, $m \gg 1$, we obtain the simplified condition

$$\frac{b}{c} > 1 + \frac{n}{m}. \quad [25]$$

Note that the inequalities Eqs. **20** and **22** both lead to condition Eq. **24** with payoff matrix Eq. **23**, whereas Eq. **21** reduces to the opposite condition. Therefore, $b/c > 1 + n/m$ is equivalent to $\rho_C > 1/N > \rho_D$ (for large m , weak selection and rare group splitting).

2.2. Migration

Let us now introduce the possibility that individuals can migrate between groups. An offspring has the probability λ to migrate to a random group. If the new group exceeds the maximum size, n , after the arrival of the migrant, then a randomly chosen individual from the group is removed with probability $1 - q$. The arrival of the mutant leads to the splitting of the group with probability q .

If migration is rare, $\lambda \ll 1$, a migrant has either invaded the whole group or is eliminated before the next migration or group splitting takes place. Because $q \ll 1$ and $\lambda \ll 1$, migration processes in which the group is split occurring with probability λq are neglected. Defector groups arise when a member of a defector group produces an offspring that migrates to a cooperator group and reaches fixation. They also arise when a defector group splits and replaces a cooperator group. For $q \ll 1$ and $\lambda \ll 1$, groups are usually homogeneous when they split or when a new migrant arrives. Therefore, new defector groups arise with probability

$$P_{j,j-1} = \frac{1}{q + \lambda} \frac{g(0)(m-j)}{f(n)j + g(0)(m-j)} \frac{j}{m} [q + \lambda\phi_D]. \quad [26]$$

New cooperator groups emerge with probability

$$P_{j,j+1} = \frac{1}{q + \lambda} \frac{f(n)j}{f(n)j + g(0)(m-j)} \frac{m-j}{m} [q + \lambda\phi_C]. \quad [27]$$

The quotient of these two probabilities simplifies to

$$\Omega_j = \frac{P_{j,j-1}}{P_{j,j+1}} = \frac{g(0)}{f(n)} \frac{q + \lambda\phi_D}{q + \lambda\phi_C} \quad [28]$$

For weak selection, Ω_j can be written as $\Omega_j \approx 1 - \Gamma w$. Here, Γ is given by

$$\Gamma = \frac{n}{\lambda + qn} \left[q(R - P) - \frac{\lambda}{2} (T - R + P - S) \right] \quad [29]$$

For the fixation probabilities, we obtain

$$\rho_D = \frac{1}{N} \left[1 + w \left(+\frac{\delta_D}{6} - \frac{m-1}{2} \Gamma \right) \right] \quad [30]$$

and

$$\rho_C = \frac{1}{N} \left[1 + w \left(-\frac{\delta_C}{6} + \frac{m-1}{2} \Gamma \right) \right]. \quad [31]$$

Consider a population structure in which cooperators dominate, i.e., which fulfills the condition shown in Eq. **25**. Because migration favors defectors, there is a critical λ_c defined by $\rho_C = \rho_D$ for which cooperators no longer fixate with higher probability than defectors. The critical λ_c is given by

$$\lambda_c = nq \frac{2m - 4 + n \left(1 - \frac{T-S}{R-P} \right)}{2 - mn \left(1 - \frac{T-S}{R-P} \right)} \quad [32]$$

For payoff matrix Eq. **23**, this can be written as

$$\lambda_c = nq \frac{(m-2) \left(1 - \frac{b}{c} \right) + n}{1 - \frac{b}{c} - mn}. \quad [33]$$

Cooperators fixate with higher probability if the migration rate λ is below the critical migration rate λ_c . This is equivalent to

$$\frac{b}{c} > 1 + \frac{n + m \frac{\lambda}{q}}{m - 2 - \frac{\lambda}{qn}}. \quad [34]$$

For $\lambda = 0$, we obtain Eq. **24** again. Note that $z = \lambda/q$ is exactly the number of migrants arising from a group before it is eliminated. For small q , the time in which a group grows back to n after the splitting can be neglected. A certain group is

eliminated due to the splitting of another group with probability $p = q(m - 1)/m^2$. Hence, the average lifetime of a group is $T = 1/p \approx m/q$. Because the probability that this group produces a migrant is λ/m in each time step, it produces $z = \lambda/q$ migrants during its lifetime. Note that, on average, a group splits once during its lifetime. For $n \gg 1$, we have, from Eq. 34

$$\frac{b}{c} > 1 + \frac{n}{m-2} + z \frac{m}{m-2}. \quad [35]$$

If the number of groups is large, $m \gg 1$, we obtain from Eq. 35

$$\frac{b}{c} > 1 + z + \frac{n}{m}. \quad [36]$$

3. Multilevel Selection

Here, we extend our analysis to an arbitrary number of levels of selection that we denote as h . The fitness is frequency-dependent only on the lowest level with group size $m_1 = n$, where the fixation probability of a cooperator for weak selection is

$$\Phi_C^1(m_1) = \phi_C \approx \frac{1}{m_1} \left(1 - \frac{w}{2}(c m_1 + b - c) \right). \quad [37]$$

On the remaining $h - 1$ levels, the fitness is constant. The probability that a metagroup of cooperators at level i takes over a population consisting of $m_i - 1$ metagroups of defectors is

$$\Phi_C^i(m_i) \approx \frac{1}{m_i} \left[1 + \frac{w}{2}(m_i - 1)(b - c) \right], \quad [38]$$

valid for weak selection. If all splitting probabilities q_i are small, the fixation probability of a single cooperator is simply the product of the fixation probabilities on the different levels, $\rho_c = \prod_{i=1}^h \Phi_C^i(m_i)$. Again, we ask under which circumstances

a single cooperator reaches fixation with higher probability than a neutral mutant, $\rho_c > 1/N$, where the population size is $N = \prod_{i=1}^h m_i$. For weak selection, this condition reduces to

$$\frac{b}{c} > 1 + \frac{m_1}{-h + \sum_{i=2}^h m_i}. \quad [39]$$

For $h = 2$, we recover again the condition Eq. **24**. For $h > 2$, only the sum of the number of metagroups on the different levels enters. Levels that consist of just one metagroup do not contribute at all.

4. Other Stochastic Processes

Our results hold not only for the frequency dependent Moran process, but also extend to other models of population dynamics. Consider the following process: *(i)* Select two individuals at random. Because only mixed pairs can change the state of the population, we discuss only the case in which a cooperator and a defector are chosen. *(ii)* Replace the defector (payoff g) by a copy of the cooperator (payoff f) with probability $p = 1/2 + w'(f - g)/(2C)$, where C is the maximum possible payoff difference. The cooperator is replaced by a copy of the defector with probability $1 - p$. For weak selection, $w = w'/C \ll 1$, this process has the same fixation probability as the frequency dependent Moran process (5). Hence, the conditions shown in Eqs. **24** and **34** derived for weak selection are the same for this process. Another possibility is to choose $p = 1/(1 + \exp[(g - f)w])$ instead of the linear dependence on the fitness described above. This also leads to the same fixation probability and, hence, again, to the same conditions for small w .

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