



Strategy selection in structured populations

Corina E. Tarnita^{a,b,*}, Hisashi Ohtsuki^{c,d}, Tibor Antal^{a,b}, Feng Fu^{a,b,e}, Martin A. Nowak^{a,b}

^a Program for Evolutionary Dynamics, Department of Mathematics, Harvard University, Cambridge, MA 02138, USA

^b Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

^c Department of Value and Decision Science, Tokyo Institute of Technology, Tokyo 152-8552, Japan

^d PRESTO, Japan Science and Technology Agency, Saitama 332-0012, Japan

^e Center for Systems and Control, State Key Laboratory for Turbulence and Complex Systems, College of Engineering, Peking University, Beijing 100871, China

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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 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 a mutation and selection process. 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, games in phenotype space and games on sets. We give a proof for the existence of such a σ , which holds for all population structures and update rules that have certain (natural) properties. We assume weak selection, but allow 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.

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1. Introduction

Game theory was invented by John von Neumann and Morgenstern (1944) to study strategic and economic decisions of humans (Fudenberg and Tirole, 1991; Binmore, 1994; Weibull, 1995; Samuelson, 1997; Binmore, 2007). Evolutionary game theory was introduced by John Maynard Smith in order to explore the evolution of animal behavior (Maynard Smith and Price, 1973; Maynard Smith, 1982; Houston and 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 and Leonard, 1975; Doebeli and Knowlton, 1998), host–parasite interactions (Turner and Chao, 1999; Nowak and 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 and Hamilton, 1981; Boyd and Richerson, 2005; Nowak and 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 and Sigmund, 2004).

In evolutionary game theory there is always a population of players. The interactions of the game lead to payoffs, which are 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 and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1980; Hofbauer and Sigmund, 1988; Hofbauer et al., 1998; Hofbauer and Sigmund, 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 and Sigmund, 1988). For example, a stable equilibrium of the replicator equation

* Corresponding author at: Program for Evolutionary Dynamics, Department of Mathematics, Harvard University, Cambridge, MA 02138, USA. Tel.: +1 617 496 4737; fax: +1 617 496 4629.

E-mail address: corina@math.harvard.edu (C.E. Tarnita).

is a Nash equilibrium of the underlying game. Another approach to evolutionary game theory is given by adaptive dynamics (Nowak and Sigmund, 1990; Hofbauer and Sigmund, 1990; Metz et al., 1996; Dieckmann et al., 2000) which also assumes infinitely large population size.

However, 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 and 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 and Nowak, 2006; Nowak, 2006a, Traulsen et al., 2006; Lessard and Ladret, 2007; Bomze and 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 and May, 1992, 1993; Ellison, 1993; Herz, 1994; Lindgren and Nordahl, 1994; Ferriere and Michod, 1996; Killingback and Doebeli, 1996; Nakamaru et al., 1997, 1998; Nakamaru and Iwasa, 2005, 2006; van Baalen and Rand, 1998; Yamamura et al., 2004; Helbing and Yu, 2008). Here most interactions occur among nearest neighbors. The typical geometry for spatial games are regular lattices (Nowak et al., 1994; Hauert and Doebeli, 2004; Szabó and Töke, 1998; Szabó et al., 2000), but evolutionary game dynamics have also been studied in continuous space (Hutson and 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; Ohtsuki and Nowak, 2006; Pacheco et al., 2006; Szabó and 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 and Nowak, 2006). There is also a modified condition for what it means to be a Nash equilibrium for games on graphs (Ohtsuki and Nowak, 2008).

Spatial models have also a long history of investigation in the study of ecosystems and ecological interactions (Levin and Paine, 1974; Durrett, 1988; Hassell et al., 1991; Durrett and Levin, 1994). There is also a literature on the dispersal behavior of animals (Hamilton and May, 1977; Comins et al., 1980; Gandon and Rousset, 1999). Boerlijst and Hogeweg (1991) studied spatial models in prebiotic evolution. Evolution in structured populations can also be studied with the methods of inclusive fitness theory (Seeger, 1981; Grafen, 1985, 2006; Queller, 1985; Taylor, 1992; Taylor and Frank, 1996; Frank, 1998; Rousset and Billiard, 2000; Rousset, 2004; Taylor et al., 2000, 2007b).

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

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

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 (Nowak et al., 2004). 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. 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, the condition for strategy A to be favored over strategy B is

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

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).

In this paper we focus on structured populations and the limit of weak selection. We analyze (3) to deduce that the condition for strategy A to be favored over strategy B is equivalent to

$$\sigma a + b > c + \sigma d. \quad (4)$$

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 and Selten, 1988). 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, the main result and the necessary assumptions. In Section 3 we give the proof of the single-parameter condition, which holds for weak selection and any mutation rate. In Section 4 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. Several specific consequences are then discussed. In Section 5 we present several examples of evolutionary dynamics 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, games in phenotype space and games on sets. 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., 2009b). 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 $[a \times (\text{number of } A\text{-interactants}) + b \times (\text{number of } B\text{-interactants})]$. The effective payoff of an individual is given by $1 + w \cdot \text{Payoff}$. Parameter w denotes the intensity of selection. The limit of weak selection is given by $w \rightarrow 0$.

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.

A state S of the population assigns to each player a strategy (A or B) and a 'location' (in space, phenotype space, etc.). A state must include all information that can affect the payoffs of players. For our proof, we assume a finite state space. We study a Markov process on this state space. We denote by P_{ij} the transition probability from state S_i to state S_j . These transition probabilities depend on the update rule and on the effective payoffs of individuals. Since the effective payoff is of the form $1 + w \cdot \text{Payoff}$ and the payoff is linear in a, b, c, d , it follows that the transition probabilities are functions $P_{ij}(wa, wb, wc, wd)$.

We show the following theorem

Theorem. Consider a population structure and an update rule such that

- (i) the transition probabilities are differentiable at $w = 0$;
- (ii) the update rule is symmetric for the two strategies and
- (iii) in the game given by the matrix $\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}$, strategy A is not disfavored.

Then, in the limit of weak selection, the condition that strategy A is favored over strategy B is a one parameter condition:

$$\sigma a + b > c + \sigma d, \quad (5)$$

where σ depends on the model and the dynamics (population structure, update rule, the mutation rates) but not on the entries of the payoff matrix, a, b, c, d .

Let us now discuss the three natural assumptions.

- (i) The transition probabilities are differentiable at $w = 0$. We require the transition probabilities $P_{ij}(wa, wb, wc, wd)$ to have first-order Taylor expansions at $w = 0$. Examples of update rules that satisfy Assumption (i) include: the death–birth (DB) and birth–death (BD) updating on graphs (Ohtsuki et al., 2006), the synchronous updating based on the Wright–Fisher process (Ewens, 2004; Antal et al., 2009b; Tarnita et al., 2009) and the pairwise comparison (PC) process (Traulsen et al., 2008).

- (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 .
- (iii) In the game given by the matrix $\begin{pmatrix} 0 & 1 \\ 0 & 0 \end{pmatrix}$, strategy A is not disfavored.

We will show in the proof that the first two assumptions are sufficient to obtain a single-parameter condition. We need the third assumption simply to determine the direction of the inequality in this condition. Thus, if (iii) is satisfied, then the condition that A is favored over B has the form (5). Otherwise, it has the form $\sigma a + b < c + \sigma d$.

3. Proof

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

$$k_1 a + k_2 b > k_3 c + k_4 d. \quad (6)$$

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 a σ . Furthermore, using Assumption (iii) we show that the condition that A is favored over B becomes

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

3.1. Linearity

As we already mentioned, we study a Markov process on the 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 B.

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 $\langle x \rangle$. Thus

$$\langle x \rangle = \sum_S x_S \pi_S, \quad (8)$$

where π_S is the stationary probability that the system is in state S . The condition for strategy A to be favored over strategy B is that the average frequency of A is greater than $1/2$

$$\langle x \rangle > \frac{1}{2}. \quad (9)$$

This is equivalent to saying that, on average, A individuals are more than 50%.

We analyze this condition in the limit of weak selection $w \rightarrow 0$. The frequency x_S of A individuals in state S does not depend on the game; hence, it does not depend on w . However, the probability π_S that the system is in state S does depend on w . For update rules satisfying Assumption (i), we show in Appendix B that π_S is differentiable as a function of w . Thus, we can write its first-order

Taylor expansion at $w = 0$

$$\pi_S = \pi_S^{(0)} + w\pi_S^{(1)} + \mathcal{O}(w^2). \tag{10}$$

The (0) superscript refers to the neutral state $w = 0$ and $\pi_S^{(1)} = d\pi_S/dw$ evaluated at $w = 0$. The notation $\mathcal{O}(w^2)$ denotes terms of order w^2 or higher. They are negligible for $w \rightarrow 0$.

Hence, we can write the first-order Taylor expansion of the average frequency of A

$$\langle x \rangle = \sum_S x_S \pi_S^{(0)} + w \sum_S x_S \pi_S^{(1)} + \mathcal{O}(w^2). \tag{11}$$

Since $\pi_S^{(0)}$ is the probability that the neutral process (i.e. when $w = 0$) is in state S , the first sum is simply the average number of A individuals at neutrality. This is $1/2$ for update rules that satisfy Assumption (ii) because in the neutral process, A and B individuals are only differentiated by labels.

Thus, in the limit of weak selection, the condition (9) that A is favored over B becomes

$$\sum_S x_S \pi_S^{(1)} > 0. \tag{12}$$

As we already mentioned, the frequency x_S of A individuals in state S does not depend on the game. However, $\pi_S^{(1)}$ does depend on the game. We will show in Appendix B that $\pi_S^{(1)}$ is linear in a, b, c, d with no constant terms. Hence, from (12) 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 (6).

3.2. 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 (6): $k_1 a + k_2 b > k_3 c + k_4 d$. For structures which moreover satisfy our symmetry condition (Assumption (ii)), we obtain the symmetric relation by simply relabeling the two strategies. Thus, strategy B is favored over strategy A if and only if

$$k_1 d + k_2 c > k_3 b + k_4 a. \tag{13}$$

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

$$k_4 a + k_3 b > k_2 c + k_1 d. \tag{14}$$

Since both conditions (6) and (14) are if and only if conditions that A is favored over B , they must be equivalent. Thus, it must be that (14) is a scalar multiple of (6), so there must exist some $\lambda > 0$ such that $k_4 = \lambda k_1 = \lambda^2 k_4$ and $k_3 = \lambda k_2 = \lambda^2 k_3$. Hence, 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

$$ka + k'b > k'c + kd. \tag{15}$$

Note that this condition depends only on the parameter $\sigma = k/k'$. Thus, in general, the condition that A is favored over B can be written as a single-parameter condition. However, one must exercise caution in dividing by k' because its sign can change the direction of the inequality. This is where we need Assumption (iii). Assumption (iii) holds if and only if $k' \geq 0$ and then we can rewrite (15) as

$$\sigma a + b > c + \sigma d. \tag{16}$$

If (iii) does not hold, then $k' < 0$ and hence (15) becomes $\sigma a + b < c + \sigma d$.

Note that σ could also be infinite (if $k' = 0$) and then the condition that A is favored over B reduces to $a > d$. If $\sigma = 0$ then the condition is simply $b > c$.

4. Evolution of cooperation

In this section we find 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, c , for another individual to receive a benefit, b . We have $b > c > 0$. Defectors, D , distribute no benefits and pay no costs. We obtain the payoff matrix

$$\begin{matrix} & C & D \\ C & (b-c, -c) \\ D & (b, 0) \end{matrix}. \tag{17}$$

For structures for which condition (5) holds, we can apply it for payoff matrix (17) to obtain

$$\sigma(b-c) - c > b. \tag{18}$$

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

$$\left(\frac{b}{c}\right)^* = \frac{\sigma + 1}{\sigma - 1}. \tag{19}$$

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

$$\sigma = \frac{(b/c)^* + 1}{(b/c)^* - 1}. \tag{20}$$

Here we have $\sigma > 1$. Note that even without the assumption $b > c > 0$, the same σ is obtained from (18), only some care is required to find the correct signs.

Thus, for any population structure and update rule for which condition (5) holds, 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 (20), this implies $\sigma = (k + 1)/(k - 1)$ which is in agreement with (27).

This demonstrates the practical advantage of relationship (20). In order to derive σ for the general game (1), it suffices to study the specific game (17) and to derive the critical benefit-cost ratio, $(b/c)^*$. Then (20) gives us the answer. Thus we have

Corollary. *In the limit of weak selection, for all structures for which strategy dominance is given by a single-parameter condition (5), for the purpose of studying strategy dominance, it suffices to analyze one-parameter games (e.g. the simplified Prisoner's Dilemma).*

The practical advantage comes from the fact that it is sometimes easier to study the specific game (17) than to study the general game (1). Specifically, using (17) often spares the calculation of probabilities that three randomly chosen players share the same strategy (for example, coefficient η in Antal et al., 2009b).

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 (17) 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 (17). 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 and Nowak (2006, 2008) or Taylor and 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

$$\begin{pmatrix} 1 & b \\ 0 & 0 \end{pmatrix} \text{ or } \begin{pmatrix} 1 & 0 \\ c & 0 \end{pmatrix}. \tag{21}$$

5. Examples

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 .

Moreover, for some of the examples, we use the corollary to find the parameter σ for structures where only the Prisoner's Dilemma has been studied. Such structures include: the regular graph of degree k and the different interaction and replacement graphs when the population size is not much larger than the degree, as well as the phenotype space.

5.1. 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 both DB and BD updating we find for weak selection and any mutation rate

$$\sigma = \frac{N - 2}{N}. \tag{22}$$

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, $a + b > c + d$.

For a wide class of update rules—including pairwise comparison (Traulsen et al., 2008)—it can be shown that (22) holds for any intensity of selection and for any mutation rate (Antal et al., 2009a). The σ given by (22) can also be found in Kandori et al. (1993), who study a process that is stochastic in the generation of mutants, but deterministic in following the gradient of selection.

5.2. 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

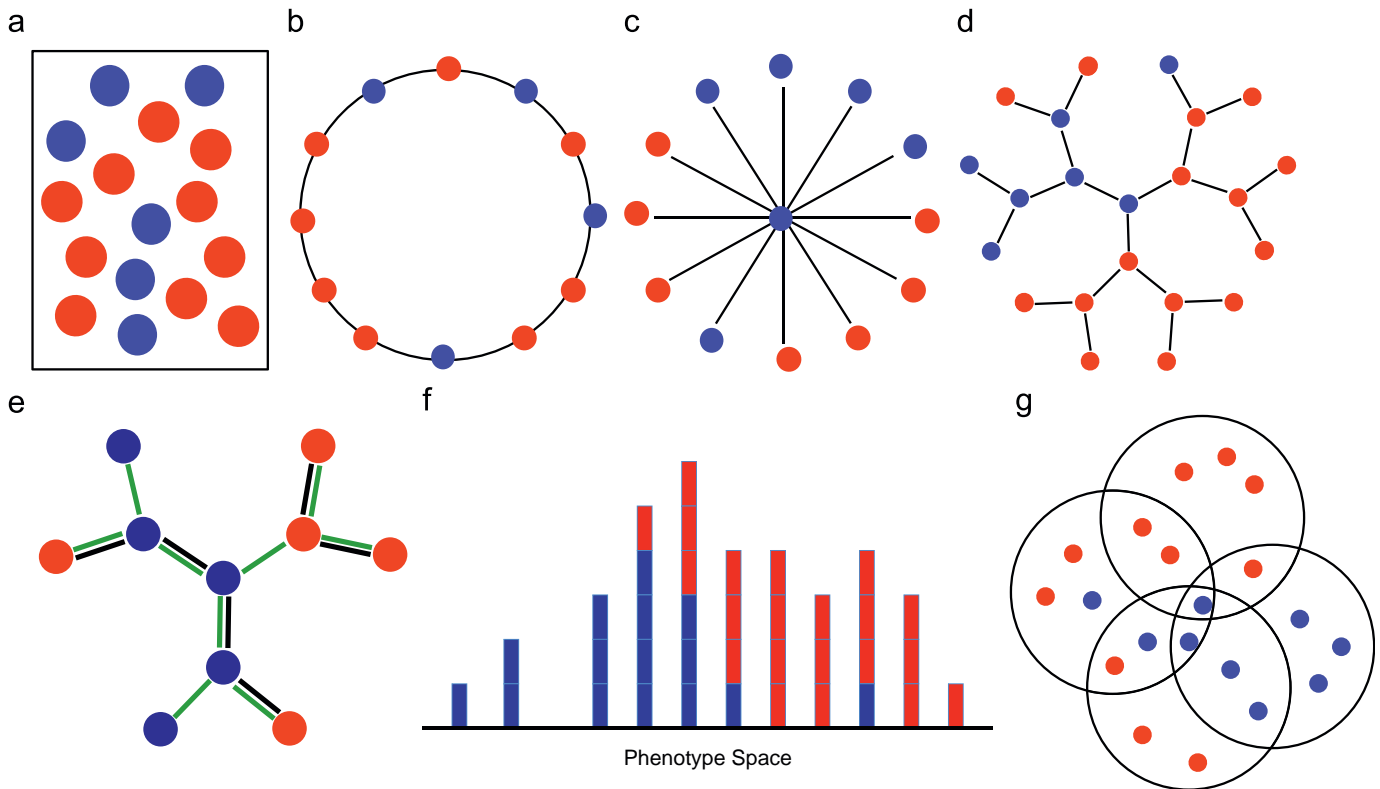


Fig. 1. Various population structures for which σ values are known. (a) For the well-mixed population we have $\sigma = (N - 2)/N$ for any mutation rate. (b) For the cycle we have $\sigma = (3N - 8)/N$ (DB) and $\sigma = (N - 2)/N$ (BD) for low mutation. (c) For DB on the star we have $\sigma = 1$ for any mutation rate and any population size, $N \geq 3$. For BD on the star we have $\sigma = (N^3 - 4N^2 + 8N - 8)/(N^3 - 2N^2 + 8)$, for low mutation. (d) For regular graphs of degree k we have $\sigma = (k + 1)/(k - 1)$ (DB) and $\sigma = 1$ (BD) for low mutation and large population size. (e) If there are different interaction and replacement graphs, we have $\sigma = (gh + l)/(gh - l)$ (DB) and $\sigma = 1$ (BD) 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 $\sigma = 1 + \sqrt{3}$ (DB or synchronous) for a one dimensional phenotype space, low mutation rates and large population size. (g) For 'games on sets' σ is more complicated and is given by (36). All results hold for weak selection.

reproduction. Individuals play a game only with their neighbors and an average (or total) payoff is calculated. In this section we consider death–birth updating and birth–death updating. In 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 effective payoffs. In BD updating, at any one time step, an individual is chosen to reproduce proportional to effective payoff; his offspring replaces randomly one of the neighbors (Ohtsuki et al., 2006).

5.2.1. 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 and Nowak (2006). The following result can be found in Ohtsuki and Nowak (2006) and holds for weak selection.

For DB updating and low mutation ($u \rightarrow 0$) we have

$$\sigma = \frac{3N - 8}{N}. \tag{23}$$

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 DB on a cycle with non-vanishing mutation (Fig. 2a). We confirm (23) and also find that σ depends on the mutation rate, u .

For BD updating we have

$$\sigma = \frac{N - 2}{N}. \tag{24}$$

Hence, for BD updating on a cycle we obtain the same σ -factor as for the well-mixed population, which corresponds to a complete graph. The cycle and the complete graph are on the extreme ends of the spectrum of population structures. Among all regular graphs, the cycle has the smallest degree and the complete graph has the largest degree, for a given population size. We

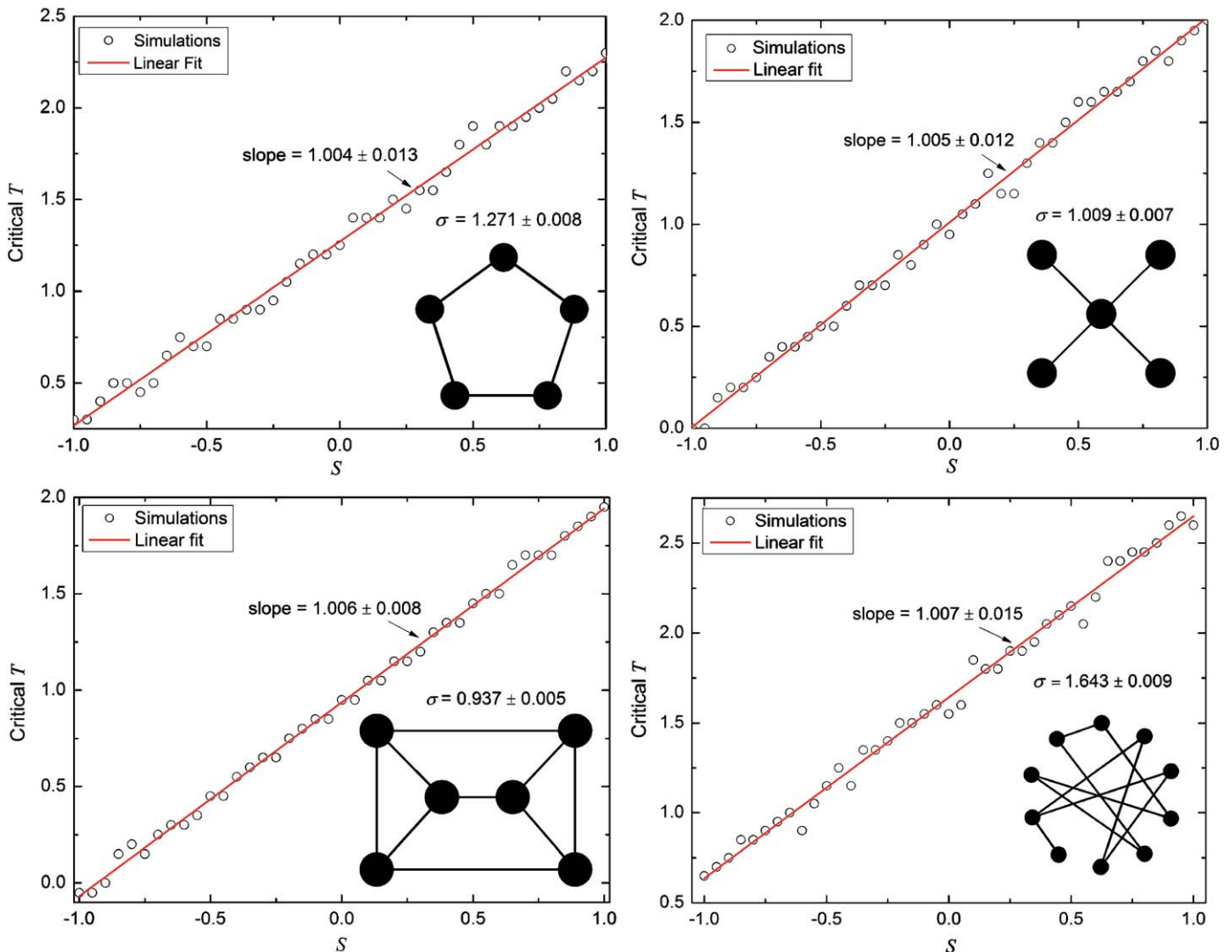


Fig. 2. Numerical simulations for DB updating confirm the linear inequality $\sigma a + b > c + \sigma d$. We study the payoff matrix $a = 1, b = S, c = T$ and $d = 0$ for $-1 \leq S \leq 1$ and $0 \leq T \leq 2$. The red line is the equilibrium condition $T = S + \sigma$. Below this line A is favored. (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 (29) 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 we calculate total payoffs and use as intensity of selection $w = 0.005$. Each point is an average over 2×10^6 runs. (For interpretation of the reference to color in this figure legend, the reader is referred to the web version of this article.)

conjecture that the σ -factor given by (24) holds for weak selection on any regular graph.

We have also performed simulations for BD on a cycle with non-vanishing mutation (Fig. 3a). They confirm (24).

5.2.2. 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. The calculation for the star for both BD and DB updating is shown in Appendix A.

For DB updating on a star we find

$$\sigma = 1. \quad (25)$$

This result holds for weak selection and for any population size $N \geq 3$ and any mutation rate u . Simulations for the star are in agreement with this result (Fig. 2b).

For BD updating on a star we find

$$\sigma = \frac{N^3 - 4N^2 + 8N - 8}{N^3 - 2N^2 + 8}. \quad (26)$$

This result holds in the limit of low mutation, $u \rightarrow 0$. Note also that in the limit of N large we have $\sigma = 1$. Simulations confirm our result (Fig. 3b).

5.2.3. 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

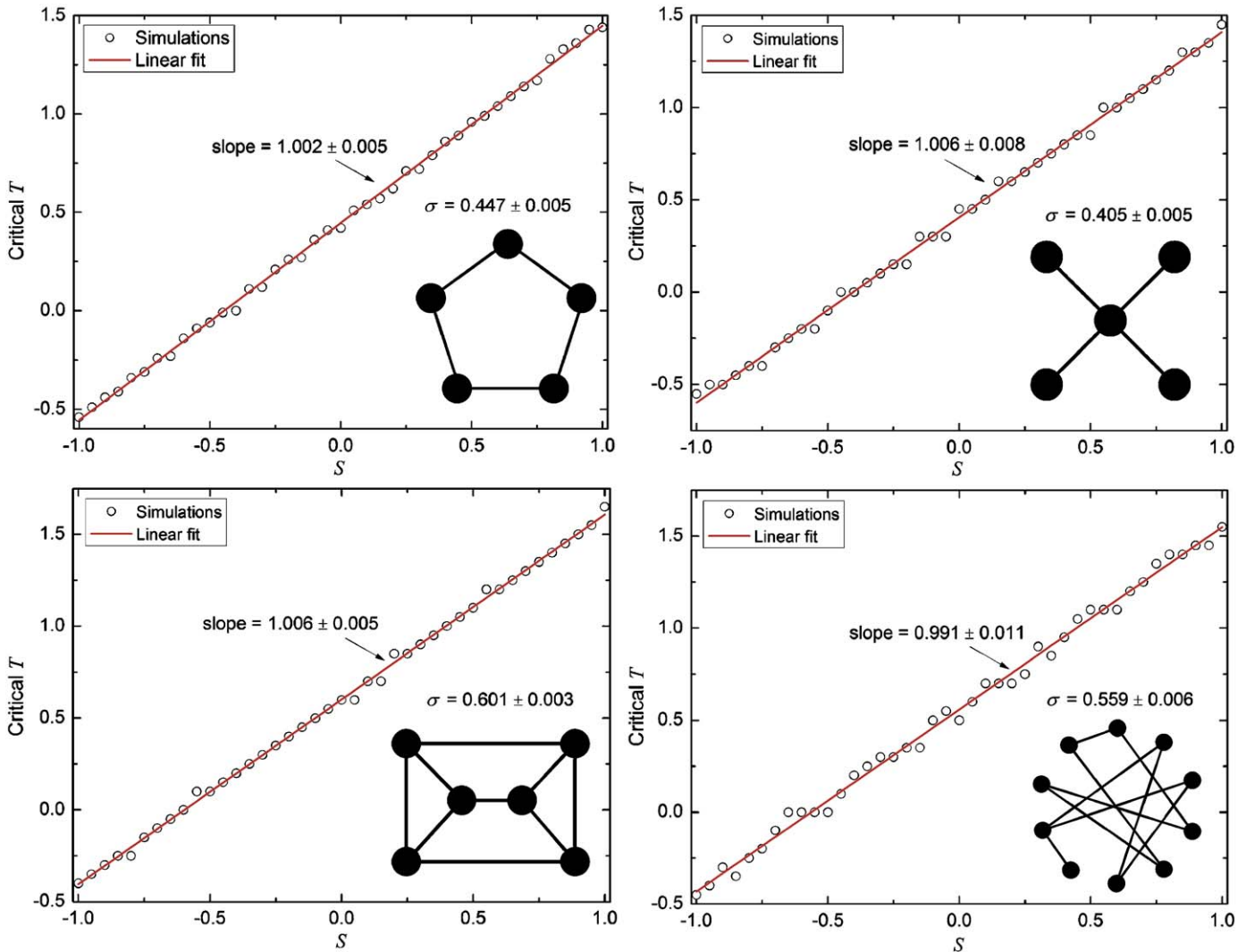


Fig. 3. Numerical simulations for BD updating confirm the linear inequality $\sigma a + b > c + \sigma d$. We study the payoff matrix $a = 1$, $b = S$, $c = T$ and $d = 0$ for $-1 \leq S \leq 1$ and $0 \leq T \leq 2$. The red line is the equilibrium condition $T = S + \sigma$. Below this line A is favored. (a) For a cycle with $N = 5$ and mutation rate, $u = 0.2$, we find $\sigma = 0.447$. The theoretical result for low mutation is $\sigma = 0.6$. Thus, σ depends on the mutation rate. (b) For a star with $N = 5$ we find $\sigma = 0.405$ for $u = 0.1$. The theoretical result for low mutation is $\sigma = 0.686$. This shows that σ depends on the mutation rate. (c) For a regular graph with $k = 3$ and $N = 6$ we find $\sigma = 0.601$ for $u = 0.1$. The theoretical prediction for low mutation is $\sigma = 0.666$. Here again σ depends on the mutation rate. (d) For this random graph with $N = 10$ and average degree $k = 2$ we find $\sigma = 0.559$ for $u = 0.05$. For all simulations we calculate total payoffs and use as intensity of selection $w = 0.005$. Each point is an average over 2×10^6 runs. (For interpretation of the reference to color in this figure legend, the reader is referred to the web version of this article.)

degree $k \geq 2$. Each individual is connected to exactly k other individuals (Fig. 1d).

For DB updating on this structure, Ohtsuki et al. (2006) obtain (see Eq. (24) in their online material)

$$\sigma = \frac{k + 1}{k - 1}. \tag{27}$$

This result holds for 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 BD updating on a regular graph of degree $k \ll N$, in the limit of weak selection and low mutation, Ohtsuki et al. (2006) find

$$\sigma = 1. \tag{28}$$

Hence, for any degree k , we have the simple condition of risk-dominance. Population structure does not seem to affect strategy selection under BD updating for weak selection and large population size.

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 computer simulations for a random graph with $N = 10$ and average degree $k = 2$. We find a linear condition with $\sigma = 1.636$ for DB updating and $\sigma = 0.559$ for BD updating (see Figs. 2d, 3d).

For a regular graph of degree k , the calculation of Ohtsuki et al. (2006) is only applicable if the population size is much larger than the degree of the graph, $N \gg k$. For general population size N , however, we can obtain the σ parameter using our corollary and the results of Taylor et al. (2007a) and Lehmann et al. (2007). They obtained a critical benefit-to-cost ratio of $(b/c)^* = (N - 2)/(N/k - 2)$. Using relationship (20), we obtain

$$\sigma = \frac{(k + 1)N - 4k}{(k - 1)N}. \tag{29}$$

As a consistency check, taking $N \rightarrow \infty$ in (29) leads to (27). Moreover, setting $k = 2$ in (29) leads to (23), and setting $k = N - 1$ in (29) agrees with (22), 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 (29) for low mutation is $\sigma = 1$. Thus we conclude that σ depends on the mutation rate u (Fig. 2c).

For the BD updating on a regular graph with general population size N , we can similarly obtain the relevant σ from the result of Taylor et al. (2007a). For the Prisoner’s Dilemma they find a critical benefit-to-cost ratio of $(b/c)^* = -1/(N - 1)$. Hence, using relationship (20) we obtain

$$\sigma = \frac{N - 2}{N}. \tag{30}$$

Note that the results in Taylor et al. (2007a) hold for any homogeneous graph that satisfies certain symmetry conditions (‘bi-transitivity’). Hence, for BD updating on a wide class of graphs, the condition for strategy dominance is the same as the risk-dominance condition in a well-mixed population.

Computer simulations for a regular graph with $k = 3$ and $N = 6$, for mutation rate $u = 0.1$ suggest that $\sigma = 0.601$. The corresponding prediction of (29) for low mutation is $\sigma = 0.666$. Thus we conclude that σ depends on the mutation rate u (Fig. 3c).

5.2.4. 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 results hold for weak selection and large population size (Ohtsuki and Nowak, 2007):

For DB updating we find

$$\sigma = \frac{gh + l}{gh - l}. \tag{31}$$

For BD updating we find

$$\sigma = 1. \tag{32}$$

Again BD updating does not lead to an outcome that differs from well-mixed populations.

For different replacement and interaction graphs with general population size, N , we can obtain σ via the critical benefit-to-cost ratio in the Prisoner’s Dilemma game (17). Using the result of Taylor et al. (2007b), we obtain $(b/c)^* = (N - 2)/(Nl/gh - 2)$. Hence, we have

$$\sigma = \frac{(gh + l)N - 4gh}{(gh - l)N}. \tag{33}$$

As a consistency check, $g = h = l = k$ reproduces (29).

5.3. Games in phenotype space

Antal et al. (2009b) proposed a model for the evolution of cooperation based on phenotypic similarity. In addition to the usual strategies A and B , each player also has a phenotype. The phenotype is given by an integer o , in other words, each player is positioned in a one-dimensional discrete phenotype space (Fig. 1f). Individuals interact only 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 (in a Wright–Fisher type process). There is an independent mutation probability for the strategy of players, u , and for the phenotype of players, v . When an individual reproduces, its offspring has the same phenotype with probability $1 - 2v$ and mutates to either one of the two neighboring phenotypes with equal probability v . During the dynamics, the whole population stays in a finite cluster, and wanders together in the infinite phenotype space (Moran, 1975; Kingman, 1976).

The resulting expression for σ is derived using the corollary. It is complicated and depends on all parameters, including the two mutation rates, u and v . The expression simplifies for large population sizes, where the main parameters are the scaled mutation rates $\mu = Nu$, $\nu = Nv$ for BD updating (or $\mu = 2Nu$, $\nu = 2Nv$ for synchronous updating). It turns out that σ is a monotone decreasing function of μ , and a monotone increasing function of ν . Hence cooperation is favored (larger σ) for smaller strategy mutation rate and larger phenotypic mutation rate. In the optimal case for cooperation, $\mu \rightarrow 0$, σ becomes only a function of the phenotypic mutation rate

$$\sigma = \frac{1 + 4v}{2 + 4v} \left(1 + \sqrt{\frac{3 + 12v}{3 + 4v}} \right). \tag{34}$$

The largest possible value of σ is obtained for very large phenotypic mutation rate $\nu \rightarrow \infty$, where

$$\sigma = 1 + \sqrt{3}. \tag{35}$$

This is the largest possible sigma for games in a one-dimensional phenotype space.

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. (2009b).

5.4. Games on sets

Tarnita et al. (2009) propose a model based on set memberships (Fig. 1g). They consider a population of N individuals distributed over M sets. To obtain analytical results, we also assume that each individual belongs to exactly K sets, where $K \leq M$. If two individuals belong to the same set, they interact; if they have more than one set in common, they interact several times. An interaction is an evolutionary game given by (1).

The system evolves according to synchronous updating (Wright–Fisher process). There are discrete, non-overlapping generations. All individuals update at the same time. The population size is constant. Individuals reproduce proportional to their effective payoffs. An offspring inherits the sets of the parent with probability $1 - v$ or adopts a random configuration (including that of the parent) with probability v . Any particular configuration of set memberships is chosen with probability $v / \binom{M}{K}$. Similarly, the offspring inherits the strategy of the parent with probability $1 - u$; with probability u , he picks a random strategy. Thus, we have a strategy mutation rate, u , and a set mutation rate, v .

The resulting expression for σ is complicated and depends on all parameters, including the two mutation rates. The expression simplifies for large population size, where the main parameters are the two effective mutation rates $\mu = 2Nu$ and $\nu = 2Nv$ as well as M and K . We find

$$\sigma = \frac{1 + v + \mu}{3 + v + \mu} \cdot \frac{K(v^2 + 2v + v\mu) + M(3 + 2v + \mu)}{K(v^2 + 2v + v\mu) + M(1 + \mu)}. \quad (36)$$

Note that sigma is a one humped function of the set mutation rate v . There is an optimum value of v , which maximizes sigma.

For low effective strategy mutation rate ($\mu \rightarrow 0$) and effective set mutation rate $v \gg 1$ we obtain the simplified expression of σ as

$$\sigma = 1 + \frac{2M}{vK}. \quad (37)$$

Note that for large values of v , sigma decreases with v and increases with M/K .

For low effective strategy mutation rate and low effective set mutation rate $v \rightarrow 0$, we obtained the following simplified expression for σ

$$\sigma = 1 + v \frac{4}{3} \left(1 - \frac{K}{M}\right). \quad (38)$$

Note that, on the other hand, for low values of v , σ increases with v . Hence, there will be an optimum set mutation rate.

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

$$\begin{matrix} & A & B \\ A & \begin{pmatrix} a & b \end{pmatrix} \\ B & \begin{pmatrix} c & d \end{pmatrix} \end{matrix}. \quad (39)$$

We have shown that the condition for A to be more abundant than B in the stationary state of the mutation–selection process can be

written as a simple linear inequality

$$\sigma a + b > c + \sigma d. \quad (40)$$

This condition holds for all population structures that fulfill three natural assumptions, for any mutation rate, but for weak selection. The parameter σ captures the effect of population structure on ‘strategy selection’. We say that ‘strategy A is selected over strategy B ’ if it is more abundant in the stationary distribution of the mutation–selection process. It is important to note that σ does not capture all aspects of evolutionary dynamics in structured populations, but only those that determine strategy selection.

The single parameter, σ , 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. Therefore, σ describes the degree of positive or negative assortment among players who use the same strategy (for the purpose of analyzing strategy selection). Note that our theory does not imply that σ must be positive; negative values of σ are possible in principle, although for all of the examples presented in this paper we have $\sigma > 0$. 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 exists a simple linear inequality with a single parameter, σ , given that some very natural assumptions hold.

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Appendix A. Calculations for the star

A.1. DB updating

We consider a star structured population of size N . A hub is the node lying in the center that is connected to the other $N - 1$ nodes, each of which is called a leaf. Each leaf is connected only to the hub.

We consider the two strategies, A and B . A state of the population is fully described by the number of A -players in the hub and the number of A -players in the leaves. Thus, 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.

DB updating on a star satisfies our Assumptions (i) and (ii). It can be shown (as we do in general in Appendix B) 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.

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

$$\begin{cases} P((0, i) \rightarrow (0, i - 1)) = \frac{i}{N}, \\ P((0, i) \rightarrow (0, i + 1)) = u \frac{N - i - 1}{N}, \\ P((0, i) \rightarrow (1, i)) = \frac{u}{N} + (1 - u) \frac{i}{N(N - 1)} \left(1 + w \frac{N - i - 1}{N - 1} (b - d) \right), \\ P((0, i) \rightarrow (0, i)) = (1 - u) \frac{N - i - 1}{N} \left(1 + \frac{1}{N - 1} \left(1 + w \frac{i}{N - 1} (d - b) \right) \right) \end{cases} \quad (41)$$

and

$$\begin{cases} P((1, i) \rightarrow (1, i - 1)) = \frac{i}{N}, \\ P((1, i) \rightarrow (1, i + 1)) = \frac{N - i - 1}{N}, \\ P((1, i) \rightarrow (0, i)) = \frac{u}{N} + (1 - u) \frac{N - i - 1}{N(N - 1)} \left(1 + w \frac{i}{N - 1} (c - a) \right), \\ P((1, i) \rightarrow (1, i)) = (1 - u) \frac{i}{N} \left(1 + \frac{1}{N - 1} \left(1 + w \frac{N - i - 1}{N - 1} (a - c) \right) \right), \end{cases} \quad (42)$$

So all these transition probabilities do not 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.

Hence, we conclude that our expression (12) which gives the sigma condition depends on $a - c$ and $b - d$ linearly. Thus, it must be of the form:

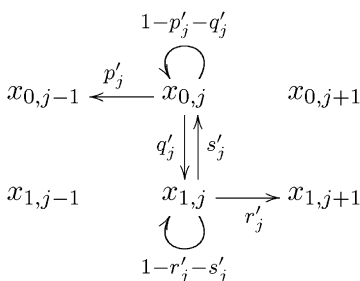
$$(a - c)g(N, u) + (b - d)h(N, u) > 0, \quad (43)$$

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 (12)), 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 .

A.2. BD updating

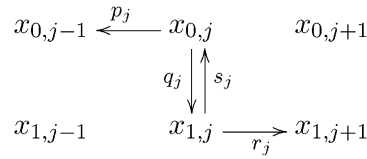
Let $x_{i,j}$ be the probability that A fixates in the population given initial state is (i, j) . Also, let p'_j, q'_j, r'_j and s'_j be the transition probabilities as in the diagram below.



We normalize these probabilities as follows:

$$p_j \equiv \frac{p'_j}{p'_j + q'_j}, \quad q_j \equiv \frac{q'_j}{p'_j + q'_j}, \quad r_j \equiv \frac{r'_j}{r'_j + s'_j}, \quad s_j \equiv \frac{s'_j}{r'_j + s'_j}. \quad (44)$$

Now we have the following diagram. We have $p_j + q_j = 1$ and $r_j + s_j = 1$ there



Direct calculation shows

$$\begin{aligned} x_{0,1} &= q_1 / \left[\sum_{j=1}^{N-2} q_j \left(\prod_{i=1}^{j-1} \frac{p_i}{r_i} \right) + \left(\prod_{i=1}^{N-2} \frac{p_i}{r_i} \right) \right], \\ x_{1,0} &= r_0 / \left[\sum_{j=1}^{N-2} q_j \left(\prod_{i=1}^{j-1} \frac{p_i}{r_i} \right) + \left(\prod_{i=1}^{N-2} \frac{p_i}{r_i} \right) \right]. \end{aligned} \quad (45)$$

For BD updating, we obtain

$$\begin{aligned} x_{0,1} &= \frac{N - 1}{N^2 - 2N + 2} + \mathcal{O}(w), \\ x_{1,0} &= \frac{1}{N^2 - 2N + 2} + \mathcal{O}(w), \\ \rho_A &\equiv \frac{(N - 1)x_{0,1} + x_{1,0}}{N} = \frac{1}{N} + wZ(\lambda_1 a + \lambda_2 b - \lambda_3 c - \lambda_4 d) + \mathcal{O}(w^2), \end{aligned} \quad (46)$$

where

$$\begin{aligned} Z &= \frac{(N - 1)^2}{6N^2(N^2 - 2N + 2)}, \\ \lambda_1 &= N^3 - 3N^2 + 5N - 6, \quad \lambda_2 = 2N^3 - 6N^2 + 7N + 6, \\ \lambda_3 &= N^3 - 7N + 18, \quad \lambda_4 = 2N^3 - 9N^2 + 19N - 18. \end{aligned} \quad (47)$$

The result suggests that a leaf is $(N - 1)$ times more advantageous than the hub.

As before we obtain the σ -factor as

$$\sigma = \frac{\lambda_1 + \lambda_4}{\lambda_2 + \lambda_3} = \frac{N^3 - 4N^2 + 8N - 8}{N^3 - 2N^2 + 8}. \quad (48)$$

Appendix B. 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 $w = 0$, 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 first-order Taylor expansions at $w = 0$.

Note that given the effective payoff function $1 + w \cdot \text{payoff}$, we introduce w together with a, b, c and d . Thus, our transition probabilities from state S_i to state S_j will be functions $P_{ij}(wa, wb, wc, wd)$. So, unless we differentiate with respect to w or evaluate at $w = \text{const}$, whenever we have a degree k term in w , it must be accompanied by a degree k term in a, b, c or d and vice versa. Moreover, w cannot be accompanied by a constant term, i.e. a term that does not contain a, b, c or d .

The probability π_S that the system is in state S also depends on w . For our structures and update rules we will now show that π_S is continuous and differentiable at $w = 0$. 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 :

$$v_1 = -v_n h_1, \quad \dots \quad v_i = -v_n h_i, \quad \dots \quad v_{n-1} = -v_n h_{n-1}. \quad (49)$$

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

$$1 = v_n(-h_1 - \dots - h_{n-1} + 1). \quad (50)$$

For our structures and update rules, the transition probabilities have Taylor expansions around $w = 0$ and thus can be written as polynomials in w . As before, since any w 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 w . 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 w). Thus, h_i above are all rational functions of w . Therefore, from (50) we conclude that v_n must also be a rational function of w . This implies that in our vector of probabilities, all the entries are rational functions. Thus π_S is a fraction of polynomials in w which we write in irreducible form. The only way that this is not continuous at $w = 0$ is if the denominator is zero at $w = 0$. But in that case, $\lim_{w \rightarrow 0} \pi_S = \infty$ which is impossible since π_S is a probability. Therefore, π_S is continuous at $w = 0$.

Moreover, we can write

$$\pi_S = \frac{b_{0S} + b_{1S}w + \mathcal{O}(w^2)}{c_{0S} + c_{1S}w + \mathcal{O}(w^2)}. \quad (51)$$

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 w 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

$$\pi_S^{(1)}(w) = \frac{b_{1S}c_{0S} - b_{0S}c_{1S} + \mathcal{O}(w)}{c_{0S}^2 + \mathcal{O}(w)}. \quad (52)$$

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

$$\pi_S^{(1)} = \frac{b_{1S}c_{0S} - b_{0S}c_{1S}}{c_{0S}^2}. \quad (53)$$

Since b_{0S}, c_{0S} contain no a, b, c, d and b_{1S}, c_{1S} are linear in a, b, c, d for all S 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.

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