Aspiration can promote cooperation in well-mixed populations as in regular graphs

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Abstract

Classical studies on aspiration-based dynamics suggest that a dissatisfied individual changes strategy without taking into account the success of others. This promotes defection spreading. The imitation-based dynamics allow individuals to imitate successful strategies without taking into account their own-satisfactions. In this article, we propose to study a dynamic based on aspiration which takes into account imitation of successful strategies for dissatisfied individuals. This helps cooperative members to resist. Individuals compare their success to their desired satisfaction level before making a decision to update their strategies. This mechanism helps individuals with a minimum of self-satisfaction to maintain their strategies. If an individual is dissatisfied, it will learn from others by choosing successful strategies. We derive an exact expression of the fixation probability in well-mixed populations as in structured populations in networks. As a result, we show that selection may favor cooperation more than defection in well-mixed populations as in populations ranged over a regular graph. We show that the best scenario is a graph with a small connectivity.

Keywords and phrases: Fixation probability; Evolutionary game dynamics; Pair approximation; Cooperation; Evolutionary graph theory; Imitation; Aspiration

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1 Introduction

Evolutionary game theory is the framework where the frequency of a strategy depends on the fitnesses of the different individuals in the population (Maynard Smith and Price [Maynard(1973)], Maynard Smith [Maynard(1982)], Hofbauer and Sigmund [Hofbauer(1988)], Weibull [Weibull(1995)], Samuelson [Samuelson(1997)], Cressman [Cressman(2003)], Vincent and Brown [Vincent(2005)], Nowak [Nowak(2006)]). Individuals interact and gain payoffs, which are seen as biological fitness or reproductive rates.

The standard model, called the replicator equation, was formulated in an infinitely large well-mixed population where any two individuals have the same probability to interact (Taylor and Jonker [Taylor(1978)], Zeeman [Zeeman(1980)], Hofbauer and Sigmund [Hofbauer(1998), Hofbauer(2003)]). Suppose that there are $n$ strategies $\{S_1, S_2, \ldots, S_n\}$. The game is described by a payoff matrix $A = \{a_{i,j}\}_{i,j=1}^n$, where $a_{i,j}$ is the payoff of an $S_i$-player if its partner is $S_j$-player. Let $x_i$ be the frequency of $S_i$-players in the population. The dynamic is

$$\frac{dx_i}{dt} = x_i(f_i - \overline{f}), \quad (1)$$

where $f_i = \sum_{j=1}^n x_j a_{i,j}$ and $\overline{f} = \sum_{i=1}^n x_i f_i$ refer to the expected payoff on an $S_i$-player, and the average payoff in the population, respectively.

Real populations are finite and deterministic approaches cannot capture this finiteness. Recently, a stochastic approach is introduced to model this finiteness by a Markov chain with a finite state space. In the absence of mutation, the Markov chain has absorbing states represented by a population of a unique type. A strategy is said to be favored by selection if its fixation probability is greater than what it would be under neutrality (Nowak et al. [Nowak(2004)], Imhof and Nowak [Imhof(2006)]). In the presence of symmetric mutation, this Markov chain is irreducible, and as a result, it has a stationary state. An interest in the frequency of a given strategy in this equilibrium states arises. In this case, a strategy is said to be favored by selection if its average frequency in the stationary state is greater than what it would be under neutrality (absence of selection) (Antal et al. [Antal(2007)], Imhof and Nowak [Imhof(2006)]).
al. [Antal(2009)]. Both models, without mutation and with mutation, share the same favored strategy if the mutation rate is small enough (Rousset and Billiard [Rousset(2000)], Rousset [Rousset(2003)], Fudenberg and Imhof [Fudenberg(2006)]).

Further advances in evolutionary game theory study structured populations. The traditional setting is the island model where individuals are structured into isolated islands (Ladret and Lessard [Ladret(2007)]; Lessard [Lessard(2011)]). Interactions occur only within islands. After reproduction, individuals can migrate or stay in the parent’s island. The case of isolation by distance, called stepping stone model, is considered in Rousset and Billiard [Rousset(2000)], and Rousset [Rousset(2006)]. Islands are numbered 1, 2, . . . , d and the migrate rates are $m_{i,i+1} = m_{i,i-1} = m/2$, $m_{i,i} = 1 - m$, and 0 otherwise.

In these structured models, individuals share the same neighborhood if they belong to the same group, or they do not have any common neighbor if they belong to two different groups. Evolutionary graph theory is a natural extension to take into account that individuals can share only some of their neighbors (Nowak and May [Nowak(1992)], Hauert and Doebeli [Hauert(2004)], Lieberman et al. [Lieberman(2005)], Ohtsuki et al. [Ohtsuki(2006)], Taylor et al. [Taylor(2007)]). It is a powerful framework that includes social networks in the evolutionary process. N individuals occupy N nodes. Each node is linked to k nodes by edges. Each edge indicates who can interact with whom.

For a graph of degree $k = 2$, the evolutionary process is described in many studies (Ohtsuki and Nowak [Ohtsuki(2006)], van Valen and Nowak [Veelen(2012)]). The population state is described completely by the frequency of each strategy. A condition, to favor a strategy over another strategy in a finite population, can be derived as in well-mixed populations.

For general degree, the frequencies of the different strategies are not enough to describe the evolutionary process. To simplify the complexity of such a graph, a technique of pair approximation (Matsuda et al. [Matsuda(1987)], Matsuda(1992), Nakamura et al. [Nakamaru(1997)], Keeling [Keeling(1999)], Haraguchi and Sasaki [?], Van
Baalen ([Baalen(2000)]) is introduced in regular graphs (Ohtsuki et al.[Ohtsuki(2006), Ohtsuki(2006), Ohtsuki(2007)]). It is a framework to study the stochastic dynamics in graphs not only by considering the global frequency $p_C$ of a given strategy $C$, but also by considering $q_{C|C}$, the probability that a neighbor of a $C$-player, is of type $C$. This technique is limited to a large population such that $k << N$.

Besides, update rules, in which individuals correct their strategies following a selection mechanism, are of greater importance for their confirmed impact on the evolutionary process. For this reason, one of the most open questions is how do individuals update their current strategy based on their knowledge of themselves and others.

Many update rules have been proposed. The most used are based in two representative models: imitation-based rule (Ohtsuki et al. [Ohtsuki(2006)], Szabó and Tke [ST(1998)], Traulsen et al. [Traulsen(2007)]) and aspiration-based rule (Chen and Wang [Chen(2008)], Du et al. [Du(2014)]). Under imitation-based rule, individuals update their strategies based on their knowledge of others. An individual compares its payoff with its neighbors’ payoffs before making a decision. If its payoff is lower, it would imitate its neighbors with a higher probability. Under aspiration-based rule, individuals update their strategies based on their knowledge about themselves. An individual compares its payoff to an aspiration level, which represents its tolerance with its current strategy. If its payoff is lower, it would switch its strategy with a higher probability.

Aspiration-driven update rules help individuals to keep their successful strategies if they reach the aspirated levels. For instance, in case of conflict between the private information (memory of the route) and social information (trail pheromone), experienced ants choose to follow the route to their previous trips (Grüter et al. [Gruter(2011)]). The same conclusion was inferred in experiments on fish stickleback, where an experienced forager ignored conflicting public information in favor of trustworthy private information (van Bergen et al. [Bergen(2004)]). Also, it has been shown that self-evaluation mechanisms, called "Satisficing", is a mainstream to understand social and economic problems
in human interactions (Simon [Simon(1955), Simon(1957)]).

In case of dissatisfaction, rational individuals will not randomly explore their neighborhood. A dissatisfied individual will take into account the success of its neighbors. Here, we proposed an update rule based on aspiration and imitation to explain cooperation spreading in structured populations as in well-mixed populations. If the strategy gives its player a certain benefit, it will be maintained with a higher probability. A dissatisfied individual will explore its neighborhood by considering their success.

In this article, we study a regular graph of degree $k$, where the update mechanism is composed of two rounds. In the first round, individuals compares their payoffs to a personal tolerance index. Satisfied individuals keep their current strategy with higher probability. Dissatisfied individuals will explore the success of their neighbors with a higher probability. The focal individual used its payoff only to decide if it will keep its strategy, in case of satisfaction, or if it will imitate a neighbor, in case of dissatisfaction. More precisely, a random individual $I$ compares its payoff $\Pi_I$ to its satisfaction level $\alpha_I$. It will maintain its current strategy with probability proportional to $\Pi_I - \alpha_I$. Otherwise, it will adopt a neighbor’s strategy proportional to its fitness.

This model is equivalent to the following death-birth update. At each time step, a randomly chosen individual survives with probability proportional to the relative size $\Pi_I - \alpha_I$. Otherwise, it dies. In this case, a competition between its neighbors arises. A neighbour is chosen proportional to its fitness to produce a copy, which will occupy the vacant position. It is similar to the death-birth update rule (Ohtsuki et al. Ohtsuki(2006)), where the death event occurs with probability 1.

As Ohtsuki et al. Ohtsuki(2006), we use a pair approximation technique and a diffusion approximation, to derive an estimation of the fixation probability in graphs of degree $3 \leq k << N$. We use an exact calculation technique for circular model, $k = 2$, and well-mixed model, $k = N$. Then, we compare the success of cooperation and defection. We show that cooperation is favored if the ratio benefit-to-cost $b/c$ exceeds some critical
value that depends on the graph degree, \( k \).

The remainder of this paper is divided in 5 sections. In Section 2, we describe our model. In Section 3, we study the global frequency \( p_C \) and the local frequency \( q_{C|C} \). We describe the quasi-steady state and then we derive an approximation of the fixation probability of strategy \( C \) in Section 4. In Section 5, we test the success of cooperation comparing to defection. We study the additive prisoner dilemma in Section 6. We finish this article by a discussion in Section 7.

## 2 Model

Consider a finite population composed of \( N \) individuals distributed over \( N \) nodes of a graph. Each node is related by edges to other \( k \) nodes. \( k \), called the graph degree, is the same for all individuals (see Figure 1). Each edge indicates who interacts with whom. Any two individuals who are related by an edge are called neighbors. Suppose that there is no loops to cancel self-interaction. Moreover, suppose that the graph is connected in the sense that any two nodes are linked by a finite number of edges. Each individual can adopt a strategy among \( \{C, D\} \): \( C \) for cooperation and \( D \) for defection.

At each time step, each individual interacts with its neighbors through the game matrix

\[
\begin{pmatrix}
C & D \\
C & R & S \\
D & T & P
\end{pmatrix}
\]

(2)

Two cooperators receive a reward, \( R \), whereas two defectors receive a punishment, \( P \). if they interact, a cooperator receives a sucker, \( S \), while a defector receives a temptation, \( T \). After interactions with its neighbors, any individual accumulates a payoff denoted by \( \Pi \). Then, a randomly chosen individual \( I \) will compare its payoff \( \Pi_I \) to its satisfaction index \( \alpha_I \), which represents its tolerance with its current strategy. Here, we study the simplest case where the satisfaction level depends on the strategy. Individual \( I \) will keep its current
strategy with probability
\[ g\left(\delta (\alpha_I - \Pi_I)\right), \]  
\[ (3) \]
where \( \delta \) is a non-negative constant called the selection intensity. It will update its current strategy with the complementary, probability
\[ 1 - g\left(\delta (\alpha_I - \Pi_I)\right). \]  
\[ (4) \]
In this case, it adopts the strategy of one of its neighbors, say \( J \), chosen with probability proportional to its fitness \( f_J = 1 + \delta \Pi_J \). More precisely, let \( J_1, J_2, \ldots, J_k \) the neighbors of individual \( I \). Individual \( I \) will adopt the strategy of one of a neighbor \( J_i \) with probability \( f_{J_i}/\sum_{l=1}^k f_{J_l} \), for \( i = 1, \ldots, k \). This mechanism helps individual \( I \) to learn from its neighbors by selecting the most successful strategy. This does not mean that the chosen strategy will be suitable for individual \( I \) since it has a different neighborhood than individual \( J \).
Here, we assume that \( g \) is a function such that

- \( g(0) = 1/2 \): under neutrality \( \delta = 0 \), updating and maintaining occur with the same probability, that is \( 1/2 \).

- \( g'(0) < 0 \): for \( \delta > 0 \) very small, we have
  \[
  g\left(\delta(\alpha_I - \Pi_I)\right) \approx \frac{1}{2} - \delta \cdot g'(0)(\alpha_I - \Pi_I).
  \]

Then maintaining occurs proportional to the individual satisfaction \( \Pi_I - \alpha_I \).

If \( \Pi_I > \alpha_I \), individuals maintain their strategies with a probability higher than \( 1/2 \). If \( \Pi_I < \alpha_I \), individuals maintain their strategies with a probability lower than \( 1/2 \). If \( \Pi_I = \alpha_I \), individuals maintain their strategy with probability \( 1/2 \). The most used function is the Fermi rule

\[
g(x) = \frac{1}{1 + e^{-x}}.
\]

Neutral model is the case \( \delta = 0 \). The case of weak selection corresponds to \( \delta > 0 \) very small. This case is presented in most studies in genetic populations, molecular evolution and cultural evolution (Kimura [Kimura(198)], Traulsen et al. [Traulsen(2007)], Traulsen et al. [Traulsen(2010)], Wu et al. [Wu(2014)]). In this case, the effect of payoff differences on the evolutionary process is small. Weak selection is a reasonable assumption for two reasons:

- It is a standard case to derive many analytic results which are not possible for any selection intensity, but these results stay a good approximation for other selection intensities

- In real biological populations, the fitness of an individual depends on many competitions (games), and then each game makes a small contribution, and here we interested only by a game.

In the remainder, we are interested in the effect of weak selection on the evolutionary process. We use Fermi rule (5), where \( g'(0) = -1/4 < 0 \).
3 Rate of change under weak selection

Define $p_X$ and $p_{XY}$ as the frequencies of strategy $X$ and pairs of type $XY$, respectively, for $X, Y \in \{C, D\}$. Denote by $q_{Y|X} = p_{XY}/p_X$ the probability that a given neighbor of an $X$-strategist is a $Y$-strategist. As a result of basic probability properties, these quantities are related by the following relations

$$p_C + p_D = 1,$$
$$p_{XY} = q_{X|Y} p_Y = q_{Y|X} p_X = p_{YX},$$
$$q_{A|Y} + q_{B|Y} = 1.\quad (6)$$

Using these identities, we can express all these probabilities in terms of $p_C$ and $q_{C|C}$

$$p_D = 1 - p_C,$$
$$p_{CC} = q_{C|C} p_C,$$
$$q_{D|C} = 1 - q_{C|C},$$
$$p_{CD} = q_{D|C} p_C = (1 - q_{C|C}) p_C;$$
$$q_{C|D} = \frac{p_{CD}}{p_D} = \frac{(1 - q_{C|C}) p_C}{1 - p_C};$$
$$q_{D|D} = 1 - q_{C|D} = 1 - \frac{(1 - q_{C|C}) p_C}{1 - p_C},$$
$$p_{DD} = q_{D|D} p_D = 1 - p_C - (1 - q_{C|C}) p_C.\quad (7)$$

Based on the above identities, the evolutionary process is completely described through $p_C$ and $q_{C|C}$.

In next subsections, we derive the changes in one times steps of $p_C$ and $q_{C|C}$, respectively, to characterize the evolutionary process of our model.
3.1 Payoffs

Assume that the selected individual, \( I \), is an \( X \)-strategist, and that its neighborhood is formed by \( k_C \) cooperators and \( k_D = k - k_C \) defectors. Therefore, its expected payoff is

\[
\Pi_X = \begin{cases} 
    \frac{k_C R + k_D S}{k} & \text{if } X = C, \\
    \frac{k_C T + k_D P}{k} & \text{if } X = D.
\end{cases}
\]  

(8)

In the second round, individual \( I \) will adopt a neighbor’s strategy. Then, we must consider the neighborhood’s payoffs of \( I \). Let individual \( J \), a \( Y \)-player, be a random neighbor of individual \( I \), and let \( \Pi_{Y|X} \) be its expected payoff of individual \( J \). Hence, with reasoning based on the strategies of individuals \( I \) and \( J \), we have

\[
\Pi_{C|C} = \frac{[1 + (k - 1)q_{C|C}]R + (k - 1)q_{D|C}S}{k}, \\
\Pi_{C|D} = \frac{(k - 1)q_{C|C}R + [1 + (k - 1)q_{D|C}]S}{k}, \\
\Pi_{D|C} = \frac{[1 + (k - 1)q_{C|D}]T + (k - 1)q_{D|D}P}{k}, \\
\Pi_{D|D} = \frac{(k - 1)q_{C|D}T + [1 + (k - 1)q_{D|D}]P}{k}.
\]  

(9)

Proof. Start with the first payoff in Eq. (9). Assume that \( I \) and \( J \) are two cooperators. In addition of \( I \), individual \( J \) has other \( k - 1 \) neighbors. Each one of them is of type \( C \) with probability \( q_{C|C} \), or of type \( D \) with probability \( q_{D|C} = 1 - q_{C|C} \). In average, the neighborhood of individual \( J \) is composed of \( 1 + (k - 1)q_{C|C} \) cooperators and \( (k - 1)q_{D|C} \) defectors. This explains the form of the expected payoff. Similarly, we have the other payoffs in Eq. (9).

3.2 Change in \( p_C \)

The frequency of \( C \), \( p_C \), increases if a defector becomes a cooperator. A defector is selected to update its strategy with probability \( p_D \). Its neighborhood is formed by \( k_C \) cooperators and \( k_D = k - k_C \) defectors with probability \( \binom{k}{k_C} q_{C|D}^{k_C} q_{D|D}^{k-k_C} \), for \( k_C = 0, 1, \ldots, k \). It will
choose to update its strategy with probability

$$\frac{1}{1 + e^{\delta (\Pi_D - \alpha_D)}} = \frac{1}{2} + \delta \cdot \frac{\alpha_D - \Pi_D}{4} + \mathcal{O}(\delta^2).$$

Here \(\mathcal{O}(\delta^n)\) means that the error is of order of \(\delta^n\) for \(n \in \mathbb{N}\). Finally, it becomes a cooperator with probability

$$\frac{k_C(1 + \delta \Pi_{C|D})}{k_C(1 + \delta \Pi_{C|D}) + (k - k_C)(1 + \delta \Pi_{D|D})} = \frac{k_C}{k} + \frac{k_C(k - k_C)}{k^2}(\Pi_{C|D} - \Pi_{D|D}) + \mathcal{O}(\delta^2). \quad (10)$$

In this case, the change is \(\Delta p_C = \frac{1}{N}\). Summarize this event in the following probability

$$\mathbb{P}(\Delta p_C = \frac{1}{N}) = \frac{p_D}{2k} \sum_{k_C=0}^{k} k_C \left( \binom{k}{k_C} q_{C|D}^{k-k_C} q_{D|D}^{k} + \frac{\delta p_D}{2} \sum_{k_C=0}^{k} k_C \left( \binom{k}{k_C} q_{C|D}^{k-k_C} q_{D|D}^{k} \right) \right)$$

$$\times \left[ \frac{k - k_C}{k}(\Pi_{C|D} - \Pi_{D|D}) + \frac{\alpha_D - \Pi_D}{2} \right] + \mathcal{O}(\delta^2). \quad (11)$$

Using Eq. (10) and the first two moments of the binomial distribution,

$$\sum_{k_C=0}^{k} k_C \times \binom{k}{k_C} q_{C|D}^{k-k_C} = \sum_{k_C=0}^{k} k_C \times \binom{k}{k_C} (1 - q_{C|D})^{k-k_C} = kq_{C|D},$$

$$\sum_{k_C=0}^{k} k_C^2 \times \binom{k}{k_C} q_{C|D}^{k-k_C} = \sum_{k_C=0}^{k} k_C^2 \times \binom{k}{k_C} (1 - q_{C|D})^{k-k_C} = kq_{C|D} + k(k - 1)q_{C|D}^2.$$  

yield

$$\mathbb{P}(\Delta p_C = \frac{1}{N}) = \frac{p_D q_{C|D}}{2} + \frac{\delta p_D}{4k} \left[ 2(k - 1)q_{C|D}q_{D|D}(\Pi_{C|D} - \Pi_{D|D}) + kq_{C|D}\alpha_D \right. \right.\right.$$

$$\left. - (1 + (k - 1)q_{C|D})q_{C|D}T - (k - 1)q_{C|D}q_{D|D}P \right] + \mathcal{O}(\delta^2)$$

$$= \frac{p_{CD}}{2} + \frac{\delta p_{CD}}{4k} \left[ I_R^+ R + I_S^+ S - I_T^+ T - I_P^+ P + k\alpha_D \right] + \mathcal{O}(\delta^2), \quad (13)$$
where

\[
I_R^+ = \frac{2(k-1)^2}{k} q_{C|C} q_{D|D}, \\
I_S^+ = \frac{2(k-1)}{k} q_{D|D} \left( 1 + (k-1) q_{D|C} \right), \\
I_T^+ = 1 + (k-1) q_{C|D} + \frac{2(k-1)^2}{k} q_{D|D} q_{C|C}, \\
I_P^+ = \frac{k-1}{k} q_{D|D} \left( k + 2 + 2(k-1) q_{D|D} \right).
\]  

\[(14)\]

The frequency of \( C, p_C \), decreases if a cooperator becomes a defector. In this case, the change is \( \Delta p_C = -\frac{1}{N} \). This happens with probability

\[
\mathbb{P} \left( \Delta p_C = -\frac{1}{N} \right) = \frac{p_C}{k} \sum_{k=0}^{k} \binom{k}{k} q_{C|C} q_{D|D}^{k-k_C} \frac{1}{1 + e^{\delta (\Pi_D - \Pi_C)}}\frac{(k-k_C)(1+\delta \Pi_D)}{(k-k_C)(1+\delta \Pi_D) + (k-k_C)(1+\delta \Pi_D)}
\]

\[
= \frac{p_C}{2k} \sum_{k=0}^{k} (k-k_C) \binom{k}{k_C} q_{C|C}^{k-k_C} q_{D|C}^{k-k_C} + \frac{\delta p_C}{2k} \sum_{k=0}^{k} (k-k_C) \binom{k}{k_C} q_{C|C}^{k-k_C} q_{D|C}^{k-k_C}
\]

\[
\times \left( \frac{k_C}{k} (\Pi_D - \Pi_C) + \frac{\alpha_C - \Pi_C}{2} \right) + O(\delta^2)
\]

\[
= \frac{p_{CD}}{2} + \frac{\delta p_{CD}}{4k} \left( -I_R R - I_S S + I_T T + I_P P + k \alpha_C \right) + O(\delta^2),
\]  

\[(15)\]

where

\[
I_R = \frac{k-1}{k} q_{C|C} \left( k + 2 + 2(k-1) q_{C|C} \right), \\
I_S = 1 + (k-1) q_{D|C} + \frac{2(k-1)^2}{k} q_{C|C} q_{D|C}, \\
I_T = \frac{2(k-1)}{k} q_{C|C} \left( 1 + (k-1) q_{D|C} \right), \\
I_P = \frac{2(k-1)^2}{k} q_{C|C} q_{D|D}.
\]  

\[(16)\]

Denote by \( \dot{p}_A \) the rate of change of \( p_C \) in one time step. Using Eqs \[(13)\] and \[(15)\], we obtain

\[
\dot{p}_C = \frac{1}{N} \mathbb{P} \left( \Delta p_C = -\frac{1}{N} \right) - \frac{1}{N} \mathbb{P} \left( \Delta p_C = \frac{1}{N} \right)
\]

\[
= \frac{\delta p_{CD}}{4Nk} \left[ I_R R + I_S S - I_T T - I_P P + k \Delta \alpha \right] + O(\delta^2),
\]  

\[(17)\]
where

\[ I_R = I_R^+ + I_R^- = \left[ k + 2 + 2(k - 1)(q_{C|C} + q_{D|D}) \right] \frac{k - 1}{k} q_{C|C}, \]
\[ I_S = I_S^+ + I_S^- = 1 + (k - 1)q_{D|C} + \frac{2(k - 1)^2}{k} (q_{C|C} + q_{D|D})q_{D|C} + \frac{2(k - 1)q_{D|D}}{k}, \]
\[ I_T = I_T^+ + I_T^- = 1 + (k - 1)q_{C|D} + \frac{2(k - 1)^2}{k} (q_{C|C} + q_{D|D})q_{C|D} + \frac{2(k - 1)q_{C|C}}{k}, \]
\[ I_P = I_P^+ + I_P^- = \left[ k + 2 + 2(k - 1)(q_{C|C} + q_{D|D}) \right] \frac{k - 1}{k} q_{D|D}, \]

and ∆α = α_D − α_C. ∆α is the satisfaction level difference between defectors and cooperators.

### 3.3 Change in q_{C|C}

Since \( q_{C|C} = p_{CC}/p_C \), we must start by the rate of change of \( p_{CC} \), the frequency of CC-pairs. Note that the total number of all pairs is \( kN/2 \) as each individual has \( k \) neighbors. \( p_{CC} \) changes if a defector becomes a cooperator or a cooperator becomes a defector. Let \( I \) be the selected individual and assume that its neighborhood is formed by \( k_C \) cooperators and \( k - k_C \) defectors.

The number of pairs CC will increase by \( k_C \) if a defector becomes a cooperator. This occurs with probability

\[
P\left( \Delta p_{CC} = \frac{2k_C}{kN} \right) = p_D \left( \frac{k}{k_C} \right) q_{C|D}^{k-k_C} \left( q_{D|C}^{k_C} \right) \frac{1}{1 + e^{\delta(\Pi_{C|D} - \alpha_D)}} \times \frac{k_C(1 + \delta \Pi_{C|D})}{k_C(1 + \delta \Pi_{C|D}) + (k - k_C)(1 + \delta \Pi_{D|C})} \]
\[
= \frac{p_{C}(k - k_C)}{2k} \left( \frac{k}{k_C} \right) q_{D|C}^{k_C} q_{C|C}^{k_D} + O(\delta), \tag{19} \]

The number of pairs CC will decrease by \( k_C \) if a cooperator becomes a defector. This occurs with probability

\[
P\left( \Delta p_{CC} = -\frac{2k_C}{kN} \right) = p_C \left( \frac{k}{k_C} \right) q_{C|C}^{k-k_C} \times \frac{1}{1 + e^{\delta(\Pi_{C|C} - \alpha_C)}} \times \frac{k_D(1 + \delta \Pi_{D|C})}{k_D(1 + \delta \Pi_{D|C}) + (k - k_C)(1 + \delta \Pi_{C|D})} \]
\[
= \frac{p_C(k - k_C)}{2k} \left( \frac{k}{k_C} \right) q_{D|C}^{k_C} q_{C|C}^{k_D} + O(\delta). \tag{20} \]

Let \( \dot{p}_{CC} \) be the rate of change of \( p_{CC} \) in one time step. Using Eqs (12), (20) and (20),
yield

\[
\dot{p}_{CC} = \sum_{k_C=0}^{k} \frac{2k_C}{kN} \left[ \mathbb{P}( \Delta p_{CC} = \frac{2k_C}{kN} ) - \mathbb{P}( \Delta p_{CC} = -\frac{2k_C}{kN} ) \right]
\]

\[
= \sum_{k_C=1}^{k} \frac{2k_C}{kN} \left[ \frac{k_{CPD}}{2k} \left( \frac{k}{k_C} \right) q_{C|D}^{k_C} q_{D|D}^{k_C} - \frac{(k - k_C)p_C}{2k} \left( \frac{k}{k_C} \right) q_{C|C}^{k_C} q_{D|C}^{k_C} \right] + \mathcal{O}(\delta)
\]

\[
= \frac{p_D}{k^2 N} \sum_{k_C=0}^{k} k^2 \left( \frac{k}{k_C} \right) q_{C|D}^{k_C} q_{D|D}^{k_C} - \frac{p_C}{k^2 N} \sum_{k_C=0}^{k} k_C(k - k_C) \left( \frac{k}{k_C} \right) q_{C|C}^{k_C} q_{D|C}^{k_C} + \mathcal{O}(\delta)
\]

\[
= \frac{p_D}{k^2 N} \left( k q_{C|D} - k(k - 1)q_{C|D}^2 \right) - \frac{p_C}{k^2 N} \left( k^2 q_{C|C} - k q_{C|C} - k(k - 1)q_{C|C}^2 \right) + \mathcal{O}(\delta)
\]

\[
= \frac{p_C D}{kN} \left( 1 + (k - 1)(q_{C|D} - q_{C|C}) \right) + \mathcal{O}(\delta).
\]

As a result, the rate of change of \( q_{C|C} \) in one time step is

\[
\dot{q}_{C|C} = \frac{\dot{p}_{CC}}{p_C} = \frac{p_C D}{kN p_C} \left( 1 + (k - 1)(q_{C|D} - q_{C|C}) \right) + \mathcal{O}(\delta)
\]

\[
= \frac{1 - q_{C|C}}{kN} \left( 1 + (k - 1) \frac{p_C - q_{C|C}}{1 - p_C} \right) + \mathcal{O}(\delta).
\]

In the last step, we have used Eq (7).

4 The quasi-steady state

As a consequence of Eqs (17) and (22), the local density \( q_{C|C} \) equilibrates much more quickly than the global density \( p_C \) (Ohtsuki and Nowak [Ohtsuki(2006)]). Therefore, the dynamical system rapidly converges onto a quasi-steady state, defined by \( \dot{q}_{C|C} = 0 \), or more explicitly,

\[
q_{C|C} = \frac{1}{k - 1} + \frac{k - 2}{k - 1} p_C.
\]

It is the key relationship, which is obtained in many studies of structured populations in regular graphs (Ohtsuki et al. [Ohtsuki(2006)]). Instead of studying a diffusion process in terms of two variables, \( p_C \) and \( q_{C|C} \), by this relation we describe the system by one-dimensional diffusion process in terms of \( p_C \) only.
With a short interval $\Delta t$, we have
\[
\mathbb{E}[\Delta p_C|p_C(0) = p] = \dot{p}_C \Delta t \left( \equiv \mu(p) \Delta t \right). \tag{24}
\]

Using Eq (17) and the coefficients $I_i$ for $i = R, S, T, P$, derived in Appendix A, we obtain
\[
\mu(p) = \frac{\delta(k-2)}{4Nk^2(k-1)} p(1-p) \left( \Gamma_0 + k^2 \Delta \alpha + \Gamma_1 p \right). \tag{25}
\]

Here
\[
\Gamma_0 = (3k+2)R + (3k^2 - 3k - 2)S - (k+2)T - (3k+2)(k-1)P,
\]
\[
\Gamma_1 = (3k+2)(k-2)(R - S - T + P). \tag{26}
\]

For the variance, we have
\[
\text{var} \left[ \Delta p_C|p_C(0) = p \right] = \mathbb{E} \left[ (\Delta p_C)^2 | p_C(0) = p \right] - \mathbb{E} \left[ \Delta p_C | p_C(0) = p \right]^2
\]
\[
= \frac{1}{N^2} \left( \mathbb{P} \left( \Delta p_C = -\frac{1}{N} \right) + \mathbb{P} \left( \Delta p_C = \frac{1}{N} \right) \right) \Delta t + O(\delta^2) \Delta t
\]
\[
\simeq \frac{(k-2)}{N^2(k-1)} p(1-p) \Delta t \left( \equiv \nu(p) \Delta t \right). \tag{27}
\]

Conditions (25) and (27) ensure the diffusion approximation with drift function $\mu(x)$ and diffusion function $\nu(x)$.

Suppose that a proportion $p$ of cooperators appears in a population of defectors, $p \in (0, 1)$. As a result, there are two possibilities for the evolutionary dynamics. The first scenario is that this proportion produces a lineage, which will eventually invade the entire population (extinction of defectors $x = 1$). The second scenario is that these proportion might die before reproducing or generate a lineage that disappears after sometime (extinction of cooperators $x = 0$). Then, $x = 0$ and $x = 1$ are absorbing states of the diffusion process.

Let $\phi_C^\delta(p, t)$ be the probability that absorption has occurred at $x = 1$ at or before $t$. The backward Kolomogov equation (Kimura [Kimura(1962)], Crow and Kimura [Crow(1970)],
Ewens ([Ewens(2004)]) can be written as

\[
\frac{\partial \phi_C^\delta(p,t)}{\partial t} = \mu(p) \frac{\partial \phi_C^\delta(p,t)}{\partial p} + \frac{\nu(p)}{2} \frac{\partial^2 \phi_C^\delta(p,t)}{\partial p^2}
\]  
(28)

with boundary conditions \( \phi_C^\delta(0,t) = 0 \) and \( \phi_C^\delta(1,t) = 1 \).

By letting \( t \to \infty \), the limit

\[
\phi_C^\delta(p) = \lim_{t \to \infty} \phi_C^\delta(p,t)
\]

represents the fixation probability of cooperators given an initial frequency \( p \). As \( t \to \infty \), the left-hand side in (28) tends to 0, since \( \phi_C^\delta(p,t) \) tends to be constant. Therefore, Eq. 28 becomes

\[
\mu(x) \frac{d\phi_C^\delta}{dx}(x) + \frac{\nu(x)}{2} \frac{d^2\phi_C^\delta}{dx^2}(x) = 0,
\]

with the boundary conditions, \( \phi_C^\delta(0) = 0 \) and \( \phi_C^\delta(1) = 1 \). The solution of Eq (30) is

\[
\phi_C^\delta(p) = \int_0^p \exp \left\{ - \int_0^x \frac{2\mu(y)}{\nu(y)} dy \right\} dx / \int_0^1 \exp \left\{ - \int_0^x \frac{2\mu(y)}{\nu(y)} dy \right\} dx. 
\]

(31)

Using Eqs (25) and (27), we have

\[
\exp \left\{ - \int_0^x \frac{2\mu(y)}{\nu(y)} dy \right\} = \exp \left\{ - \int_0^x \frac{\delta N}{2k^2} (\Gamma_1 y + \Gamma_0) dy \right\} 
= \exp \left\{ - \frac{\delta N}{4k^2} (\Gamma_1 x^2 + 2\Gamma_0 x + k^2 \Delta \alpha x) \right\} 
= 1 - \delta \cdot \frac{N}{4k^2} \left[ \Gamma_1 x^2 + 2\Gamma_0 x + k^2 \Delta \alpha x \right] + O(\delta^2).
\]

(32)

Integrating Eq (32), we have the key approximation

\[
\phi_C^\delta(p) = \frac{\int_0^p \left(1 - \delta \cdot \frac{N}{4k^2} (\Gamma_1 x^2 + 2\Gamma_0 x + k^2 \Delta \alpha x)\right) dx + O(\delta^2)}{\int_0^1 \left(1 - \delta \cdot \frac{N}{4k^2} (\Gamma_1 x^2 + 2\Gamma_0 x + k^2 \Delta \alpha x)\right) dx + O(\delta^2)} 
= \frac{p - \delta \cdot \frac{N}{4k^2} \left[ \Gamma_1 p^3 + \Gamma_0 p^2 + k^2 \Delta \alpha p^2 \right] + O(\delta^2)}{1 - \delta \cdot \frac{N}{4k^2} \left[ \Gamma_1 + \Gamma_0 + k^2 \Delta \alpha \right] + O(\delta^2)} 
\]

\[
= \left[ p - \delta \cdot \frac{Np}{12k^2} \left[ \Gamma_1 p^3 / 3 + \Gamma_0 p^2 + k^2 \Delta \alpha p^2 \right] \right] \times \left[ 1 + \delta \cdot \frac{N}{4k^2} \left( \Gamma_1 / 3 + \Gamma_0 + k^2 \Delta \alpha \right) \right] + O(\delta^2) 
= p + \delta \cdot \frac{Np(1-p)}{12k^2} \left[ \Gamma_1 + 3\Gamma_0 + 3k^2 \Delta \alpha + \Gamma_1 p \right] + O(\delta^2).
\]

(33)
Similarly, let $\phi_D^\delta(p)$ be the probability that a proportion $p$ of defectors takes over a population of cooperators. Since there is ultimate fixation of cooperation or defection with probability 1, we have

$$\phi_D^\delta(p) = 1 - \phi_C^\delta(1-p) = p - \delta \cdot \frac{Np(1-p)}{12k^2} \left[ 2\Gamma_1 + 3\Gamma_0 + 3k^2\Delta\alpha - \Gamma_1p \right] + \mathcal{O}(\delta^2). \quad (34)$$

5 Fixation probabilities

5.1 First test: $\rho_C(\delta) > \rho_C(0)$

A first criterion, for weak selection to favor the emergence and stabilization of cooperation, is the comparison of the fixation probability under weak selection, $\rho_C(\delta) = \phi_C^\delta(1/N)$, to what it would be under neutrality, $\rho_C(0) = \phi_C^0(1/N)$ (Rousset and Billiard, Nowak et al., Nowak(2004), Taylor et al. [?]). We say that selection favors the fixation of cooperation if $\rho_C(\delta) > \rho_C(0)$. Otherwise, that is $\rho_C(\delta) < \rho_C(0)$, we say that selection opposes the fixation of cooperation. Using Eq (33), we have

$$\rho_C(0) = \frac{1}{N},$$

$$\rho_C(\delta) = \rho_C(0) + \delta \cdot \frac{N - 1}{12Nk^2} \left[ \Gamma_1 + 3\Gamma_0 + 3k^2\Delta\alpha \right] + \mathcal{O}(\delta^2). \quad (35)$$

Accordingly, $\rho_C(\delta) > \rho_C(0)$ if $\Gamma_0 + 3\Gamma_1 + 3k^2\Delta\alpha > 0$, which is equivalent to

$$\frac{3k^2 + 5k + 2}{3k^2} R + \frac{6k^2 - 5k - 2}{3k^2} S - \frac{3k^2 - k + 2}{3k^2} T - \frac{6k^2 + k - 2}{3k^2} P + \Delta\alpha > 0. \quad (36)$$

This condition is valid for $k \geq 3$. Note that the above calculation is valid only for $k \geq 3$ since both the expectation and the variance, given by Eqs (25) and (27), are zero.

For $k = 2$ and finite population, the fixation probability $\rho_C(\delta)$ is derived in Eq. (33), in Appendix B. In this case $\rho_C(\delta) > \rho_C(0)$ if

$$\frac{2N^2 - 7N + 7}{N(N-1)} R + \frac{N^2 + 2N - 3}{N(N-1)} S - \frac{N^2 - 2N + 5}{N(N-1)} T - \frac{2N^2 - 3N - 5}{N(N-1)} P + \Delta\alpha > 0. \quad (37)$$

For large population, $N \to \infty$, it is equivalent to

$$2R + S - T - 2P + \Delta\alpha > 0,$$
which extends Eq. (36) for $k = 2$.

If inequality (36) is reversed, weak selection opposes the fixation of cooperation, $\rho_C(\delta) < \rho_C(0)$. This does not mean that weak selection favors the fixation of defection. Similarly, from Eq. (34), we have $\rho_D(\delta) > \rho_D(0)$ if $2\Gamma_0 + 3\Gamma_1 + 3k^2\Delta\alpha < 0$, which is equivalent to

$$
\frac{6k^2 + k - 2}{3k^2}R + \frac{3k^2 - k + 2}{3k^2}S - \frac{6k^2 - 5k - 2}{3k^2}T - \frac{3k^2 + 5k + 2}{3k^2}P + \Delta\alpha < 0. \quad (38)
$$

5.2 Second test: $\rho_C(\delta) > \rho_D(\delta)$

It is possible that weak selection favors the fixation of cooperation and defection or opposes the fixation of cooperation and defection. As a result, comparing the fixation probability to what it would be under neutrality does not give a complete view of the success of a strategy. Then, a second criterion is introduced (Nowak et al. [Nowak(2004)]), based on the comparison of the fixation probabilities, to measure the most successful strategy. If $\rho_C(\delta) > \rho_D(\delta)$, then the invasion of a single cooperating in an all defecting population is more likely than the reverse situation. In such a case, we say that the evolution of cooperation is more favored by selection than the evolution of defection.

Using Eqs (33) and (34), we have

$$
\frac{\phi_C(\delta)(p)}{\phi_D(\delta)(p)} = 1 + \delta \cdot \frac{N(1-p)}{4k^2} \left[ \Gamma_1 + 2\Gamma_0 + 2k^2\Delta\alpha \right] + O(\delta^2). \quad (39)
$$

Particularly for $p = N^{-1}$, we have

$$
\frac{\rho_C(\delta)}{\rho_D(\delta)} = 1 + \delta \cdot \frac{N - 1}{4k^2} \left[ \Gamma_1 + 2\Gamma_0 + 2k^2\Delta\alpha \right] + O(\delta^2). \quad (40)
$$

Accordingly, we have $\rho_C(\delta) > \rho_D(\delta)$ if $\Gamma_1 + 2\Gamma_0 + 2k^2\Delta\alpha > 0$, which is equivalent to

$$
\frac{3k + 2}{2k} (R - P) + \frac{3k - 2}{2k} (S - T) + \Delta\alpha > 0 \quad (41)
$$

This equation predicts the success of cooperators more often than defectors. It is valid for $k \geq 3$. 

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For $k = 2$ and by using Eq. (70), $\rho_C(\delta) > \rho_D(\delta)$ if

$$\rho_C(\delta) > \rho_D(\delta) \text{ if } (2N - 5)(R - P) + N(S - T) + N\Delta \alpha > 0.$$ (42)

For large population size $N \to \infty$, it is equivalent to

$$2R + S - T - 2P + \Delta \alpha > 0,$$ (43)

which extends Eq. (41) for $k = 2$.

For symmetric aspiration, $\alpha_D = \alpha_C$, Eq (41) can be written as

$$\sigma R + S > T + \sigma P,$$ (44)

where $\sigma = \frac{3k+2}{3k-2}$ is the structure coefficient (Tarnita et al. [Tarnita(2009)]). $\sigma$ describes the structure and the update rule effects on the evolutionary process. It depends only on the population structure and the update rule and not on the game matrix. It quantifies the degree for which individuals of the same type are more likely to meet than individuals of different types. If we select two neighbors, then with probability $1/(1 + \sigma)$ we have different types and with probability $\sigma/(1 + \sigma)$ we have the same type.

The game is equivalent to a well-mixed population without structure, where each individual can interact with any other individual through the effective game matrix (Lessard [Lessard(2011)]), given by

$$A_{eff} = \begin{bmatrix} \sigma R & S \\ T & \sigma P \end{bmatrix}. \tag{45}$$

Note that $\sigma$ converges to 1 as $k \to \infty$. Therefore, the normal payoff matrix (2) is obtained in the limit where each individual interacts with any other individuals. This describes exactly a well-mixed population and the limit of condition (44) is

$$R + S > T + P.$$ 

This is exactly condition derived from Eq. (77) for a large well-mixed population.
6 Example: Simplified prisoner’s Dilemma

Consider the simplified additive prisoner’s Dilemma given by matrix

\[
\begin{pmatrix}
C & D \\
C & (b - c) \\
D & b
\end{pmatrix}.
\]

(46)

A cooperator pays a cost, \(c > 0\), to receive a benefit, \(b > c\), if its partner is a cooperator. A defector benefits by receiving \(b\) if its partner cooperates. This is one of the most important social dilemmas, which can be used to quantify the effectiveness of cooperation via the benefit-to-cost ratio \(b/c\). This ratio is an indicator of the performance of cooperation in structured populations as in well-mixed populations.

Using conditions (36) and (38) with the new entries, we have \(\rho_C(\delta) > \frac{1}{N} > \rho_C(\delta)\) if

\[
\frac{2}{k}b - 3c + \Delta\alpha > 0.
\]

(47)

The difference in aspiration level, \(\Delta\alpha = \alpha_D - \alpha_C\), is a form of compensation to cooperators for their behavior. If the compensation \(\Delta\alpha\) exceeds the payoff difference, then, selection favors cooperation more than defection.

Otherwise, that is \(\frac{2}{k}b - 3c + \Delta\alpha < 0\), we have \(\rho_C(\delta) < \frac{1}{N} < \rho_C(\delta)\). In this case, the difference in aspiration level, \(\Delta\alpha\), is not enough to compensate cooperators to evolve and take over the population. Selection should promote defection more than cooperation.

Positive values of \(\Delta\alpha = \alpha_D - \alpha_C > 0\) play in favor of cooperation since this reduces the cooperation effort \(c\). With an appropriate values of \(\Delta\alpha\), a cooperator will be more satisfied than a defector since its tolerance index \(\alpha_C\) is lower than that one a defector, \(\alpha_D\). This allows cooperators to maintain their strategy more frequently than defectors. This increases the updating frequency of defectors until they finish by accepting cooperation.

Consider the case where each type aspirates the maximum payoff that can receive it, \(\alpha_C = (b - c)\) and \(\alpha_D = b\). Then, the difference in aspiration level is \(\Delta\alpha = c\). Condition
for selection to favor cooperation more than defection becomes
\[ \frac{b}{c} > k. \] (48)

This is typically the condition derived by Ohtsuki et al. \cite{Ohtsuki2006} for death-birth updating. At each time step, an individual is selected to die. A neighbour is selected with probability proportional to its fitness to give birth a copy, which will take the vacant position.

If both strategies have the same satisfaction level, \( \Delta \alpha = 0 \), then weak selection favors cooperation more often than defection if
\[ \frac{b}{c} > (\frac{b}{c})^* = \frac{\sigma + 1}{\sigma - 1} = \frac{3}{2} k. \] (49)

Small values of \( k \) decrease the crucial ratio \( (\frac{b}{c})^* \). This gives more advantage to cooperators to emerge more likely than defectors. This is a natural consequence of the key relationship \( q_{C|C} - q_{C|D} = 1/(k - 1) \). A cooperator is connected to more cooperators than a defector. A graph with fewer connection increases the formation of cooperators’ clusters.

A graph with a large connections should promote defection. Since \( q_{C|C} - q_{C|D} = 1/(k - 1) \approx 0 \), then a cooperator is linked to the same number of cooperators as a defector, \( q_{C|C} \approx q_{C|D} \). An increasing value of \( k \) demands a large cooperation effort, for selection to favor cooperation more than defection.

7 Discussion

In this paper, we have studied an updating rule of two rounds. In the first round, an individual compares its payoff to a tolerance index. Satisfied individuals will keep their current strategies with a probability higher than 1/2. Dissatisfied individuals will keep their current strategies with probability lower than 1/2.

Before investing their efforts in gathering social information, individuals play with their strategies to reach their aspiration levels. Satisfied individuals will maintain their
strategies. Unsatisfied individuals will invest their resources in gathering social information to imitate successful strategies.

These mechanisms help to maintain the best strategies, which give a satisfactory return to their players. For rational dissatisfied individuals, it would make the best sense, if they imitate successful strategies by turning to their neighborhood. The classical aspiration-based update rule suggests that dissatisfied individuals will switch their strategies, which stands in contradiction with their rationality. It will be more realistic to let dissatisfied individuals choose successful strategies.

Individuals are ranged over $N$ nodes, where each node is occupied by an individual. Each node is linked to $k$ other nodes, where $k$ is a constant. The traditional well-mixed population is represented by a complete graph, $k = N$. The circular mode is represented by a very limited connections, $k = 2$.

Under the classical aspiration mechanisms, dissatisfied individuals discover randomly other strategies. The aspiration level is a constant, $\Delta \alpha = 0$. In such a case, weak selection favors defection more than cooperation (Du et al. [Du(2014)]). This is natural since cooperators have a lower payoff than defectors. As a result, they will update their strategies more frequently than defectors, which promotes defection.

For a general game and by pair approximation for $k \geq 3$, we have shown the selection favors cooperation more often than defection if

$$\frac{3k + 2}{2k}(R - P) + \frac{3k - 2}{2k}(S - T) + \Delta \alpha > 0.$$  \hspace{1cm} (50)

$\frac{3k + 2}{2k}(R - P) + \frac{3k - 2}{2k}(S - T)$ quantifies the effect of payoff difference between cooperators and defectors. $\Delta \alpha$ quantifies the effect of difference in aspiration level. Pair approximation fails to characterize the evolutionary process for $k = 2$ and $k \approx N$. For circular model $k = 2$ and by an exact calculation, we extend these results.

In the limit case $k \to \infty$, condition [50] becomes

$$\frac{3}{2}(R + S - T - P) + \Delta \alpha > 0,$$  \hspace{1cm} (51)
which is exactly the same condition obtained in well-mixed population by an exact calcu-
lation. For symmetric aspiration, $\Delta \alpha = 0$, it is exactly the risk dominance condition in
a coordination game (Harsanyi and Selten [Harsanyi(1988)]). A coordination game is the
case where $R > T$ and $P > S$. In a coordination game, selection always favors the risk
dominance equilibrium more often than the other strategy.

Under the additive prisoner’s Dilemma, cooperators have a higher fitness if they are
linked to a higher number of cooperators, while defectors have a lower fitness if they are
linked to a higher number of defectors. The key relationship is $q_{C|C} - q_{C|D} = \frac{1}{k-1}$. For $k$
small enough, we have $q_{C|C} \gg q_{C|D}$, which means that a cooperator is linked to a higher
number of cooperators than a defector. As a result, cooperators have a higher fitness
than defectors. A graph with a fewer connections should promote cooperative behavior.
For $k$ too large, we have $q_{C|C} \approx q_{C|D}$. In this case, both cooperators and defectors are
linked to the same number of cooperators. This plays in favor of defectors since they have
a higher fitness than cooperators. A graph with a large number of connections should
oppose cooperative behavior.

Moreover, the level of cooperation in structured populations is not the same as in well-
mixed populations. Cooperative behavior is favored in certain networks as in a well-mixed
populations. Other networks favors defection.

For symmetric aspiration, $\Delta \alpha = 0$, selection favors cooperation more than defection if
$b/c > \frac{3k}{4}$, where $k$ is the connectivity. However, in a well-mixed population always weak
selection favors defectors spreading in the population (Appendix C). Networks with a
fewer connections should promote cooperation. Networks with a large connections should
promote defection.

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8 Appendix A: Coefficients in Eq (18) in the quasi-steady state

In the quasi-steady state and by using Eq (23), we express the different probabilities of Eq (7) in terms of $p_C$ as

$$
p_D = 1 - p_C,
q_{D|C} = 1 - q_{C|C} = \frac{k - 2}{k - 1} (1 - p_C),
q_{C|D} = \frac{q_{D|C}p_C}{1 - p_C} = \frac{k - 2}{k - 1} p_C,
q_{D|D} = 1 - q_{C|D} = 1 - \frac{k - 2}{k - 1} p_C,
p_{CD} = q_{D|C}p_C = \frac{k - 2}{k - 1} (1 - p_C)p_C.
$$

(52)

This leads to an important equality

$$
q_{C|C} + q_{D|D} = \frac{k}{k - 1}.
$$

(53)
Hence, by using Eqs (52) and (53), the quantity of interest in Eq (18) become

\[ I_R = \left[ k + 2 + 2(k - 1)(q_{C|C} + q_{D|D}) \right] \frac{k - 1}{k} q_{C|C} \]
\[ = \left[ k + 2 + 2(k - 1) \times \frac{k}{k - 1} \right] \frac{k - 1}{k} \left( p_C + \frac{1 - p_C}{k - 1} \right) \]
\[ = \frac{3k + 2 + (3k + 2)(k - 2)p_C}{k}, \]

\[ I_S = 1 + (k - 1)q_{D|C} + \frac{2(k - 1)^2}{k} (q_{C|C} + q_{D|D})q_{D|C} + \frac{2(k - 1)q_{D|D}}{k} \]
\[ = 1 + (k - 1)k - 2 \frac{k - 2}{k - 1} (1 - p_C) + \frac{2(k - 1)^2}{k} \frac{k - 2}{k - 1} (1 - p_C) + \frac{2(k - 1)}{k} \left( 1 - \frac{k - 2}{k - 1} p_C \right) \]
\[ = \frac{3k^2 - 3k - 2 - (k - 2)(3k + 2)p_C}{k}, \]

\[ I_T = 1 + (k - 1)q_{C|D} + \frac{2(k - 1)^2}{k} (q_{C|C} + q_{D|D})q_{C|D} + \frac{2(k - 1)q_{C|C}}{k} \]
\[ = 1 + (k - 1)k - 2 \frac{k - 2}{k - 1} p_C + \frac{2(k - 1)^2}{k} \frac{k - 2}{k - 1} p_C + \frac{2(k - 1)}{k} \left( \frac{1}{k - 1} + \frac{k - 2}{k - 1} p_C \right) \]
\[ = \frac{(k + 2) + (3k + 2)(k - 2)p_C}{k}, \]

\[ I_P = \left[ k + 2 + 2(k - 1)(q_{C|C} + q_{D|D}) \right] \frac{k - 1}{k} q_{D|D} \]
\[ = \left[ k + 2 + 2(k - 1) \times \frac{k}{k - 1} \right] \frac{k - 1}{k} \left( 1 - \frac{k - 2}{k - 1} p_C \right) \]
\[ = \frac{(3k + 2)(k - 1) - (3k + 2)(k - 2)p_C}{k}. \] (54)

9 Appendix B: Circular model \((k = 2)\)

Suppose that we have \(N\) sites over a circle numbered 1, 2, \ldots, \(N\). Each site is occupied by an individual. Individual who is located at site \(l\) can interact with its neighbors located at sites \(l - 1\) and \(l + 1\), through game matrix (2). The same graph is used for the replacement graph. Dissatisfied individuals imitate their direct neighbors.

At each time step, each individual interacts with its direct neighbors. Then, an individual \(I\) is chosen at random. It will update its strategy with probability (4). In this case, it will imitate the strategy of a direct neighbor \(J\), with probability proportional to its fitness \(f_J = 1 + \delta \Pi_J\). Otherwise, individual \(I\) will keep its current strategy.

The population is initially consisted entirely of defectors. A new cooperator is intro-
duced on a particular site. We have two scenarios. This cooperator will generate a lineage of cooperators without overlapping one beside the other, which will take over the population. In this case, the population ends with only cooperators (extinction of defectors). The second scenario is that this individual might die before reproducing or generate a lineage that disappears (extinction of cooperators). Let $\rho_C(\delta)$ the probability of the first scenario. Likewise, $\rho_D(\delta)$ is the probability that a single defector placed in a population of cooperators will generate a lineage, which will take over the population. Using a recursive argument (Karlin and Taylor [Karlin(1975)]), we have

$$
\rho_C(\delta) = \frac{1}{1 + \sum_{i=1}^{N-1} \prod_{j=1}^{i} \frac{T_j^+}{T_j^-} }.
$$

$$
\frac{\rho_C(\delta)}{\rho_D(\delta)} = \prod_{i=1}^{N-1} \frac{T_i^+}{T_i^-}.
$$

(55)

where $T_i^+$ (resp. $T_i^-$) is the transition probability of "the number of cooperators increases from $i$ to $i+1$ in one time step" (resp."the number of cooperators decreases from $i$ to $i-1$ in one times step").

9.1 Payoffs

Without loss of generality, suppose that sites $l+1, \ldots, l+i$ are occupied by cooperators, while the other sites are occupied by defectors. Changes in the composition of the population take place at the boundary between the two clusters: cooperators’ cluster formed by sites $l+1, \ldots, l+i$ and defectors’ cluster formed by the other sites. Changes in one time step may happen at sites $l, l+1, l+i, l+i+1$.

To find the transition probabilities $T_i^+$ and $T_i^-$, the different payoffs of individuals around the boundary should be known. The payoff of an individual depends on the
number of its neighbors of each type. We have the following types of payoffs

\[ \Pi_{C,(1,1)} = \frac{R + S}{2}, \]
\[ \Pi_{D,(1,1)} = \frac{T + P}{2}, \]
\[ \Pi_{C,(2,0)} = R, \]
\[ \Pi_{C,(0,2)} = S, \]
\[ \Pi_{D,(2,0)} = T, \]
\[ \Pi_{D,(0,2)} = P, \]

where \( \Pi_{X,(l,j)} \) refer to the payoff of an \( X \)-player, who has \( l \) cooperators and \( j \) defectors as neighbors, for \( X \in \{C, D\} \) and \( l + j = 2 \) is the graph degree.

### 9.2 Ratio of transition probabilities

The transition \( i \to i + 1 \) takes place only if a defector, who is located at the boundary, becomes a cooperator. This occurs with probability

\[
T_i^+ = \frac{2}{N} \times \frac{1}{1 + e^{\delta (\alpha_C - \Pi_{C,(1,1)})}} \times \frac{f_{C,(1,1)}}{f_{C,(1,1)} + f_{D,(0,2)}} = \frac{1}{2N} + \frac{\delta}{4N} \left[ \Pi_{C,(1,1)} + \alpha_D - \Pi_{D,(0,2)} - \Pi_{D,(1,1)} \right] + O(\delta^2). \tag{57}
\]

The transition \( i \to i - 1 \) takes place only if a defector, who is located at the boundary, becomes a cooperator. This occurs with probability

\[
T_i^- = \frac{2}{N} \times \frac{1}{1 + e^{\delta (\alpha_C - \Pi_{C,(1,1)})}} \times \frac{f_{D,(1,1)}}{f_{C,(2,0)} + f_{D,(1,1)}} = \frac{1}{2N} + \frac{\delta}{4N} \left[ \Pi_{D,(1,1)} + \alpha_C - \Pi_{C,(2,0)} - \Pi_{C,(1,1)} \right] + O(\delta^2). \tag{58}
\]

Dividing Eq (57) by Eq (58), we obtain

\[
\frac{T_i^+}{T_i^-} = 1 + \frac{\delta}{2} \left[ 2(\Pi_{C,(1,1)} - \Pi_{D,(1,1)}) + \Pi_{C,(2,0)} - \Pi_{D,(0,2)} + \Delta \alpha \right] + O(\delta^2). \tag{59}
\]

Note that Eq (59) is valid for \( i = 3, \ldots, N - 3 \).
For $i = 2$, only two cooperators are present in the population. Their payoffs are of type $\Pi_{C,(1,1)}$. As a result, we have

$$T_2^- = \frac{2}{N} \times \frac{1}{1 + e^{\delta(\alpha_C - \Pi_{C,(1,1)})}} \times \frac{f_{D,(1,1)}}{f_{C,(1,1)} + f_{D,(1,1)}}$$

$$= \frac{1}{2N} + \frac{\delta}{4N} \left[ \Pi_{D,(1,1)} - 2\Pi_{C,(1,1)} + \alpha_C \right] + \mathcal{O}(\delta^2). \quad (60)$$

The transition probability $T_2^+$ is the same in Eq (57). Then, the ratio becomes

$$\frac{T_2^+}{T_2^-} = 1 + \frac{\delta}{2} \left[ 2(\Pi_{C,(1,1)} - \Pi_{D,(1,1)}) + \Pi_{C,(1,1)} - \Pi_{D,(0,2)} + \Delta \alpha \right] + \mathcal{O}(\delta^2). \quad (61)$$

Likewise, for $i = N - 2$, we have

$$\frac{T_{N-2}^+}{T_{N-2}^-} = 1 + \frac{\delta}{2} \left[ 2(\Pi_{C,(1,1)} - \Pi_{D,(1,1)}) + \Pi_{C,(2,0)} - \Pi_{D,(1,1)} + \Delta \alpha \right] + \mathcal{O}(\delta^2). \quad (62)$$

Finally, for $i = 1$, only one cooperator is in the competition with $N - 1$ defectors. If it decides to update its strategy, it will switch its strategy with probability 1 since its direct neighbors are defectors. Therefore, we obtain

$$T_1^- = \frac{1}{N} \times \frac{1}{1 + e^{\delta(\alpha_C - \Pi_{C,(0,2)})}}$$

$$= \frac{1}{2N} + \frac{\delta}{4N} \left[ \alpha_C - \Pi_{C,(0,2)} \right] + \mathcal{O}(\delta^2), \quad (63)$$

whereas

$$T_1^+ = \frac{2}{N} \times \frac{1}{1 + e^{\delta(\alpha_D - \Pi_{D,(1,1)})}} \times \frac{f_{C,(0,2)}}{f_{C,(0,2)} + f_{D,(0,2)}}$$

$$= \frac{1}{2N} + \frac{\delta}{4N} \left[ \Pi_{C,(0,2)} - \Pi_{D,(0,2)} + \alpha_D - \Pi_{D,(1,1)} \right] + \mathcal{O}(\delta^2). \quad (64)$$

Accordingly, the ratio becomes

$$\frac{T_1^+}{T_1^-} = 1 + \frac{\delta}{2} \left[ 2\Pi_{C,(0,2)} - \Pi_{D,(0,2)} - \Pi_{D,(1,1)} + \Delta \alpha \right] + \mathcal{O}(\delta^2). \quad (65)$$

Likewise, for $i = N - 1$, we have

$$\frac{T_{N-1}^+}{T_{N-1}^-} = 1 + \frac{\delta}{2} \left[ \Pi_{C,(2,0)} + \Pi_{C,(1,1)} - 2\Pi_{D,(2,0)} + \Delta \alpha \right] + \mathcal{O}(\delta^2). \quad (66)$$
9.3 Approximation of the fixation probabilities

We expand \( \prod_{j=1}^{i} \frac{T_j^-}{T_j^+} \) up to the first-order in \( \delta \),

\[
\prod_{j=1}^{i} \frac{T_j^-}{T_j^+} = \prod_{j=1}^{i} \left[ 1 + \delta \cdot \frac{d}{d\delta} \left( \frac{T_j^-}{T_j^+} \right) \big|_{\delta=0} \right] = 1 + \delta \cdot \sum_{j=1}^{i} \frac{d}{d\delta} \left( \frac{T_j^-}{T_j^+} \right) \big|_{\delta=0} + O(\delta^2). \tag{67}\]

Accordingly, we have

\[
\rho_C(\delta) = \frac{1}{N + \delta \cdot \sum_{i=1}^{N-1} \sum_{j=1}^{i} \frac{d}{d\delta} \left( \frac{T_j^-}{T_j^+} \right) \big|_{\delta=0} + O(\delta^2)} = 1 + \frac{\delta}{N} \sum_{i=1}^{N-1} \sum_{j=1}^{i} \frac{d}{d\delta} \left( \frac{T_j^-}{T_j^+} \right) \big|_{\delta=0} + O(\delta^2), \tag{68}\]

\[
\frac{\rho_C}{\rho_D}(\delta) = 1 + \delta \cdot \sum_{j=1}^{N-1} \frac{d}{d\delta} \left( \frac{T_j^+}{T_j^-} \right) \big|_{\delta=0} + O(\delta^2). \tag{69}\]

Substituting Eqs (59, 61, 62, 65, 66) in Eq (68) yield to

\[
\rho_C(\delta) = \frac{1}{N} + \frac{\delta}{4N^2} \left[ (2N^2 - 7N + 7)R + (N^2 + 2N - 3)S - (N^2 - 2N + 5)T \right.
\]

\[
- (2N^2 - 3N - 5)P + N(N - 1)\Delta \alpha \big] + O(\delta^2), \tag{69}\]

and

\[
\frac{\rho_C}{\rho_D}(\delta) = 1 + \frac{\delta}{2} \left[ (2N - 5)(R - P) + N(S - T) + N\Delta \alpha \big] + O(\delta^2. \tag{70}\]

10 Appendix C: Well-mixed population

Consider a well-mixed population of size \( N \), where each individual can interact with any other individual with the same probability through game matrix \( \mathbf{2} \). At any time step, all individuals interact by pairs to accumulate payoffs. Then, an individual \( I \) is chosen at random to update its strategy. It will update its strategy with probability \( \mathbf{3} \). In this case, it imitates individual \( J \), one of its neighbors, probability proportional to its fitness
\( f_J = 1 + \delta \Pi_J \). Otherwise, the current strategy of individual \( I \) will be maintained. Similarly to appendix \( B \), we have

\[
\rho_C(\delta) = \frac{1}{1 + \sum_{i=1}^{N-1} \prod_{j=1}^{i} \frac{T_j}{T_j}},
\]

\( \rho_C(\delta) = \frac{N^{-1} T_i^+}{T_i^-} \).

(71)

where \( T_i^+ \) (resp. \( T_i^- \)) is the transition probability \( i \rightarrow i + 1 \) (resp. \( i \rightarrow i - 1 \)).

Suppose that the population is composed of \( i \) cooperators and \( N - i \) defectors. Then, the payoffs of a cooperator and a defector are given, respectively, by

\[
\Pi_{C,i} = \frac{(i-1)R + (N-i)S}{N-1}
\]

\[
\Pi_{D,i} = \frac{iT + (N-i-1)P}{N-1}.
\]

(72)

\( T_i^+ \) is the probability that a defector, chosen to update its strategy, becomes a cooperator. This occurs with probability

\[
T_i^+ = \frac{N-i}{N} \times \frac{1}{1 + e^{\delta(\alpha_D - \Pi_{D,i})}} \times \frac{if_{C,i}}{if_{C,i} + \frac{(N-i)if_{D,i}}{2(N-1)}} \times \frac{(N-i)i}{2N(N-1)} + \delta \cdot \frac{(N-i)i}{2N(N-1)} \left[ \frac{\alpha_D - \Pi_{D,i}}{2} + \frac{N-i-1}{N-1} (\Pi_{C,i} - \Pi_{D,i}) \right] + \mathcal{O}(\delta^2).
\]

(73)

\( T_i^- \) is the probability that a cooperator, chosen to update its strategy, becomes a defector. This occurs with probability

\[
T_i^- = \frac{i}{N} \times \frac{1}{1 + e^{\delta(\alpha_C - \Pi_{C,i})}} \times \frac{(N-i)if_{D,i}}{(i-1)f_{C,i} + (N-i)f_{D,i}}.
\]

\[
= \frac{(N-i)i}{2N(N-1)} + \delta \cdot \frac{(N-i)i}{2N(N-1)} \left[ \frac{\alpha_C - \Pi_{C,i}}{2} + \frac{i-1}{N-1} (\Pi_{D,i} - \Pi_{C,i}) \right] + \mathcal{O}(\delta^2).
\]

(74)

Therefore, the ratio of transition probabilities is

\[
\frac{T_i^+}{T_i^-} = 1 + \delta \left[ \frac{3N-5}{N-1}(\Pi_{C,i} - \Pi_{D,i}) + \Delta \alpha \right] + \mathcal{O}(\delta^2).
\]

(75)
Inserting Eq (75) in Eq (71) after expanding it up to the first-order in $\delta$, we have

$$
\rho_C(\delta) = \frac{1}{N} + \delta \cdot \frac{1}{N} \sum_{i=1}^{N-1} (N - i) \frac{d}{d\delta} \left( \frac{T_i^+}{T_i^-} \right) \bigg|_{\delta=0} + O(\delta^2)
$$

$$
= \frac{1}{N} + \delta \cdot \frac{N - 1}{4} \left[ \frac{3N - 5}{3(N - 1)^2} \left( (N - 2)R + (2N - 1)S - (N + 1)T - (2N - 4)P \right) + \Delta \alpha \right]
$$

(76)

and

$$
\frac{\rho_C}{\rho_D}(\delta) = 1 + \delta \cdot \sum_{i=1}^{N-1} \frac{d}{d\delta} \left( \frac{T_i^+}{T_i^-} \right) \bigg|_{\delta=0} + O(\delta^2)
$$

$$
= 1 + \delta \cdot \frac{N - 1}{2} \left[ \frac{3N - 5}{2(N - 1)^2} \left( (N - 2)R + NS - NT - (N - 2)P \right) + \Delta \alpha \right] + O(\delta).
$$

(77)

Note that Eqs (76) and (77) is valid for any finite population size $N \geq 2$.

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