Evolutionary game dynamics with non-uniform interaction rates

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Abstract

The classical setting of evolutionary game theory, the replicator equation, assumes uniform interaction rates. The rate at which individuals meet and interact is independent of their strategies. Here we extend this framework by allowing the interaction rates to depend on the strategies. This extension leads to non-linear fitness functions. We show that a strict Nash equilibrium remains uninvadable for non-uniform interaction rates, but the conditions for evolutionary stability need to be modified. We analyze all games between two strategies. If the two strategies coexist or exclude each other, then the evolutionary dynamics do not change qualitatively, only the location of the equilibrium point changes. If, however, one strategy dominates the other in the classical setting, then the introduction of non-uniform interaction rates can lead to a pair of interior equilibria. For the Prisoner's Dilemma, non-uniform interaction rates allow the coexistence between cooperators and defectors. For the snowdrift game, non-uniform interaction rates change the equilibrium frequency of cooperators.
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1. Introduction: replicator equation with uniform interaction rates

Consider a two strategy game with payoff matrix

	A	B
A	a	b
B	c	d

Strategy A receives payoffs a and b when playing against strategy A and B, respectively. Strategy B receives payoffs c and d when playing against A and B, respectively. We denote by x and y the frequency of individuals adopting strategy A and B, respectively. We have $x + y = 1$.

With uniform interaction rates, where players interact with each other indiscriminantly, the selection dynamics can be described by the standard replicator equation (Taylor and Jonker, 1978; Hofbauer et al., 1979; Hofbauer and Sigmund, 1998, 2003):

$$\dot{x} = x(f_A - \phi)$$
$$\dot{y} = y(f_B - \phi). \tag{1}$$

The fitness of A and B players are linear functions of x, given by

$$f_A = ax + by,$$
$$f_B = cx + dy.$$

The average fitness of the population is given by

$$\phi = f_A x + f_B y.$$

The replicator equation assumes that the rate (or probability) of interaction between two players is independent of their strategies.

There are three generic evolutionary outcomes:

(1) *A dominates B*: if $a > c$ and $b > d$, then the entire population will eventually consist of A players. The only stable equilibrium is $x = 1$. A is a strict Nash equilibrium, and therefore an evolutionarily stable

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strategy (ESS), while B is not. We use the notation $A \longleftarrow B$.

(2) A and B co-exist in a stable equilibrium: if $a < c$ and $b > d$, then the interior equilibrium $x = (b - d)/(b + c - a - d)$ is stable. Neither A nor B are Nash equilibria. We use the notation $A \rightarrow \leftarrow B$.

(3) A and B are bi-stable: if $a > c$ and $b < d$, the interior equilibrium $x = (d - b)/(a + d - b - c)$ is unstable. The two boundary points, $x = 0$ and 1 are attracting. A and B are both strict Nash equilibria. We use the notation $A \longleftrightarrow B$. If $a + b > c + d$, then strategy A is risk dominant. It has the larger basin of attraction. If $a > d$, then strategy A is Pareto optimal, i.e. there is no other strategies the two players can employ to have payoff at least as high as a, and at least one player having payoff higher than a.

2. Replicator equation with non-uniform interaction rates

Now suppose that the probability of interaction between two players is not independent of their strategies. Analogous to a chemical reaction, an A player interacts with another A player with reaction rate r_1, an A player and a B player interact with reaction rate r_2, and a B player interacts with another B player with reaction rate r_3.

$$A + A \xrightarrow{r_1} AA,$$
$$A + B \xrightarrow{r_2} AB,$$
$$B + B \xrightarrow{r_3} BB.$$
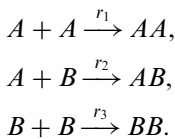
We assume that the fitness of individuals is determined by the average payoff over a large number of interactions. Therefore, the fitness of A and B players are non-linear functions of x and y, given by

$$f_A = \frac{ar_1 x + br_2 y}{r_1 x + r_2 y},$$
$$f_B = \frac{cr_2 x + dr_3 y}{r_2 x + r_3 y}.$$

The rates r_1, r_2 and r_3 are non-negative. The normal replicator equation with uniform interaction rates corresponds to the special case $r_1 = r_2 = r_3 > 0$. If $r_1 > r_2$ and $r_3 > r_2$, then players prefer to interact with their own kind. If, however, $r_1 < r_2$ and $r_3 < r_2$, then mixed interactions (between A and B) are more likely.

2.1. A comparison with kin selection

In the context of kin selection (Hamilton, 1964), games between relatives have been studied in the late 1970s by Grafen (1979), Hines and Maynard Smith (1979), Mirmirani and Oster (1978), Orlove (1978, 1979a,b), and Treisman (1977). The "inclusive fitness" approach simply modifies the original payoff matrix M to

	A	B
A	$(1+r)a$	$b + rc$
B	$c + rb$	$(1+r)d$

where r is the coefficient of relatedness. In this framework, all individuals of the population are assumed to be related equally. The payoff to a player in a pairwise interaction is the sum of his own payoff plus r times the opponent's payoff. Grafen proposed a "personal fitness" approach to account for the fact that an individual is more likely to play an opponent with the same strategy. In Grafen's model,

$$f_A = ra + (1-r)(ax + by), \quad f_B = rd + (1-r)(cx + dy),$$

where r is the probability than a player will meet an opponent with the same strategy because of some genetic or social relationship.

More recently, (Tao and Lessard, 2002) developed the ESS theory for frequency-dependent selection in family-structure populations. In particular, they use the payoff matrix

	A	B
A	$(1+r/2)a$	$b + cr/2$
B	$c + br/2$	$(1+r/2)d$

where r is the probability to interact with a sib, to show the effect of kin selection involving full sibs on ESS conditions.

All these approaches contain linear fitness functions. In contrast, our model is based on non-linear fitness functions and can therefore not be studied by a simple transformation of the payoff matrix. In our model, there will be new dynamical features which are not present in the standard replicator equation.

Queller (1985) used a definition of relatedness which depends on the covariance of the strategies of interacting individuals. Non-uniform interaction rates lead to high covariance of players' strategies, and hence a degree of relatedness in Queller's formulation.

2.2. Invariant transformations

For the standard replicator equation, there exist some useful transformations of the payoff matrix that do not change the evolutionary dynamics. Here we show that some of these transformations can also be used for non-uniform interaction rates.

Consider the equations

$$\dot{x} = x(f_A - \phi),$$
$$\dot{y} = y(f_B - \phi),$$

with $\phi = x f_A + y f_B$ and

$$f_A = \frac{ar_1 x + br_2 y}{r_1 x + r_2 y} \quad \text{and} \quad f_B = \frac{cr_2 x + dr_3 y}{r_2 x + r_3 y}.$$

(1) Adding the same constant to all payoff values, a, b, c and d, does not change the evolutionary dynamics. We have

	A	B
A	$a + f_0$	$b + f_0$
B	$c + f_0$	$d + f_0$

Therefore, we obtain the substitutions

$$f_A \rightarrow f_A + f_0, \quad f_B \rightarrow f_B + f_0, \quad \phi \rightarrow \phi + f_0.$$

The corresponding fitness of A and B players, and hence the average fitness of the population, are all increased by the base fitness f_0. Therefore, the evolutionary outcome and speed remain invariant when background fitness is introduced.

(2) Multiplying all payoff values, a, b, c and d, by the same factor does not change the evolutionary dynamics. We have

	A	B
A	ka	kb
B	kc	kd

Therefore, we have the substitutions

$$f_A \rightarrow k f_A, \quad f_B \rightarrow k f_B, \quad \phi \rightarrow k\phi.$$

The corresponding fitness of A and B players, and hence the average fitness of the population, are all multiplied by k. The evolutionary outcome is still the same, while the evolutionary speed is increased k-fold.

(3) For the replicator equation with uniform interaction rates, it is possible to add arbitrary constants to each column of the payoff matrix

	A	B
A	$a + f_0$	$b + g_0$
B	$c + f_0$	$d + g_0$

We have the substitutions

$$f_A \rightarrow f_A + f_0 + (g_0 - f_0)\frac{r_2 y}{r_1 x + r_2 y},$$

$$f_B \rightarrow f_B + f_0 + (g_0 - f_0)\frac{r_3 y}{r_2 x + r_3 y},$$

$$\phi \rightarrow \phi + f_0 + (g_0 - f_0)\left(\frac{r_2 xy}{r_1 x + r_2 y} + \frac{r_3 y^2}{r_2 x + r_3 y}\right).$$

Hence

$$f_A - \phi \rightarrow f_A - \phi + (g_0 - f_0)xy^2 \frac{r_2^2 - r_1 r_3}{(r_1 x + r_2 y)(r_2 x + r_3 y)},$$

$$f_B - \phi \rightarrow f_B - \phi + (g_2 - f_0)x^2 y \frac{r_2^2 - r_1 r_3}{(r_1 x + r_2 y)(r_2 x + r_3 y)}.$$

This transformation does not change the evolutionary dynamics for uniform interaction rates. For non-uniform interaction rates, however, such transformations will

change the evolutionary dynamics, in general. Only for the specific case, $r_1 r_3 = r_2^2$, the evolutionary dynamics remain invariant.

2.3. Evolutionary stability

When players do not interact with players of the opposite strategy, $r_2 = 0$, then A dominates B if and only if $a > d$, while B dominates A if and only if $a < d$.

With uniform interaction rates, if ε many B players enter a population of $1 - \varepsilon$ many A players, the fitness of A and B players are given by

$$f_A = a(1 - \varepsilon) + b\varepsilon, \quad f_B = c(1 - \varepsilon) + d\varepsilon.$$

A is stable against invasion by B if $f_A > f_B$ for small ε. Hence A is an evolutionary stable strategy (ESS), if

(1) either $a > c$,
(2) or $a = c$ and $b > d$.

The concept of an ESS was introduced by Maynard Smith and Price (1973). With non-uniform interaction rates, if ε many B players enter a population of $1 - \varepsilon$ many A players, the fitness of A and B players are given by

$$f_A = \frac{ar_1(1 - \varepsilon) + br_2\varepsilon}{r_1(1 - \varepsilon) + r_2\varepsilon} \quad \text{and} \quad f_B = \frac{cr_2(1 - \varepsilon) + dr_3\varepsilon}{r_2(1 - \varepsilon) + r_3\varepsilon}.$$

In this case, strategy A is ESS if either

(1) $a > c$, or
(2) $a = c$ and $(b - a)r_2^2 > (d - a)r_1 r_3$.

Therefore, the conditions for evolutionary stability does depend on the interaction rates r_1, r_2, and r_3.

If $a > c$, then A is a strict Nash equilibrium and cannot be invaded by B for any choice of r_1, r_2 and r_3 with $r_1, r_2, r_3 > 0$. Therefore, a strict Nash equilibrium remains uninvadable for non-uniform interaction rates, while the condition for ESS changes.

Consider the following example:

	A	B
A	1	3
B	1	2

For uniform interaction rates, strategy A is ESS and therefore cannot be invaded by B. We have $A \longleftarrow B$. For non-uniform interaction rates, however, if

$$2r_2^2 < r_1 r_3,$$

then B can invade A.

2.4. Evolutionary dynamics

From now on, we consider the case $r_2 > 0$. Without loss of generality, let $r_2 = 1$. We will show that for non-uniform interaction rates, there are four generic outcomes, one of which is entirely new.

Let us introduce the parameters

$$\alpha = r_1 r_3 (a - d) + (b - c),$$
$$\beta = r_1 (a - c),$$
$$\gamma = r_3 (b - d). \tag{2}$$

We list below the evolutionary outcomes of a deterministic two strategy game with non-uniform interaction rates. We will prove these results in the Appendix.

2.5. B dominates A

If $a < c$ and $b < d$, then B dominates A in the normal replicator equation. We have to distinguish two cases:

(1) If $c > a > d > b$ and

$$r_1 r_3 > \left(\frac{\sqrt{(a-b)(c-d)} + \sqrt{(a-c)(b-d)}}{d - a} \right)^2$$

then we have

$$A \rightarrow \cdot \leftarrow \cdot \rightarrow B.$$

The stable interior equilibrium is given by

$$x_1 = \frac{-(\alpha - 2\gamma) + \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}.$$

The unstable interior equilibrium is given by

$$x_2 = \frac{-(\alpha - 2\gamma) - \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}.$$

The bifurcation occurs when

$$r_1 r_3 = \left(\frac{\sqrt{(a-b)(c-d)} + \sqrt{(a-c)(b-d)}}{d - a} \right)^2.$$

As $r_1 r_3$ increases above this threshold, $\alpha^2 - 4\beta\gamma$ increases.

(2) If $d > b > c > a$ and

$$r_1 r_3 < \left(\frac{\sqrt{(a-b)(c-d)} - \sqrt{(a-c)(b-d)}}{d - a} \right)^2$$

then we again have

$$A \rightarrow \cdot \leftarrow \cdot \rightarrow B.$$

The stable interior equilibrium is given by

$$x_1 = \frac{-(\alpha - 2\gamma) - \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}.$$

The unstable interior equilibrium is given by

$$x_2 = \frac{-(\alpha - 2\gamma) - \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}.$$

The bifurcation occurs when

$$r_1 r_3 = \left(\frac{\sqrt{(a-b)(c-d)} - \sqrt{(a-c)(b-d)}}{d - a} \right)^2.$$

As $r_1 r_3$ decreases below this threshold, $\alpha^2 - 4\beta\gamma$ increases.

(3) Otherwise, if conditions in case (1) and (2) are not met, namely when $\alpha^2 - 4\beta\gamma < 0$, we have the usual scenario where B dominates A. The entire population will converge to all B

$$A \longrightarrow B.$$

Hence, for the first two classes of games where strategy B is strictly dominant, the evolutionary outcome can be altered by varying the reaction rates r_1 and r_3. Note, however, that the invasion dynamics do not change. B can invade A, but A cannot invade B. If initially most of the population play B, then everyone will play B. If initially most of the population play A, then A and B players will co-exist.

The bifurcation point is where the evolutionary outcome changes its course. In particular, bifurcation occurs when

$$\alpha^2 = 4\beta\gamma.$$

When $\alpha^2 - 4\beta\gamma < 0$, we simply have $A \longrightarrow B$.

When $\alpha^2 = 4\beta\gamma$, and $\alpha = 2\sqrt{\beta\gamma}$, we have a tangent (or fold) bifurcation point at

$$x^* = \frac{\sqrt{-\gamma}}{\sqrt{-\beta} + \sqrt{-\gamma}} = \frac{\sqrt{(d-b)r_3}}{\sqrt{(c-a)r_1} + \sqrt{(d-b)r_3}}.$$

As $\alpha^2 - 4\beta\gamma$ increases above zero, the two equilibria move symmetrically away from

$$x^* = \frac{-(\alpha - 2\gamma)}{2(\beta + \gamma - \alpha)}$$

toward the neighboring end points.

When $r_1 = r_3$, we find that the bifurcation point is at

$$x^* = \frac{\sqrt{d - b}}{\sqrt{c - a} + \sqrt{d - b}}.$$

Obviously when $a > c$ and $b > d$, then the situation is similar with A and B exchanged.

2.6. A and B coexist

If $a < c$ and $b > d$, then A and B co-exist in a stable equilibrium,

$$A \rightarrow \leftarrow B.$$

The interior stable equilibrium is given by

$$x^* = \frac{-(\alpha - 2\gamma) - \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}.$$

The evolutionary dynamics do not change by introducing non-uniform interaction rates. However, the location of the interior stable equilibrium, x^*, can be shifted by varying r_1 and r_3.

We find that x^* increases monotonically with respect to r_1 and r_3. As $r_3 \rightarrow \infty$, $x^* \rightarrow 1$; as $r_3 \rightarrow 0$, $x^* \rightarrow 0$. In particular, we can increase the equilibrium frequency of A

by increasing r_1 and r_3, and we can increase the equilibrium frequency of B by decreasing r_1 and r_3.

2.7. A and B are bi-stable

If $a > c$ and $b < d$, then A and B are bi-stable,

$$A \longleftrightarrow B.$$

Both strategies are strict Nash equilibria. The unstable interior equilibrium is given by

$$x^* = \frac{-(\alpha - 2\gamma) + \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}.$$

For a bi-stable game, the evolutionary outcome stays the same with non-uniform interaction rates. However, the location of the interior unstable equilibrium, x^*, can be shifted by varying r_1 and r_3.

We find that x^* decreases monotonically with respect to r_1 and r_3. As $r_1 \to \infty$, $x^* \to 0$; as $r_1 \to 0$, $x^* \to 1$. In particular, we can minimize the invasion barrier for A by increasing r_1 and r_3, and we can minimize the invasion barrier for B by decreasing r_1 and r_3.

For uniform interaction rates, A is risk dominant if

$$a + b > c + d.$$

This implies $x^* < \frac{1}{2}$ and, hence, A has a larger basin of attraction.

For non-uniform interaction rates, A has the larger basin of attraction if

$$\alpha + \beta + \gamma > 0.$$

This inequality can be written as

$$\frac{ar_1 + b}{r_1 + 1} > \frac{c + dr_3}{1 + r_3}.$$

This is the condition that the fitness an A player is greater than that of a B player when the proportion of A and B players are equal. We argue that this condition is the relevant criterion for risk-dominance in the context of non-uniform interaction rates as it generates the larger basin of attraction.

Given $a > c$ and $d > b$, it is not possible that a strategy is risk-dominant for any choice of r_1 and r_3.

Let us focus on the special case where $r_1 = r_3 = r > 0$ and $r_2 = 1$. Strategy A is risk dominant if

$$(a - d)r > c - b.$$

Consider the example

	A	B
A	4	1
B	3	3

For uniform interaction rates, B is risk dominant. For non-uniform interaction rates, if $r < 2$, B is risk dominant, and if $r > 2$, then A is risk dominant. If $a > d > b > c$, then A is risk dominant for any choice of r.

3. Application to Prisoner's Dilemma

In the Prisoner's Dilemma, the two strategies C and D denote cooperation and defection. The payoff matrix is given by

	C	D
C	R	S
D	T	P

The Prisoner's Dilemma is defined by $T > R > P > S$ and $R > (T + S)/2$, and it corresponds to the case outlined in case (1) in Section 2.5.

For uniform interaction rates $r_1 = r_2 = r_3$, defection is the dominant strategy. Hence, the entire population will consist of defectors eventually. We have $C \longrightarrow D$.

However, if players only interact with opponents of the same strategy, then cooperators cannot be exploited by defectors. In this case, where $r_2 = 0$ and $r_1, r_3 > 0$, cooperation is the dominant strategy, because $R > P$. Hence $C \longleftarrow D$.

Assume $r_2 \neq 0$, which means that cooperators and defectors do interact. Without loss of generality, assume that $r_2 = 1$. The selection dynamics depend on the size of $r_1 r_3$ relative to ρ^2, where

$$\rho = \frac{\sqrt{(T - R)(P - S)} + \sqrt{(R - S)(T - P)}}{R - P}.$$

Note that ρ is always greater than 1. We use the values set in Axelrod and Hamilton (1981), $T = 5, R = 3, P = 1$, $S = 0$, we obtain $\rho \simeq 2.44$.

If $r_1 r_3 < \rho^2$, then defection is the dominant strategy. If $r_1 r_3 > \rho^2$, then there are two interior equilibria, one stable and the other unstable, in addition to the two equilibria on the boundary. We have $C \to \cdot \leftarrow \cdot \to D$.

At the bifurcation point, we have $r_1 r_3 = \rho^2$. As $r_1 r_3$ increases above ρ^2, the two interior equilibria move further apart from the bifurcation point, given by

$$x^* = \frac{\rho}{\rho + \sqrt{2}r_1}.$$

Now let $r = r_1 = r_3$. Thus the cooperator–cooperator interaction rate is the same as that of defector–defector. When $r = \rho$, we have the bifurcation point at

$$x^* = \frac{\rho}{\rho + \sqrt{2}\rho} = \frac{1}{1 + \sqrt{2}} \simeq 0.41.$$

The frequency of cooperators, x^*, at the bifurcation point is independent of any parameter. As r increases, the interior stable equilibrium point moves closer toward 1, while the unstable equilibrium moves closer toward 0. So the proportion of cooperators tend to increase monotonically as r increases. As $r \to \infty$, we recover the case where $r_2 = 0$, and cooperation is the dominant strategy, $C \longleftarrow D$, as defectors can no longer exploit cooperators. See Fig. 1.

Location of Interior Equilibria for Prisoner's
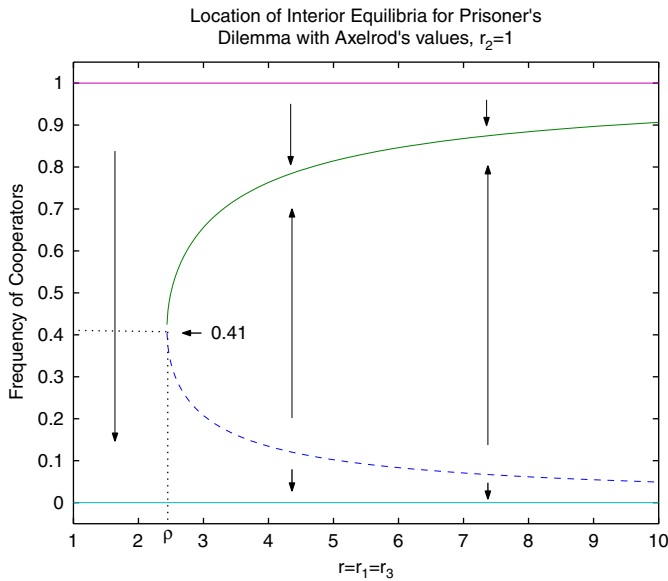Dilemma with Axelrod's values, $r_2=1$

Fig. 1.

4. Application to the snowdrift game

In a snowdrift game (Hauert and Doebeli, 2004), two drivers who are caught in a blizzard and trapped on either side of a snowdrift. They can shovel (cooperate) or remain in the car (defect). If both cooperate, they have the benefit e of getting home while sharing the labor cost f, so the net payoff to each player is $e - f/2$. If both defect, they do not get home, and the net payoff is 0. If one cooperates while the other defects, the cooperator receives $e - f$, and the defector receives e.

	C	D
C	$e - f/2$	$e - f$
D	e	0

If $e > f > 0$, the payoffs generate the snowdrift game, in which it is best to play the strategy different from one's opponent: stay in the car if the other is shoveling, and shovel if the other is idle in the car. This corresponds the situation outlined in Section 2.6. The equilibrium frequency of cooperators is $1 - f/(2e - f)$, where $f/(2e - f)$ is the cost-to-benefit ratio of mutual cooperation. The average payoff of the population at equilibrium is $2e(e - f)/(2e - f)$, which is smaller than the average population payoff, $e - f/2$, if the entire population consists of cooperators only.

The equilibrium frequency of cooperators, x^*, is always an increasing function of r_1 and r_3. Hence the equilibrium frequency of cooperators can be maximized by increasing the interaction rates between players with the same strategies.

5. Conclusion

Evolutionary game theory was pioneered by John Maynard Smith (Maynard Smith and Price, 1973;

Maynard Smith, 1982). His ideas brought game theory to biology and population thinking to game theory. Maynard Smith invented the important concept of an evolutionarily stable strategy (ESS), which can resist invasion of other strategies in infinitely large populations. Evolutionary game theory has been used to study the interaction among genes, cells, viruses, animals and humans. For a recent review see Nowak and Sigmund (2004). Evolutionary game theory offers an framework to explore the evolution of altruistic behavior (Trivers, 1971; Axelrod and Hamilton, 1981; Nowak and Sigmund, 1992; Killingback and Doebeli, 2002) and human language (Nowak et al., 2002). Mathematical approaches to evolutionary game dynamics are based on ordinary differential equations (Taylor and Jonker, 1978; Hofbauer et al., 1979; Zeeman, 1980; Fudenberg and Tirole, 1991; Weibull, 1995; Tao and Lessard, 2000), partial differential equations (Hutson and Vickers, 1993), stochastic differential equation (Imhof, 2004; Fudenberg and Imhof, 2004), cellular automata (Nowak and May, 1992; Herz, 1994; Lindgren and Nordahl, 1994; Killingback and Doebeli, 1996; Mitteldorf and Wilson, 2000; Irwin and Taylor, 2001; Hauert et al., 2002; Le Galliard et al., 2003), and stochastic processes (Nowak et al., 2004; Taylor et al., 2004). There is much current interest to study evolutionary game dynamics on graphs, which also leads to non-uniform interaction rates (Ellison, 1993; Nakamaru et al., 1997, 1998; Epstein, 1998; Abramson and Kuperman, 2001; Ebel and Bornholdt, 2002; Szabo and Vukov, 2004; Iftin et al., 2004; Nakamaru and Iwasa, 2005; Lieberman et al., 2005). The fundamental Lotka–Volterra equation of ecology is equivalent to the replicator equation of evolutionary game theory (Hofbauer and Sigmund, 2003).

In this paper, we have studied the effect of non-uniform interaction rates on evolutionary game dynamics. In the classical approach of the replicator equation, the rate of interaction between any two individuals is the same and does not depend on the strategies (phenotypes) of these individuals. Here we assume that the interaction rates are not uniform. For example, players who use the same strategy might interact more frequently than players who use different strategies. Non-uniform interaction rates lead to non-linear fitness functions and therefore allow richer dynamics than the classical replicator equation, which is based on linear fitness functions. We have analyzed the evolutionary dynamics of all symmetric two-strategy games.

If strategy A is a strict Nash equilibrium, then it remains uninvadable for positive non-uniform interaction rates. If A dominates B then non-uniform interaction rates can introduce a pair of interior equilibria; one of them is stable the other one unstable. If A and B coexist, then non-uniform interaction rates cannot change the qualitative dynamics, but alter the location of the stable equilibrium. If A and B are bi-stable, then again non-uniform interaction rates cannot change the qualitative dynamics, but alter the location of the unstable equilibrium. There is a

new condition for risk dominance that depends on the interaction rates.

For the non-repeated Prisoner's Dilemma, coexistence between cooperators and defectors is possible if the ratio of homogeneous $(C{-}C, D{-}D)$ over heterogeneous $(C{-}D)$ interaction rates exceeds a critical value. If $C{-}C$ interactions are as likely as $D{-}D$ interactions, then the pair of equilibria arises at a cooperator frequency of $x^* = 1/(1 + \sqrt{2}) \approx 0.41$ which is entirely independent of the payoff matrix, as long as $T > R > P > S$. Both equilibria are stable, one consists of defectors alone, and the other consists of a mixture of defectors and cooperators.

For the snowdrift game, the equilibrium of frequency of cooperators is increased if homogeneous interactions are more likely than heterogeneous ones.

Spatial dynamics of the Prisoner's Dilemma (Nowak and May, 1992; Killingback and Doebeli, 1999, 2002) leads to clustering of cooperators and therefore always favors cooperators. Spatial dynamics of the snowdrift game, however, can lead to intricate patterns of cooperators intermixed with defectors and can therefore enhance heterogeneous interactions. This effect can reduce the equilibrium frequency of cooperators (Hauert and Doebeli, 2004). Both phenomena are in accordance with the findings of the present paper.

The analysis of non-uniform interaction rates should be extended to stochastic game dynamics of finite populations. Furthermore, we can distinguish the rate, r_{AB}, a strategy A player interacts with a strategy B player, and the rate, r_{BA}, a strategy B player interacts with strategy A player. Here we have analyzed $r_{AA} = r_1$, $r_{BB} = r_3$, and $r_{AB} = r_{BA} = r_2$. It would also be interesting to study evolutionary dynamics for $r_{AB} \neq r_{BA}$.

Acknowledgments

Appendix

We prove our main results concerning non-uniform reaction rates. We first consider the generic case where none of the reaction rates r_i is zero.

Since f_A and f_B are homogeneous in r_i's, after a change of variable (dividing the denominator and nominator by r_2, assuming $r_2 \neq 0$), we can write

$$f_A = \frac{ar_1x + by}{r_1x + y},$$

$$f_B = \frac{cx + dr_3y}{x + r_3y}.$$

The replicator equations can be reduced to

$$\dot{x} = x(1 - x)(f_A - f_B),$$

where x is the proportion of A players and

$$f_A - f_B = \frac{(ar_1x + by)(x + r_3y) - (cx + dr_3y)(r_1x + y)}{(r_1x + y)(x + r_3y)}.$$

The equilibrium points are either on the boundary or in the interior.

At $x = 0$, the Jacobian is

$$J(x = 0) = f_A(0) - f_B(0) = b - d.$$

So $x = 0$ is a stable equilibrium if $b < d$, and an unstable equilibrium if $b > d$.

At $x = 1$, the Jacobian is

$$J(x = 1) = -f_A(1) + f_B(1) = c - a.$$

So $x = 1$ is a stable equilibrium if $a > c$, and an unstable equilibrium if $a < c$.

At the interior equilibrium x^*, where x^* is the polynomial root of the nominator of $f_A - f_B$, call it $h(x)$, where

$$
\begin{aligned}
h(x) &= (ar_1x + b(1 - x))(x + r_3(1 - x)) \\
&\quad - (cx + dr_3(1 - x))(r_1x + (1 - x)) \\
&= (r_1(a - c) - r_1r_3(a - d) - (b - c) + r_3(b - d))x^2 \\
&\quad + (r_1r_3(a - d) + (b - c) - 2r_3(b - d))x + r_3(b - d) \\
&= (\beta + \gamma - \alpha)x^2 + (\alpha - 2\gamma)x + \gamma,
\end{aligned}
$$

where

$$\alpha = r_1r_3(a - d) + (b - c),$$
$$\beta = r_1(a - c),$$
$$\gamma = r_3(b - d),$$

$$x^* = \frac{-(\alpha - 2\gamma) \pm \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}.$$

At $x = x^*$, the Jacobian is directly proportional to

$$h'(x^*) = 2x^*(\beta + \gamma - \alpha) + (\alpha - 2\gamma) = \pm\sqrt{\alpha^2 - 4\beta\gamma}$$

depending on the root x^*.

For x^* to be an interior equilibrium, we require that

$$0 < x^* < 1.$$

This condition and the sign of the Jacobian at $x = x^*$ will help us to determine the evolutionary outcomes of this game.

In order for both roots $(-(\alpha - 2\gamma) \pm \sqrt{\alpha^2 - 4\beta\gamma})/2(\beta + \gamma - \alpha)$ to be in $(0, 1)$, $\alpha^2 > 4\beta\gamma$ must hold. In addition, we find that either

$$\beta + \gamma < \alpha, \quad \alpha > 2\gamma, 2\beta, \quad 4\beta(\beta + \gamma) > 4\alpha\beta, \quad 4\gamma(\beta + \gamma) > 4\alpha\gamma,$$

or

$$\beta + \gamma > \alpha, \quad \alpha < 2\gamma, 2\beta, \quad 4\beta(\beta + \gamma) > 4\alpha\beta, \quad 4\gamma(\beta + \gamma) > 4\alpha\gamma.$$

We focus on the case where β and γ are both positive, hence with uniform reaction rates, A is a strict Nash equilibrium. However, with non-uniform reaction rates,

the selection dynamics depends on the magnitude of $r_1 r_3$ versus $r_2^2 = 1$.

Under the conditions that $a > c$ and $b > d$, $\beta, \gamma > 0$. Hence, we have $A \leftarrow \cdot \rightarrow \cdot \leftarrow B$ when $\alpha < 2\beta, 2\gamma$. Since $\alpha^2 > 4\alpha\beta$, $\alpha < 0$ must hold. Since $\alpha < 0$, we find if $a > d$, then $b < c$, so $a > c > b > d$; if $a < d$, since $b > d$ and $a > c$, we have $b > d > a > c$. The conditions $\alpha < 0$ and $\alpha^2 > 4\beta\gamma$ together imply that $A \leftarrow \cdot \rightarrow \cdot \leftarrow B$ if and only if one of the following holds:

(1) $b > d > a > c$,

$$r_1 r_3 > \left(\frac{\sqrt{(a-c)(b-d)} + \sqrt{(a-b)(c-d)}}{a-d} \right)^2,$$

(2) $a > c > b > d$,

$$r_1 r_3 < \left(\frac{\sqrt{(a-c)(b-d)} - \sqrt{(a-b)(c-d)}}{a-d} \right)^2.$$

The two interior equilibria are located at

$$\frac{-(\alpha - 2\gamma) \pm \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}.$$

In summary, the two-strategy games whose evolutionary outcome could be altered by non-uniform reaction rates fall in one of the following four categories, where either A or B is a dominant strategy:

(1) $b > d > a > c$

     and $r_1 r_3 > \left(\dfrac{\sqrt{(a-c)(b-d)} + \sqrt{(a-b)(c-d)}}{a-d} \right)^2.$

(2) $a > c > b > d$

     and $r_1 r_3 < \left(\dfrac{\sqrt{(a-c)(b-d)} - \sqrt{(a-b)(c-d)}}{a-d} \right)^2.$

(3) $a < c < b < d$

     and $r_1 r_3 < \left(\dfrac{\sqrt{(a-c)(b-d)} - \sqrt{(a-b)(c-d)}}{a-d} \right)^2.$

(4) $b < d < a < c$

     and $r_1 r_3 > \left(\dfrac{\sqrt{(a-c)(b-d)} + \sqrt{(a-b)(c-d)}}{a-d} \right)^2.$

The location of interior equilibria at

$$\frac{-(\alpha - 2\gamma) \pm \sqrt{\alpha^2 - 4\beta\gamma}}{2(\beta + \gamma - \alpha)}$$

depend largely on the reaction rates r_1, r_2, and r_3, as well as the signs of $a - d$ and $b - c$.

When $r_1 r_3 \gg r_2^2$, we need to compare the payoffs a and d:

(1) $d > a$:
if $b > d$, we have an interior stable equilibrium at

$$x_1^* = \frac{r_3(b-d)}{r_1(a-c) + r_3(b-d) + r_1 r_3(d-a)}$$

we can make $x_1^* \to 0$ by increasing r_1.
If $a > c$, we have an interior unstable equilibrium at

$$x_2^* = \frac{r_3(b-d) + r_1 r_3(d-a)}{r_1(a-c) + r_3(b-d) + r_1 r_3(d-a)}$$

we can make $x_2^* \to 1$ by increasing r_3.

(2) $a > d$:
if $c > a$, we have an interior stable equilibrium at

$$x_1^* = \frac{r_3(b-d) - r_1 r_3(a-d)}{r_1(a-c) + r_3(b-d) - r_1 r_3(a-d)}$$

we can make $x_1^* \to 1$ by increasing r_3.
If $d > b$, we have an interior unstable equilibrium at

$$x_2^* = \frac{r_3(b-d)}{r_1(a-c) + r_3(b-d) - r_1 r_3(a-d)}$$

we can make $x_2^* \to 0$ by increasing r_1.

When $r_2^2 \gg r_1 r_3$, we need to compare the payoffs b and c.

(1) $b > c$:
if $c > a$, we have an interior stable equilibrium at

$$x_1^* = \frac{r_3(b-d) - (b-c)}{r_1(a-c) + r_3(b-d) - (b-c)}$$

we can make $x_1^* \to 1$ by decreasing r_1.
If $d > b$, we have an interior unstable equilibrium at

$$x_2^* = \frac{r_3(b-d)}{r_1(a-c) + r_3(b-d) - (b-c)}$$

we can make $x_2^* \to 0$ by decreasing r_3.

(3) $b < c$:
if $b > d$, we have an interior stable equilibrium at

$$x_1^* = \frac{r_3(b-d)}{r_1(a-c) + r_3(b-d) - (b-c)}$$

we can make $x_1^* \to 0$ by decreasing r_3.
If $a > c$, we have an interior unstable equilibrium at

$$x_2^* = \frac{r_3(b-d) - (b-c)}{r_1(a-c) + r_3(b-d) - (b-c)}$$

we can make $x_2^* \to 1$ by decreasing r_1.

Finally, we consider the special cases when $r_i = 0$ when $i = 1, 2$, or 3.

If $r_1 = 0$, $r_2 = 1$, then A dominates B if and only if $b > c, d$. If $b < c, d$, then B dominates A. If however, $c < b < d$, then we have a bi-stable game where $x = 0, 1$ are both Nash equilibria, and $(d - b)r_3 / ((d - b)r_3 + (b - c))$ is an unstable interior equilibrium. Otherwise, when $d < b < c$, we have a mixed strategy game where $x = 0, 1$ are

unstable equilibria, but $(d-b)r_3/((d-b)r_3+(b-c))$ is a stable interior equilibrium.

Similarly, if $r_3 = 0$, $r_2 = 1$, we have $A \longleftarrow B$ when $c < a, b$; $A \longrightarrow B$ when $c > a, b$; $A \leftarrow \cdot \rightarrow B$ when $b < c < a$; and $A \rightarrow \cdot \leftarrow B$ when $a < c < b$. The interior equilibrium is at $(c-b)/(c-b+(a-c)r_1)$. Here, the greater r_1 is, the closer the interior equilibrium is to $x = 0$.

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