



Multi-player games on the cycle

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ABSTRACT

In multi-player games n individuals interact in any one encounter and derive a payoff from that interaction. We assume that individuals adopt one of two strategies, and we consider symmetric games, which means the payoff depends only on the number of players using either strategy, but not on any particular configuration of the encounter. On the cycle we assume that any string of n neighbouring players interacts. We study fixation probabilities of stochastic evolutionary dynamics. We derive analytical results on the cycle both for linear and exponential fitness for any intensity of selection, and compare those to results for the well-mixed population. As particular examples we study multi-player public goods games, stag hunt games and snowdrift games.

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1. Introduction

Evolutionary game theory is an approach to study frequency dependent selection or social evolution: the fitness of individuals is not constant, but depends on interactions with others in the population (Maynard Smith and Price, 1973; Maynard Smith, 1982; Hofbauer and Sigmund, 1998; Weibull, 1995; Samuelson, 1997; Cressman, 2003; Hofbauer and Sigmund, 2003; Nowak and Sigmund, 2004). The traditional theory is based on deterministic dynamics in infinitely large, well-mixed populations, but can be extended to spatial games (Nowak and May, 1992, 1993; Nakamaru et al., 1997, 1998; Szabó and Töke, 1998; Hauert, 2001, 2002; Szabó and Fáth, 2007; Nowak et al., 2010) and stochastic dynamics in finite populations (Nowak et al., 2004; Taylor et al., 2004; Fudenberg and Imhof, 2006; Imhof and Nowak, 2006; Traulsen et al., 2007a,b; Antal et al., 2009a,c). Evolutionary graph theory explores evolutionary dynamics on general (fixed) population structures or social networks (Lieberman et al., 2005; Ohtsuki and Nowak, 2006; Ohtsuki et al., 2006; Grafen, 2007; Ohtsuki et al., 2007a,b; Taylor et al., 2007). Some models study evolution on dynamic graphs (Bala and Goyal, 2000; Skyrms and Pemantle, 2000; Pacheco et al., 2006a,b) or clustering in phenotype space (Antal et al., 2009b). In evolutionary set theory individuals can cluster within and move between sets (Tarnita et al., 2009a). General results for spatial games are often derived for the limit of weak selection (Tarnita et al., 2009b, 2011).

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Many of those results concern dyadic interactions. In order to understand the essential features of mechanisms for evolution of cooperation much can be learned from studying such pairwise interactions (Nowak, 2006). But there are also many cooperative enterprises with more than two participants. An ant colony, a firm, a rock band, an orchestra or a football team are relevant situations where the number of players in any one encounter is not limited to two. Therefore generalizing evolutionary games to more than two players is a natural endeavor (see Hauert et al., 2002; Milinski et al., 2006; Zheng et al., 2007; Santos et al., 2008; Kurokawa and Ihara, 2009; Pacheco et al., 2009; Souza et al., 2009; Wang et al., 2009; van Veelen, 2009, 2011a,b; Gokhale and Traulsen, 2010, 2011; Roca and Helbing, 2011; Santos and Pacheco, 2011).

It is of general interest to study how population structure affects evolutionary dynamics. One extreme case is the well-mixed population where every individual of the population is equally likely to interact with every other individual. In terms of evolutionary graph theory the well-mixed population is given by a complete graph with identical weights. Another extreme case is a one-dimensional population structure where the individuals of the population are arranged along a line. If the ends of the line are joined (in order to avoid boundary effects) then we obtain a cycle. It is useful to study games in well-mixed populations and on cycles, because most (static) population structures have behaviors between these two extreme cases. For a population of $N=3$ individuals the well-mixed population is equivalent to the cycle.

Furthermore, when studying evolutionary game dynamics in finite sized populations one quickly realizes the importance of varying the intensity of selection. Strong selection means that the fitness differences between individuals can be large, which can dominate the stochastic effects caused by the finiteness of the population.

Weak selection means that the fitness differences between individuals are small and therefore stochastic effects are very important. The limit of weak selection is the case where the evolutionary dynamics are almost entirely dominated by random drift and the effects of the game provide only a small perturbation to random drift. The limit of weak selection can be seen as a ‘high temperature’ situation, and it is worth exploring how robust results in this limit are to changes in the intensity of selection (see also Wu et al., 2010).

Here we study n -player games on cycles, where every unbroken sequence of n players is assumed to play the game. For 2-player games on cycles, Ohtsuki and Nowak (2006) ask the question whether strategy A will replace strategy B with a higher probability than vice versa, and find simple conditions. Their derivations use Taylor expansions, apply to 2 player games with linear fitness, and hold either at one extreme (strong selection) or at the other (weak selection). In this paper we use a different (more direct) method to derive our results, which is not based on Taylor expansions. This allows us to obtain results for any intensity of selection. We also allow for exponential as well as linear fitness, and expand the results to games with any number of players. The results in Ohtsuki and Nowak (2006) are confirmed as special cases.

The conditions for cooperation to evolve on the cycle are compared to those for the well mixed population derived by Kurokawa and Ihara (2009) for linear fitness and weak selection, and by Gokhale and Traulsen (2010) for exponential fitness and any intensity of selection. We study four examples: (i) a linear public goods game, (ii) a multi-player stag hunt game, (iii) a multi-player snowdrift game and (iv) a game which is non-linear in the production of the public good.

2. Results for multi-player games

Consider a symmetric game with n players that all can choose between two strategies, A and B . A game is symmetric if all permutations of the strategy profile leave the payoffs of A -players and B -players unchanged. For example, if we have $n=3$ players, then the payoffs of players 1 and 3 in strategy profile (A, B, A) are equal to each other, and equal to the payoffs of players 2 and 3 in strategy profile (B, A, A) . In other words, a game is symmetric if the payoffs only depend on how many A (and B) players occur in an interaction group. In a symmetric n player game, P_i is the payoff to an A -player in a group of i many A players (and $n-i$ many B players). In contrast, Q_i is the payoff to a B -player in a group of i many B players (and $n-i$ many A players). See also Gokhale and Traulsen (2010).

There are various possibilities for translating payoff into reproductive success (fitness). One option is that the fitness of an individual is proportional to e^{wP} , where P is the total payoff of that individual and w is a parameter that determines the intensity of selection (Traulsen et al., 2008). For this exponential fitness function w can range between 0 and ∞ . The limit of weak selection is given by $w \rightarrow 0$.

Another possibility is that fitness is proportional to a linear function of payoff, $1-w+wP$ (Nowak et al., 2004). Again P is the individual's total payoff and w is a parameter that determines the intensity of selection, which can vary between 0 and 1 if all payoffs are non-negative. In other words, if there are no negative payoffs, then $w_{\max} = 1$. If there are negative payoffs, however, and $P_{\min} < 0$ is the smallest possible total payoff that an individual could achieve, then the maximum intensity of selection is given by $w_{\max} = 1/(1-P_{\min})$. The reason is that in the stochastic processes of evolutionary dynamics the fitness of an individual is proportional to the probability of being chosen for reproduction. These probabilities must be non-negative. The limit of weak selection is again given by $w \rightarrow 0$.

We consider two update rules: (i) ‘birth–death’ (BD) means that an individual is selected for reproduction proportional to

fitness and the offspring replaces a randomly selected individual, or a randomly selected neighbour (ii) ‘death–birth’ (DB) means that a random individual is eliminated, and the remaining individuals, or the neighbours, compete for the empty site proportional to their fitness (Lieberman et al., 2005; Ohtsuki and Nowak, 2006; Ohtsuki et al., 2006).

Imagine now that a single A individual arises in a population of B individuals. The A individual could die before reproducing or generate a lineage of A , which becomes extinct after some time. In both cases, the population returns to a state of ‘all- B ’. The other possibility is that A produces a lineage which will eventually take over the entire population, which means that B becomes extinct. In this case, the population will end up in the state ‘all- A ’. Denote by ρ_A the probability that a single A individual will take over a population of B . Denote by ρ_B the probability that a single B individual will take over a population of A . The quantities ρ_A and ρ_B are called the fixation probabilities of A and B , respectively (see Karlin and Taylor, 1975; Ewens, 2004).

A neutral mutant has fixation probability $1/N$. Therefore, if $\rho_A > 1/N$, then selection favours the fixation of A . If $\rho_A < 1/N$, then selection opposes the fixation of A . If $\rho_A > \rho_B$, then selection favours A over B (see Nowak et al., 2004).

2.1. Well-mixed populations

We begin by restating two known results for the well-mixed population. In a well-mixed population every possible combination of n individuals plays the game. The total payoff of an individual is the sum over all its interactions. In terms of evolutionary graph theory, the well-mixed population is defined by a complete graph with identical weights.

For the exponential fitness function, and for any intensity of selection, Gokhale and Traulsen (2010) find that A is favored over B if and only if

$$\sum_{i=1}^n NP_i + (N-n)P_n > \sum_{i=1}^{n-1} NQ_i + (N-n)Q_n \quad (1)$$

Gokhale and Traulsen (2010) assume BD updating, but their result also holds for DB updating. In Appendix A we restate this result in Theorem-Proof form. A core element of the proof is a combinatoric identity, which we state as a separate Lemma. Our proof of that identity is shorter than the derivation in Gokhale and Traulsen (2010) and might be easier to follow. Gokhale and Traulsen (2010) use average instead of total payoffs, but dividing by the total number of interactions only scales the intensity of selection (see the proof in Appendix A).

Gokhale and Traulsen (2010) note that their result holds true “for any birth–death process in which the ratio of transition probabilities can be approximated under weak selection by a term linear in the payoff difference in addition to the neutral result”. Proposition 3 in Appendix A makes this statement explicit for linear fitness, and includes DB updating. The proof there can be used for a range of update process that are similar in the limit of weak selection.

For large population size, $N \gg n$, condition (1) reduces to the result obtained by Kurokawa and Ihara (2009):

$$\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i \quad (2)$$

Kurokawa and Ihara (2009) derive this condition for large N , linear fitness, and weak selection, while the result of Gokhale and Traulsen (2010) implies that condition (2) also holds for large N , exponential fitness, and any intensity of selection (see also Kurokawa et al., 2010).

For the special case of $n=2$, Antal et al. (2009a) find the same conditions (1) and (2) for any intensity of selection for a wide

class of evolutionary processes. In a somewhat different setting, Kandori et al. (1993) derive the $n=2$ condition for a process with deterministic selection. Theorem 3 in Young (1993), where selection is stochastic, shows that the risk dominant equilibrium in 2×2 games with two strict Nash equilibria is “generically stable”.

2.2. The cycle

The simplest spatial model is a one-dimensional population structure. If the ends of this structure are joined, then we obtain a cycle. For games on cycles see for instance Ellison (1993), Eshel et al. (1998), Lieberman et al. (2005), Ohtsuki et al. (2006), Ohtsuki and Nowak (2006), Grafen (2007), and Nowak et al. (2010). For multi-player games individuals do not just interact with one neighbour on the left and one on the right, but also with individuals that are further away. Every unbroken sequence of n players on the cycle plays the game, which implies that every player is contained in n such sequences. It interacts with its $n-1$ neighbours on the left in one game, with $n-2$ neighbours on the left and 1 on the right in another, and so on until the game in which it interacts only with its $n-1$ neighbours on the right. Each player’s payoffs are affected by the strategies of all neighbours that are less than n places away, although the nearer ones have a larger effect than the more distant ones. The closer two individuals are on the cycle, the more games they have in common. For $n=2$ we are back in the case where individuals only interact with direct neighbours, which is studied by Ohtsuki and Nowak (2006), Grafen (2007) and Nowak et al. (2010).

Ohtsuki and Nowak (2006) use Taylor expansions to derive results for games with two players, linear fitness, and either for strong selection or for the limit of weak selection. Here we use a direct approach, without approximations, which allows us to derive results that hold for any intensity of selection. We also extend the analysis to exponential fitness and, obviously, to games with more than two players. Our results are summarized below. They can also be found as propositions with proofs in Appendix C.

For BD updating, we find that selection favors A over B if

$$\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i \tag{3}$$

This condition holds for large N for any intensity of selection, both for exponential fitness and for linear fitness. Condition (3) is the same as condition (2), which is obtained for large, well-mixed populations. Therefore BD updating on a cycle does not modify the selection criterion for n player games when compared with a well-mixed population (if we use exponential fitness, or linear fitness with weak selection).

For DB updating on the cycle we obtain different conditions. For exponential fitness and any intensity of selection, we find that A is favored over B if

$$(P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n) > 0 \tag{4}$$

For linear fitness and varying intensity of selection, $w \in (0, w_{\max})$, we find

$$(1-w)C_0 + wC_1 > 0 \tag{5}$$

Here

$$C_0 = (P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n)$$

and

$$C_1 = \sum_{i=1}^n P_i \left(\sum_{i=2}^n P_i + P_n \right) - \sum_{i=1}^n Q_i \left(\sum_{i=2}^n Q_i + Q_n \right)$$

Note that for linear fitness and weak selection ($w \downarrow 0$) we get the same condition as for exponential fitness with any intensity of selection. The general condition for linear fitness, however, is nonlinear in the payoff values.

3. Examples

3.1. The n -player linear public goods game

We consider a linear public goods game, where n players participate in any one interaction. Being a cooperator costs $c > 0$ and leads to a benefit $b > c$, which is distributed among other $n-1$ players.¹ If strategy A is cooperate, and B is defect, then we obtain the following payoff functions:

$$P_i = \frac{i-1}{n-1} b - c$$

$$Q_i = \frac{n-i}{n-1} b$$

While economists tend to refer to this game as a linear public goods game, it can also be described as public goods games with generalized equal gains from switching, or with additive fitnesses (van Veelen, 2009, 2011a,b, see also Nowak and Sigmund, 1990; Wild and Traulsen, 2007; Traulsen et al., 2008).

The lowest possible payoff in the game is obtained by one cooperator in a world of defectors, which is nP_1 . Thus, for linear fitness, the largest possible w is $w_{\max} = 1/(1-nP_1) = 1/(1+nc)$. For exponential fitness there is no upper bound on w .

The condition for the evolution of cooperation in large, well mixed populations translates to the following (see Appendix D.1 for all computations):

$$-nc > 0. \tag{2a}$$

This is never the case for $c > 0$. Thus, in the well mixed population, both for exponential fitness and any intensity of selection, and for linear fitness in the limit of weak selection, we never have $\rho_C > \rho_D$.

The same condition applies to BD updating on the cycle, both for exponential fitness and linear fitness, and for any intensity of selection. Again, we never have $\rho_C > \rho_D$ for large populations.

For DB updating on the cycle, exponential fitness, and any intensity of selection, we find that $\rho_C > \rho_D$ for large populations if and only if

$$\frac{b}{c} > n. \tag{4a}$$

For DB updating on the cycle, linear fitness, and any intensity of selection $w \in (0, 1/(1+nc))$, we find that $\rho_C > \rho_D$ for large populations if and only if

$$(1-w)2(b-cn) + wn(n-1)(b-cn)(b-c) > 0. \tag{5a}$$

This inequality can be written as $(b-cn)[2(1-w) + wn(n-1)(b-c)] > 0$. Because the second term is always positive, this condition reduces to

$$\frac{b}{c} > n.$$

Table 1 summarizes our results.

¹ This is an “others only” description of the game, which has the obvious advantage that c is the actual net cost of the cooperative behaviour. At Example 3, we will switch to a description where the individual itself also shares in the benefits.

Table 1

Conditions for evolution of cooperation in n -player linear public goods games. For exponential fitness, all of those conditions apply for any intensity of selection. For linear fitness they apply for the cycle for any intensity of selection $w \in (0, 1/(1+nc))$, but only in the limit of weak selection for the well-mixed population.

	Well-mixed population	Cycle
Birth-death	Never	Never
Death-birth	Never	$\frac{b}{c} > n$

Table 2

Conditions for evolution of cooperation in n -player stag hunt games. For exponential fitness, all of these conditions apply for any intensity of selection. For linear fitness they all apply in the limit of weak selection. For linear fitness and BD updating on the cycle, the condition also applies for any intensity of selection, whereas the condition for DB updating on the cycle and any intensity of selection ranges from $b/c > 2n/3$ at $w \downarrow 0$ to $b/c > n/\sqrt{2}$ at $w \uparrow 1/(1+nc)$.

	Well-mixed population	Cycle
Birth-death	$\frac{b}{c} > n$	$\frac{b}{c} > n$
Death-birth	$\frac{b}{c} > n$	$\frac{b}{c} > \frac{2}{3}n$

3.2. The n -player stag hunt game

In the n player stag hunt game, cooperation implies a cost $c > 0$, regardless of group size n (see Skyrms, 2004; Pacheco et al., 2009). If everyone cooperates, then everyone gets $b > c$ in return. If not everyone cooperates, then no one gets anything in return. This gives the following payoff functions, where as before i is the number of cooperators in the group

$$P_i = \begin{cases} -c, & i \neq n \\ b-c, & i = n \end{cases}$$

$$Q_i = 0$$

For linear fitness the largest possible intensity of selection is $w_{\max} = 1/(1-nP_1) = 1/(1+nc)$.

The condition for the evolution of cooperation in large, well mixed populations is given by (see Appendix D.2)

$$\frac{b}{c} > n. \tag{2b}$$

The same condition applies to BD updating on the cycle, both for exponential fitness and linear fitness, and for any intensity of selection.

For DB updating on the cycle, exponential fitness and any intensity of selection, we have $\rho_C > \rho_D$ for large populations if and only if

$$\frac{b}{c} > \frac{2}{3}n. \tag{4b}$$

For DB updating on the cycle, linear fitness, and any intensity of selection $w \in (0, 1/(1+nc))$, we find that $\rho_C > \rho_D$ for large populations if and only if

$$(1-w)(3b-2nc) + w(b-nc)(2b-nc) > 0. \tag{5b}$$

This implies that for DB updating on the cycle, linear fitness and weak selection ($w \downarrow 0$), the condition becomes

$$\frac{b}{c} > \frac{2}{3}n.$$

For $w \uparrow 1/(1+nc)$ the condition becomes

$$\frac{b}{c} > \frac{n}{\sqrt{2}}.$$

The threshold is more restrictive for higher intensity of selection.

Table 2 summarizes our results.

For BD updating, the condition for the fixation probability of cooperators to be larger than the fixation probability of defectors ($\rho_C > \rho_D$) is the same for the well mixed population and the cycle. This result, however, does not imply that for a given stag hunt game the fixation probabilities ρ_C and ρ_D are the same for the two structures, nor that the conditional fixation times are the same (see Antal and Scheuring, 2006; Traulsen et al., 2007a,b; Wu et al., 2010). If j denotes the population state with j cooperators and $N-j$ defectors, and T_j^+ (resp. T_j^-) is the probability of a transition from state j to $j+1$ (resp. $j-1$), then on the cycle, the ratio's of transition probabilities T_j^+/T_j^- are the same for all but the first and last $n-1$ states—that is, for all states $j \in \{n, \dots, N-n\}$ (see Appendix C). If $b/c > n$, then T_j^+/T_j^- is somewhat larger than 1 for all those states. For the well-mixed population, on the contrary, the ratios of transition probabilities T_j^+/T_j^- changes between every two population states, with T_{N-1}^+/T_{N-1}^- being very large, and T_1^+/T_1^- being very small, implying that the closer the population is to either one of the monomorphic states, the stronger the selection is towards that monomorphic state. This effect makes the fixation of a single mutant of either kind an unlikely event in the well-mixed population with strong selection, because single mutants are typically eliminated from the population.

3.3. The n -player snowdrift game

Another extreme case is for a benefit to materialize if only a single individual cooperates, while any extra cooperator does not add to the benefits gained from cooperation (see Zheng et al., 2007; Souza et al., 2009; Santos and Pacheco, 2011). This case is represented by the following payoff function, where we still assume that $b > c$ and where i denotes the number of cooperators in the group:

$$P_i = b-c$$

$$Q_i = \begin{cases} b, & i \neq n \\ 0, & i = n \end{cases}$$

Note that there are different ways to generalize the snowdrift game to n players. In Zheng et al. (2007) the payoff of a cooperator is $P_i = b-c/i$, which implies that the costs of the collective effort are divided by the number of cooperators. In Souza et al. (2009) that feature is combined with a threshold M such that the benefit only materializes if at least M players cooperate. Here we chose not to divide the costs by the number of cooperators. That choice makes the game a special case of the more general set of games discussed in Section 3.4, of which also the n -player stag hunt game is a special case.

The lowest possible payoff for an individual is 0. Hence for linear fitness we can consider all intensities of selection $w \in (0, 1)$.

The condition for the evolution of cooperation in large, well mixed populations is given by (see Appendix D.3 for all computations)

$$\frac{b}{c} > n. \tag{2c}$$

The same condition applies to BD updating on the cycle, both for exponential fitness and linear fitness, and for any intensity of selection.

For DB updating on the cycle, exponential fitness and any intensity of selection, we have $\rho_C > \rho_D$ for large populations if and only if

$$\frac{b}{c} > \frac{2}{3}n. \tag{4c}$$

For DB updating, linear fitness, and intensity of selection $w \in (0, 1)$, we find that $\rho_C > \rho_D$ for large populations if and only if

$$(1-w)(3b-2nc) + w(b^2(3n-2)-2bcn^2 + c^2n^2) > 0. \tag{5c}$$

Table 3
 Conditions for evolution of cooperation in n -player snowdrift games. For exponential fitness, all of these conditions apply to any intensity of selection. For linear fitness they all apply in the limit of weak selection. For linear fitness and BD updating on the cycle, the condition also applies to any intensity of selection, whereas the condition for DB updating on the cycle and any intensity of selection ranges from $b/c > 2n/3$ at $w \downarrow 0$ to $b/c > (n^2 + n\sqrt{(n-1)(n-2)})/(3n-2)$ at $w \uparrow 1$.

	Well-mixed population	Cycle
Birth–death	$\frac{b}{c} > n$	$\frac{b}{c} > n$
Death–birth	$\frac{b}{c} > n$	$\frac{b}{c} > \frac{2}{3}n$

This inequality implies that for DB updating, linear fitness and weak selection ($w \downarrow 0$), the condition becomes

$$\frac{b}{c} > \frac{2}{3}n.$$

For $w \uparrow 1$ the condition becomes

$$\frac{b}{c} > \frac{n^2 + n\sqrt{(n-1)(n-2)}}{3n-2}.$$

Again, the critical benefit-to-cost ratio increases (moderately) with increasing intensity of selection.

Table 3 summarizes those results.

As with the n -player stag hunt game and BD updating, the fixation probabilities ρ_C and ρ_D do not have to be the same for the two structures, even if the condition for ρ_C to be larger than ρ_D is the same. For the n -player snowdrift game the conditional fixation time in the well mixed population increases exponentially with population size (see Antal and Scheuring, 2006). Also the ratios of transition probabilities T_j^+ / T_j^- change between every two population states, but now T_{N-1}^+ / T_{N-1}^- is very small, and T_1^+ / T_1^- is very large, implying that the closer the population is to either one of the monomorphic states, the stronger selection is away from that monomorphic state. Thus it is common for rare mutants to initially increase in numbers. Once present in the population in reasonable numbers, however, it takes very long for the mutant to either fixate or become extinct. Even for very low mutation rate, the system would still spend much time in mixed states. On the cycle, on the other hand, mixtures are no more or less stable in the n -player snowdrift game than they are in the n -player stag hunt game.

3.4. A multi-player game with non-linear production of a public good

The two examples above can be seen as two special cases of a more general set of games. Suppose that the payoff functions are as follows:

$$P_i = \left(\frac{i}{n}\right)^\alpha b - c$$

$$Q_i = \left(\frac{n-i}{n}\right)^\alpha b$$

One can see this as a case where a public good is produced. How much is produced depends on the number of cooperators: it is proportional to the fraction of cooperators raised to the power α . The cost of cooperation is always c .

The n -player stag hunt game is the limiting case for $\alpha \rightarrow \infty$, when a public good of size b is produced if all individuals cooperate, but nothing otherwise. The n -player snowdrift game is the limiting case for $\alpha \downarrow 0$, when one cooperator suffices to produce the public good, while additional cooperators have no effect.

The lowest possible payoff is $\min\{(1/n)^\alpha b - c, 0\}$. For linear fitness, the largest possible intensity of selection is $w_{\max} = 1/(1 - nP_1) = \min\{1/(1 + c - n^{1-\alpha}b), 1\}$.

The condition for the evolution of cooperation in large, well mixed populations is given by (see Appendix D.4)

$$\frac{b}{c} > n. \tag{2d}$$

The same condition applies to BD updating on the cycle, both with exponential fitness and linear fitness, and for any intensity of selection.

For DB updating on the cycle, exponential fitness and any intensity of selection, we have $\rho_C > \rho_D$ for large populations if and only if

$$\frac{b}{c} > \frac{2n}{3 + \left(\frac{n-1}{n}\right)^\alpha - \left(\frac{1}{n}\right)^\alpha}. \tag{4d}$$

For DB updating on the cycle, linear fitness, and intensity of selection $w \in (0, w_{\max})$, we find that $\rho_C > \rho_D$ for large populations if and only if

$$(1-w) \left(\frac{3n^\alpha + (n-1)^\alpha - 1}{n^\alpha} b - 2nc \right) + w \left(\begin{aligned} & n^2 c^2 \\ & - \left(2 \sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha + \left(\frac{1}{n}\right)^\alpha + 1 \right) bnc \\ & + \left(\sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha + \frac{(n-1)^\alpha + (n-2)^\alpha}{n^\alpha} \sum_{i=1}^{n-1} \left(\frac{i}{n}\right)^\alpha \right) b^2 \end{aligned} \right) > 0. \tag{5d}$$

This inequality implies that for DB updating on the cycle, linear fitness and weak selection ($w \downarrow 0$), the condition is

$$\frac{b}{c} > \frac{2n^{\alpha+1}}{3n^\alpha + (n-1)^\alpha - 1} = \frac{2n}{3 + \left(\frac{n-1}{n}\right)^\alpha - \left(\frac{1}{n}\right)^\alpha}.$$

Also the linear public goods game falls within this set of games, provided that we switch from the “others only” presentation from Section 3.1, to a representation where the contributor also shares in the benefits. If we take $\alpha = 1$, then we get a linear public goods game where the net costs of cooperation are $c - b/n$ and the net benefits to the other group members are $(1 - 1/n)b$ (see also van Veelen, 2009, 2011b).

4. Conclusion

We have studied multi-player games on the cycle and compared our results to those for the well-mixed population derived by Gokhale and Traulsen (2010). These two population structures represent opposite extremes for the level of spatial assortment. Therefore, we expect these results to bracket conditions that might be found for many other static population structures. We explore the competition of two strategies, A and B , and ask when the fixation probability of one strategy is greater than the fixation probability of the other strategy, $\rho_A > \rho_B$. For a mutation–selection process in the limit of vanishingly small mutation rate, the strategy with the larger fixation probability is also the more abundant one in the stationary distribution. We can therefore say that this strategy is favored by natural selection.

We have studied two update rules: birth–death (BD) and death–birth (DB) updating. In the first case an individual is chosen for reproduction proportional to payoff, and the offspring replaces a randomly chosen neighbor. In the second case, a random individual is chosen to update its strategy; it will adopt the strategy of one of its neighbors proportional to payoff.

We have considered two fitness functions: exponential and linear. We derive the selection criterion $\rho_A > \rho_B$ for a cycle with large population size N . For BD updating we derive a condition, given by inequality (3), which is linear in the payoff values.

This condition holds both for exponential and linear fitness functions for any intensity of selection. Moreover the condition is equivalent to what can be derived for the well-mixed population for exponential fitness and any intensity of selection or for linear fitness and weak selection. As for $n=2$ player games we find that BD updating on a cycle does not lead to spatial effects that modify the selection criterion, $\rho_A > \rho_B$, for large N . Of course, the expected fixation times can differ (Antal and Scheuring, 2006).

For DB updating with exponential fitness and any intensity of selection we find a selection criterion, given by inequality (4), which is also linear in the payoff values but differs from the equivalent condition for the well-mixed population. Therefore DB updating on a cycle can favor strategies which would not be selected in a well-mixed population. In particular DB updating on a cycle can promote the evolution of cooperation.

For DB updating with linear fitness and varying intensity of selection we find a selection criterion, given by inequality (5), which is nonlinear in the payoff values. The condition contains both linear and quadratic terms.

We use these main results to study four examples: a linear public goods game, a multi-player stag-hunt game, a multi-player snowdrift game, and finally a game with nonlinear production of a public good.

For the linear public goods game we find that only DB updating on the cycle can favor evolution of cooperation. The crucial condition here is that the benefit-to-cost ratio, b/c , exceeds the group size, n , of the multi-player game.

For the stag-hunt game we find that cooperation is favored for both geometries (the well-mixed population and the cycle) and both update rules (BD and DB) provided $b/c > n$. DB updating on a cycle relaxes the condition to $b/c > 2n/3$. The same conditions hold for the snowdrift game. The only differences in selection criteria between the stag-hunt and the snowdrift game arise for linear fitness and non-weak selection. It is not surprising that for these two relaxed social dilemmas evolution of cooperation is possible even in a well-mixed population. It is perhaps somewhat surprising that for exponential fitness the selection criteria are identical for these two games. This fact can be understood by looking at a more general game with nonlinear production of a public good, of which both games are special cases ($\alpha \rightarrow \infty$ and $\alpha \downarrow 0$). The condition for the well mixed population as well as for BD updating on the cycle for this more general set of games do not depend on the parameter α , and the condition for DB updating on the cycle turns out to be the same in either limit.

Our analysis generalizes the results of Ohtsuki and Nowak (2006), who consider 2-player games on cycles, and derive results for games with linear fitness at either one extreme (weak selection) or the other (strong selection). We have generalized their results to conditions that apply to any intensity of selection, allow for exponential as well as linear fitness, and consider games with any number of players. The conditions we find are concise, and turn out to become even simpler when applied to standard examples such as multi-player public goods, stag hunt, or snowdrift games.

Our approach for studying multi-player games on a one-dimensional spatial structure uses different interaction and replacement graphs (Ohtsuki et al., 2007a,b). For the accumulation of payoff each player interacts with up to $n-1$ players on the left and on the right side, but the competition for replacement only occurs between immediate neighbors. Other choices are possible and will be investigated in due course.

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Appendix A. Results for n -player games in well mixed populations

We will use the following identity for $1 \leq k \leq n$:

$$\sum_{j=k}^{N-n+k} \binom{j-1}{k-1} \binom{N-j}{n-k} = \binom{N}{n}$$

Showing that this is indeed an identity uses a simple induction argument:

Lemma 1. $\sum_{j=k}^{N-n+k} \binom{j-1}{k-1} \binom{N-j}{n-k} = \binom{N}{n}$ for $1 \leq k \leq n$.

Proof. The recursion $\binom{N}{n} = \binom{N-1}{n} + \binom{N-1}{n-1}$ together with the initialization

$$\binom{0}{i} = \begin{cases} 1 & \text{if } i = 0 \\ 0 & \text{if } i \neq 0 \end{cases}$$

defines $\binom{N}{n}$. Because each term in the summation satisfies this recursion, the sum as a whole does too:

$$\begin{aligned} \sum_{j=k}^{N-n+k} \binom{j-1}{k-1} \binom{N-j}{n-k} &= \sum_{j=k}^{N-n+k} \binom{j-1}{k-1} \binom{N-j-1}{n-k} \\ &\quad + \sum_{j=k}^{N-n+k} \binom{j-1}{k-1} \binom{N-j-1}{n-k-1} \end{aligned}$$

or, written in a shorter way

$$S_k(N, n) = S_k(N-1, n) + S_k(N-1, n-1)$$

With the observation that $S_1(N, 1) = N \forall N > 0$, this initializes the same recursion that defines $\binom{N}{n}$, and therefore $S(N, n) = \binom{N}{n}$. \square

Gokhale and Traulsen (2010) use the same identity, but provide a longer derivation (see pages 3 and 4 of their Supporting Information).

A.1. Well mixed population, exponential fitness

We assume that interactions as well as replacements occur on full graphs (Ohtsuki et al., 2007a,b). With birth–death updating, an individual is selected for reproduction at random, but proportional to its fitness, and another individual is chosen at random for death. With j individuals that play strategy A in a population of size N , the number of A -players increases from j to $j+1$ if an A -player is selected for reproduction and a B -player dies, which happens with probability T_j^+ , where

$$T_j^+ = \frac{j e^{w\pi_{A,j}}}{j e^{w\pi_{A,j}} + (N-j) e^{w\pi_{B,N-j}}} \frac{N-j}{N}$$

and

$$\pi_{A,j} = \sum_{k=\max\{1, n-N+j\}}^{\min\{n, j\}} \binom{j-1}{k-1} \binom{N-j}{n-k} P_k$$

$$\pi_{B,N-j} = \sum_{k=\max\{1, n-j\}}^{\min\{n, N-j\}} \binom{N-j-1}{k-1} \binom{j}{n-k} Q_k$$

Similarly the number of A -players decreases from j to $j-1$ with probability T_j^- , where

$$T_j^- = \frac{(N-j) e^{w\pi_{B,N-j}}}{j e^{w\pi_{A,j}} + (N-j) e^{w\pi_{B,N-j}}} \frac{j}{N}$$

This defines the Moran process, in which the “up/down ratios” are as follows.

$$\frac{T_j^+}{T_j^-} = \frac{\exp\left(w \sum_{k=\max\{1, n-N+j\}}^{\min\{n, j\}} \binom{j-1}{k-1} \binom{N-j}{n-k} P_k\right)}{\exp\left(w \sum_{k=\max\{1, n-j\}}^{\min\{n, N-j\}} \binom{N-j-1}{k-1} \binom{j}{n-k} Q_k\right)}$$

With death–birth updating on the full graph, the up/down ratios are the same; conditional on not being chosen for elimination, the probability of being chosen for reproduction depends on an individuals total payoff in the same way, and the probability of not being chosen is $N-1$ for all.

For BD as well as DB we therefore have

$$\prod_{j=1}^{N-1} \frac{T_j^+}{T_j^-} = \exp w \sum_{j=1}^{N-1} \left(\sum_{k=\max\{1, n-N+j\}}^{\min\{n, j\}} \binom{j-1}{k-1} \binom{N-j}{n-k} P_k - \sum_{k=\max\{1, n-j\}}^{\min\{n, N-j\}} \binom{N-j-1}{k-1} \binom{j}{n-k} Q_k \right) \quad (A.1)$$

Proposition 2 (Gokhale and Traulsen, 2010). For any intensity of selection $w \in (0, \infty)$, and exponential fitness, $\prod_{j=1}^{N-1} T_j^+ / T_j^- > 1$ (and hence $\rho_A > \rho_B$) if and only if $\sum_{i=1}^{n-1} NP_i + (N-n)P_n > \sum_{i=1}^{n-1} NQ_i + (N-n)Q_n$.

Proof. First we rewrite the term with the payoffs for cooperators by changing the summation order and using Lemma 1. In order to properly apply that identity, note that the only term missing in the second summation on the second line below is the one for $j = k = n$.

$$\begin{aligned} \sum_{j=1}^{N-1} \sum_{k=\max\{1, n-N+j\}}^{\min\{n, j\}} \binom{j-1}{k-1} \binom{N-j}{n-k} P_k &= \sum_{k=1}^n P_k \sum_{j=k}^{\min\{N-n+k, N-1\}} \binom{j-1}{k-1} \binom{N-j}{n-k} \\ &= \binom{N}{n} \sum_{k=1}^n P_k - \binom{N-1}{n-1} P_n \end{aligned}$$

In a similar way we find

$$\sum_{j=1}^{N-1} \sum_{k=\max\{1, n-j\}}^{\min\{n, N-j\}} \binom{N-j-1}{k-1} \binom{j}{n-k} Q_k = \binom{N}{n} \sum_{k=1}^n Q_k - \binom{N-1}{n-1} Q_n$$

This implies that

$$\begin{aligned} \prod_{j=1}^{N-1} \frac{T_j^+}{T_j^-} > 1 \text{ if and only if} \\ \binom{N}{n} \sum_{k=1}^n P_k - \binom{N-1}{n-1} P_n > \binom{N}{n} \sum_{k=1}^n Q_k - \binom{N-1}{n-1} Q_n \\ \Leftrightarrow \binom{N}{n} \sum_{k=1}^{n-1} P_k + \binom{N-1}{n} P_n > \binom{N}{n} \sum_{k=1}^{n-1} Q_k + \binom{N-1}{n} Q_n \\ \Leftrightarrow \sum_{i=1}^{n-1} NP_i + (N-n)P_n > \sum_{i=1}^{n-1} NQ_i + (N-n)Q_n. \quad \square \end{aligned}$$

Here we have used every individual’s total payoff. In the well-mixed population, the total payoff of all individuals depends on N , and goes to infinity if N does. This can be perceived as unnatural, and therefore it is worth noticing that if we would take average payoffs, as Gokhale and Traulsen (2010) do, all payoffs would be

divided by $\binom{N-1}{n-1}$, which is the number of interactions. This would leave all results unchanged, as they cancel out, and only have an effect on the effective intensity of selection.

A.2. Well mixed population, linear fitness

With linear fitness, the “up/down ratios” for DB as well as BD are as follows:

$$\frac{T_j^+}{T_j^-} = \frac{1-w+w \sum_{k=\max\{1, n-N+j\}}^{\min\{n, j\}} \binom{j-1}{k-1} \binom{N-j}{n-k} P_k}{1-w+w \sum_{k=\max\{1, n-j\}}^{\min\{n, N-j\}} \binom{N-j-1}{k-1} \binom{j}{n-k} Q_k}$$

In the limit of weak selection,

$$\begin{aligned} \prod_{j=1}^{N-1} \frac{T_j^+}{T_j^-} &= 1 + w \sum_{j=1}^{N-1} \left(\sum_{k=\max\{1, n-N+j\}}^{\min\{n, j\}} \binom{j-1}{k-1} \binom{N-j}{n-k} P_k - \sum_{k=\max\{1, n-j\}}^{\min\{n, N-j\}} \binom{N-j-1}{k-1} \binom{j}{n-k} Q_k \right) \quad (A.2) \end{aligned}$$

With this ratio of fixation probabilities, we can repeat the argument from Proposition 2 for linear fitness. Note that the same argument applies to a range of update processes, and ways to go from payoff to fitness, that give the same criterion in the limit of weak selection (Gokhale and Traulsen, 2010)

Proposition 3 (Kurokawa and Ihara, 2009). For $w \downarrow 0$ and linear fitness

$$\prod_{j=1}^{N-1} \frac{T_j^+}{T_j^-} > 1 \text{ (and hence } \rho_A > \rho_B \text{) if and only if} \\ \sum_{i=1}^{n-1} NP_i + (N-n)P_n > \sum_{i=1}^{n-1} NQ_i + (N-n)Q_n.$$

Proof. See Proposition 2. \square

Appendix B. Payoffs on the cycle

On the cycle, only draws on the border between A-players and B-players can affect the state of the population, both for BD and for DB updating (see for instance Ohtsuki and Nowak, 2006). The relevant payoffs on the border are given below.

If the number of A-players is 1:

$$\begin{aligned} A & nP_1 \\ B & (n-1)Q_{n-1} + Q_n \\ B & (n-2)Q_{n-1} + 2Q_n \\ \dots & \dots \end{aligned}$$

If the number of A-players is 2:

$$\begin{aligned} A & (n-1)P_2 + P_1 \\ A & (n-1)P_2 + P_1 \\ B & (n-2)Q_{n-2} + \sum_{i=0}^1 Q_{n-i} \\ B & (n-3)Q_{n-2} + \sum_{i=0}^1 Q_{n-i} + Q_n \\ \dots & \dots \end{aligned}$$

If the number of A-players is j , with $3 \leq j \leq n-1$:

$$\begin{array}{l}
 \dots \\
 A \quad (n-j)P_j + P_{j-1} + \sum_{i=2}^j P_i \\
 A \quad (n-j)P_j + \sum_{i=1}^j P_i \\
 B \quad (n-j)Q_{n-j} + \sum_{i=0}^{j-1} Q_{n-i} \\
 B \quad (n-(j+1))Q_{n-j} + Q_n + \sum_{i=0}^{j-1} Q_{n-i} \\
 \dots
 \end{array}$$

If the number of A-players is j , with $n \leq j \leq N-n$:

$$\begin{array}{l}
 \dots \\
 A \quad \sum_{i=2}^n P_i + P_n \\
 A \quad \sum_{i=1}^n P_i \\
 B \quad \sum_{i=1}^n Q_i \\
 B \quad \sum_{i=2}^n Q_i + Q_n \\
 \dots
 \end{array}$$

If the number of A-players is j , with $N-n+1 \leq j \leq N-3$:

$$\begin{array}{l}
 \dots \\
 B \quad (n-(N-j))Q_{N-j} + Q_{N-j-1} + \sum_{i=2}^{N-j} Q_i \\
 B \quad (n-(N-j))Q_{N-j} + \sum_{i=1}^{N-j} Q_i \\
 A \quad (n-(N-j))P_{n-(N-j)} + \sum_{i=0}^{N-j-1} P_{n-i} \\
 A \quad (n-((N-j)+1))P_{n-(N-j)} + P_n + \sum_{i=0}^{N-j-1} P_{n-i} \\
 \dots
 \end{array}$$

If the number of A-players is $N-2$:

$$\begin{array}{l}
 B \quad (n-1)Q_2 + Q_1 \\
 B \quad (n-1)Q_2 + Q_1 \\
 A \quad (n-2)P_{n-2} + \sum_{i=0}^1 P_{n-i} \\
 A \quad (n-3)P_{n-2} + \sum_{i=0}^1 P_{n-i} + P_n \\
 \dots
 \end{array}$$

If the number of A-players is $N-1$

$$\begin{array}{l}
 B \quad nQ_1 \\
 A \quad (n-1)P_{n-1} + P_n \\
 A \quad (n-2)P_{n-1} + 2P_n \\
 \dots
 \end{array}$$

Appendix C. Results for n -player games on the cycle

C.1. Birth-death updating, exponential fitness

With exponential fitness and for $w \in (0, \infty)$, the “up/down ratio” (see Ohtsuki and Nowak, 2006) is given by

$$\frac{T_j^+}{T_j^-} = \begin{cases} \frac{e^{w((n-j)P_j + \sum_{i=1}^j P_i)}}{e^{w((n-j)Q_{n-j} + \sum_{i=0}^{j-1} Q_{n-i})}}, & 1 \leq j \leq n-1 \\ e^{w(\sum_{i=1}^n P_i)} / e^{w(\sum_{i=1}^n Q_i)}, & n \leq j \leq N-n \\ \frac{e^{w((n-(N-j))P_{n-(N-j)} + \sum_{i=0}^{N-j-1} P_{n-i})}}{e^{w((n-(N-j))Q_{N-j} + \sum_{i=1}^{N-j} Q_i)}}, & N-n+1 \leq j \leq N-1 \end{cases}$$

Hence

$$\prod_{j=1}^{N-1} \frac{T_j^+}{T_j^-} = \left(\prod_{j=1}^{n-1} \frac{e^{w((n-j)P_j + \sum_{i=1}^j P_i)}}{e^{w((n-j)Q_{n-j} + \sum_{i=0}^{j-1} Q_{n-i})}} \right) \left(\frac{e^{w(\sum_{i=1}^n P_i)}}{e^{w(\sum_{i=1}^n Q_i)}} \right)^{N-2n+1} \times \left(\prod_{j=N-n+1}^{N-1} \frac{e^{w((n-(N-j))P_{n-(N-j)} + \sum_{i=0}^{N-j-1} P_{n-i})}}{e^{w((n-(N-j))Q_{N-j} + \sum_{i=1}^{N-j} Q_i)}} \right) \quad (C.1)$$

It is easy to see that for any $w > 0$, the condition for the fixation probability of A-players ρ_A to be larger than the fixation probability of B-players ρ_B is $\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$, in the following sense.

Proposition 4. For any intensity of selection $w \in (0, \infty)$, and with exponential fitness, if $\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$ then there is a population size \bar{N} such that $\prod_{j=1}^{N-1} T_j^+ / T_j^- > 1$ (and hence $\rho_A > \rho_B$) for all $N > \bar{N}$ and if $\sum_{i=1}^n P_i < \sum_{i=1}^n Q_i$ then there is a population size \bar{N} such that $\prod_{j=1}^{N-1} T_j^+ / T_j^- < 1$ (and hence $\rho_A < \rho_B$) for all $N > \bar{N}$.

Proof. This is a straightforward result from the observation that the first and the last term in (C.1) are larger than 0 and independent of N . For any $w \in (0, \infty]$, $\exp(w \sum_{i=1}^n P_i) / \exp(w \sum_{i=1}^n Q_i) > 1$ if and only if $\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$. \square

C.2. Birth-death updating, linear fitness

Provided that $w \in (0, 1/(1-P_{\min}))$, which implies that T_j^+ and T_j^- are larger than 0 for all j , the “up/down ratio” is given by

$$\frac{T_j^+}{T_j^-} = \begin{cases} \frac{1-w+w((n-j)P_j + \sum_{i=1}^j P_i)}{1-w+w((n-j)Q_{n-j} + \sum_{i=0}^{j-1} Q_{n-i})}, & 1 \leq j \leq n-1 \\ \frac{1-w+w(\sum_{i=1}^n P_i)}{1-w+w(\sum_{i=1}^n Q_i)}, & n \leq j \leq N-n \\ \frac{1-w+w((n-(N-j))P_{n-(N-j)} + \sum_{i=0}^{N-j-1} P_{n-i})}{1-w+w((n-(N-j))Q_{N-j} + \sum_{i=1}^{N-j} Q_i)}, & N-n+1 \leq j \leq N-1 \end{cases}$$

Hence

$$\prod_{j=1}^{N-1} \frac{T_j^+}{T_j^-} = \left(\prod_{j=1}^{n-1} \frac{1-w+w((n-j)P_j + \sum_{i=1}^j P_i)}{1-w+w((n-j)Q_{n-j} + \sum_{i=0}^{j-1} Q_{n-i})} \right) \times \left(\frac{1-w+w(\sum_{i=1}^n P_i)}{1-w+w(\sum_{i=1}^n Q_i)} \right)^{N-2n+1} \times \left(\prod_{j=N-n+1}^{N-1} \frac{1-w+w((n-(N-j))P_{n-(N-j)} + \sum_{i=0}^{N-j-1} P_{n-i})}{1-w+w((n-(N-j))Q_{N-j} + \sum_{i=1}^{N-j} Q_i)} \right) \quad (C.2)$$

Now we can show the following:

Proposition 5. For any intensity of selection $w \in (0, 1/(1-P_{\min}))$, and with linear fitness, if $\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$ then there is a

population size \bar{N} such that $\prod_{j=1}^{N-1} T_j^+ / T_j^- > 1$ (and hence $\rho_A > \rho_B$) for all $N > \bar{N}$ and if $\sum_{i=1}^n P_i < \sum_{i=1}^n Q_i$ then there is a population size \bar{N} such that $\prod_{j=1}^{N-1} T_j^+ / T_j^- < 1$ (and hence $\rho_A < \rho_B$) for all $N > \bar{N}$.

Proof. This is a straightforward result from the observation that the first and the last term in (C.2) are larger than 0—since $w \in (0, 1/(1-P_{\min}))$ —and independent of N . For any $w \in (0, 1/(1-P_{\min}))$, $(1-w+w\sum_{i=1}^n P_i)/(1-w+w\sum_{i=1}^n Q_i) > 1$ if and only if $\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$. \square

Note that, in contrast to Ohtsuki and Nowak, we do not use a Taylor expansion to prove this result for n -player games. Using a Taylor expansion, we can, as an intermediate step, show that the condition is

$$N \sum_{i=1}^{n-1} P_i + (N-n)P_n > N \sum_{i=1}^{n-1} Q_i + (N-n)Q_n,$$

and then let N be large compared to n . See also Propositions 2 and 3.

C.3. Death–birth updating, exponential fitness

It is not hard to see that with exponential fitness and DB updating, the first and the last $n+1$ “up/down ratios” are again unaffected by N , if $N > 2n+2$. Therefore we will now in one go focus on the up/down ratio for $n+1 \leq j \leq N-(n+1)$:

$$\begin{aligned} \frac{T_j^+}{T_j^-} &= \frac{e^{w(\sum_{i=1}^n P_i)}}{e^{w(\sum_{i=1}^n P_i) + e^{w(\sum_{i=2}^n Q_i + Q_n)}}} \times \frac{e^{w(\sum_{i=1}^n Q_i)} + e^{w(\sum_{i=2}^n P_i + P_n)}}{e^{w(\sum_{i=1}^n Q_i)}} \\ &= \frac{e^{w(\sum_{i=1}^n P_i + \sum_{i=1}^n Q_i)} + e^{w(\sum_{i=1}^n P_i + \sum_{i=2}^n P_i + P_n)}}{e^{w(\sum_{i=1}^n P_i + \sum_{i=1}^n Q_i)} + e^{w(\sum_{i=2}^n Q_i + Q_n + \sum_{i=1}^n Q_i)}} \end{aligned}$$

Hence

$$\begin{aligned} \prod_{j=1}^{N-1} \frac{T_j^+}{T_j^-} &= \left(\prod_{i=1}^{n-1} \frac{\lambda_i}{\mu_i} \right) \\ &\times \left(\frac{e^{w(\sum_{i=1}^n P_i + \sum_{i=1}^n Q_i)} + e^{w(\sum_{i=1}^n P_i + \sum_{i=2}^n P_i + P_n)}}{e^{w(\sum_{i=1}^n P_i + \sum_{i=1}^n Q_i)} + e^{w(\sum_{i=2}^n Q_i + Q_n + \sum_{i=1}^n Q_i)}} \right)^{N-2n+1} \\ &\times \left(\prod_{i=N-n+1}^{N-1} \frac{\lambda_i}{\mu_i} \right) \end{aligned} \tag{C.3}$$

Proposition 6. For any intensity of selection $w \in (0, \infty)$, and exponential fitness, if $(P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n) > 0$ then there is a population size \bar{N} such that $\prod_{i=1}^{N-1} \lambda_i / \mu_i > 1$ for all $N > \bar{N}$ and if $(P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n) < 0$ then there is a population size \bar{N} such that $\prod_{i=1}^{N-1} \lambda_i / \mu_i < 1$ for all $N > \bar{N}$.

Proof. This is a straightforward result from the observation that the first and the last term in (C.3) are larger than 0 (since we are using exponential fitness) and independent of N (easy to verify). For any $w \in (0, \infty)$,

$$\begin{aligned} &\frac{e^{w(\sum_{i=1}^n P_i + \sum_{i=1}^n Q_i)} + e^{w(\sum_{i=1}^n P_i + \sum_{i=2}^n P_i + P_n)}}{e^{w(\sum_{i=1}^n P_i + \sum_{i=1}^n Q_i)} + e^{w(\sum_{i=2}^n Q_i + Q_n + \sum_{i=1}^n Q_i)}} > 1 \\ &\Leftrightarrow \frac{e^{w(\sum_{i=1}^n P_i + \sum_{i=2}^n P_i + P_n)}}{e^{w(\sum_{i=2}^n Q_i + Q_n + \sum_{i=1}^n Q_i)}} > 1 \\ &\Leftrightarrow \sum_{i=1}^n P_i + \sum_{i=2}^n P_i + P_n > \sum_{i=2}^n Q_i + Q_n + \sum_{i=1}^n Q_i \end{aligned}$$

$$\Leftrightarrow (P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n) > 0 \quad \square$$

C.4. Death–birth updating, linear fitness

It is not hard to see that with linear fitness and DB updating, the first and the last $n+1$ “up/down ratios” are again unaffected by N , if $N > 2n+2$. Therefore we will in one go focus on the up/down ratio for $n \leq j \leq N-n$. Provided that $w \in (0, 1/(1-P_{\min}))$, which implies that T_j^+ and T_j^- are larger than 0 for all j , the “up/down ratio” is given by

$$\begin{aligned} \frac{T_j^+}{T_j^-} &= \frac{1-w+w(\sum_{i=1}^n P_i)}{2-2w+w(\sum_{i=1}^n P_i + \sum_{i=2}^n Q_i + Q_n)} \\ &\times \frac{2-2w+w(\sum_{i=1}^n Q_i + \sum_{i=2}^n P_i + P_n)}{1-w+w(\sum_{i=1}^n Q_i)} \end{aligned}$$

This gives us

$$\begin{aligned} \prod_{j=1}^{N-1} \frac{T_j^+}{T_j^-} &= \left(\prod_{i=1}^{n-1} \frac{\lambda_i}{\mu_i} \right) \left(\frac{1-w+w(\sum_{i=1}^n P_i)}{2-2w+w(\sum_{i=1}^n P_i + \sum_{i=2}^n Q_i + Q_n)} \right. \\ &\times \left. \frac{2-2w+w(\sum_{i=1}^n Q_i + \sum_{i=2}^n P_i + P_n)}{1-w+w(\sum_{i=1}^n Q_i)} \right)^{N-2n+1} \\ &\times \left(\prod_{i=N-n+1}^{N-1} \frac{\lambda_i}{\mu_i} \right) \end{aligned} \tag{C.4}$$

In this case we find that the condition is not independent of the intensity of selection; it is a convex combination of two conditions; for intensity of selection $w \in (0, 1/(1-P_{\min}))$, the condition is

$$C_w = (1-w)C_0 + wC_1 > 0$$

in which

$$C_0 = (P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n)$$

and

$$C_1 = \sum_{i=1}^n P_i \left(\sum_{i=2}^n P_i + P_n \right) - \sum_{i=1}^n Q_i \left(\sum_{i=2}^n Q_i + Q_n \right)$$

Proposition 7. For intensity of selection $w \in (0, 1/(1-P_{\min}))$, and with linear fitness, if $C_w > 0$ then there is a population size \bar{N} such that $\prod_{j=1}^{N-1} T_j^+ / T_j^- > 1$ for all $N > \bar{N}$ and if $C_w < 0$ then there is a population size \bar{N} such that $\prod_{j=1}^{N-1} T_j^+ / T_j^- < 1$ for all $N > \bar{N}$.

Proof. This is a slightly less straightforward result from the observation that the first and the last term in (C.4) are larger than 0—since $w \in (0, 1/(1-P_{\min}))$ —and independent of N (easy to verify).

If we write

$$A = \sum_{i=1}^n P_i$$

$$B = \sum_{i=1}^n Q_i$$

$$C = \sum_{i=2}^n P_i + P_n$$

and

$$D = \sum_{i=2}^n Q_i + Q_n$$

then we can write

$$\frac{1-w+w(\sum_{i=1}^n P_i)}{2-2w+w(\sum_{i=1}^n P_i + \sum_{i=2}^n Q_i + Q_n)} \times \frac{2-2w+w(\sum_{i=1}^n Q_i + \sum_{i=2}^n P_i + P_n)}{1-w+w(\sum_{i=1}^n Q_i)}$$

as

$$\frac{1-w+wA}{2-2w+w(A+D)} \frac{2-2w+w(C+B)}{1-w+wB}$$

The condition then becomes

$$\frac{1-w+wA}{2-2w+w(A+D)} \frac{2-2w+w(C+B)}{1-w+wB} > 1 \Leftrightarrow$$

$$(1+w(A-1))(2+w(C+B-2)) > (1+w(B-1))(2+w(A+D-2)) \Leftrightarrow$$

$$2+w(2A+C+B-4)+w^2(A-1)(C+B-2) > 2+w(2B+A+D-4)+w^2(B-1)(A+D-2) \Leftrightarrow$$

$$w(2A+C+B)+w^2(A-1)(C+B-2) > w(2B+A+D)+w^2(B-1)(A+D-2) \Leftrightarrow$$

$$(2A+C+B)+w(A-1)(C+B-2) > (2B+A+D)+w(B-1)(A+D-2) \Leftrightarrow$$

$$(1-w)(2A+C+B)+wA(C+B) > (1-w)(2B+A+D)+wB(A+D) \Leftrightarrow$$

$$(1-w)(A+C-B-D)+w(AC-BD) > 0$$

This gives us $(1-w)C_0 + wC_1 > 0$. \square

Note that the limit of weak selection ($w \downarrow 0$) always exists and returns the first condition. On the other hand, $1/(1-P_{\min})$ may be smaller than 1. If that is the case, in the limit of the largest w that has a well defined dynamics ($w \uparrow 1/(1-P_{\min})$) it does not have to be the case that $C_1 > 0$.

On the cycle, the number of interactions does not depend on N and therefore remains constant, even if N goes to infinity. Still, we can replace total fitness by average fitness here as well. Again, that would be inconsequential for the results. This can be seen easily, because changing to average fitness would imply that we should divide total payoffs by n , which would be equivalent to taking $\bar{P}_i = (1/n)P_i$ and $\bar{Q}_i = (1/n)Q_i$ instead of P_i and Q_i for all i in all of the results above, although that of course rescales the intensity of selection.

With linear fitness, where there is a maximum to the strength of selection, this implies that $\bar{w}_{\max} = 1/(1-\bar{P}_{\min}) = n/(n-P_{\min})$. This implies that also in the limit of the largest w that has a well defined dynamics, the condition remains the same; with obvious definitions for \bar{C}_0 and \bar{C}_1 , a bit of algebra shows that $(1-\bar{w}_{\max})\bar{C}_0 + \bar{w}_{\max}\bar{C}_1 > 0$ is equivalent to $(1-w_{\max})C_0 + w_{\max}C_1 > 0$:

$$\begin{aligned} (1-\bar{w}_{\max})\bar{C}_0 + \bar{w}_{\max}\bar{C}_1 > 0 \\ \Leftrightarrow \left(1 - \frac{n}{n-P_{\min}}\right) \frac{1}{n} C_0 + \frac{n}{n-P_{\min}} \frac{1}{n^2} C_1 > 0 \\ \Leftrightarrow -P_{\min} \frac{1}{n} C_0 + \frac{1}{n^2} C_1 > 0 \\ \Leftrightarrow -nP_{\min} C_0 + C_1 > 0 \end{aligned}$$

$$\begin{aligned} \Leftrightarrow \left(1 - \frac{1}{1-nP_{\min}}\right) C_0 + \frac{1}{1-P_{\min}} C_1 > 0 \\ \Leftrightarrow (1-w_{\max})C_0 + w_{\max}C_1 > 0 \end{aligned}$$

Appendix D. Examples

D.1. The n -player linear public goods game

The payoff function for the n -player linear public goods game is

$$P_i = \frac{i-1}{n-1} b - c$$

$$Q_i = \frac{n-i}{n-1} b$$

With this payoff function we find that the two relevant sums return relatively simple values:

$$\sum_{i=1}^n P_i = \sum_{i=1}^n \left(\frac{i-1}{n-1} b - c\right) = \frac{1}{2} nb - nc$$

$$\sum_{i=1}^n Q_i = \sum_{i=1}^n \frac{n-i}{n-1} b = \frac{1}{2} nb$$

Condition 2 for the n -player public goods game then reads

$$\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$$

$$\frac{1}{2} nb - nc > \frac{1}{2} nb$$

$$-nc > 0$$

Condition (4) for the n -player public goods game is

$$(P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n) > 0$$

$$(-c-b) + 2 \sum_{i=2}^{n-1} \left(\frac{i-1}{n-1} b - c - \frac{n-i}{n-1} b\right) + 3(b-c) > 0$$

$$-c-b-2 \sum_{i=2}^{n-1} c + 3(b-c) > 0$$

$$2(b-cn) > 0$$

Thereby we also obtain $C_0 = 2(b-cn)$ in Proposition 7.

For C_1 we obtain

$$\begin{aligned} C_1 &= \sum_{i=1}^n P_i \left(\sum_{i=2}^n P_i + P_n\right) - \sum_{i=1}^n Q_i \left(\sum_{i=2}^n Q_i + Q_n\right) \\ &= \left(\frac{1}{2} nb - nc\right) \left(\left(\frac{1}{2} n + 1\right) b - nc\right) - \left(\frac{1}{2} nb\right) \left(\left(\frac{1}{2} n - 1\right) b\right) \\ &= n \left\{ \left(\frac{1}{2} b - c\right) \left(\left(\frac{1}{2} n + 1\right) b - nc\right) - \frac{1}{2} b(n-2) \frac{1}{2} b \right\} \\ &= n \left\{ \frac{1}{2} b^2 \left(\frac{1}{2} n + 1\right) - cb(n+1) + c^2 n - \frac{1}{4} b^2 (n-2) \right\} \\ &= n \{ b^2 - bc(n+1) + c^2 n \} \\ &= n(b-cn)(b-c) \end{aligned}$$

Substituting these values for C_0 and C_1 we get selection for cooperation in n -player public goods game for intensities of

selection $w \in (0, 1/(1+nc))$ if
 $(1-w)2(b-cn) + wn(b-cn)(b-c) > 0$

or

$$(b-cn)((1-w)2 + wn(b-c)) > 0$$

Provided that $b > c$, this is equivalent to $b > cn$.

D.2. The n -player stag hunt game

The payoff function for the n -player stag hunt game is

$$P_i = \begin{cases} -c, & i \neq n \\ b-c, & i = n \end{cases}$$

$$Q_i = 0$$

With this payoff function we find that the two relevant sums return relatively simple values:

$$\sum_{i=1}^n P_i = b-nc$$

$$\sum_{i=1}^n Q_i = 0$$

Condition (A.2) for the n -player stag hunt game then reads

$$\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$$

$$b-nc > 0$$

Condition (4) for the n -player stag hunt game is

$$(P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n) > 0$$

$$-c + 2 \sum_{i=2}^{n-1} (-c) + 3(b-c) > 0$$

$$3b - 2nc > 0$$

Thereby we also obtain $C_0 = 3b - 2nc$ in Proposition 7.

For C_1 we get

$$C_1 = \sum_{i=1}^n P_i \left(\sum_{i=2}^n P_i + P_n \right) - \sum_{i=1}^n Q_i \left(\sum_{i=2}^n Q_i + Q_n \right) \\ = (b-nc)(2b-nc)$$

Substituting these values for C_0 and C_1 we get selection for cooperation in n -player stag hunt game for intensities of selection $w \in (0, 1/(1+nc))$ if

$$(1-w)(3b-2nc) + w(b-nc)(2b-nc) > 0$$

In the limit of weak selection ($w \downarrow 0$), this condition then becomes

$$b > \frac{2}{3}nc$$

Approaching the largest possible intensity of selection ($w \uparrow 1/(1+nc)$), this condition then becomes

$$\left(1 - \frac{1}{1+nc} \right) (3b-2nc) + \frac{1}{1+nc} (b-nc)(2b-nc) > 0$$

$$nc(3b-2nc) + (b-nc)(2b-nc) > 0$$

$$2b^2 > c^2n^2$$

$$b > \frac{1}{2}\sqrt{2}cn$$

D.3. n -Player snowdrift games

The payoff function for n -player snowdrift games is

$$P_i = b-c$$

$$Q_i = \begin{cases} b, & i \neq n \\ 0, & i = n \end{cases}$$

With this payoff function we find that the two relevant sums return relatively simple values:

$$\sum_{i=1}^n P_i = n(b-c)$$

$$\sum_{i=1}^n Q_i = (n-1)b$$

Condition (2) for n -player snowdrift games then reads

$$\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$$

$$n(b-c) > (n-1)b$$

$$b > nc$$

Condition (4) for n -player snowdrift games is

$$(P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n) > 0$$

$$(b-c-b) + 2 \sum_{i=2}^{n-1} (b-c-b) + 3(b-c) > 0$$

$$3b - 2nc > 0$$

Thereby we also obtain $C_0 = 3b - 2nc$ in Proposition 7.

For C_1 we get

$$C_1 = \sum_{i=1}^n P_i \left(\sum_{i=2}^n P_i + P_n \right) - \sum_{i=1}^n Q_i \left(\sum_{i=2}^n Q_i + Q_n \right) \\ = n^2(b-c)^2 - (n-1)b(n-2)b \\ = b^2(3n-2) - 2bcn^2 + c^2n^2 \\ = \left(b-cn \frac{n + \sqrt{(n-1)(n-2)}}{3n-2} \right) \left(b-cn \frac{n - \sqrt{(n-1)(n-2)}}{3n-2} \right)$$

Substituting these values for C_0 and C_1 we get selection for cooperation in n -player snowdrift games for intensities of selection $w \in (0, 1)$:

$$(1-w)(3b-2nc) + w(b^2(3n-2) - 2bcn^2 + c^2n^2) > 0$$

In the limit of weak selection ($w \downarrow 0$), this condition then becomes

$$b > \frac{2}{3}nc$$

Approaching the largest possible intensity of selection ($w \uparrow 1$), this condition then becomes

$$\left(b-cn \frac{n + \sqrt{(n-1)(n-2)}}{3n-2} \right) \left(b-cn \frac{n - \sqrt{(n-1)(n-2)}}{3n-2} \right) > 0$$

With $b > c$, and knowing that $0 < (n - \sqrt{(n-1)(n-2)}) / (3n-2) < 1/n$, this is equivalent to

$$b > \frac{n^2 + n\sqrt{(n-1)(n-2)}}{3n-2} c$$

D.4. n-Player games with non-linear production of a public good

The payoff function for this more general set of n-player games is

$$P_i = \left(\frac{i}{n}\right)^\alpha b - c$$

$$Q_i = \left(\frac{n-i}{n}\right)^\alpha b$$

With this payoff function, the two relevant sums return somewhat less simple values than the less general examples:

$$\sum_{i=1}^n P_i = \sum_{i=1}^n \left(\frac{i}{n}\right)^\alpha b - nc$$

$$\sum_{i=1}^n Q_i = \sum_{i=1}^n \left(\frac{n-i}{n}\right)^\alpha b = \sum_{i=0}^{n-1} \left(\frac{i}{n}\right)^\alpha b$$

Condition (2) for this n-player game then reads

$$\sum_{i=1}^n P_i > \sum_{i=1}^n Q_i$$

$$\sum_{i=1}^n \left(\frac{i}{n}\right)^\alpha b - nc > \sum_{i=0}^{n-1} \left(\frac{i}{n}\right)^\alpha b$$

$$b - nc > 0$$

This implies that the condition for cooperation to evolve in large, well mixed population and any intensity of selection does not depend on α .

Condition (4) is

$$(P_1 - Q_1) + 2 \sum_{i=2}^{n-1} (P_i - Q_i) + 3(P_n - Q_n) > 0$$

$$\left(\frac{1}{n}\right)^\alpha b - c - \left(\frac{n-1}{n}\right)^\alpha b + 2 \sum_{i=2}^{n-1} \left(\left(\frac{i}{n}\right)^\alpha b - c\right) - 2 \sum_{i=2}^{n-1} \left(\frac{n-i}{n}\right)^\alpha b + 3(b-c) > 0$$

$$\left(\frac{n-1}{n}\right)^\alpha b - \left(\frac{1}{n}\right)^\alpha b + 3b - 2nc > 0$$

This implies that for exponential fitness and any selection, as well as linear fitness and weak selection, $\rho_C > \rho_D$ for large populations if and only if

$$\frac{b}{c} > \frac{2n}{3 + \left(\frac{n-1}{n}\right)^\alpha - \left(\frac{1}{n}\right)^\alpha}$$

Both for $\alpha \downarrow 0$ and for $\alpha \rightarrow \infty$ that reduces to $b/c > \frac{2}{3}n$. For $\alpha = 1$ this equals $n^2 / (2n-1)$.

With condition (4) we also obtain $C_0 = ((n-1)/n)^\alpha b - (1/n)^\alpha b + 3b - 2nc$ in Proposition 7. For C_1 we get

$$\begin{aligned} C_1 &= \sum_{i=1}^n \left(\left(\frac{i}{n}\right)^\alpha b - c\right) \left(\sum_{i=2}^n \left(\left(\frac{i}{n}\right)^\alpha b - c\right) + b - c\right) \\ &\quad - \sum_{i=1}^n \left(\frac{n-i}{n}\right)^\alpha b \left(\sum_{i=2}^n \left(\frac{n-i}{n}\right)^\alpha b\right) \\ &= \left(\sum_{i=1}^n \left(\frac{i}{n}\right)^\alpha b - nc\right) \left(\sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha b + b - nc\right) \end{aligned}$$

$$\begin{aligned} & - \sum_{i=1}^{n-1} \left(\frac{i}{n}\right)^\alpha b \left(\sum_{i=1}^{n-2} \left(\frac{i}{n}\right)^\alpha b\right) \\ &= n^2 c^2 - \left(\sum_{i=1}^n \left(\frac{i}{n}\right)^\alpha b + \sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha b + b\right) nc \\ &\quad + \left(\sum_{i=1}^n \left(\frac{i}{n}\right)^\alpha \sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha - \sum_{i=1}^{n-1} \left(\frac{i}{n}\right)^\alpha \sum_{i=1}^{n-2} \left(\frac{i}{n}\right)^\alpha\right) b^2 \\ &= n^2 c^2 - \left(2 \sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha + \left(\frac{1}{n}\right)^\alpha + 1\right) bnc \\ &\quad + \left(\sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha + \frac{(n-1)^\alpha + (n-2)^\alpha}{n^\alpha} \sum_{i=1}^{n-1} \left(\frac{i}{n}\right)^\alpha\right) b^2 \end{aligned}$$

Substituting these values for C_0 and C_1 we get selection for cooperation in n-player games with non-linear production of a public good for intensities of selection $w \in (0, 1)$ if

$$(1-w) \left(\frac{3n^\alpha + (n-1)^\alpha - 1}{n^\alpha} b - 2nc\right) + w \left(\begin{aligned} & n^2 c^2 \\ & - \left(2 \sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha + \left(\frac{1}{n}\right)^\alpha + 1\right) bnc \\ & + \left(\sum_{i=2}^n \left(\frac{i}{n}\right)^\alpha + \frac{(n-1)^\alpha + (n-2)^\alpha}{n^\alpha} \sum_{i=1}^{n-1} \left(\frac{i}{n}\right)^\alpha\right) b^2 \end{aligned}\right) > 0.$$

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