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Modelling Moran Process with Network Dynamics for the Evolution of Cooperation *

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We introduce a simple model based on the Moran process with network dynamics. Using pair approximation, the cooperation frequencies at equilibrium states are deduced for general interactions. Three usual social dilemmas are discussed in the framework of our model. It is found that they all have a phase transition at the same value of cost-to-benefit ratio. For the prisoner's dilemma game, notably it is exactly the simple rule reported in the literature [Nature 441 (2006) 502]. In our model, the simple rule results from the parent-offspring link. Thus the basic mechanism for cooperation enhancement in network reciprocity is in line with the Hamilton rule of kin selection. Our simulations verify the analysis obtained from pair approximation.

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Cooperation, which is essential for the construction of a new level of organization, has been expected to be a third fundamental principle of evolutionary dynamics apart from mutation and selection.^[1] Darwinian evolution represents an intrinsically frequency-dependent process.^[2,3] The fitness of an individual is determined by environmental condition as well as the frequency of its competitors.^[4] How can Darwinian dynamics based on mutation and selection lead to cooperation? The evolutionary game theory^[5,6] provides a common mathematical framework for modelling the dynamics of evolution. Traditionally, the well-known replicator equation^[2] describes the change in frequency of the two types in infinite populations. In nature, stochastic effects and random drift disturb the deterministic selection process when populations are finite in size.^[7] The Moran process^[8] has been introduced to describe the balance between selection and drift with a finite but constant population size. However, both the replicator equation and the Moran process tell us that defection dominates over cooperation in the well-mixed population.

Hence, the evolution of cooperation needs specific mechanisms which allow natural selection to favor cooperation over defection. Several such mechanisms including kin selection,^[9] direct reciprocity,^[10] indirect reciprocity,^[11] group selection,^[12] network reciprocity,^[13–15] and so on have been broadly investigated. Network reciprocity, such as spatial reciprocity^[16] and heterogeneous reciprocity,^[17–20] is well recognized as one of the key mechanisms for the evolution of cooperation. Generally, it is reported that cooperation is viable in the death-birth Moran process on various graphs only if $k < b/c$,^[21] where k is the average degree (number of neighbors) of the network, and b and c are the benefit for defectors and cost for cooperators, respectively, when cooperators meet de-

factors. Recently, similar results have also been reported in Ref. [22] on a stochastic nongrowth network evolution model. In that model the offspring inherits a strategy of its parent and definitely links to its parent. In fact, this parent-offspring link leads assortative players to be closer and disassortative players to be alienated. This mechanism is also an implicit assumption for network reciprocity and is not so obvious to be paid much importance. Their results are in line with Hamilton's rule of kin selection,^[9] which is that frequent kin interactions promote cooperation.

In this Letter, we introduce a simple model of the coevolution based on the Moran process and the above mechanism of parent-offspring link with dynamical networks. Importantly, our work shows that it is just the parent-offspring link that Darwinian dynamics based on selection can take advantage of network structure to enhance cooperation, even though the network evolves. Thus this parent-offspring link plays a key role in network reciprocity, especially when the strategy dynamics co-evolve with the network structure. Firstly, we derive the cooperation frequency at equilibrium state by pair approximation and then discuss three usual social dilemmas: The prisoner's dilemma game (PD),^[10] the snowdrift game (SG),^[16] and the boundary prisoner's dilemma (BPD). In the framework of our model, we find that they all have a phase transition at the same value of cost-to-benefit ratio r . Our result expands the simple transition rule reported in Ref. [21] in the PD to SG and BPD cases. In PD, it is a first order transition, while in SG and BPD, it is a continuous phase transition. In our model, the simple rule results just from the parent-offspring link. We also verify our analysis with numerical simulations.

In our model, the players occupy the vertices of a graph. The edges denote links between individuals in

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terms of game interaction but not replacement. We assume that the graph varies only when reproduction and death occur. The interaction is represented by the social dilemmas associated with symmetric 2×2 games between two pure strategies, cooperators C and defectors D , in which the payoff matrix is given by

	C	D
C	R	S
D	T	P

The entries refer to payoffs of the row player. In the payoff matrix, R is the reward for mutual cooperation; P is the punishment for mutual defection. When a cooperator meets a defector, the former gets the sucker's payoff S and the latter gets the temptation to defect T . The orderings of the four values define different well-known social dilemmas: the prisoner's dilemma game (PD) ($T > R > P > S$) and the snowdrift game (SG) ($T > R > S > P$).

Initially, the players interconnect randomly to make up a random network with the average degree k and adopt either strategy C or D with equal probability. Each individual plays with all his neighbors along the network, accumulating a total payoff $\pi_C = k_C R + k_D S$ for the cooperator or $\pi_D = k_C T + k_D P$ for the defector, where k_C and k_D denote the numbers of C and D players among its k neighbors. The effective reproductive fitness of an individual of type X is then given by $1 - \omega + \omega \pi_X$, where ω determines the relative contributions of the baseline fitness and the payoff π_X resulting from interactions with its neighbors. Then, we conduct the Moran process with dynamical networks as follows:

- (i) *Selection*. An individual is selected for reproduction with a probability proportional to his fitness.
- (ii) *Reproduction*. His offspring is introduced with the same strategy of his parent and connects to his parent always and other $k - 1$ individuals randomly.
- (iii) *Replacement*. The offspring replaces a random individual except for his parent. Remove the randomly selected individual with all his links.

Here we employ global selection different from the model in Ref. [21], where their model is based on tournament selection. Firstly they randomly choose a group from the population for tournament and then select an individual with highest payoff in this group for reproduction. Thus in every generation the individual with lowest payoff in the population will have no chance to reproduce in their model. Thus, their model is a little deviated from the Moran process. In addition, our model can facilitate the analysis by pair approximation.

Now, we apply pair approximation^[16,23–25] to deduce the steady state of the system. Let P_C and P_D denote the frequencies of C and D in the population. Let $P_{CC}, P_{CD}, P_{DC}, P_{DD}$ denote the frequencies

of CC, CD, DC, DD pairs. Let $q_{X|Y}$ denote the conditional probability to find an X -player given that the adjacent node is occupied by a Y -player. The whole system can be described by only two variables, p_C and p_{CC} , with the identities^[21]

$$\begin{aligned} p_C + p_D &= 1, & q_{C|X} + q_{D|X} &= 1, \\ p_{XY} &= q_{X|Y} \cdot p_Y, & p_{CD} &= p_{DC}. \end{aligned} \quad (1)$$

The replicator dynamics of p_C is given as

$$\begin{aligned} \frac{\partial p_C}{\partial t} &= \frac{1}{N} p_D \frac{p_C f_C}{f} - \frac{1}{N} p_C \frac{p_D f_D}{f} \\ &= \frac{p_C p_D}{N f} (f_C - f_D), \end{aligned} \quad (2)$$

where the fitness of C -players and D -players read

$$\begin{cases} f_C = 1 - \omega + \omega(k q_{C|C} R + k q_{D|C} S), \\ f_D = 1 - \omega + \omega(k q_{C|D} T + k q_{D|D} P), \end{cases} \quad (3)$$

the mean fitness is

$$\bar{f} = p_C f_C + p_D f_D. \quad (4)$$

In Eq. (2), the first term denotes that a D -player is randomly selected to die and a C -player is selected for reproduction proportional to his fitness and the second term is derived vice versa.

The evolution of p_{CC} can be described as

$$\frac{\partial p_{CC}}{\partial t} = \frac{p_C f_C}{p_C f_C + p_D f_D} \frac{1 + (k - 1)p_C}{kN/2} - \frac{p_C}{kN/2} k q_{C|C}, \quad (5)$$

where the first term denotes that a C -player is selected to reproduce with probability proportional to his fitness and his offspring links to him and $(k - 1)p_C$ other C -players in the population in average. The other term denotes that a C -player, who links to $k q_{C|C}$ C -players in pair approximation, is randomly selected to die with probability p_C . There are always $kN/2$ edges in the network approximately. When the system reach stable state, $\frac{\partial p_C}{\partial t} = 0$ and $\frac{\partial p_{CC}}{\partial t} = 0$, which can be reduced to

$$f_C = f_D, \quad (6)$$

$$1 + (k - 1)p_C = k q_{C|C}. \quad (7)$$

Equation (6) tells us that C and D players have the same fitness in average at the stable system. Under this condition, the strength of selection ω will be cancelled out implying that our model is valid with any strength of selection. Equation (7) is of identity with

$$k(q_{C|C} - p_C) = p_D, \quad (8)$$

which indicates that the C -players in our model always get closer than that of the well-mixed condition at the stable state and the more D -players in the population, the closer C -players get together just due to this parent-offspring link. Then the C -players will get more benefits by assortative reciprocity so as to

promote cooperative behavior. We also find that the larger the average degree k is, the less important this parent-offspring link performs and the weaker the assortative effect is.

With the identity

$$q_{C|D} = \frac{p_C}{1 - p_C}(1 - q_{C|C}), \quad (9)$$

we can reach

$$p_C = \begin{cases} 1 + \frac{1}{k-1} \frac{R-P-(k-1)(T-R)}{T+S-R-P}, & \frac{T-R}{R-P} > \frac{1}{k-1}, \\ 1, & \frac{T-R}{R-P} < \frac{1}{k-1}, \end{cases} \quad (10)$$

from Eqs. (6) and (7). Note that the system undergoes a phase transition at

$$\frac{T-R}{R-P} = \frac{1}{k-1}, \quad (11)$$

either first-order or second-order, dependent on the value of $T + S - R - P$.

Our model can be used to discuss different social dilemmas, such as PD and SG. In the PD, a cooperator incurs a cost c to the donor and results in a benefit b to the recipient with $b > c > 0$, but a defector has no cost and does not deal out benefits. In evolutionary biology, cost and benefit are measured in terms of reproductive success. Reproduction can be genetic or cultural. The payoff matrix for the PD is given as

$$\begin{array}{c|cc} & C & D \\ \hline C & 1 & -r \\ D & 1+r & 0 \end{array}$$

with $r = c/(b - c)$ being the cost-to-benefit ratio for cooperation in the normalized form. In this game, $T - P - R + S = 0$, which is in game theory sometimes referred to as “equal gains from shifting”. The system undergoes a first-order phase transition at the critical value $r_c = 1/(k - 1)$ between 1 and 0. The population will evolve to a homogenous state with all cooperators when $r < r_c$ or all defectors when $r > r_c$. This is exactly the simple rule $b/c > k$ for network reciprocity in Ref. [21]. Our model indicates that this simple rule comes out just due to this parent-offspring link, which is the basis of kin selection in Hamilton’s rule for cooperation. In our simple model, the simple rule is satisfied in any strength of selection. The strength of selection does not affect the equilibrium frequency but just affects the convergent velocity.

In the SG,^[16,26–29] imagine two drivers on their way home that are caught in a blizzard and trapped on either side of a snowdrift. Each driver has the option to get out and start shovelling or to remain in the cozy warmth of the car. If both start shovelling each has the benefit b of getting home while sharing the labor costs c with $b > c > 0$. However, if only one shovels both drivers still get home but the lazy bum

avoids the labor costs. Thus, the payoff matrix for the SG can be given as

$$\begin{array}{c|cc} & C & D \\ \hline C & 1 & 1-r \\ D & 1+r & 0 \end{array}$$

with $r = c/(2b - c)$ being the cost-to-benefit ratio of mutual cooperation in the normalized form. As a result, evolution under replicator dynamics carried out in well-mixed populations leads to an equilibrium frequency for cooperators given by $1 - r$. But cooperation is inhibited whenever evolution in the SG takes place in a spatially structured population. Our model gives out

$$p_C = \begin{cases} 1 - r + 1/(k - 1), & r > 1/(k - 1), \\ 1, & r < 1/(k - 1), \end{cases} \quad (12)$$

which enhances cooperation compared to mixed population for any r . A continuous phase transition can also be found at $r_c = 1/(k - 1)$. The parent-offspring link is also the key role in enhancing cooperation.

Let us consider another game with payoff ordering $T > R > S = P$ between PD and SG, which has often been considered to be qualitatively equal to the PD game in the previous studies. Here we refer to it as boundary PD (BPD). The payoff matrix is commonly chosen as

$$\begin{array}{c|cc} & C & D \\ \hline C & 1 & 0 \\ D & 1+r & 0 \end{array}$$

with r being the cost-to-benefit ratio in the normalized form. In this game, the system also goes through a continuous transition at $r_c = 1/(k - 1)$. The equilibrium frequencies of cooperators p_C are given as

$$p_C = \begin{cases} \frac{1}{(k-1)r}, & r > r_c, \\ 1, & r < r_c, \end{cases} \quad (13)$$

which indicates that the assortative link can promote cooperation greatly when k is small.

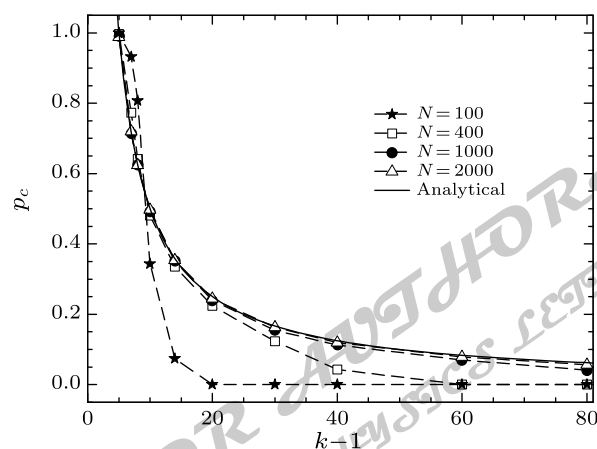


Fig. 1. Cooperation frequencies as a function of $k - 1 = [5, 7, 8, 10, 14, 20, 30, 40, 60, 80]$ with various system size N . The simulations are carried out on BPD with $r = 0.2$ and the analytical results are derived from pair approximation.

Now we do some simulations to verify our analytic discussions. In our simulations, each time step involves N three-step circular procedures in our model. As mentioned in Ref. [30], stochastic replication without mutation will enter one of the absorbing states eventually in any finite system. However the time to absorption is dependent on the system size and may be beyond our computing abilities. Thus we just refer to the transient states as equilibrium. Equilibrium frequencies of cooperators (p_c) are averaged over 100 time steps after a transient of 200 time steps. Our results are averaged on 100 different initial conditions. Here we employ global selection different from the model in Ref. [22], where they first choose a group from the population randomly and then perform selection on this group. Although their model has less time-cost for simulation, it is a little deviation from the Moran process. However, our simulations, as shown in Fig. 1, confirm that their results are very consistent with ours which are based on the Moran process. We verify their results that the small system size introduces large fluctuation which leads the results to deviate from pair approximation predictions.

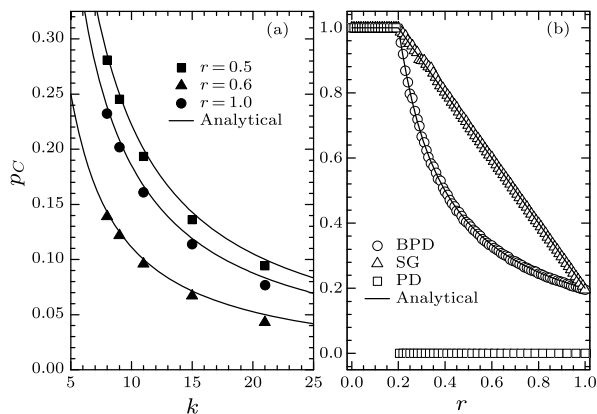


Fig. 2. (a) Cooperation frequencies as a function of average degree k for various r in BPD. The results are consistent with analysis. (b) Cooperation frequencies as a function of r in various social dilemmas with $k = 6$. All of them have a phase transition at $r = 0.2$, either first-order or continuous, which are predicted by pair approximation in main text. In both cases the system size is set as $N = 1000$, except for the conditions near the critical point, where we simulate with N from 2000 to 20000.

We also confirm the analytical results from pair approximation with numerical simulation as shown in Fig. 2. When the system size is large enough with the fluctuation being ignored, the simulated results fit well with the analytical results, whatever the cooperation frequency depends on average degree k (Fig. 2(a)) or the cost-to-benefit ratio r (Fig. 2(b)) in any of last three social dilemmas. Note that simulations verify the phase transitions at the same critical point for all dilemmas.

In summary, a simple model based on the Moran process with network dynamics has been discussed by theoretical analysis and numerical simulations. Using pair approximation, the cooperation frequencies at equilibrium states are deduced to discuss three usual social dilemmas: PD, SG and BPD. In the framework of our model, we find that they all have a phase transition at the same value of cost-to-benefit ratio. Our result expands the simple transition rule reported in Ref. [21] in the PD to SG and BPD cases. In PD, it is a first order transition, while in SG and BPD, it is a continuous phase transition. In our model, the simple rule results just from the parent-offspring link. Thus the basic mechanism for cooperation enhancement in network reciprocity is in line with Hamilton's rule of kin selection.

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