

A MODIFIED REPLICATOR EQUATION ON GRAPHS WITH TRIANGLES

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ABSTRACT: Under the assumption of weak selection, and using a new closure method for the pair approximation technique, we build a modified replicator equation on infinitely large regular graphs, for birth-death updating. The closure method that we propose takes into account the probability of triangles in the graph. Using this new equation, we study how graph structure can affect cooperation in some games with two different strategies, namely the Prisoner's Dilemma, the Snow-Drift Game and the Coordination Game.

KEYWORDS: evolutionary graph theory, game dynamics, pair approximation.

1. Introduction

The replicator equation was introduced for the first time by Peter Taylor and Leo Joker [1] and quickly played an important role in evolutionary game dynamics, for instance in the work of Christopher Zeeman [2], Josef Hofbauer, Peter Schuster and Karl Sigmund [3]. These last two authors were also responsible for its name [4]. Since then, the equation has been adapted to include other elements, such mutation, but the original form was the first important tool to connect game dynamics, where individuals change their strategy over time, with evolutionary game theory, developed by Maynard Smith and Price [5, 6] to predict the prevalence of competing strategies in evolving populations. The replicator equation in evolutionary games with n strategies, is given by:

$$\dot{x}_i = x_i(f_i - \phi), \quad i = 1, \dots, n$$

where x_i is the frequency of strategy i , f_i is the fitness of strategy i and ϕ is the average fitness of the population. Fitness is calculated from the

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$n \times n$ payoff matrix A whose entries correspond to the payoff for strategy i versus strategy j . The fitness of strategy i is given by $f_i = \sum_{j=1}^n x_j a_{ij}$ and the average fitness is obtained from $\phi = \sum_{i=1}^n x_i f_i$. This replicator equation describes the dynamics in the deterministic limit of an infinitely large and well-mixed population. It is assumed that the population is infinitely large so that one can look at x_i as differentiable functions. (There have been attempts to connect this deterministic approach to the stochastic models; see [7] for a good example.) If we think of each individual as a vertex, a well-mixed population can be represented by a complete graph, in which every pair of vertices is connected by an edge. However, this is not often the case when one looks at the structure of a population. Frequently, each individual interacts only with some of the others, not all of them. In this paper, we will deal with structured populations, although only considering regular graphs, in which all the vertices have the same valency. Therefore, we will need to apply some changes to the traditional replicator equation. We will do that under the assumption of weak selection, meaning that differences in reproductive success are small. This approach has been brought into evolutionary game theory more than two decades ago [8]. In infinitely large populations, if structure is ignored, the intensity of selection merely results in a rescaling of time, it does not change the outcome [9, 10]. However, if we take into account the structure, the assumption of weak selection allows us to separate the timescales of local and global dynamics, and regard global frequencies as constant while local frequencies equilibrate [11]. If each individual derives a payoff P interacting with its neighbours, then the fitness of that individual is given by $1 - w + wP$, where w is the parameter of selection. In the limit of weak selection: $w \approx 0$. In 2006, Ohtsuki and Nowak [12] derived a replicator equation on graphs with great similarities with the classic one for well-mixed populations

$$\dot{x}_i = x_i(f_i + g_i - \phi) = x_i \left[\sum_l x_j (a_{ij} + b_{ij}) - \phi \right], \quad i = 1 \dots n,$$

where $g_i = \sum_{j=1}^n x_j b_{ij}$ and $B = [b_{ij}]$ is a well defined $n \times n$ matrix. In a sense, the only change in the equation, moving from well-mixed populations to structured populations, is the payoff matrix. Instead of $[a_{ij}]$, we have now $[a_{ij} + b_{ij}]$. The entries of the matrix $B = [b_{ij}]$ depend on the details of the update rule that is used; since population size is assumed to be fixed, death

and reproduction are fundamentally linked. There exist many different update rules that depend on the detail of how players interact and reproduce. Some of the most common ones are birth-death updating, death-birth updating and imitation. Death-birth (DB) updating means that a player is randomly chosen to die and to be replaced by the offspring of one of its neighbours according to their relative fitness. For imitation updating (IM), a random player is chosen and he will either keep his strategy or imitate one of the neighbours' strategies proportional to fitness. Here, however, we will just deal with birth-death updating (BD): a player is chosen with probability proportional to its fitness, and the offspring of this player replaces a random neighbour.

2. A Modified Pair Approximation MPA

If populations are not well-mixed, what happens locally, around each individual player (located at a vertex in an interaction network), becomes very important. It follows that, instead of global frequencies, one has to look at local frequencies. If we use $q_{i|j}$ as the notation for local frequency of strategy i around strategy j (the probability of a given neighbour of a j player playing i), this conditional probability can be expressed as $q_{i|j} = x_{ij}/x_j$, where x_{ij} and x_j are, respectively, the global frequency of $i - j$ pairs and the global frequency of j -strategy. However, if one has to calculate $q_{i|jl}$ (for instance to track the dynamics of jl -pairs [11]), the probability that a neighbouring player uses strategy i given that the focal player uses strategy j and is also connected to a player using strategy l , one has to take into account x_{ijl} , the global frequency of triples. The easiest way to avoid this, is to assume $q_{i|jl} = q_{i|j}$, ignoring the effect that a two-step adjacent player might have on the neighbour. This method is called *pair approximation* and was first developed by Matsuda [11]. Some approaches, instead of focusing only on pairs, have taken triplet correlations into account. For instance, in [13, 14], the difference between open and closed triple configurations was ignored in order to obtain a new estimate; later, Morita [15] used the Kirkwood closure [16] to build his approximation rule. We have taken a different approach here (see Table 1 to compare the different approaches).

A complication arises from the fact that one cannot pick just any arbitrary form to try to improve the approximation for $q_{i|jl}$, as the approximation should satisfy the condition that $\sum_i q_{i|jl} = 1$ (where the index i sums over

Van Baalen	$q_{a ab} = q_{a a} \left[(1 - \gamma) + \gamma \frac{q_{a b}}{x_a} \right]$ $q_{b ab} = 1 - q_{a ab}$
Morita	$q_{a ab} = (1 - \gamma)q_{a a} + \gamma \frac{q_{a a}}{q_{a a} + q_{b b}}$ $q_{b ab} = 1 - q_{a ab}$
MPA	$q_{a ab} = \left(1 - \frac{\gamma}{2}\right)q_{a a} + \frac{\gamma}{2}q_{a b}$ $q_{b ab} = \left(1 - \frac{\gamma}{2}\right)q_{b a} + \frac{\gamma}{2}q_{b b}$

TABLE 1. Approximations taking into account the probability of triples

all possible strategies). Many published approximations do not satisfy this consistency condition.

By looking at local frequencies instead of global frequencies, one is acknowledging the importance that structure has in population dynamics. Nevertheless, when one uses the *standard pair approximation* (SPA), the particular structure of a population is not taken into account. The same approximation is chosen, regardless of the graph that represents interactions between players. What we will do here is to slightly change the pair approximation, according to the probability of finding triangular triples in the graph. If we denote by γ the probability of triangular triples in the graph, then we take the following approximation (that we will call MPA):

$$q_{i|lj} = \left(1 - \frac{\gamma}{2}\right)q_{i|l} + \frac{\gamma}{2}q_{i|j}$$

The idea behind this modified pair approximation is that if we have a triangular triple and we want, for instance, to calculate $q_{i|lj}$ in that configuration, we can either approximate it using $q_{i|l}$ or $q_{i|j}$ because there's an edge connecting the vertice i to both l and j (Figure 1).

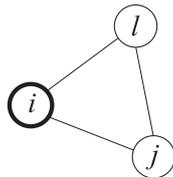


FIGURE 1. Triangular triple where i is both a neighbour of j and of l

What we do here is to take the average of these two probabilities ($[q_{i|l} + q_{i|j}]/2$) instead of picking either one of them. For triangles, we use

$$q_{i|lj}^{\Delta} = \frac{q_{i|l} + q_{i|j}}{2}.$$

However, not all triples are closed, as this depends on the topology of the network. We will represent by $q_{i|lj}^{-} = q_{i|l}$, so we ignore that, in a linear triple, player l has another neighbour that uses strategy j . Then,

$$q_{i|lj} = (1 - \gamma)q_{i|lj}^{-} + \gamma q_{i|lj}^{\Delta} = (1 - \gamma)q_{i|l} + \gamma \frac{q_{i|l} + q_{i|j}}{2} = \left(1 - \frac{\gamma}{2}\right)q_{i|l} + \frac{\gamma}{2}q_{i|j}.$$

If $l = j$ this is similar to the standard pair approximation (SPA) since $q_{i|jj} = q_{i|j}$. The consistency conditions are also satisfied by this modified approximation because $\sum_i q_{i|lj} = 1$, as it can easily be checked.

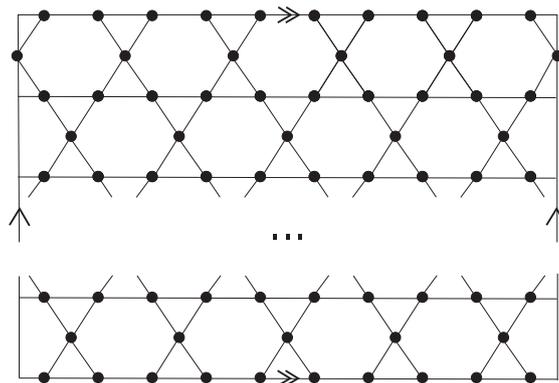


FIGURE 2. Regular graph with vertices of valency 4 on a torus (identifying opposites sides of the rectangle).

To test the accuracy of this modified pair approximation (MPA) we have run some computer simulations. Our method is the following: we start with a triangular lattice of 1000 vertices, all of them with A players. At the beginning of each run, we substitute n of those A players by random clusters (of random length) of B players. We then compare the exact $q_{A|BA}$ and $q_{A|AB}$ with the predictions that we get using SPA and MPA. We conduct this simulation 10^4 times and we calculate the average absolute errors of both approximations. The results are summarized in Table 2. If $n = 250$ and $n = 500$, MPA does always better than SPA. If $n = 10$ (very few B's), SPA does better for $q_{A|BA}$ but it is not so good to predict $q_{A|AB}$, which is what we could expect from the definition of MPA (when the spatial clumping of B is

high, $q_{B|B}$ will also be high and it will counterbalance the low $q_{B|A}$, if B is rare). And if we look carefully at the table, even when the number of B 's is very small, what we lose in accuracy, while calculating $q_{A|BA}$ with MPA, is slightly less than what we gain when predicting $q_{A|AB}$. The same conclusions can be achieved when simulations are run in the regular graph represented in Figure 2, which has vertices of degree 4, and faces of degree 3 (triangles) and 6 (hexagons). A summary of these simulations is presented in Table 3.

	10 B's	250 B's	500 B's		10 B's	250 B's	500 B's
SPA error	0,0249	0,1253	0,1709	SPA error	0,1403	0,3170	0,3048
MPA error	0,0728	0,0357	0,0383	MPA error	0,0734	0,1804	0,1647
	(A) $q_{A BA}$				(B) $q_{A AB}$		

TABLE 2. Triangular lattice on torus with 1000 vertices.

	10 B's	250 B's	500 B's		10 B's	250 B's	500 B's
SPA error	0,0466	0,1021	0,1414	SPA error	0,1175	0,2758	0,2727
MPA error	0,0700	0,0419	0,0643	MPA error	0,0766	0,1992	0,1945
	(A) $q_{A BA}$				(B) $q_{A AB}$		

TABLE 3. Graph in Figure 2, with 990 vertices of valency 4.

From the definition of MPA and from these simulations, we can estimate that, by substituting SPA by MPA, we are slightly increasing the accuracy of the approximation, while keeping the simplicity of the original pair approximation, which is very important for applications.

2.1. Dynamics of local frequencies. The dynamics of local frequencies on an infinite regular graph of degree $k > 2$, assuming weak selection $w \ll 1$ and birth-death updating can be described by the following equation [12]:

$$\dot{q}_{i|j} = \frac{\dot{x}_{ij}}{x_j} = \frac{2}{k} \left[\delta_{ij} + (k-1) \left(\sum_l q_{i|lj} q_{l|j} \right) - k q_{i|j} \right] + O(w).$$

If we adopt the standard pair approximation (SPA) then $q_{i|lj} = q_{i|l}$ and the equilibrium local frequencies are, according to Ohtsuki and Nowak [12], given by

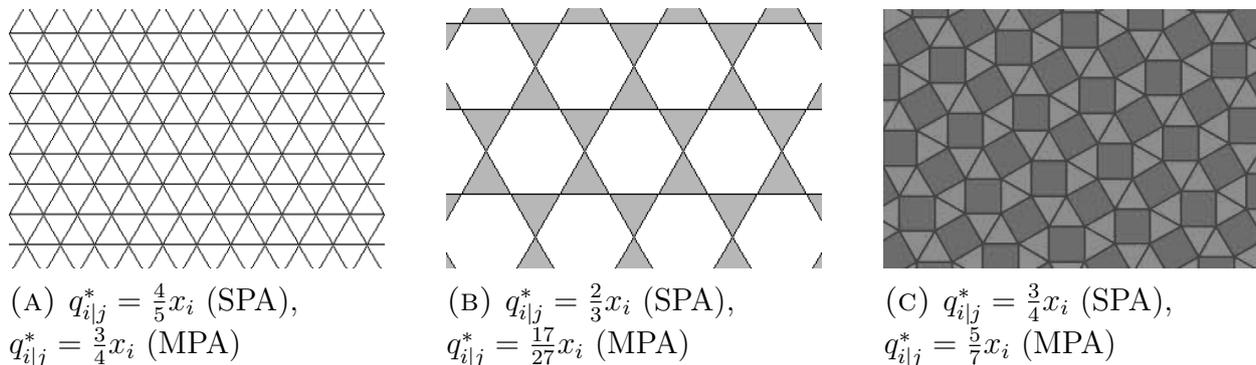


FIGURE 3. Equilibrium frequencies for the triangular lattice (a) and two other regular graphs.

$$q_{i|j}^* = \frac{(k-2)x_i + \delta_{ij}}{k-1},$$

where x_i is the global frequency of strategy i and δ is the Kronecker delta function. We should note that since $w \ll 1$, while the local frequencies (fast variables) equilibrate we can look at global frequencies (slow variables) as constant.

Although most of the results could easily be adapted to other kind of populations, throughout this paper, to simplify our calculations, we will only deal with populations whose elements have only one of two distinct strategies (i or j). If, instead of the standard pair approximation (SPA), we take our modified pair approximation (MPA), the equilibrium frequencies would be given by

$$q_{i|j}^* = \left[1 - \frac{2}{(2-\gamma)(k-1)} \right] x_i = x_i - \frac{2x_i}{(2-\gamma)(k-1)}$$

$$q_{j|j}^* = 1 - x_i + \frac{2x_i}{(2-\gamma)(k-1)} = x_j + \frac{2-2x_j}{(2-\gamma)(k-1)}$$

Or, in a single expression:

$$q_{l|m}^* = x_l - \frac{2x_l}{(2-\gamma)(k-1)} + \frac{2}{(2-\gamma)(k-1)} \delta_{lm},$$

where δ is the Kronecker function (see Appendix A for details). Some examples can be found in Figure 3.

It follows that, in these new approaches (as in the standard one), we have

$$q_{i|j}^* < x_i < q_{i|i}^*, \text{ for all } \gamma.$$

This is the same as saying that j -players have fewer i -neighbours than is expected by global frequencies, while i -players have more. But here, we can conclude something else: if γ (the probability of triangular triples) increases and the degree of the graph does not change, the difference between $q_{i|j}^*$ and x_i , as well as the difference between $q_{i|i}^*$ and x_i , also increases. Since the difference between local frequencies and global frequencies grows with the probability of triangular triples, we have to take into account local dynamics in graphs with abundant triangles, if we do not want to ignore the spatial effects.

3. Replicator equation on graphs for BD updating

The traditional replicator equations for well-mixed populations is given by $\dot{x}_i = x_i(f_i - \phi)$. Using the standard pair approximation, Ohtsuki and Nowak [12] have obtained a replicator equation on graphs,

$$\dot{x}_i = x_i(f_i + g_i - \phi),$$

where $f_i = \sum_{j=1}^n x_j a_{ij}$, $g_i = \sum_{j=1}^n x_j b_{ij}$ and ϕ is the average fitness of the population. In the case of BD-updating,

$$b_{ij} = \frac{a_{ii} + a_{ij} - a_{ji} - a_{jj}}{k - 2}.$$

3.1. MPA. Our goal is to obtain a modified replicator equation but using MPA instead of SPA. To stress the differences and similarities between both equations, we will try, whenever possible, to use the same notation Ohtsuki and Nowak have used in [12]. Their replicator equation was obtained from the following deterministic evolutionary dynamics (here we present a simplified expression, assuming there are only two different strategies: i and j):

$$\begin{aligned} \dot{x}_i = & \sum_{k_i+k_j=k} \left[x_i \left(\frac{k!}{k_i!k_j!} q_{i|i}^{k_i} q_{j|i}^{k_j} \right) \frac{W(i; k_i, k_j)}{\tilde{W}} \right] - \\ & - \sum_{r \in \{i, j\}} x_r \sum_{k_i+k_j=k} \left[\left(\frac{k!}{k_i!k_j!} q_{i|r}^{k_i} q_{j|r}^{k_j} \right) \right] \frac{k_i}{k} \frac{W(r; k_i, k_j)}{\tilde{W}}, \end{aligned} \quad (1)$$

where $W(i; k_i, k_j) = 1 - w + w(k_i a_{ii} + k_j a_{ij})$ is the fitness of a player using strategy i , with k_i neighbours using strategy i and k_j neighbours using strategy j , and \tilde{W} is the average fitness in the population.

If we use MPA, instead of SPA, from the subtraction of these two terms, we obtain the following replicator equation on graphs (see Appendix B):

$$\dot{x}_i = \frac{wyz^2}{2(2-\gamma)} x_i (f_i + g_i - \phi),$$

with $z = (2 - \gamma)(k - 1) - 2$ and $y = \frac{2}{(2-\gamma)(k-1)}$. Neglecting the factor $\frac{wyz^2}{2(2-\gamma)}$, which is equivalent to a change of time scale, we obtain the MPA replicator equation on graphs:

$$\dot{x}_i = x_i (f_i + g_i - \phi) = x_i \left[\sum_l x_l (a_{il} + b_{il}) - \phi \right],$$

with

$$b_{il} = \frac{2a_{ii} + (2 - \gamma)a_{il} - (2 - \gamma)a_{li} - 2a_{ll}}{(2 - \gamma)(k - 1) - 2}. \quad (2)$$

Hence, the structure of the replicator equation is preserved but the transformation of the payoff matrix is not independent of the graph, since $B = [b_{ml}]$ depends on the probability of triangles (and on the degree of the graph). The 2×2 matrix B has the following property: $b_{ii} = b_{jj} = 0$ and $b_{ij} = -b_{ji}$. In [12], the contributions from assortativeness (characterized by the terms a_{ii} and a_{jj}) and spite (characterized by the terms a_{ij} and a_{ji}) are equally strong but here, assuming $\gamma > 0$, assortativeness has a stronger influence than spite, as one can see in equation (2).

4. Games on graphs

4.1. The Prisoner's Dilemma. In the Prisoner's Dilemma [17, 18, 19], a cooperator pays a cost c for his opponent to receive a benefit $b > c$. It is a dilemma because, for each player, the best option is to defect, regardless of the other player's behaviour. However, if both decide to defect, their benefit will be smaller than if both decide to cooperate. The payoff matrix of this simplified Prisoner's Dilemma [20] is the following:

$$A = \begin{bmatrix} b - c & -c \\ b & 0 \end{bmatrix}.$$

According to our model, the matrix that describes local competition around a vertex, in a graph of degree $k > 2$ and with γ being the probability of triangular triples, is given by

$$B = \begin{bmatrix} 0 & \frac{2(b-c)+(2-\gamma)(-b-c)}{z} \\ \frac{2(c-b)+(2-\gamma)(b+c)}{z} & 0 \end{bmatrix}.$$

If we denote by x the frequency of cooperators in the population, the replicator equation would be the following (see Appendix C):

$$\dot{x} = x(1-x) \left[-c + \frac{(\gamma-4)c + \gamma b}{z} \right].$$

Defectors always win if $-c + \frac{(\gamma-4)c + \gamma b}{z} < 0$. This happens when $\gamma < \frac{2kc}{kc+b}$. Hence, if $b \leq kc$ then defectors always win, regardless of the graph, but if $b > kc$ (which happens when the ratio benefit/cost is greater than k) then cooperators will win if the probability of triangles is high enough. In previous models (for complete graphs, for cycles [21] and for other non-complete regular graphs [12]), structure does not favor cooperation for BD updating. However, in our case, if the benefit/cost ratio a player can get is big enough ($b/c > k$), cooperators might win. This also means that cooperation is the only EES (Evolutionary Stable Strategy) on the graph if $b/c > k$ and $\gamma > \frac{2kc}{kc+b}$, which is a different conclusion than the one obtained for well-mixed populations and the one derived from the replicator equation in [12] (in both cases, defection is the only ESS in the game). Hence, if we take our modified replicator equation, evolutionary stability is also affected by structure for BD updating, and not only for DB (death-birth) updating and IM (imitation) updating [22].

4.2. The Snow-Drift Game. Two drivers are trapped on opposite sides of a snow-drift. Each driver has two options: to get out of the car and shoveling to clear the path (cooperate) or stay warm in the car (defect). If at least one player cooperates they will get a benefit b . The cost of getting out of the car and shovel is c (which is shared if both get out of the car). It follows that the payoff matrix of this game is given by

$$A = \begin{bmatrix} b - \frac{c}{2} & b - c \\ b & 0 \end{bmatrix},$$

so that

$$B = \begin{bmatrix} 0 & \frac{2b-c-(2-\gamma)c}{z} \\ \frac{c-2b+(2-\gamma)c}{z} & 0 \end{bmatrix}.$$

If we denote by x the frequency of cooperators in the population, the replicator equation would be the following (see Appendix C):

$$\dot{x} = x(1-x) \left[\left(\frac{c}{2} - b \right) x + \frac{(b-c)z + 2b - c - (2-\gamma)c}{z} \right]$$

Then $x^* = 1 + \frac{-zc/2 + 2b - c - (2-\gamma)c}{z(b-c/2)}$ is a stable equilibrium solution.

If $b/c > (3-\gamma)/2$ this equilibrium solution is greater than in the well-mixed populations. For Ohtsuki and Nowak [12] and for Morita [23] this occurs when $b/c > 3/2$, while our condition also depends on γ , the probability of triples (but not on the valency k of the vertices). It can be easily verified that if $\gamma = 0$ our new approach coincides with previous ones, as expected. Some choices of parameters can lead to dominance of one strategy over the other. If $\frac{b}{c} < 1 + \frac{1-\gamma}{(2-\gamma)(k-1)}$ then defectors always win. If $\frac{b}{c} > \frac{2k-(k+1)\gamma+2}{4}$ then cooperators always win. Here again, the probability of triples becomes relevant to the final result (although, in this case, the degree k of the graph has also to be taken into account). For instance, in the triangular lattice, the equilibrium solution is greater than in the well-mixed population if $b/c > 13/10$. If $b/c < 43/40$ then defectors always win. If $b/c > 14/5$ then cooperators always win.

4.3. Coordination Game. In a Coordination Game, both strategies (S_1 and S_2) are strict Nash equilibria and it is best to do the same as the opponent. A strategy is called risk-dominant [24] if its basin of attraction is greater than $1/2$, and is called Pareto-efficient if a player can get the best outcome by choosing it. To make comparisons easier, let us consider the same specific coordination game chosen in [12], given by the payoff matrix

$$A = \begin{bmatrix} a & 0 \\ 1 & 2 \end{bmatrix}.$$

We are assuming $1 < a < 3$. In this case, S_2 is always risk-dominant. If $a < 2$ then S_2 is both risk dominant and Pareto-efficient. If $2 < a < 3$ then S_1 becomes Pareto-efficient, while S_2 remains risk-dominant. This last case

is the most interesting, since a conflict arises, and it might be useful to know how structure can affect the dynamics of this game.

According to our model, the matrix that describes local competition around a vertex, in a graph of degree k and with γ being the probability of triangular triples, is given by

$$B = \begin{bmatrix} 0 & 2a + \gamma - 6 \\ 6 - 2a - \gamma & 0 \end{bmatrix}.$$

If we denote by x the frequency of S_1 in the population, the replicator equation would be the following (see Appendix C):

$$\dot{x} = x(1-x) \left[x(1+a) + \frac{2a + \gamma - 6 - 2z}{z} \right].$$

Then $x^* = \frac{2z-2a-\gamma+6}{z(1+a)}$ is an unstable equilibrium solution. If we compare it to $x^{**} = \frac{2}{a+1}$, the equilibrium solution for a well-mixed population, we conclude that, if $a < 2.5$, the basin of attraction of strategy S_2 is always larger than in a well-mixed population. But in the case where $2.5 < a < 3$, that is true only if $\gamma < 6 - 2a$. Hence, differently from [12], BD updating not always favors risk dominance; it depends on the graph and, consequently, on the way the population is structured.

5. Alternative Modified Replicator Equations

In previous sections, we have dealt with the approximation $q_{i|lj} \approx (1 - \frac{\gamma}{2})q_{i|l} + \frac{\gamma}{2}q_{i|j}$. However, if we just look at the mathematical accuracy, we could have chosen any constant $\alpha \in [0, 1]$ instead of $\frac{\gamma}{2}$. Any approximation $q_{i|lj}(1 - \alpha)q_{i|l} + \alpha q_{i|j}$ would satisfy the consistency conditions. The replicator equation would be the same as for MPA, only with a slight modification,

$$b_{il} = \frac{a_{ii} + (1 - \alpha)a_{il} - (1 - \alpha)a_{il} - a_{ll}}{(1 - \alpha)(k - 1) - 1}.$$

In some cases, choosing a constant α different from $\frac{\gamma}{2}$ would give better results, but that would require some experimental tests for each graph, and, here, we are trying to be as general as possible.

6. Discussion

The replicator equation on graphs can be improved, keeping its simplicity, by including more information about the graph of interactions than just the valency of the vertices [12]. Inspired by previous approaches [13, 14], we take into account the probability of triangles in the graph but in a much simpler way. This results in a change in the matrix that describes local competition, which becomes dependent on that probability and, consequently, on the way the elements of the population are linked to each other.

In previous models for BD updating, structure seems not to favor cooperation in the Prisoner's Dilemma game. However, if we use our modified approximation and replicator equation, that might not be the case if the ratio b/c is big enough. In the snow-drift game, if the probability of triangles increases, the b/c ratio that one needs to consider to make the equilibrium solution greater than in the case of well-mixed populations, becomes smaller. In our model, BD updating not always favors risk dominance in coordination games.

Appendices

Appendix A.

$$\begin{aligned}
 \dot{q}_{i|j} &= \frac{\dot{x}_{ij}}{x_j} = \frac{2}{k} \left[\delta_{ij} + (k-1) \left(\sum_l q_{i|lj} q_{l|j} \right) - k q_{i|j} \right] + O(w) \\
 &= \frac{2}{k} \left[(k-1) (q_{i|i|j} q_{i|j} + q_{i|j|j} q_{j|j}) - k q_{i|j} \right] + O(w) \\
 &= \frac{2}{k} \left[(k-1) \left(\left[\left(1 - \frac{\gamma}{2}\right) q_{i|i} + \frac{\gamma}{2} q_{i|j} \right] q_{i|j} + q_{i|j} q_{j|j} \right) - k q_{i|j} \right] + O(w) \\
 &= \frac{2}{k} q_{i|j} \left[(k-1) \left(\left(1 - \frac{\gamma}{2}\right) q_{i|i} + \frac{\gamma}{2} q_{i|j} + q_{j|j} \right) - k \right] + O(w)
 \end{aligned}$$

Hence, if $q_{i|j} \neq 0$,

$$\begin{aligned}
\dot{q}_{i|j} = 0 &\iff (k-1)\left(\left(1 - \frac{\gamma}{2}\right)q_{i|i} + \frac{\gamma}{2}q_{i|j} + q_{j|j}\right) - k = 0 \\
&\quad \left(1 - \frac{\gamma}{2}\right)q_{i|i} + \frac{\gamma}{2}q_{i|j} + q_{j|j} = \frac{k}{k-1} \\
&\quad \left(1 - \frac{\gamma}{2}\right)q_{i|i} + \frac{\gamma}{2}(1 - q_{j|j}) + q_{j|j} = \frac{k}{k-1} \\
&\quad \left(1 - \frac{\gamma}{2}\right)q_{i|i} + \left(1 - \frac{\gamma}{2}\right)q_{j|j} = \frac{k}{k-1} - \frac{\gamma}{2} \\
&\quad \quad \quad q_{i|i} + q_{j|j} = \frac{\frac{k}{k-1} - \frac{\gamma}{2}}{1 - \frac{\gamma}{2}} \\
&\quad \quad \quad q_{i|i} + q_{j|j} = 1 + \frac{2}{(2-\gamma)(k-1)}
\end{aligned}$$

Since $q_{i|j} + q_{j|j} = q_{j|i} + q_{i|i} = 1$ we have

$$q_{i|j} + q_{j|i} = 2 - (q_{i|i} + q_{j|j}) = 1 - \frac{2}{(2-\gamma)(k-1)}.$$

Hence, $(q_{i|j} + q_{j|i})x_i = \left[1 - \frac{2}{(2-\gamma)(k-1)}\right]x_i$ and, because $q_{j|i}x_i = q_{i|j}x_j$, we have

$$q_{i|j}(x_i + x_j) = \left[1 - \frac{2}{(2-\gamma)(k-1)}\right]x_i.$$

From this equality, since $x_i + x_j = 1$, we can obtain the equilibrium frequency

$$q_{i|j}^* = \left[1 - \frac{2}{(2-\gamma)(k-1)}\right]x_i = x_i - \frac{2x_i}{(2-\gamma)(k-1)}.$$

Appendix B. Notation:

$$a_{i\bullet} = \sum_l x_l a_{il} \quad , \quad a_{\bullet i} = \sum_l x_l a_{li} \quad , \quad a_{\bullet} = \sum_l x_l a_{ll} \quad , \quad a_{\bullet\bullet} = \sum_{l,m} x_l x_m a_{lm}.$$

As in [12], we can use properties of the multinomial distribution to obtain the equality

$$\tilde{W} = 1 - w + w \sum_m x_m \sum_l k q_{l|m} a_{ml}.$$

Considering

$$\theta = \sum_m x_m \sum_l k q_{l|m} a_{ml},$$

we have

$$\tilde{W} = 1 - w + w\theta.$$

And, since $w \ll 1$:

$$\frac{W(i; k_i, k_j)}{\tilde{W}} \approx 1 + w \left(\sum_l k_l a_{il} - \theta \right).$$

If $y = \frac{2}{(2-\gamma)(k-1)}$, then we can write $q_{i|j} = x_i(1-y) + y\delta_{ij}$. Thus, both terms of equation (1) can be presented in a simplified way.

The first term of equation (1) is

$$\begin{aligned} \sum_{k_i+k_j=k} \left[x_i \left(\frac{k!}{k_i!k_j!} q_{i|i}^{k_i} q_{j|i}^{k_j} \right) \frac{W(i; k_i, k_j)}{\tilde{W}} \right] &= x_i \left[1 + w \left(\sum_l k q_{l|i} a_{il} - \theta \right) \right] \\ &= x_i \left[1 + w \left(\sum_l k (x_l(1-y) + y\delta_{li}) a_{il} - \theta \right) \right] \\ &= x_i \left[1 + wyka_{ii} + w \left(\sum_l k x_l(1-y) a_{il} - \theta \right) \right] \\ &= x_i \left[1 + wy \left(ka_{ii} + k \left(\frac{1}{y} - 1 \right) \sum_l x_l a_{il} - \frac{\theta}{y} \right) \right] \\ &= x_i \left[1 + wy \left(ka_{ii} + k \left(\frac{1}{y} - 1 \right) a_{i\bullet} - \frac{\theta}{y} \right) \right]. \end{aligned}$$

The second term of equation (1) is

$$\begin{aligned} &\sum_{r \in \{i, j\}} x_r \sum_{k_i+k_j=k} \left[\left(\frac{k!}{k_i!k_j!} q_{i|r}^{k_i} q_{j|r}^{k_j} \right) \right] \frac{k_i W(r; k_i, k_j)}{k \tilde{W}} = \\ &= \sum_r x_r q_{i|r} \left[1 + w \left(\sum_l \{ \delta_{il} + (k-1) q_{l|r} \} a_{rl} - \theta \right) \right] = \\ &= \sum_r x_r (x_i(1-y) + y\delta_{ir}) \left[1 + w \left(\sum_l \{ \delta_{il} + (k-1)(x_l(1-y) + y\delta_{lr}) \} a_{rl} - \theta \right) \right] = \\ &= \sum_r x_r (x_i(1-y) + y\delta_{ir}) \left[1 + w \{ a_{ri} + (k-1)(1-y)a_{r\bullet} + (k-1)ya_{rr} - \theta \} \right] = \\ &= x_i(1-y) \left[1 + w \{ a_{\bullet i} + (k-1)(1-y)a_{\bullet\bullet} + (k-1)ya_{\bullet} - \theta \} \right] + \\ &\quad + x_i y \left[1 + w \{ a_{ii} + (k-1)(1-y)a_{i\bullet} + (k-1)ya_{ii} - \theta \} \right] = \\ &= x_i \left[1 + w (a_{\bullet i} + (k-1)(1-y)a_{\bullet\bullet} + (k-1)ya_{\bullet} - \theta) \right] + \end{aligned}$$

$$\begin{aligned}
& +x_iyw[(1+y(k-1))a_{ii}+(k-1)(1-y)a_{i\bullet}-a_{\bullet i}-(k-1)(1-y)a_{\bullet\bullet}-y(k-1)a_{\bullet}] = \\
& \quad = x_i[1+wy(\frac{1}{y}a_{\bullet i}+(k-1)(\frac{1}{y}-1)a_{\bullet\bullet}+(k-1)a_{\bullet}-\frac{\theta}{y})]+ \\
& +x_iyw[(1+y(k-1))a_{ii}+(k-1)(1-y)a_{i\bullet}-a_{\bullet i}-(k-1)(1-y)a_{\bullet\bullet}-y(k-1)a_{\bullet}] = \\
& = x_i[1+wy\{(\frac{1}{y}-1)a_{\bullet i}+(k-1)(1-y)a_{\bullet}+(1+y(k-1))a_{ii}+(k-1)(1-y)a_{i\bullet}+ \\
& \quad \quad \quad +(k-1)(\frac{1}{y}-2+y)a_{\bullet\bullet}-\frac{\theta}{y}\}].
\end{aligned}$$

Hence, when we subtract the second term from the first term, we get the following expression:

$$\begin{aligned}
& x_iwy[(k-1-y(k-1))a_{ii}+(k(\frac{1}{y}-1)-(k-1)(1-y))a_{i\bullet}-(\frac{1}{y}-1)a_{\bullet i}- \\
& \quad \quad \quad -(k-1)(1-y)a_{\bullet}-(k-1)(\frac{1}{y}+y-2)a_{\bullet\bullet}].
\end{aligned}$$

If $z = (2-\gamma)(k-1)-2$ then $\frac{1}{y}-1 = \frac{z}{2}$ and the previous expression can be rewritten as:

$$\begin{aligned}
& x_iwy[\frac{z}{2-\gamma}a_{ii}+z(\frac{k}{2}-\frac{1}{2-\gamma})a_{i\bullet}-\frac{z}{2}a_{\bullet i}-\frac{z}{2-\gamma}a_{\bullet}-z(\frac{k-1}{2}-\frac{1}{2-\gamma})a_{\bullet\bullet}] = \\
& \quad = x_i\frac{wyz}{2(2-\gamma)}[za_{i\bullet}+(2a_{ii}+(2-\gamma)a_{i\bullet}-(2-\gamma)a_{\bullet i}-2a_{\bullet})-za_{\bullet\bullet}] = \\
& \quad = x_i\frac{wyz^2}{2(2-\gamma)}[a_{i\bullet}+\frac{2a_{ii}+(2-\gamma)a_{i\bullet}-(2-\gamma)a_{\bullet i}-2a_{\bullet}}{z}-a_{\bullet\bullet}].
\end{aligned}$$

Appendix C.

Prisoner's Dilemma.

$$\begin{aligned}
\dot{x} & = x[x(b-c)+(1-x)(-c+\frac{2(b-c)+(2-\gamma)(-b-c)}{z})-x(b-c)] \\
& = x(1-x)[-c+\frac{(\gamma-4)c+\gamma b}{z}]
\end{aligned}$$

Defectors always win if $-c + \frac{(\gamma-4)c+\gamma b}{z} < 0$.

But then, since $z = (2 - \gamma)(k - 1) - 2$,

$$\begin{aligned} -c + \frac{(\gamma - 4)c + \gamma b}{(2 - \gamma)(k - 1) - 2} &< 0 \\ [(2 - \gamma)(k - 1) - 2](-c) + (\gamma - 4)c + \gamma b &< 0 \\ -kc(2 - \gamma) + \gamma b &< 0 \\ \gamma &< \frac{2kc}{kc + b}. \end{aligned}$$

Snow-Drift.

$$\begin{aligned} \dot{x} &= x \left[x \left(b - \frac{c}{2} \right) + (1 - x) \left(b - c + \frac{2b - c - (2 - \gamma)c}{z} \right) - x^2 \left(b - \frac{c}{2} \right) - x(1 - x)(2b - c) \right] \\ &= x(1 - x) \left[x \left(\frac{c}{2} - b \right) + \frac{(b - c)z + 2(b - \frac{c}{2}) - (2 - \gamma)c}{z} \right] \end{aligned}$$

The non trivial equilibrium solution is given by the following expression:

$$x^* = \frac{z(b - c) + 2b - c - (2 - \gamma)c}{z(b - c/2)} = 1 + \frac{-zc/2 + 2b - c - (2 - \gamma)c}{z(b - c/2)}.$$

If we take $\bar{x} = 1 - \frac{c}{2b - c}$, the equilibrium solution for a well-mixed population, then

$$x^* > \bar{x} \iff 1 + \frac{-zc/2 + 2b - c - (2 - \gamma)c}{z(b - c/2)} > 1 - \frac{c}{2b - c} \iff \frac{b}{c} > \frac{3 - \gamma}{2}.$$

Defectors always win if

$$1 + \frac{-zc/2 + 2b - c - (2 - \gamma)c}{z(b - c/2)} < 0 \iff \frac{b}{c} < \frac{z + 3 - \gamma}{z + 2} = 1 + \frac{1 - \gamma}{(2 - \gamma)(k - 1)}.$$

Cooperators always win if

$$1 + \frac{-zc/2 + 2b - c - (2 - \gamma)c}{z(b - c/2)} > 1 \iff \frac{b}{c} > \frac{z + 6 - 2\gamma}{4} = \frac{2k - (k + 1)\gamma + 2}{4}.$$

Coordination Game.

$$\dot{x} = x(1 - x) \left[x(1 + a) + \frac{2a + \gamma - 6 - 2z}{z} \right]$$

The non trivial equilibrium solution is given by the following expression:

$$x^* = \frac{6 + 2z - a - \gamma}{z(1 + a)}.$$

If we denote by x^{**} the equilibrium solution for well-mixed populations,

$$x^* > x^{**} \iff \frac{6 + 2z - a - \gamma}{z(1 + a)} > \frac{2}{a + 1} \iff \gamma < 6 - 2a.$$

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