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Strategy selection in structured populations

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Abstract

Evolutionary game theory studies frequency dependent selection. The fitness of a strategy is not constant, but depends on the relative abundances (=frequencies) of strategies in the population. This type of evolutionary dynamics occurs in many settings of ecology, infectious disease dynamics, animal behavior and social interactions of humans. Traditionally evolutionary game dynamics are studied in well-mixed populations, where the interaction between any two individuals is equally likely. There have also been several approaches to study evolutionary games in structured populations. In this paper we present a simple result that holds for a large variety of population structures. We consider the game between two strategies, A and B , described by the payoff matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$. We study mutation and selection. If the payoffs are linear in a, b, c and d , then for weak selection strategy A is favored over B if and only if $\sigma a + b > c + \sigma d$. This means the effect of population structure on strategy selection can be described by a single parameter, σ . We present the values of σ for various examples including the well-mixed population, games on graphs and games in phenotype space. We give a proof for the existence of σ , which holds for all population structures and update rules that have certain (very natural) properties. Our proof assumes weak selection, but allows any mutation rate. We discuss the relationship between σ and the critical benefit to cost ratio for the evolution of cooperation. The single parameter, σ , allows us to quantify the ability of a population structure to promote the evolution of cooperation or to choose efficient equilibria in coordination games.

1 Introduction

Game theory was invented by John von Neuman and Oskar Morgenstern (1944) to study strategic and economic decisions of humans (Fudenberg & Tirole 1991, Binmore 1994, Weibull 1995, Samuelson 1997). Evolutionary game theory was introduced by John Maynard Smith in order to explore the evolution of animal behavior (Maynard Smith & Price 1973, Maynard Smith 1982, Houston & McNamara 1999, McNamara et al 1999, Bshary et al 2008). In the meanwhile, evolutionary game theory has been used in many areas of biology including ecology (May & Leonard 1975, Doebeli & Knowlton 1998), host-parasite interactions (Turner & Chao 1999, Nowak & May 1994), bacterial

population dynamics (Kerr et al 2002), immunological dynamics (Nowak et al 1995), the evolution of human language (Nowak et al 2002) and the evolution of social behavior of humans (Trivers 1971, Axelrod & Hamilton 1981, Boyd & Richerson 2005, Nowak & Sigmund 2005). Evolutionary game theory is the necessary tool of analysis whenever the success of one strategy depends on the frequency of strategies in the population. Therefore, evolutionary game theory is a general approach to evolutionary dynamics with constant selection being a special case (Nowak & Sigmund 2004).

In evolutionary game theory there is always a population of players. The interactions of the game lead to payoff, which is interpreted as reproductive success. Individuals, who receive a higher payoff, leave more offspring. Thereby, successful strategies outcompete less successful ones. Reproduction can be genetic or cultural.

The traditional approach to evolutionary game theory is based on the replicator equation (Taylor & Jonker 1978, Hofbauer et al 1979, Zeeman 1980, Hofbauer & Sigmund 1988,1998, 2003, Cressman 2003), which examines deterministic dynamics in infinitely large, well-mixed populations. Many of our intuitions about evolutionary dynamics come from this approach (Hofbauer & Sigmund 1988). For example, a stable equilibrium of the replicator equation is a Nash equilibrium of the underlying game. Another approach to evolutionary game theory is given by adaptive dynamics (Nowak & Sigmund 1990, Hofbauer & Sigmund 1990, Metz et al 1996, Dieckman et al 2000) which also assumes infinitely large population size.

But if we want to understand evolutionary game dynamics in finite-sized populations, we need a stochastic approach (Riley 1979, Schaffer 1988, Fogel et al 1998, Ficici & Pollack 2000, Alos-Ferrer 2003). A crucial quantity is the fixation probability of strategies; this is the probability that a newly introduced mutant, using a different strategy, takes over the population (Nowak et al 2004, Taylor et al 2004, Imhof & Nowak 2006, Nowak 2006a, Traulsen, Pacheco & Imhof 2006, Lessard & Ladret 2007, Bomze & Pawlowitsch 2008). In this new approach, the Nash equilibrium condition no longer implies evolutionary stability.

There has also been much interest in studying evolutionary games in spatial settings (Nowak & May 1992, 1993, Ellison 1993, Herz 1994, Lindgren & Nordahl 1994, Ferriere & Michod 1996, Killingback & Doebeli 1996, Nakamaru et al 1997, 1998, Nakamaru & Iwasa 2005, 2006, van Baalen & Rand 1998, Yamamura et al 2004, Helbing & Wu 2008). Here most interactions occur among nearest neighbors. The typical geometry for spatial games are regular lattices (Nowak et al 1994, Hauert & Doebeli 2004, Szabó & Tóke 1998, Szabó et al. 2000), but evolutionary game dynamics has also been studied in continuous space (Hutson & Vickers 1992, 2002, Hofbauer 1999).

Evolutionary graph theory is an extension of spatial games to more general population structures and social networks (Lieberman et al 2005, Ohtsuki et al 2006, Pacheco et al 2006, Szabó & Fath 2007, Taylor et al 2007a, Santos et al 2008, Fu et al 2008). The members of the population occupy the vertices of a graph. The edges determine who interacts with whom. Different update rules can lead to very different outcomes of the evolutionary process, which emphasizes the general idea that population structure greatly affects evolutionary dynamics. For example, death-birth updating on graphs allows the evolution of cooperation, if the benefit-to-cost ratio exceeds the average degree of the graph $b/c > k$ (Ohtsuki et al 2006). Birth-death updating on graphs does not favor evolution of cooperation. A replicator equation with a transformed payoff matrix can describe deterministic evolutionary dynamics on regular graphs (Ohtsuki & Nowak 2007). There is also a modified condition for what it means to be a Nash equilibrium for games on graphs (Ohtsuki & Nowak 2008).

Spatial models have also a long history of investigation in the study of ecosystems and ecological interactions (Levin & Paine 1974, Durrett 1988, Hassel et al 1991, Durrett & Levin 1994). There is also a literature on the dispersal behavior of animals (Hamilton & May 1977, Comins et al 1980, Gandon & Rousset 1999). Boerlijst & Hogeweg (1991) studied spatial models in prebiotic evolution. The concept of a viscous population (Hamilton 1964) has given rise to the study of population structure in the context of inclusive fitness theory (Seger 1981, Grafen 1985, 2006, Queller 1985, Taylor 1992b, Taylor & Frank 1996, Frank 1998, Rousset & Billiard 2000, Rousset 2004, Taylor et al 2000, 2007b).

In this paper, we study the interaction between two strategies, A and B , given by the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \quad (1)$$

We consider a mutation-selection process in a population of fixed size N . Whenever an individual reproduces, the offspring adopts the parent's strategy with probability $1 - u$ and adopts a random strategy with probability u . We say that strategy A is selected over strategy B , if it is more abundant in the stationary distribution of the mutation-selection process. We call this concept 'strategy selection'.

In the limit of low mutation ($u \rightarrow 0$), the stationary distribution is non-zero only for populations that are either all- A or all- B . The system spends only an infinitesimal small fraction of time in the mixed states. In this case, the question of strategy selection reduces to the comparison of the fixation probabilities, ρ_A and ρ_B . Here, ρ_A is the probability that a single A mutant introduced in a population of $N - 1$ many B players generates a lineage of offspring that takes over the entire population. In contrast, the probability that the A lineage becomes extinct is $1 - \rho_A$. Vice versa, ρ_B denotes the probability that a single B mutant introduced in a population of $N - 1$ many A players generates a lineage that takes over the entire population. The fixation probabilities measure global selection over the entire range of relative abundances (Nowak et al 2004). The condition for A to be favored over B in the limit of low mutation is

$$\rho_A > \rho_B. \quad (2)$$

For positive mutation rate ($0 < u < 1$), the stationary distribution includes both homogeneous and mixed states. In this case, strategy selection is determined by the inequality

$$\langle x \rangle > 1/2. \quad (3)$$

Here x is the frequency of A individuals in the population. The angular brackets denote the average taken over all states of the system, weighted by the probability of finding the system in each state. In the limit of low mutation, (3) is equivalent to (2).

Nowak et al (2004) have shown that in a well mixed population, in the limit of weak selection, condition (2) is equivalent to

$$\frac{N-2}{N}a + b > c + \frac{N-2}{N}d. \quad (4)$$

Antal et al (2008a) have shown that condition (4) holds for a large variety of stochastic processes that describe evolutionary dynamics in well-mixed populations, for any mutation rate and for any

intensity of selection. But in this paper we focus on structured populations and the limit of weak selection. A particular example of strategy selection in structured populations for any mutation rate is studied by Antal et al (2008b).

In this paper we analyze (3) to show that for a wide variety of population structures the condition for strategy A to be favored over strategy B can be written in the form

$$\sigma a + b > c + \sigma d. \tag{5}$$

This condition holds for the limit of weak selection. The parameter σ depends on the population structure, the update rule and the mutation rate, but it does not depend on the payoff values a, b, c, d . Thus, in the limit of weak selection, strategy selection in structured populations is determined by a linear inequality. The effect of population structure can be summarized by a single parameter, σ . Therefore, we call inequality (5) the ‘single-parameter condition’.

Note that $\sigma = 1$ corresponds to the standard condition for risk-dominance (Harsanyi & Selten 1988, Gintis, 2000, Binmore, 2007). If $\sigma > 1$ then the diagonal entries of the payoff matrix, a and d , are more important than the off-diagonal entries, b and c . In this case, the population structure can favor the evolution of cooperation in the Prisoner’s Dilemma game, which is defined by $c > a > d > b$. If $\sigma > 1$ then the population structure can favor the Pareto-efficient strategy over the risk-dominant strategy in a coordination game. A coordination game is defined by $a > c$ and $b < d$. Strategy A is Pareto efficient if $a > d$. Strategy B is risk-dominant if $a + b < c + d$. If $\sigma < 1$ then the population structure can favor the evolution of spite.

The paper is structured as follows. In Section 2 we present the model and the necessary assumptions that allow us to prove (5). In Section 3 we show the relationship between σ and the critical benefit-to-cost ratio for the evolution of cooperation. An interesting consequence is that for the purpose of calculating σ it suffices to study games that have simplified payoff matrices. In Section 4 we present a number of examples of games in structured populations that lead to a single-parameter condition. These examples include games in the well-mixed population, games on regular and heterogeneous graphs, games on replacement and interaction graphs, and games in phenotype space. In Section 5 we give a proof of the single-parameter condition, which holds for weak selection and any mutation rate. Section 6 is a summary of our findings.

2 Model and results

We consider stochastic evolutionary dynamics (with mutation and selection) in a structured population of finite size, N . Individuals adopt either strategy A or B . Individuals 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 (Ohtsuki et al 2006), inhabitants of the same island or individuals that share certain phenotypic properties (Antal et al 2008b). Based on these interactions, an average (or total) payoff is calculated according to the payoff matrix (1). We assume that the payoff is linear in a, b, c, d , with no constant terms. For instance, the total payoff of an A individual is $[a \times (\text{number of A-interactants}) + b \times (\text{number of B-interactants})]$. The effective payoff of an individual is given by $1 + \delta \cdot \text{Payoff}$. The parameter δ denotes the intensity of selection. The limit of weak selection is given by $\delta \rightarrow 0$.

Reproduction is subject to mutation. With probability u the offspring adopts a random strategy (which is either A or B). 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.

Our proof of the single parameter condition (5) holds for update rules that have the following two (very natural) properties.

- (i) The update is payoff-proportional with either constant birth rate or constant death rate.

Each update event consists of two steps: birth and death. One individual is chosen to give birth, and one individual is chosen to die. The order of the two steps is arbitrary: birth can be followed by death or vice versa. But only one of the two steps is proportional to payoff, while the other step is entirely independent of payoff and happens with the same probability to all individuals in the population. We discuss a few examples below.

- (ii) The update rule is symmetric for the two strategies.

The update rule differentiates between A and B only based on payoff. Relabeling the two strategies and correspondingly swapping the entries of the payoff matrix must yield symmetric dynamics. This assumption is entirely natural. It means that the difference between A and B is fully captured by the payoff matrix, while the population structure and update rule do not introduce any additional difference between A and B .

Let us now discuss a few update rules that fulfill assumption (i). A typical example is death-birth (DB) updating on graphs (Ohtsuki et al 2006): a random individual is chosen to die; the neighbors compete for the empty site proportional to their payoff. This means that death is entirely independent of payoff, while birth is proportional to payoff. Another example is the synchronous updating used by Antal et al (2008b) for ‘games in phenotype space’. There are discrete generations, as in a Wright-Fisher process (Ewens, 2004). Individuals reproduce proportional to payoff. All individuals die from one generation to the next and hence death is again entirely independent of payoff.

An update rule that does not fulfill assumption (i) is birth-death (BD) updating on graphs (Ohtsuki et al 2006): an individual is chosen for reproduction proportional to payoff; the offspring replaces a randomly chosen neighbor. Here the death event is not independent of payoff, because there is a correlation between strategies (and thus payoffs) of neighboring individuals on the graph. It turns out that for this update rule condition (5) still holds, but we need another proof that will be presented in a forthcoming paper.

Therefore we already know that (5) holds for a larger class of models than what is covered in this paper. Our assumption (i) of a constant birth rate or a constant death rate is needed for the type of proof that is given here, but we expect (5) to hold for most models that satisfy payoff-proportional update together with the symmetry assumption (ii).

In this paper, we first show that if assumptions (i) and (ii) are satisfied, then the condition for strategy A to be favored over strategy B can be written in the form

$$ka + k'b > k'c + kd. \tag{6}$$

The factors k and k' depend on the population structure and the update rule, but not on the entries of the payoff matrix. Condition (6) only depends on the single parameter $\sigma = k/k'$, but one has to be careful about the sign of k' , since dividing by k' can change the direction of the inequality.

Thus, in general, one can write the condition for strategy A to be favored over strategy B as a single-parameter condition. If $k' \geq 0$, this condition becomes

$$\sigma a + b > c + \sigma d \quad (7)$$

If the parameter σ tends to infinity then condition (7) becomes $a > d$. If σ is zero then condition (7) becomes $b > c$.

The condition $k' \geq 0$ is a very natural one and can be expected to hold in most cases. It holds for structures and update rules for which the game given by the payoff matrix

$$\begin{array}{cc} & A & B \\ A & (0 & 1) \\ B & (0 & 0) \end{array} \quad (8)$$

does not disfavor strategy A .

3 Evolution of cooperation

There is a relationship between the critical benefit-to-cost ratio for the evolution of cooperation (Nowak 2006b) and the parameter σ . In a simplified version of the Prisoner's Dilemma game a cooperator, C , pays a cost, \mathfrak{c} , for another individual to receive a benefit, \mathfrak{b} . We have $\mathfrak{b} > \mathfrak{c} > 0$. Defectors, D , distribute no benefits and pay no costs. We obtain the payoff matrix

$$\begin{array}{cc} & C & D \\ C & (\mathfrak{b} - \mathfrak{c} & -\mathfrak{c}) \\ D & (\mathfrak{b} & 0) \end{array} \quad (9)$$

Using condition (7) for payoff matrix (9) we obtain

$$\sigma(\mathfrak{b} - \mathfrak{c}) - \mathfrak{c} > \mathfrak{b} \quad (10)$$

For $\sigma > 1$ this condition means that cooperators are more abundant than defectors whenever the benefit-to-cost ratio $\mathfrak{b}/\mathfrak{c}$ is larger than the critical value

$$\left(\frac{\mathfrak{b}}{\mathfrak{c}}\right)^* = \frac{\sigma + 1}{\sigma - 1} \quad (11)$$

Alternatively, σ can be expressed by the critical $(\mathfrak{b}/\mathfrak{c})^*$ ratio as

$$\sigma = \frac{(\mathfrak{b}/\mathfrak{c})^* + 1}{(\mathfrak{b}/\mathfrak{c})^* - 1} \quad (12)$$

Here we have $\sigma > 1$. Note that even without the assumption $\mathfrak{b} > \mathfrak{c} > 0$, the same σ is obtained from (10), only some care is required to find the correct signs.

Thus, for any population structure and update rule that satisfy our assumptions, if the critical benefit-to-cost ratio is known, we can immediately obtain σ and vice versa. For example, for DB

updating on regular graphs of degree k we know that $(b/c)^* = k$ (Ohtsuki et al 2006). Using equation (12), this implies $\sigma = (k + 1)/(k - 1)$ which is in agreement with equation (17).

This demonstrates the practical advantage of relationship (12). In order to derive σ for the general game (1), it suffices to study the specific game (9) and to derive the critical benefit-cost ratio, $(b/c)^*$. Then (12) gives us the answer. It is sometimes easier to study the specific game (9) than to study the general game (1). Specifically, using (9) often spares the calculation of probabilities that three randomly chosen players share the same strategy (for example, coefficient η in Antal et al, 2008b).

Wild and Traulsen (2007) argue that the general payoff matrix (1) allows the study of synergistic effects between players in the weak selection limit, as opposed to the simplified matrix (9) where such effects are not present. Here we demonstrated that these synergistic effects do not matter if we are only interested in the question whether A is more abundant than B in the stationary distribution of the mutation-selection process. Of course, our observation does not suggest that the analysis of general games, given by (1), can be completely replaced by the analysis of simpler games, given by (9). Questions concerning which strategies are Nash equilibria, which are evolutionarily stable or when we have coexistence or bi-stability can only be answered by studying the general matrix. For such analyses see Ohtsuki & Nowak (2006, 2008) or Taylor & Nowak (2007).

Note also that instead of the simplified Prisoner's Dilemma payoff matrix, we can also consider other types of simplified payoff matrices in order to calculate σ . Two examples are

$$\begin{pmatrix} 1 & b \\ 0 & 0 \end{pmatrix} \quad \text{or} \quad \begin{pmatrix} 1 & 0 \\ c & 0 \end{pmatrix} \quad (13)$$

4 The single-parameter conjecture

Let us consider a game between two strategies A and B that is given by the payoff matrix (1). We study a variety of different population structures and always observe that for weak selection the condition for A to be favored over B can be written in the form $\sigma a + b > c + \sigma d$. For each example we give the value of σ . The derivations of these results have been given in papers which we cite. For the star we present a new calculation. These observations have led to the conjecture that for weak selection the effect of population structure on strategy selection can 'always' be summarized by a single parameter, σ .

4.1 The well-mixed population

As first example we consider the frequency dependent Moran process in a well mixed population of size N (Nowak et al 2004, Taylor et al 2004, Nowak 2006a) (Fig. 1a). In the language of evolutionary graph theory, a well-mixed population corresponds to a complete graph with identical weights. Each individual interacts with all other $N - 1$ individuals equally likely and obtains an average (or total) payoff. For DB updating we find for weak selection and any mutation rate (Antal et al 2008a)

$$\sigma = \frac{N - 2}{N} \quad (14)$$

Hence, for any finite well-mixed population we have $\sigma < 1$. In the limit $N \rightarrow \infty$, we obtain $\sigma = 1$, which yields the standard condition of risk-dominance, $a + b > c + d$. The σ given by eq (14) can also be found in the paper by Kandori et al (1993) who study a process that is stochastic in the generation of mutants, but deterministic in following the gradient of selection.

4.2 Graph structured populations

In such models, the players occupy the vertices of a graph, which is assumed to be fixed. The edges denote links between individuals in terms of game dynamical interaction and biological reproduction. Individuals play a game only with their neighbors and an average (or total) payoff is calculated. In this section we consider death-birth (DB) updating: at any one time step, a random individual is chosen to die, and the neighbors compete for the empty spot, proportional to their fitness (Ohtsuki et al 2006).

4.2.1 Cycle

Let us imagine N individuals that are aligned in a one dimensional array. Each individual is connected to its two neighbors, and the ends are joined up (Fig. 1b). The cycle is a regular graph of degree $k = 2$. Games on cycles have been studied by many authors including Ellison (1993), Nakamaru et al (1997), Ohtsuki et al (2006) and Ohtsuki & Nowak (2006a). The following result can be found in Ohtsuki & Nowak (2006) and holds for weak selection. For DB updating and low mutation ($u \rightarrow 0$) we have

$$\sigma = \frac{3N - 8}{N}. \quad (15)$$

Note that σ is an increasing function of the population size, N , and converges to $\sigma = 3$ for large N .

We have also performed simulations for a cycle with non-vanishing mutation (Fig. 2a). We find that σ decreases with increasing mutation rate, u .

4.2.2 Star

The star is another graph structure, which can be calculated exactly. There are N individuals. One individual occupies the center of the star and the remaining $N - 1$ individuals populate the periphery (Fig. 1c). The center is connected to all other individuals and, therefore, has degree $k = N - 1$. Each individual in the periphery is only connected to the center and, therefore, has degree $k = 1$. The average degree of the star is given by $\bar{k} = 2(N - 1)/N$. For large population size, N , the star and the cycle have the same average degree. Yet the population dynamics are very different. For DB updating on a star we find

$$\sigma = 1 \quad (16)$$

This result holds for weak selection and for any population size $N \geq 3$ and any mutation rate u . The calculation for the star is shown in Appendix A. Simulations for the star confirm that $\sigma = 1$ for any mutation rate (Fig. 2b).

4.2.3 Regular graphs of degree k

Let us now consider the case where the individuals of a population of size N occupy the vertices of a regular graph of degree $k \geq 2$. Each individual is connected to exactly k other individuals (Fig. 1d). For this structure, Ohtsuki et al (2006) obtain (see equation 24 in their online material)

$$\sigma = \frac{k + 1}{k - 1}. \quad (17)$$

This result holds for DB updating, weak selection, low mutation and large population size, $N \gg k$. The parameter σ depends on the degree of the graph and is always larger than one. For large values of k , σ converges to one. The limit of large k agrees with the result for the complete graph, which corresponds to a well-mixed population.

For general population size N , the calculation of Ohtsuki et al (2006) is not applicable, but we can obtain the parameter σ differently. Taylor et al (2007a) and Lehmann et al (2007) studied the Prisoner's Dilemma game (9) for the same structure but for general N . They obtained the critical benefit-to-cost ratio as $(\mathfrak{b}/\mathfrak{c})^* = (N - 2)/(N/k - 2)$. Using the relationship (12), we obtain

$$\sigma = \frac{(k + 1)N - 4k}{(k - 1)N}. \quad (18)$$

As a consistency check, taking $N \rightarrow \infty$ in (18) leads to (17). Moreover, setting $k = 2$ in (18) leads to (15), and setting $k = N - 1$ in (18) agrees with (14), as expected.

Computer simulations for a regular graph with $k = 3$ and $N = 6$, for mutation rate $u = 0.1$ suggest that $\sigma = 0.937$. The corresponding prediction of (18) for low mutation is $\sigma = 1$. Thus we conclude that σ depends on the mutation rate u (Fig. 2c).

Our proof of the linear inequality is not restricted to homogeneous graphs. Random graphs (Bollobás 1995) also satisfy our assumptions, and therefore we expect the single parameter condition to hold. We have performed simulations for a random graph with $N = 10$ and average degree $k = 2$. We find a linear condition with $\sigma = 1.636$ (see Fig. 2d).

4.2.4 Different interaction and replacement graphs

Individuals could have different neighborhoods for the game dynamical interaction and for the evolutionary updating. In this case, we place the individuals of the population on the edges of two different graphs (Ohtsuki et al 2007). The interaction graph determines who meets whom for playing the game. The replacement graph determines who learns from whom (or who competes with whom) for updating of strategies. The vertices of the two graphs are identical; the edges can be different (Fig. 1e).

Suppose both graphs are regular. The interaction graph has degree h . The replacement graph has degree g . The two graphs define an overlap graph, which contains all those edges that the interaction and replacement graph have in common. Let us assume that this overlap graph is regular and has degree l . We always have $l \leq \min\{h, g\}$. The following result holds for DB updating for weak selection and large population size (Ohtsuki et al 2007):

$$\sigma = \frac{gh + l}{gh - l}. \quad (19)$$

For general population size, N , we can obtain σ via the critical benefit-to-cost ratio in the Prisoner's Dilemma game (9). Using the result of Taylor et al. (2007), we obtain $(\mathfrak{b}/\mathfrak{c})^* = (N - 2)/(Nl/gh - 2)$. Hence, we have

$$\sigma = \frac{(gh + l)N - 4gh}{(gh - l)N}. \quad (20)$$

As a consistency check, $g = h = l = k$ reproduces (18).

4.3 Games in phenotype space

Antal et al (2008b) proposed a model for the evolution of cooperation based on phenotypic similarity. There is a one dimensional phenotype space given by a discrete lattice (Fig. 1f). Individuals interact with those who share the same phenotype. The population size is constant and given by N . Evolutionary dynamics can be calculated for DB updating or synchronous updating. There is a strategy mutation rate, u , and a phenotypic mutation rate, β . When an individual reproduces, its offspring has the same phenotype with probability $1 - 2\beta$ and mutates to either one of the two neighboring phenotypes with equal probability β .

The game can be generalized to the interaction between any two strategies A and B . The resulting expression for σ is complicated and depends on all parameters, including the two mutation rates, u and β . For $Nu \rightarrow 0$, $N\beta \rightarrow 0$ and weak selection we obtain

$$\sigma = 1 + \sqrt{3} \tag{21}$$

Note that this example has seemingly an infinite state space, which is not something we address in our proof, but a subtle trick turns the state space into a finite one. A detailed description can be found in Antal et al (2008b).

5 Proof of the single-parameter conjecture

In the first part of the proof we will show that for update rules that satisfy our assumption (i) in Section 2, the condition for strategy A to be favored over strategy B is linear in a, b, c, d with no constant terms. More precisely, it can be written as

$$k_1 a + k_2 b > k_3 c + k_4 d. \tag{22}$$

Here k_1, k_2, k_3, k_4 are real numbers, which can depend on the population structure, the update rule, the mutation rate and the population size, but not on the payoff values a, b, c, d .

In the second part of the proof we will show that for update rules that also satisfy our symmetry assumption (ii) in Section 2, this linearity leads to the existence of σ . Thus the condition that A is favored over B becomes

$$\sigma a + b > c + \sigma d \tag{23}$$

5.1 Linearity

A **state**, S , of the population is a list of strategies of the N individuals as well as, if any, their physical position, phenotypic state, or other information that can affect the fitness of players. For our proof, we assume a finite state space. We study a Markov process on this state space and we are concerned with the stationary probabilities of this process. A more detailed discussion of these stationary probabilities can be found in Appendix C.

In a state S , let x_S denote the frequency of A individuals in the population. Then the frequency of B individuals is $1 - x_S$. We are interested in the average frequency of A individuals, the average being taken over all possible states weighted by the stationary probability that the system is in those states. Let us denote this average frequency by $\langle x \rangle$. The condition for strategy A to be favored over strategy B is that the average frequency of A is greater than $1/2$ (i.e. on average, A individuals are more than 50%). This condition is hard to deal with analytically. However, for a

large class of update rules, in the limit of weak selection, this condition becomes equivalent to the simpler one

$$\langle \Delta x^{\text{sel}} \rangle > 0 \quad (24)$$

Here $\langle \Delta x^{\text{sel}} \rangle$ is the average effect of selection on the expected change in x . As before, the average is taken over all states S , weighted by the probability that the system is in each one of the states. In Appendix B we show that this equivalence is true for processes for which either the death rate or the birth rate is constant (eg. Death-Birth, Synchronous or a variant of Birth-Death updating).

Once we have this equivalence, we can proceed to calculate the average change in the frequency of A due to selection in one update step, which can be written as

$$\langle \Delta x^{\text{sel}} \rangle = \sum_S \Delta x_S \cdot \pi_S \quad (25)$$

where Δx_S is the expected change due to selection in the frequency of A individuals in a given state S of the system and π_S is the probability to find the system in that state.

Let s_i be the strategy of individual i , where $s_i = 1$ denotes A and $s_i = 0$ denotes B . Then, in a given state S of the system, the expected change of x due to selection in one update step is the number of offspring of A individuals minus the number of A individuals in the previous generation, divided by the population size. Thus, it is given by

$$\Delta x_S = \frac{1}{N} \left(\sum_i s_i \omega_i - \sum_i s_i \right) \quad (26)$$

where ω_i is the expected number of offspring of individual i (including himself if he survives).

For our update rules, for which who gives birth or who dies is chosen proportional to the effective payoff (assumption (i)), ω_i is continuous and infinitely differentiable at $\delta = 0$. Hence Δx_S is as well and we can write its Taylor expansion at $\delta = 0$

$$\Delta x_S = \Delta x_S^{(0)} + \delta \Delta x_S^{(1)} + \mathcal{O}(\delta^2) \quad (27)$$

Here $\Delta x_S^{(0)}$ is the change in state S , when $\delta = 0$. $\Delta x_S^{(1)}$ is the first derivative of Δx_S with respect to δ , evaluated at $\delta = 0$.

The probability π_S that the system is in state S also depends on δ . For update rules satisfying assumption (i), we show in Appendix C that π_S is also continuous and differentiable as a function of δ . Thus, we can write its Taylor expansion at $\delta = 0$

$$\pi_S = \pi_S^{(0)} + \delta \pi_S^{(1)} + \mathcal{O}(\delta^2) \quad (28)$$

As before, the (0) superscript refers to the neutral state $\delta = 0$ and $\pi_S^{(1)} = d\pi_S/d\delta$ evaluated at $\delta = 0$.

Since Δx_S and π_S are both continuous and differentiable at $\delta = 0$ it follows from (25) that $\langle \Delta x^{\text{sel}} \rangle$ is as well. Using their Taylor expansions (27) and (28) into (25) we can then write

$$\begin{aligned} \langle \Delta x^{\text{sel}} \rangle &= \sum_S \Delta x_S \cdot \pi_S \\ &= \sum_S \Delta x_S^{(0)} \cdot \pi_S^{(0)} + \delta \sum_S [\Delta x_S^{(1)} \cdot \pi_S^{(0)} + \Delta x_S^{(0)} \cdot \pi_S^{(1)}] + \mathcal{O}(\delta^2) \\ &= \delta \sum_S [\Delta x_S^{(1)} \cdot \pi_S^{(0)} + \Delta x_S^{(0)} \cdot \pi_S^{(1)}] + \mathcal{O}(\delta^2) \end{aligned} \quad (29)$$

For the last equality we used the fact that, for the neutral process, the average change in A over all states is zero, that is $\sum_S \Delta x_S^{(0)} \cdot \pi_S^{(0)} = 0$.

Thus, in the limit of weak selection, the condition (24) that A is favored over B becomes

$$\sum_S [\Delta x_S^{(1)} \cdot \pi_S^{(0)} + \Delta x_S^{(0)} \cdot \pi_S^{(1)}] > 0 \quad (30)$$

Note that $\Delta x_S^{(0)}$ and $\pi_S^{(0)}$ contain no terms in a, b, c, d because they correspond to neutral selection, $\delta = 0$. We will show in Appendix C that both $\Delta x_S^{(1)}$ and $\pi_S^{(1)}$ are linear in a, b, c, d with no constant terms. Hence, from (30) we deduce that our condition for strategy A to be favored over strategy B is linear in a, b, c, d and is of the form (22).

5.2 Existence of Sigma

We have thus shown that for structures satisfying assumption (i), the condition for strategy A to be favored over strategy B has the form (22)

$$k_1 a + k_2 b > k_3 c + k_4 d$$

For structures which moreover satisfy our symmetry condition (assumption (ii)), we obtain the symmetric relation by simply relabeling. Thus, strategy B is favored over strategy A if and only if

$$k_1 d + k_2 c > k_3 b + k_4 a \quad (31)$$

Since both strategies can not be favored at the same time, strategy A must be favored if and only if

$$k_4 a + k_3 b > k_2 c + k_1 d \quad (32)$$

Since both conditions (22) and (32) are if and only if conditions that A is favored over B , they must be equivalent. Thus, it must be that (32) is a scalar multiple of (22), so there must exist some $\lambda > 0$ such that $k_4 = \lambda k_1 = \lambda^2 k_4$ and $k_3 = \lambda k_2 = \lambda^2 k_3$. Thus, we conclude that $\lambda = 1$ and that $k_1 = k_4 = k$ and $k_2 = k_3 = k'$. So the condition that A is favored over B becomes

$$k a + k' b > k' c + k d \quad (33)$$

Note that this condition depends only on the parameter $\sigma = k/k'$. However, one must exercise caution in dividing by k' because its sign can change the direction of the inequality. If $k' \geq 0$, then we can rewrite (33) as

$$\sigma a + b > c + \sigma d \quad (34)$$

Note that in this case σ could be infinite and then the condition that A is favored over B reduces to $a > d$.

Note also that $k' \geq 0$ is a very natural condition which we expect to be satisfied in most cases. It is equivalent to saying that in the game given by the matrix

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix} \end{array} \quad (35)$$

strategy A is not disfavored.

6 Conclusion

We have studied evolutionary game dynamics in structured populations. We have investigated the interaction between two strategies, A and B , given by the payoff matrix

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \quad (36)$$

We have shown that the condition for A to be more abundant than B in the stationary distribution of the mutation selection process can be written as a simple linear inequality

$$\sigma a + b > c + \sigma d \quad (37)$$

This condition holds for all population structures, for weak selection, but any mutation rate. The parameter σ captures the effect of population structure. It quantifies the degree to which individuals using the same strategy are more likely ($\sigma > 1$) or less likely ($\sigma < 1$) to interact than individuals using different strategies. The value of σ can depend on the population structure, the update rule, the population size, the mutation rate, but it does not depend on the entries of the payoff matrix. For each particular problem the specific value of σ must be calculated. Here we have shown that there always is a simple linear inequality with a single parameter, σ , given that some very natural assumptions hold.

Specifically, our proof is based on two assumptions: (i) the update rule consists of two steps, birth and death; one of those steps is proportional to payoff, but the other step is independent of payoff; this means all individuals either die with the same probability or give birth with the same probability; (ii) the population structure does not introduce additional asymmetries between A and B ; all the differences between A and B are entirely described by the payoff matrix.

Based on previous examples we know that $\sigma a + b > c + \sigma d$ also holds for update rules that are proportional to payoff, but violate assumption (i). Although our proof does not work in this case, we can expect this result for weak selection. As explained in Appendix C, whenever δ occurs in an equation, it will occur together with a, b, c , or d and vice versa. For the limit of weak selection, only linear terms in δ remain. These terms will also be linear in a, b, c, d . Hence, the final condition must be linear. If assumption (ii) is satisfied, this condition is symmetric and will have only one parameter. Examples for such update rules include birth-death (BD) updating on graphs (Ohtsuki et al 2006) and various forms of group selection (Traulsen & Nowak 2006, Traulsen et al 2008).

Appendix A : Calculations for the star

Unlike the structures studied so far, the star is a structure for which $\Delta x_S^{(0)} \neq 0$. However, the star satisfies our assumptions. It can be shown (as we do in general in Appendix C) that for the star, $\pi_S^{(1)}$ is linear in a, b, c, d . Thus, we know that a single parameter condition must be satisfied for the star. However, it is hard to calculate directly what $\pi_S^{(1)}$ is for all states S . We use the symmetry of the star to deduce the σ for any mutation and weak selection.

For the star with N nodes we have $2N$ states which we will denote by $(0, i)$ and $(1, i)$, where $i = 0, \dots, N - 1$ is the number of A players on the leaves. $(0, i)$ means that there is a B in the hub; $(1, i)$ means that there is an A in the hub.

Then, for DB updating we can write the following transition probabilities:

$$\begin{cases} P((0, i) \rightarrow (0, i - 1)) = \frac{i}{N} \\ P((0, i) \rightarrow (0, i + 1)) = u \frac{N - i - 1}{N} \\ P((0, i) \rightarrow (1, i)) = \frac{u}{N} + (1 - u) \frac{i}{N(N - 1)} \left(1 + \delta \frac{N - i - 1}{N - 1} (b - d) \right) \\ P((0, i) \rightarrow (0, i)) = (1 - u) \frac{N - i - 1}{N} \left(1 + \frac{1}{N - 1} \left(1 + \delta \frac{i}{N - 1} (d - b) \right) \right) \end{cases} \quad (38)$$

and

$$\begin{cases} P((1, i) \rightarrow (1, i - 1)) = u \frac{i}{N} \\ P((1, i) \rightarrow (1, i + 1)) = \frac{N - i - 1}{N} \\ P((1, i) \rightarrow (0, i)) = \frac{u}{N} + (1 - u) \frac{N - i - 1}{N(N - 1)} \left(1 + \delta \frac{i}{N - 1} (c - a) \right) \\ P((1, i) \rightarrow (1, i)) = (1 - u) \frac{i}{N} \left(1 + \frac{1}{N - 1} \left(1 + \delta \frac{N - i - 1}{N - 1} (a - c) \right) \right) \end{cases} \quad (39)$$

So all these transition probabilities don't depend on a, b, c, d independently, but in fact on $b - d$ and $a - c$. Thus, π_S , the probabilities of finding the system in each state, also depend only on $a - c$ and $b - d$, and not on a, b, c, d independently.

Moreover, if we look at the change due to selection in each state we have:

- in state $(0, i)$

$$\Delta x = i \left(-\frac{N - 2}{N(N - 1)} + \delta \frac{N - i - 1}{N(N - 1)^2} (b - d) \right) \quad (40)$$

- in state $(1, i)$

$$\Delta x = \frac{N - 2}{N} + i \left(-\frac{N - 2}{N(N - 1)} + \delta \frac{N - i - 1}{N(N - 1)^2} (a - c) \right) \quad (41)$$

Here, as well, we note that Δx does not depend independently on a, b, c, d but only on $a - c$ and $b - d$ because basically it only matters who the leaves play with (an A or a B in the hub). Thus, we conclude that our expression (30) which gives the sigma condition depends on $a - c$ and $b - d$ linearly. Thus, it must be of the form:

$$(a - c)g(N, u) + (b - d)h(N, u) > 0 \quad (42)$$

where g and h are functions of the parameters N and u .

However, this has to be precisely the sigma relation for the star (since it is derived from (30)), and hence must be identical to $\sigma a + b > c + \sigma d$ (and here we know that $\sigma > 0$). This implies that the coefficients of a and $-d$ must be equal (and respectively those of b and $-c$). Hence we conclude that $g(N, u) = h(N, u)$ and hence $\sigma = 1$, for any population size N and any mutation rate u .

Appendix B: Update rules

As we explained, our approach works only for update rules for which the condition $\langle x \rangle > 1/2$ is equivalent to $\langle \Delta x^{\text{sel}} \rangle > 0$. Below we show that this equivalence holds for all update rules which have constant birth rate or constant death rate (assumption (2)). This condition is sufficient but may not be necessary. In a forthcoming paper we show, however, that there are processes for which neither the birth rate nor the death rate is constant and the two conditions above are not equivalent.

In a given state S , let $\mathbb{b}_{i,S}$ be the average number of descendants of individual i . Let $\mathbb{d}_{i,S}$ be the probability that individual i dies in state S . We denote by $\omega_{i,S}$ the average fitness of individual i at state S , which we can express as

$$\omega_{i,S} = \mathbb{b}_{i,S} + (1 - \mathbb{d}_{i,S}) \quad (43)$$

Since the total population size, N , is constant, we must have that

$$\sum_i \omega_{i,S} = N \iff \sum_i \mathbb{b}_{i,S} = \sum_i \mathbb{d}_{i,S} \quad (44)$$

In one step we can separate the total change of frequency Δx^{tot} into a part due to selection and a part due to mutation:

$$\Delta x_S^{\text{tot}} = \Delta x_S^{\text{sel}} + \Delta x_S^{\text{mut}} \quad (45)$$

In what follows, for the sake of simplicity, we will omit state S when it is obvious. In Section 3 we calculated the change in the frequency of A due to selection, in state S , to be

$$\Delta x_S^{\text{sel}} = \frac{1}{N} \left(\sum_i s_i \omega_i - \sum_i s_i \right) = \frac{1}{N} \sum_i s_i (\mathbb{b}_i - \mathbb{d}_i) \quad (46)$$

We can also write the change in the frequency of A due to both selection and mutation

$$\Delta x_S^{\text{tot}} = \frac{1}{N} \left[\sum_i s_i \left(\left(1 - \frac{u}{2}\right) \mathbb{b}_i + 1 - \mathbb{d}_i \right) + (1 - s_i) \frac{u}{2} \mathbb{b}_i - \sum_i s_i \right] \quad (47)$$

The first term is the average change in A due to selection (birth - death) and the second term is the average change due to mutation. We want to relate the average total change to the average change due to selection and to the average frequency of A individuals. In general, it is hard. However, if the death rate is constant ($\mathbb{d}_i = \mathbb{d}$) or the birth rate is constant ($\mathbb{b}_i = \mathbb{b}$) such a relationship is immediate.

If the death rate is constant, $\mathbb{d}_i = \mathbb{d}$, then using (44) and (46) we can rewrite (47) as

$$\begin{aligned} \Delta x_S^{\text{tot}} &= \frac{1}{N} \left(\sum_i s_i (\mathbb{b}_i - \mathbb{d}) + \frac{u}{2} \mathbb{d} \sum_i (1 - s_i) \right) \\ &= (1 - u) \Delta x_S^{\text{sel}} + u \cdot \mathbb{d} (1 - x_S) \end{aligned} \quad (48)$$

Here $x_S = \sum_i s_i / N$ is the frequency of A individuals in state S .

We know however that in the stationary state, the average total change is zero, i.e. $\langle \Delta x^{\text{tot}} \rangle = 0$. So averaging (48) over all possible states, weighted by the probability to find the system in those states, we obtain

$$0 = \langle \Delta x^{\text{tot}} \rangle = (1 - u) \langle \Delta x^{\text{sel}} \rangle + u \cdot \mathfrak{d}(1 - \langle x \rangle) \quad (49)$$

Thus, we conclude that the average frequency of A can be expressed in terms of the average change due to selection as

$$\langle x \rangle = \frac{1}{2} + \frac{1 - u}{u \cdot \mathfrak{d}} \langle \Delta x^{\text{sel}} \rangle \quad (50)$$

If the birth rate is constant, $\mathfrak{b}_i = \mathfrak{b}$, then a similar argument leads to the relationship

$$\langle x \rangle = \frac{1}{2} + \frac{1 - u}{u \cdot \mathfrak{b}} \langle \Delta x^{\text{sel}} \rangle \quad (51)$$

In both case, the condition $\langle x \rangle > 1/2$ is obviously equivalent to $\langle \Delta x^{\text{sel}} \rangle > 0$, as claimed.

Note that our proof does not work for the more familiar BD updating in which one individual is chosen to reproduce proportional to the effective payoff and its offspring replaces a random neighbor. The reason is that in this case neither the birth rate, nor the death rate are constant and there is no immediate relationship between them other than (44). Furthermore, we show in a forthcoming paper that for this BD updating, the conditions $\langle x \rangle > 1/2$ and $\langle \Delta x^{\text{sel}} \rangle > 0$ are not equivalent. Thus, our theory does not apply. We do show however, that in the limit of low mutation, $u \rightarrow 0$, our single parameter condition holds.

Appendix C: Continuity and Linearity for π_S

In this Appendix we will show that the probability π_S that the system is in state S is continuous at $\delta = 0$, infinitely differentiable and moreover that $\pi_S^{(1)}$ is linear in a, b, c, d . We show this for processes satisfying our assumptions. This part of the proof works not only for constant death or constant birth updates, but for any update rules that do not introduce any functions that do not have Taylor expansions at $\delta = 0$.

Note that given the payoff function $1 + \delta \cdot \text{payoff}$, we introduce δ together with a, b, c and d . So, unless we differentiate with respect to δ or evaluate at $\delta = \text{const}$, whenever we have a degree k term in δ , it must be accompanied by a degree k term in a, b, c or d and vice versa. Moreover, δ can not be accompanied by a constant term, i.e. a term that does not contain a, b, c or d .

Let ω_i denote the expected number of offspring of individual i due to selection. For processes for which the update is proportional to the effective payoff, we can write the Taylor expansion of ω_i at $\delta = 0$:

$$\omega_i = a_{i0} + a_{i1}\delta + \mathcal{O}(\delta^2) \quad (52)$$

The notation $\mathcal{O}(\delta^2)$ denotes terms of order δ^2 or higher. They are negligible for $\delta \rightarrow 0$. As we mentioned above, we only introduce δ together with linear terms in a, b, c, d and we only introduce a, b, c, d together with δ . Thus, we must have that in the expression of ω_i , a_{i0} contains no a, b, c, d terms whereas a_{i1} contains linear terms in a, b, c, d and no constant terms. Note that this is in agreement with what we obtain for the DB and Synchronous updates in Appendix C.

Since ω_i is a polynomial in δ , Δx_S is continuous in δ and in particular at $\delta = 0$. Thus, we can write the Taylor expansion of Δx_S at $\delta = 0$

$$\begin{aligned}\Delta x_S &= \Delta x_S^{(0)} + \delta \Delta x_S^{(1)} + \mathcal{O}(\delta^2) \\ &= \Delta x_S^{(0)} + \frac{\delta}{N} \sum_i s_i \left. \frac{d\omega_i}{d\delta} \right|_{\delta=0} + \mathcal{O}(\delta^2) \\ &= \Delta x_S^{(0)} + \frac{\delta}{N} \sum_i a_{i1} s_i + \mathcal{O}(\delta^2)\end{aligned}\tag{53}$$

Here $\Delta x_S^{(0)}$ is the change in state S when $\delta = 0$. From the above we conclude that $\Delta x_S^{(1)} = s_i a_{i1}/N$ which is linear in a, b, c, d and has no degree zero term.

The probability π_S that the system is in state S also depends on δ . For our structures and update rules we will now show that π_S is continuous and differentiable at $\delta = 0$. In order to find π_S , we need the transition probabilities P_{ij} to go from state S_j to state S_i . Then the vector of probabilities $\pi(S)$ is an eigenvector corresponding to eigenvalue 1 of the stochastic matrix P . The matrix P is primitive, i.e. there exists some integer k such that $P^k > 0$. This is because we study a selection-mutation process and hence our system has no absorbing subset of states.

Since the matrix P is stochastic and primitive, the Perron-Frobenius theorem ensures that 1 is its largest eigenvalue, that it is a simple eigenvalue and that to it, there corresponds an eigenvector with positive entries summing up to 1. This is precisely our vector of probabilities.

To find this eigenvector we perform Gaussian elimination (aka row echelon reduction) on the system $Pv = v$. Since 1 is a simple eigenvalue for P , the system we need to solve has only one degree of freedom; thus we can express the eigenvector in terms of the one free variable, which without loss of generality can be v_n :

$$v_1 = -v_n h_1, \quad \dots \quad v_i = -v_n h_i, \quad \dots \quad v_{n-1} = -v_n h_{n-1}\tag{54}$$

The eigenvector that we are interested in is the vector with non-zero entries which sum up to 1. For this vector we have

$$1 = v_n(-h_1 - \dots - h_{n-1} + 1)\tag{55}$$

For our structures and update rules, the transition probabilities have Taylor expansions around $\delta = 0$ and thus can be written as polynomials in δ . As before, since any δ is accompanied by a linear term in a, b, c, d , the coefficients of these polynomials have the same degree in a, b, c, d as the accompanying δ . Because of the elementary nature of the row operations performed, the elements of the reduced matrix will be fractions of polynomials (i.e. rational functions of δ). Thus, h_i above are all rational functions of δ . Therefore, from (55) we conclude that v_n must also be a rational function of δ . This implies that in our vector of probabilities, all the entries are rational functions. Thus π_S is a fraction of polynomials in δ which we write in irreducible form. The only way that this is not continuous at $\delta = 0$ is if the denominator is zero at $\delta = 0$. But in that case, $\lim_{\delta \rightarrow 0} \pi_S = \infty$ which is impossible since π_S is a probability. Therefore, π_S is continuous at $\delta = 0$.

Moreover, we can write

$$\pi_S = \frac{b_{0S} + b_{1S}w + \mathcal{O}(\delta^2)}{c_{0S} + c_{1S}w + \mathcal{O}(\delta^2)}\tag{56}$$

We have obtained this form for π_S by performing the following operations: Taylor expansions of the transition probabilities and elementary row operations on these Taylor expansions. Hence, any δ that was introduced from the beginning was accompanied by linear terms in a, b, c, d and no constants, and due to the elementary nature of the above operations, nothing changed. So b_{0S} and c_{0S} contain no a, b, c, d terms whereas b_{1S} and c_{1S} contain only linear a, b, c, d and no degree zero terms. Differentiating π_S once we obtain

$$\pi_S^{(1)}(w) = \frac{b_{1S}c_{0S} - b_{0S}c_{1S} + \mathcal{O}(w)}{c_{0S}^2 + \mathcal{O}(w)} \quad (57)$$

We want to show the linearity of $\pi_S^{(1)}$ which is $\pi_S^{(1)}(0)$. Thus, we have

$$\pi_S^{(1)} = \frac{b_{1S}c_{0S} - b_{0S}c_{1S}}{c_{0S}^2} \quad (58)$$

Since b_{0S}, c_{0S} contain no a, b, c, d and b_{1S}, c_{1S} are linear in a, b, c, d and have no free constant terms, we conclude that $\pi_S^{(1)}$ is linear in a, b, c, d and has no free constant term.

We have thus shown that both $(\Delta x)_S^{(1)}$ and $\pi_S^{(1)}$ are continuous and linear in a, b, c, d with no free constant terms. Thus, the condition

$$\sum_S [\Delta x_S^{(1)} \cdot \pi_S^{(0)} + \Delta x_S^{(0)} \cdot \pi_S^{(1)}] > 0 \quad (59)$$

derived in Section 5.1 for strategy A to be favored over strategy B is linear in a, b, c, d and has no free constant terms. Thus, it can be written as

$$k_1a + k_2b > k_3c + k_4d \quad (60)$$

as claimed. This concludes our proof.

References

- Alos-Ferrer, C., 2003. Finite population dynamics and mixed equilibria. *Int. Game Theory Review* 5, 263-290.
- Antal, T., Nowak, M. A., Traulsen, A., 2008a. Strategy abundance in 2x2 games for arbitrary mutation rates. e-print arXiv:0809.2804.
- Antal, T., Ohtsuki, H., Wakeley, J., Taylor, P.D., Nowak, M.A., 2008b. Evolutionary game dynamics in phenotype space. E-print arXiv:0806.2636.
- Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390-1396.
- Binmore, K., 1994. *Game Theory and the Social Contract*. MIT Press, Cambridge, MA.
- Binmore, K. 2007. *Playing for Real: A Text on Game Theory*. Oxford University Press.
- Boerlijst, M.C., Hogeweg, P., 1991. Spiral wave structures in pre-biotic evolution: hypercycles stable against parasites. *Physica D* 48, 17-28.
- Bollobás B., 1995. *Random Graphs*. Academic Press, New York.
- Bomze, I., Pawlowitsch, C., 2008. One-third rules with equality: second-order evolutionary stability conditions in finite populations. To be published in *J. Theor. Biol.*
- Boyd, R., Richerson, P.J., 2005. Solving the Puzzle of Human Cooperation. In: Levinson, S. (Ed.), *Evolution and Culture*. MIT Press, Cambridge, MA, pp. 105-132.
- Bshary, R., Grutter, A., Willener, A., Leimar, O., 2008. Pairs of cooperating cleaner fish provide better service quality than singletons. *Nature* 455, 964-967.
- Comins, H.N., Hamilton, W.D., May, R.M., 1980. Evolutionarily stable dispersal strategies. *J. Theor. Biol.* 82, 205-230.
- Cressman, R., 2003. *Evolutionary Dynamics and Extensive Form Games*. MIT Press, Cambridge, MA.
- Dieckmann, U., Law, R., Metz, J.A.J., (Eds.), 2000. *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge University Press, Cambridge, UK.
- Doebeli, M., Knowlton, N., 1998. The evolution of interspecific mutualisms. *P. Natl. Acad. Sci. U.S.A.* 95, 8676-8680.
- Durrett, R., 1988. *Lecture Notes on Particle Systems and Percolation*. Wadsworth & Brooks/Cole Advanced Books & Software, Stamford, CT.
- Durrett, R., Levin, S.A., 1994. The importance of being discrete (and spatial). *Theor. Popul. Biol.* 46, 363-394.
- Ellison, G., 1993. Learning, local interaction, and coordination. *Econometrica* 61, 1047-1071.
- Ewens, W. J. (2004). *Mathematical population genetics, vol. 1. Theoretical introduction*, Springer: New York.
- Ferriere, R., Michod, R.E., 1996. The evolution of cooperation in spatially heterogeneous populations. *Am. Nat.* 147, 692-717.
- Ficici, S.G., Pollack, J.B., 2000. Effects of finite populations on evolutionary stable strategies. In: Whitley, D., Goldberg, D., Cantu-Paz, E., Spector, L., Parmee, I., Beyer, H.G., (Eds.), *Proceedings of the 2000 Genetic and Evolutionary Computation Conference*. Morgan-Kaufmann, San Francisco, CA, pp. 927-934.

- Fogel, G., Andrews, P., Fogel, D., 1998. On the instability of evolutionary stable strategies in small populations. *Ecol. Model.* 109, 283-294.
- Frank, S.A., 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ.
- Fu, F., Wang, L., Nowak, M.A., Hauert C., 2008. *Evolutionary Dynamics on Graphs: Efficient Method for Weak Selection*. To be published.
- Fudenberg, D., Tirole, J., 1991. *Game Theory*. MIT Press, Cambridge, MA.
- Gandon, S., Rousset, F., 1999. The evolution of stepping stone dispersal rates. *Proc. R. Soc. B* 266, 2507-2513.
- Gintis, H. 2000. *Game Theory Evolving*. Princeton University Press: Princeton, USA.
- Grafen, A., 1985. A geometric view of relatedness. *Oxford Surv. Evol. Biol.* 2, 28-89.
- Grafen, A., 2006. Optimization of inclusive fitness. *J. Theor. Biol.* 238, 541-563.
- Hamilton, W.D., 1964. The genetical evolution of social behaviour, I and II. *J. Theor. Biol.* 7, 1-52.
- Hamilton, W.D., May, R.M., 1977. Dispersal in stable habitats. *Nature* 269, 578-581.
- Harsanyi, J. C., Selten, R. 1988. *A General Theory of Equilibrium Selection in Games*. MIT Press: Cambridge MA.
- Hassell, M.P., Comins, H.N., May, R.M., 1991. Spatial structure and chaos in insect population dynamics. *Nature* 353, 255-258.
- Hauert, C., Doebeli, M., 2004. Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature* 428, 643-646.
- Helbing, D., Yu, W. 2008. Migration as a mechanism to promote cooperation. *Advances in Complex Systems* 11 641 - 652
- Herz, A.V.M., 1994. Collective phenomena in spatially extended evolutionary games. *J. Theor. Biol.* 169, 65-87.
- Hofbauer, J., 1999. The spatially dominant equilibrium of a game. *Ann. Oper. Res.* 89, 233-251.
- Hofbauer, J., Sigmund, K., 1988. *The Theory of Evolution and Dynamical Systems*. Cambridge University Press, Cambridge, UK.
- Hofbauer, J., Sigmund, K., 1990. Adaptive dynamics and evolutionary stability. *Appl. Math. Lett.* 3, 75-79.
- Hofbauer, J., Sigmund, K., 1998. *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge, UK.
- Hofbauer, J., Sigmund, K., 2003. Evolutionary game dynamics. *B. Am. Math. Soc.* 40, 479-519.
- Hofbauer, J., Schuster, P., Sigmund, K., 1979. A note on evolutionary stable strategies and game dynamics. *J. Theor. Biol.* 81, 609-612.
- Houston, A.I., McNamara, J.M., 1999. *Models of Adaptive Behaviour: An Approach Based on State*. Cambridge University Press, Cambridge, UK.
- Hutson, V., Vickers, G.T., 1992. Travelling waves and dominance of ESSs. *J. Math. Biol.* 30, 457-471.
- Hutson, V., Vickers, G.T., 2002. Backward and forward traveling waves in evolutionary games. *Methods Appl. Anal.* 9, 159-176.

- Imhof, L.A., Nowak, M.A., 2006. Evolutionary game dynamics in a Wright-Fisher process. *J. Math. Biol.* 52, 667-681.
- Kandori, M., Mailath, G. J., Rob, R., 1993. Learning, mutation, and long run equilibria in games. *Econometrica*, 61, 29-56.
- Kerr, B., Riley, M.A., Feldman, M.W., Bohannan, B.J.M., 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418, 171-174.
- Killingback, T., Doebeli, M., 1996. Spatial evolutionary game theory: Hawks and Doves revisited. *Proc. R. Soc. B* 263, 1135-1144.
- Lehmann, L., Keller, L., Sumpter, D. J. T., 2007. The evolution of helping and harming on graphs: the return of inclusive fitness effect. *J. Evol. Biol.* 20, 2284-2295.
- Lessard, S., Ladret, V., 2007. The probability of a single mutant in an exchangeable selection model. *J. Math. Biol.* 54, 721-744.
- Levin, S.A., Paine, R.T., 1974. Disturbance, patch formation, and community structure. *P. Natl. Acad. Sci. U.S.A.* 71, 2744-2747.
- Lieberman, E., Hauert, C., Nowak, M.A., 2005. Evolutionary dynamics on graphs. *Nature* 433, 312-316.
- Lindgren, K., Nordahl, M.G., 1994. Evolutionary dynamics of spatial games. *Physica D* 75, 292-309.
- May, R.M., Leonard, W., 1975. Nonlinear aspects of competition between three species. *SIAM J. Appl. Math.* 29, 243-252.
- Maynard Smith, J., 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, UK.
- Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. *Nature*, 246, 15-18.
- McNamara, J., Gasson, C., Houston, A., 1999. Incorporating rules for responding into evolutionary games. *Nature* 401, 368-371.
- Metz, J.A.J., Geritz, S.A.H., Meszena, G., Jacobs, F.J.A., van Heerwaarden, J.S., 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In: van Strien, S.J., Verduyn Lunel, S.M., (Eds.), *Stochastic and Spatial Structures of Dynamical Systems*, K. Ned. Akad. Van Wet. B 45, 183-231. North-Holland Publishing Company, Amsterdam, Holland.
- Nakamaru, M., Matsuda, H., Iwasa, Y., 1997. The evolution of cooperation in a lattice-structured population. *J. Theor. Biol.* 184, 65-81.
- Nakamaru, M., Nogami, H., Iwasa, Y., 1998. Score dependent fertility model for the evolution of cooperation in a lattice. *J. Theor. Biol.* 194, 101-124.
- Nakamaru, M., Iwasa, Y., 2005. The evolution of altruism by costly punishment in lattice structured populations: score dependent viability versus score dependent fertility. *Evol. Ecol. Res.* 7, 853-870.
- Nakamaru, M., Iwasa, Y., 2006. The coevolution of altruism and punishment: role of the selfish punisher. *J. Theor. Biol.* 240, 475-488.
- Nowak, M.A., 2006a. *Evolutionary Dynamics*. Harvard University Press.
- Nowak, M.A., 2006b. Five rules for the evolution of cooperation. *Science* 314, 1560-1563.
- Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. *Nature* 359, 826-829.

- Nowak, M.A., May, R.M., 1993. The spatial dilemmas of evolution. *Int. J. Bifurcat. Chaos* 3, 35-78.
- Nowak, M.A., May, R.M., 1994. Superinfection and the evolution of parasite virulence. *Proc. R. Soc. B* 255, 81-89.
- Nowak, M., Sigmund, K., 1990. The evolution of stochastic strategies in the prisoner's dilemma. *Acta Appl. Math.* 20, 247-265.
- Nowak, M.A., Sigmund, K., 2004. Evolutionary dynamics of biological games. *Science* 303, 793-799.
- Nowak, M.A., Sigmund, K., 2005. Evolution of indirect reciprocity. *Nature* 427, 1291-1298.
- Nowak, M.A., Bonhoeffer, S., May, R.M., 1994. Spatial games and the maintenance of cooperation. *P. Natl. Acad. Sci. U.S.A.* 91, 4877-4881.
- Nowak, M.A., May, R.M., Phillips, R.E., Rowland-Jones, S., Lalloo, D.G., McAdam, S., Klenerman, P., Koppe, B., Sigmund, K., Bangham, C.R.M., McMichael, A.J., 1995. Antigenic oscillations and shifting immunodominance in HIV-1 infections. *Nature* 375, 606-611.
- Nowak, M.A., Komarova, N.L., Niyogi, P., 2002. Computational and evolutionary aspects of language. *Nature* 417, 611-617.
- Nowak, M.A., Sasaki, A., Taylor, C., Fudenberg, D., 2004. Emergence of cooperation and evolutionary stability in finite populations. *Nature* 428, 646-650.
- Ohtsuki, H., Nowak, M.A., 2006. Evolutionary games on cycles. *Proc. R. Soc. B* 273, 2249-2256.
- Ohtsuki, H., Nowak, M.A., 2007. Direct reciprocity on graphs. *J. Theor. Biol.* 247, 462-470.
- Ohtsuki, H., Nowak, M.A., 2008. Evolutionary stability on graphs. *J. Theor. Biol.* 251, 698-707.
- Ohtsuki, H., Hauert, C., Lieberman, E., Nowak, M.A., 2006. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441, 502-505.
- Ohtsuki, H., Pacheco, J., Nowak, M.A., 2007. Evolutionary graph theory: breaking the symmetry between interaction and replacement. *J. Theor. Biol.* 246, 681-694.
- Pacheco, JM., Traulsen, A. Nowak, M.A., 2006. Active linking in evolutionary games. *J. Theor. Biol.* 243, 437-443.
- Queller, D.C., 1985. Kinship, reciprocity and synergism in the evolution of social behaviour: a synthetic model. *Nature* 318, 366-367.
- Riley, J.G., 1979. Evolutionary equilibrium strategies. *J. Theor. Biol.* 76, 109-123.
- Rousset, F., 2004. Genetic structure and selection in subdivided populations. Princeton University Press.
- Rousset, F., Billiard, S., 2000. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. *J. Evol. Biol.* 13, 814-825.
- Samuelson, L., 1997. *Evolutionary Games and Equilibrium Selection*. MIT Press, Cambridge, MA.
- Santos, F.C., Santos, M.D., Pacheco, J.M., 2008. Social diversity promotes the emergence of cooperation in public goods games. *Nature*, 454, 213-216.
- Schaffer, M., 1988. Evolutionarily stable strategies for a finite population and variable contest size. *J. Theor. Biol.* 132, 469-478.
- Seger, J., 1981. Kinship and covariance. *J. Theor. Biol.* 91, 191-213.

- Szabó, G., Antal, T., Szabó, P. & Droz, M. 2000 Spatial evolutionary prisoner's dilemma game with three strategies and external constraints. *Phys. Rev. E* 62, 1095-1103.
- Szabó, G., Fath, G., 2007. Evolutionary games on graphs. *Phys. Rep.* 446, 97-216.
- Szabó, G. & Tóke, C. 1998 Evolutionary prisoner's dilemma game on a square lattice. *Phys. Rev. E* 58, 69-73.
- Taylor, C., Nowak, M.A., 2007. Transforming the dilemma. *Evolution* 61, 2281-2292.
- Taylor, C., Fudenberg, D., Sasaki, A., Nowak, M.A., 2004. Evolutionary game dynamics in finite populations. *B. Math. Biol.* 66, 1621-1644.
- Taylor, P.D., 1992a. Altruism in viscous populations—an inclusive fitness model. *Evol. Ecol.* 6, 352-353.
- Taylor, P.D., 1992b. Inclusive fitness in a homogeneous environment. *Proc. R. Soc. B* 249, 299-302.
- Taylor, P.D., Frank, S., 1996. How to make a kin selection argument. *J. Theor. Biol.* 180, 27-37.
- Taylor, P.D., Jonker, L.B., 1978. Evolutionary stable strategies and game dynamics. *Math. Biosci.* 40, 145-156.
- Taylor, P.D., Irwin, A., Day, T., 2000. Inclusive fitness in finite deme-structured and stepping-stone populations. *Selection* 1, 83-93.
- Taylor, P.D., Day, T., Wild, G., 2007a. Evolution of cooperation in a finite homogeneous graph. *Nature* 447, 469-472.
- Taylor, P.D., Day, T., Wild, G., 2007b. From inclusive fitness to fixation probability in homogeneous structured populations. *J. Theor. Biol.* 249, 101-110.
- Traulsen, A., Pacheco, J.M., Imhof, L., 2006. Stochasticity and evolutionary stability. *Phys. Rev. E* 74, 021905.
- Traulsen, A., Nowak, M.A., 2006. Evolution of cooperation by multi-level selection. *P. Natl. Acad. Sci. USA*, 103, 10952-10955
- Traulsen, A., Shohresh, N., Nowak, M.A., 2008. Analytical results for individual and group selection of any intensity. *B. Math. Biol.* 70, 1410-1424.
- Trivers, R.L., 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35-57.
- Turner, P.E., Chao, L., 1999. Prisoner's dilemma in an RNA virus. *Nature* 398, 441-443.
- van Baalen, M., Rand, D.A., 1998. The unit of selection in viscous populations and the evolution of altruism. *J. Theor. Biol.* 193, 631-648.
- von Neumann, J., Morgenstern, O., 1944. *Theory of Games and Economic Behavior*. Princeton University Press, Princeton, NJ.
- Wild, G., Traulsen, A., 2007. The different limits of weak selection and the evolutionary dynamics of finite populations. *J. Theor. Biol.* 247, 382-390.
- Weibull, J.W., 1995. *Evolutionary Game Theory*. MIT Press, Cambridge, MA.
- Yamamura, N., Higashi, M., Behera, N., Wakano, J., 2004. Evolution of mutualism through spatial effects. *J. Theor. Biol.* 226, 421-428.
- Zeeman, E.C., 1980. Population dynamics from game theory. In: Nitecki, Z.H., Robinson, R.C., (Eds.), *Proceedings of an International Conference on Global Theory of Dynamical Systems*. Lecture Notes in Mathematics, vol. 819. Springer, Berlin.

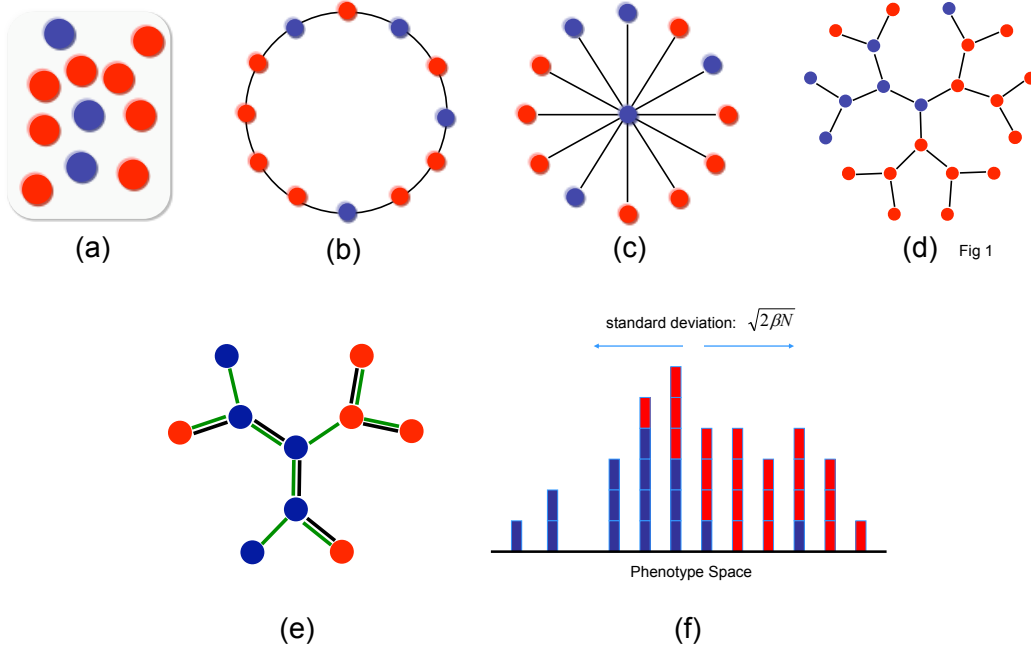


Figure 1: Various population structures for which σ values are known. **(a)** For the well-mixed population we have $\sigma = (N-2)/N$ for any mutation rate. **(b)** For the cycle we have $\sigma = (3N-8)/N$ for low mutation. **(c)** For the star we have $\sigma = 1$ for any mutation rate and any population size, $N \geq 3$. **(d)** For regular graphs of degree k we have $\sigma = (k+1)/(k-1)$ for low mutation and large population size. **(e)** If there are different interaction and replacement graphs, we have $\sigma = (gh+l)/(gh-l)$ for low mutation and large population size. The interaction graph, the replacement graph and the overlap graph between these two are all regular and have degrees, g , h and l , respectively. **(f)** For ‘games in phenotype space’ we find $\sigma = 1 + \sqrt{3}$ for a one dimensional phenotype space, low mutation rates and large population size. All results hold for DB updating and weak selection.

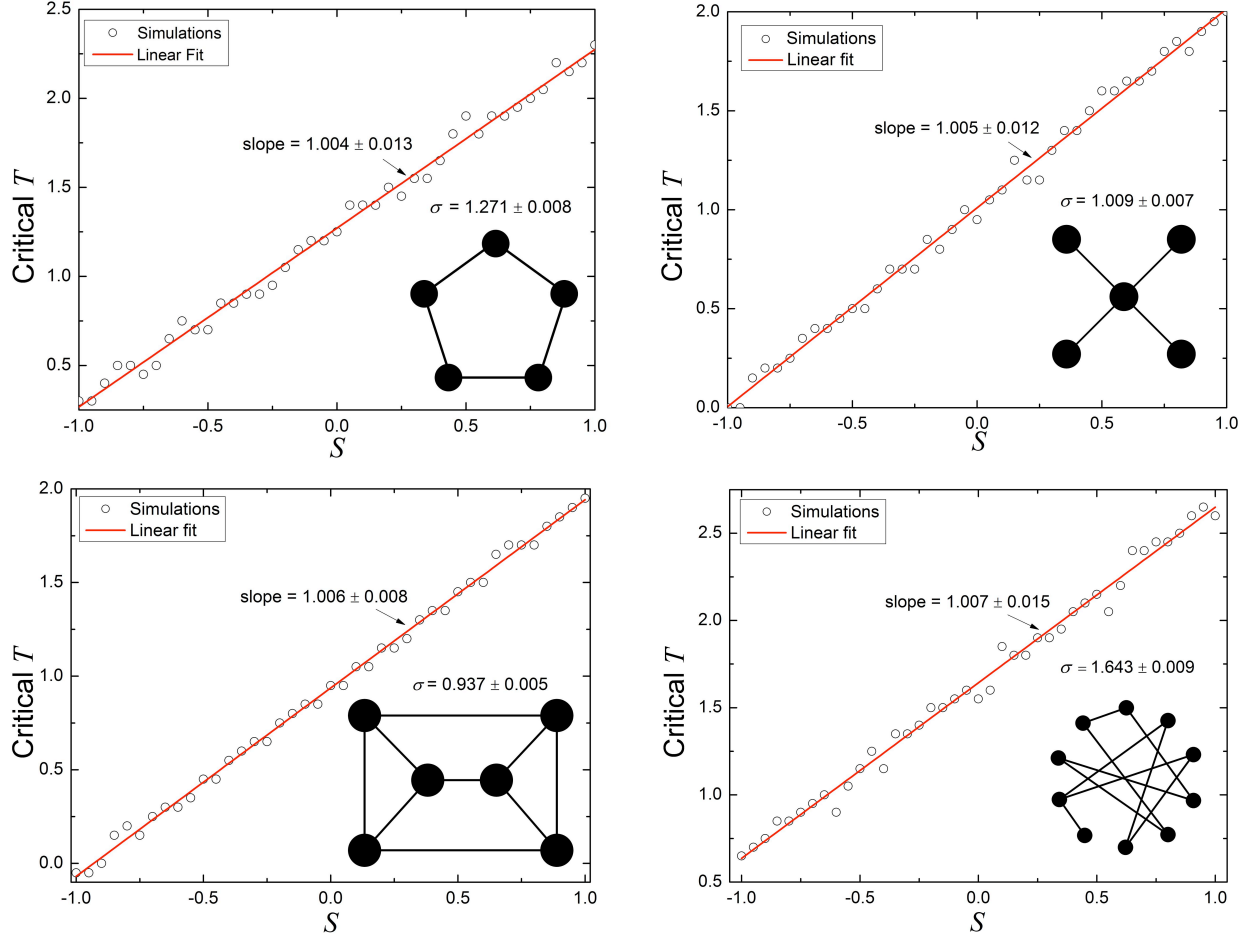


Figure 2: Numerical simulations confirm the linear inequality $\sigma a + b > c + \sigma d$. We study the payoff matrix $a = 1$, $b = S$, $c = T$, and $d = 0$ for $-1 \leq S \leq 1$ and $0 \leq T \leq 2$. The red line is the equilibrium condition $T = S + \sigma$. Below this line A is favored. **(a)** For a cycle with $N = 5$ and mutation rate, $u = 0.2$, we find $\sigma = 1.271$. The theoretical result for low mutation is $\sigma = 1.4$. Thus, σ depends on the mutation rate. **(b)** For a star with $N = 5$ we find $\sigma = 1$ for $u = 0.1$. **(c)** For a regular graph with $k = 3$ and $N = 6$ we find $\sigma = 0.937$ for $u = 0.1$. The prediction of (18) for low mutation is $\sigma = 1$. Here again σ depends on the mutation rate. **(d)** For this random graph with $N = 10$ and average degree $k = 2$ we find $\sigma = 1.636$ for $u = 0.05$. For all simulations the intensity of selection is $\delta = 0.005$. Each point is an average over 2×10^6 runs.