MIT Libraries | DSpace@MIT

MIT Open Access Articles

Evolutionary dynamics of general group interactions in structured populations

The MIT Faculty has made this article openly available. ***Please share*** how this access benefits you. Your story matters.

Citation: Li, Aming, Mark Broom, Jinming Du, and Long Wang. "Evolutionary dynamics of general group interactions in structured populations." Phys. Rev. E 93, 022407 (February 2016). © 2016 American Physical Society

As Published: http://dx.doi.org/10.1103/PhysRevE.93.022407

Publisher: American Physical Society

Persistent URL: http://hdl.handle.net/1721.1/101225

Version: Final published version: final published article, as it appeared in a journal, conference proceedings, or other formally published context

Terms of Use: Article is made available in accordance with the publisher's policy and may be subject to US copyright law. Please refer to the publisher's site for terms of use.

Massachusetts Institute of Technology

Evolutionary dynamics of general group interactions in structured populations

Aming Li,[1,2,3] Mark Broom,[4] Jinming Du,[1] and Long Wang[1,*]

[1]*Center for Systems and Control, College of Engineering, Peking University, Beijing 100871, China*

[2]*Center for Complex Network Research and Department of Physics, Northeastern University, Boston, Massachusetts 02115, USA*

[3]*Department of Physics, Physics of Living Systems Group, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, USA*

[4]*Department of Mathematics, City University London, Northampton Square, London EC1V 0HB, UK*

(Received 16 October 2015; revised manuscript received 24 January 2016; published 18 February 2016)

The evolution of populations is influenced by many factors, and the simple classical models have been developed in a number of important ways. Both population structure and multiplayer interactions have been shown to significantly affect the evolution of important properties, such as the level of cooperation or of aggressive behavior. Here we combine these two key factors and develop the evolutionary dynamics of general group interactions in structured populations represented by regular graphs. The traditional linear and threshold public goods games are adopted as models to address the dynamics. We show that for linear group interactions, population structure can favor the evolution of cooperation compared to the well-mixed case, and we see that the more neighbors there are, the harder it is for cooperators to persist in structured populations. We further show that threshold group interactions could lead to the emergence of cooperation even in well-mixed populations. Here population structure sometimes inhibits cooperation for the threshold public goods game, where depending on the benefit to cost ratio, the outcomes are bistability or a monomorphic population of defectors or cooperators. Our results suggest, counterintuitively, that structured populations are not always beneficial for the evolution of cooperation for nonlinear group interactions.

DOI: 10.1103/PhysRevE.93.022407

I. INTRODUCTION

The evolution of cooperation is an enduring conundrum in evolutionary biology since Darwin [1–7]. Serving as an indispensable mathematical model, evolutionary game theory [5,6,8–10] has become an effective method to quantify cooperation and predict evolutionary outcomes for different situations. Some further theoretical analyses on the evolution of cooperation have been achieved since the introduction of evolutionary dynamics in both infinite and finite populations [4,6,11–13]. Within the area of dynamics, two-player games [14–16] are frequently adopted to model typical pairwise interactions to understand the evolution of cooperation [17–26]. Considering the ubiquitously group interactions ranging from the natural world to human society, researchers recently generalized two-player games to their multiplayer versions [27–37], such as the N-person prisoner's dilemma [30,38], N-person snowdrift game [31,32], N-person stag hunt game [39], as well as the N-person ultimatum game [40]. In a typical collective action, an individual's payoff could be no longer the simple summation of many pairwise interactions [33,41], and instead it is replaced by the multiple interactive payoffs from multiplayer games, which depends on what strategies all other opponents hold in the same group. The various compositions of different strategies in group interactions give the possibility for the emergence of nonlinear fitness [29].

Evolutionary dynamics for strategies in group interactions are complex even in the ideally structureless (well-mixed) populations, with outcomes which cannot be obtained from pairwise interactions [28–30,33,34,37,42,43]. In reality, the introduction of not merely multiplayer games but also structured populations gives rise to polynomial as well as nonlinear fitness functions in evolutionary dynamics [28,29,33,34,38,44–47]. Hence it has added a lot of difficulty to conduct analytical explorations for this case. Even so, some significant work has emerged. For the cyclic population, van Veelen *et al.* [44] give analytical conditions for cooperation to evolve with general multiplayer games for any intensity of selection. Based on the unequal sharing of diffusible common goods in microbial colonies, with a particular population structure indicating the diffusible process, Allen *et al.* [45] give the analytic relation between benefits and costs guarantying the success of cooperation. Considering the typical discounted, linear, and synergistic group interactions, Li *et al.* [46,48] provide the theoretical rules for the emergence and stabilization of cooperation in structured populations represented by regular graphs.

Spatial reciprocity is generally accepted as one of the five rules facilitating the evolution of cooperation [7], and some theoretical results as well as experiments have validated this rule by illustrating the positive function of spatial interactions represented by lattice or complex networks [17,33,46,49–52]. However, we should not ignore some special cases where the detrimental effect of spatial structure on cooperation is revealed under the framework of the snowdrift game [18]. The presence of both multiplayer games and population structure enriches the outcomes of evolutionary dynamics. Moreover, as we consider general group interactions in structured populations, we are provided with a much greater chance to explore the effects of population structure on the evolution of cooperation. However, due to its inherent complexity, until now the evolutionary dynamics has only been given for some specific games or well-mixed populations [12,31,32,39,44,45,48,53,54]. Here we give the evolutionary dynamics for an arbitrary multiplayer game with two strategies in structured populations represented by regular

*longwang@pku.edu.cn

 ©2016 American Physical Society

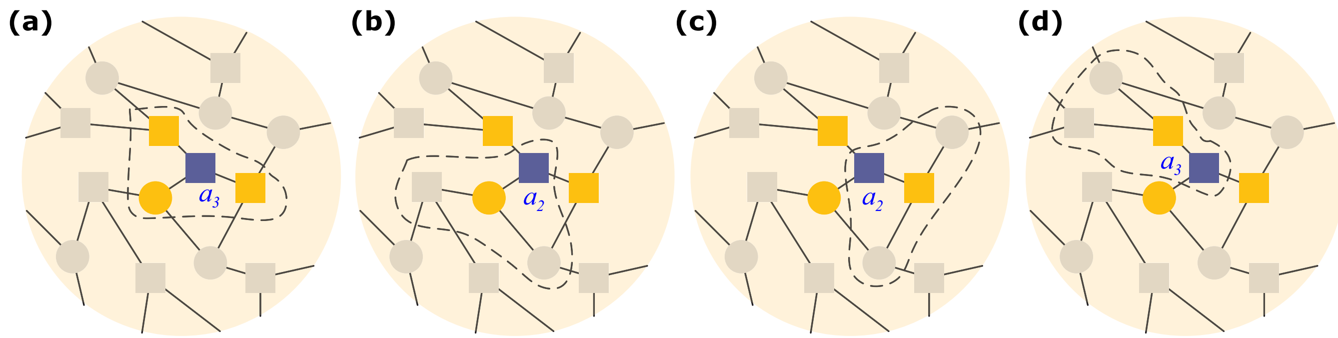

FIG. 1. Group interactions in structured populations. We choose 14 individuals from a population with degree $k = 3$ to explain group interactions in structured populations. The nodes shown as squares and circles represent individuals with strategy X and Y, respectively. The individual with a blue square has three neighbors (colored orange). During evolution, in each generation, every player will organize a game with a group of size $k + 1$ comprising itself and its neighbors. Taking the blue square as an example, we find that its payoff consists of four games: one organized by itself [circled by the dashed line in (a)] and another three organized by its three neighbors independently [circled by the dashed line in (b), (c), and (d)]. Using the payoff matrix, we give the corresponding payoff of the blue square in each panel, where the subscript indicates the number of individuals involved in the game with strategy X. Payoffs of other individuals can be calculated in the same way in each generation, and after that, a death-birth process is employed to characterize the evolution of strategies in the population.

graphs. Whatever the specific form of the payoff functions, the general multiplayer game just requires the discrete payoff values on every possible composition of strategies. Moreover, two typical multiplayer games are employed as examples to explore the evolution of cooperation in structured populations. We find that some counterintuitive results are obtained from these examples.

II. MODEL

We consider an infinitely structured population depicted by a regular graph with degree k. The vertices of the graph represent individuals. The edges determine who interacts with whom for the game payoff and who competes with whom for reproduction. In contrast to the well-mixed population, population structure allows players to interact locally; i.e., in each generation, every individual participates in k games organized by its neighbors and one game organized by itself [46,50] (see Fig. 1). Both types of game consist of $k + 1$ players. For every player in the population, after playing $k + 1$ games, they will attain payoffs accumulated from every single game in which they are involved. The payoff matrix for a general multiplayer game with size $n = k + 1$ is presented as

Opposing X players	0	1	$\cdots$	i	$\cdots$	$k-1$	k
X	a_0	a_1	$\cdots$	a_i	$\cdots$	a_{k-1}	a_k
Y	b_0	b_1	$\cdots$	b_i	$\cdots$	b_{k-1}	b_k

where a_i and b_i depict the payoffs obtained by the players with strategy X and Y, respectively. The subscript i is the number of players adopting strategy X in the game (see Fig. 1). Based on the payoffs of each individual, the "death-birth" (DB) process is employed to capture the update process, where an individual in the population is randomly chosen to die at each evolutionary step, and then all of its neighbors compete for the vacant site, gaining it with probability proportional to their fitness.

In structured populations, pair approximation is adopted to capture the evolution of strategies, where, in principle, the population structures are represented by regular graphs [19,46,55,56]. The notations p_{XY} and p_X are used to indicate the frequency of XY pairs and strategy X. For an individual with strategy Y, the probability for him or her to find someone with strategy X is $q_{X|Y}$. Hence based on the above definitions, we have the relations between these notations as

$$p_X + p_Y = 1, \quad q_{X|X} + q_{Y|X} = 1,$$
$$p_{XY} = p_Y\, q_{X|Y}, \quad p_{XY} = p_{YX},$$

where in this physical system, all variables could be represented by p_X and $q_{X|X}$.

After long calculations with the evolutionary process of the whole population captured by p_X and $q_{X|X}$, we find that the global frequency change of p_X is very slow due to the weak selection intensity w [19,46,56]. Furthermore, we have

$$q_{X|X} = \frac{k-2}{k-1} p_X + \frac{1}{k-1} \tag{1}$$

at evolutionary equilibrium based on the separation of two time scales [57]. According to the above relation between p_X and $q_{X|X}$, all variables in the dynamic evolutionary system can be expressed only by p_X mathematically when it is stable (for the detailed deviations, see [46]). It elucidates that as the composition of the structured population in term of individual strategies is stable, we could obtain the more detailed information about the population by considering only the fraction of the players with strategy X.

Hence, as we use x to indicate the expected change of the frequency of cooperators, we have the deterministic evolutionary dynamics

$$\dot{x} = \frac{w(k-2)}{k(k-1)} x(1-x) f(x), \tag{2}$$

where $f(x) = k(\pi_X^Y - \pi_Y^Y) + [(k-2)x + 1][(\pi_X^X - \pi_Y^X) - (\pi_X^Y - \pi_Y^Y)]$, and π_X^Y is the mean payoff of the player adopting strategy X, who is the neighbor of the selected individual with strategy Y. The above equation gives the evolutionary dynamics of group interactions in structured populations, from which we could obtain the deterministic evolutionary direction of the population by virtue of the sign of $f(x)$; that is, the physical change of the strategy composition is simplified by analyzing $f(x)$. Considering the configuration of the population structure around the selected individual who has k_X neighbors adopting strategy X, we have

$$\begin{aligned}
\pi_X^X &= a_{k_X} + \sum_{i=0}^{k-1} p(i) * \left[a_{i+1} + i \sum_{l=0}^{k-1} p(l) a_{l+1} \right.\\
&\quad \left. + (k-1-i) \sum_{l=0}^{k-1} q(l) a_l \right],\\
\pi_Y^X &= b_{k_X+1} + \sum_{i=0}^{k-1} q(i) * \left[b_{i+1} + i \sum_{l=0}^{k-1} p(l) b_{l+1} \right.\\
&\quad \left. + (k-1-i) \sum_{l=0}^{k-1} q(l) b_l \right],\\
\pi_X^Y &= a_{k_X-1} + \sum_{i=0}^{k-1} p(i) * \left[a_i + i \sum_{l=0}^{k-1} p(l) a_{l+1} \right.\\
&\quad \left. + (k-1-i) \sum_{l=0}^{k-1} q(l) a_l \right],\\
\pi_Y^Y &= b_{k_X} + \sum_{i=0}^{k-1} q(i) * \left[b_i + i \sum_{l=0}^{k-1} p(l) b_{l+1} \right.\\
&\quad \left. + (k-1-i) \sum_{l=0}^{k-1} q(l) b_l \right].
\end{aligned}$$

$p(i)$ and $q(i)$ are the function of i,

$$\begin{aligned}
p(i) &= \frac{(k-1)!}{i!(k-1-i)!} q_{X|X}^i q_{Y|X}^{k-1-i},\\
q(i) &= \frac{(k-1)!}{i!(k-1-i)!} q_{X|Y}^i q_{Y|Y}^{k-1-i},
\end{aligned}$$

which denote the probability for players (who are neighbors of the selected individual) adopting strategy X and Y to find i players with strategy X and $k-1-i$ with Y in the player's other $k-1$ neighbors except the selected individual, respectively, where $q_{X|X} = (k-2)x/(k-1) + 1/(k-1)$, $q_{X|Y} = (k-2)x/(k-1)$, $q_{Y|X} = (k-2)(1-x)/(k-1)$, and $q_{Y|Y} = 1-(k-2)x/(k-1)$.

III. LINEAR PUBLIC GOODS GAME

For the traditional public goods game [30], every cooperator contributes a benefit b to the group at a cost c ($b > c$), while defectors pay nothing, and eventually the totally collected benefits from all cooperators are distributed evenly to every group member irrespective of their previous strategies. As to the payoff matrix, mapping X and Y to the strategy cooperation and defection severally, we have

$$a_i = \frac{(i+1)b}{n} - c, \quad b_i = \frac{ib}{n},$$

with $0 \leqslant i \leqslant n-1$, and the corresponding evolutionary dynamics for well-mixed populations is

$$\dot{x} = x(1-x)[b/n - c], \tag{3}$$

where n is the group size. According to Eq. (2), we obtain the evolutionary dynamics (see Appendix A)

$$\dot{x} = \frac{w(n-3)}{n-2} x(1-x) \left[\frac{n+2}{n} b - nc \right] \tag{4}$$

in structured populations where every individual has k neighbors ($n = k+1$ here). Considering $n > n^2/(n+2)$, the evolutionary dynamics indicates that the structured populations could better pave the way for cooperation than the structureless cases [see Figs. 2(a), 2(b), 2(d), and 2(e)]. It has also been pointed out that the benefit and cost of the cooperative behavior only experience a linear payoff transformation as we move from the structureless population to the structured [48]. Now let us consider the net benefit $\bar{b}$ and cost $\bar{c}$ for a cooperator. We have the relations

$$\bar{c} = c - \frac{b}{n}, \quad \bar{b} = \frac{n-1}{n} b$$

between b and $\bar{b}$, c and $\bar{c}$. Hence we get that cooperation could flourish in a structured population if

$$\frac{\bar{b}}{\bar{c}} > \frac{n(n-1)}{2}. \tag{5}$$

This means that the system will always end up in full cooperation if the above condition is satisfied. As we have shown that, for the structured population represented by the regular graph with degree k, every player has k neighbors and is engaged in group interactions with size $n = k+1$. Our results for group interactions captured by the public goods game in structured populations suggest that cooperators will gain a foothold if the net benefit and net cost ratio $\bar{b}/\bar{c}$ exceeds half of the product of the number of neighbors and the size of the group interactions.

IV. THRESHOLD PUBLIC GOODS GAME

For the threshold public goods game (also called the n-person stag-hunt dilemma [39]), public goods is available as the number of cooperators in the group meets a predetermined threshold, and, if not, meaning that the collective target is not achieved, every player gets nothing while cooperators still suffer the cost they have paid. In this case, we have

$$\begin{aligned}
a_i &= \frac{i+1}{n} b\theta(i-M+1) - c,\\
b_i &= \frac{i}{n} b\theta(i-M),
\end{aligned} \tag{6}$$

where M is the threshold for the collective target, and the Heaviside step function $\theta(x)$ satisfies $\theta(x<0) = 0$ and $\theta(x \geqslant 0) = 1$. As $M = 0$ or 1, the threshold public goods game degenerates to its linear version. Here, for simplicity, we consider the largest threshold, $M = n$.

For the replicator dynamics in well-mixed populations [6], we have

$$\dot{x} = x(1-x)(bx^{n-1} - c),$$

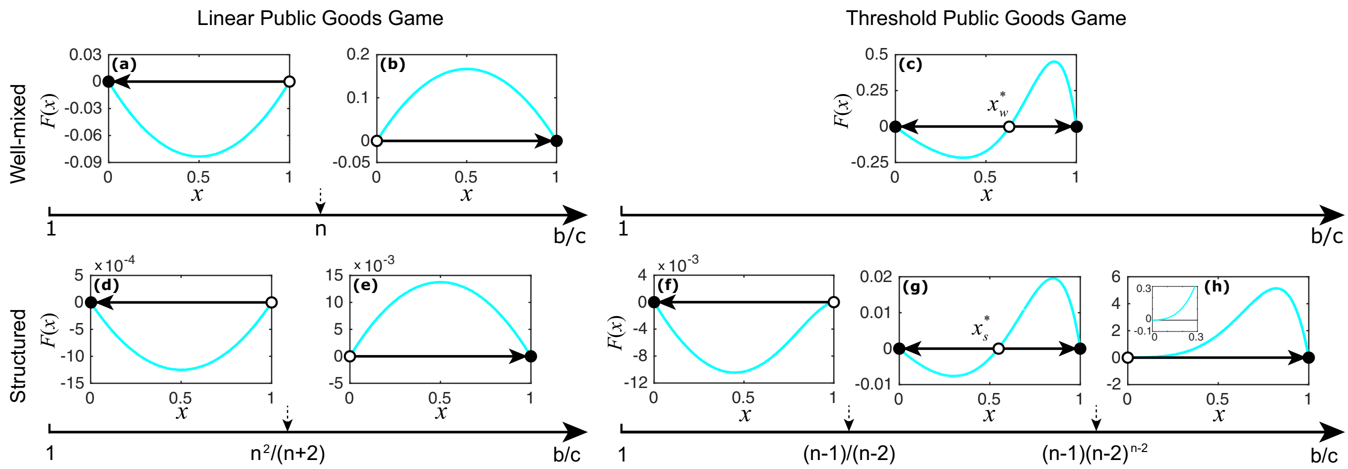

FIG. 2. Evolutionary dynamics for linear and threshold public goods games in well-mixed and structured populations. Each arrow below the panels gives the range of benefit-to-cost ratio b/c, up to which the corresponding evolutionary dynamics are shown. The direction of selection dynamics is indicated by the arrow in each panel, where the small solid circle represents a stable equilibrium and an empty circle represents an unstable equilibrium. In structured populations, the group size is $n = k + 1$. In (c), the internal unstable equilibrium is x_w^*, and for (g) it is x_s^*. In (h) the inset is employed to show that $F(x) > 0$ as $x \to 0$, and it shares the same labels as the main panel. Parameters are $w = 0.01, c = 1, k = 5, n = 6$, and the others for (a) and (d) are $b = 4$, (b), (c), (e), and (g) $b = 10$, (f) $b = 1.1$, (h) $b = 2000$.

where n is the group size. In this case, we find bistability of the evolutionary outcomes, suggesting that the simple nonlinear group interactions (with maximum threshold) give the possibility for cooperators to take over the whole population [see Fig. 2(c)] whatever the value of b/c; i.e., if the initial frequency of cooperators is bigger than $x_w^* = \sqrt[n-1]{c/b}$, cooperators will occupy the whole population. However, for the linear public goods game, it is impossible for cooperators to take over the population as $b/c < n$.

When we consider the population structure, according to the Eq. (2), the evolutionary dynamics (see Appendix B) is

$$\dot{x} = \frac{w\,(n-3)}{(n-1)(n-2)}\,x\,(1-x) \times \left\{ bn\frac{[(n-3)x+1]^{n-1}}{(n-2)^{n-2}} - n(n-1)c \right\}. \tag{7}$$

Hence we have that cooperators could take over the population (see Appendix B) if and only if

$$\frac{b}{c} > \frac{n-1}{n-2}. \tag{8}$$

For defectors, the criterion is

$$\frac{b}{c} > (n-1)(n-2)^{n-2}. \tag{9}$$

The evolutionary outcomes are divided into three cases based on the value of b/c [see Figs. 2(f) to 2(h)], where pure defectors, bistability of defectors and cooperators, and pure cooperators are presented. It shows that a structured population could favor the evolution of cooperation more than a well-mixed population when $b/c > (n-1)(n-2)^{n-2}$ [see Fig. 2(h)], given that in the former case the population will merely consist of cooperators. When b/c decreases but is bigger than $(n-1)/(n-2)$, the advantage of cooperators declines, where, similarly to the well-mixed cases, an internal unstable equilibrium $x_s^* = [\sqrt[n-1]{(n-1)(n-2)^{n-2}c/b} - 1]/(n-3)$ emerges [see Fig. 2(g)]. However, we should not miss the situation with $b/c < (n-1)/(n-2)$ where cooperators become extinct [see Fig. 2(f)], which will never happen for well-mixed populations accompanied by the cooperative attraction interval $(\sqrt[n-1]{(n-2)/(n-1)}, 1]$ [see Fig. 2(c)], telling us that population structure is not always beneficial for cooperators.

V. DISCUSSION AND CONCLUSIONS

Population structure invokes much more complexity in exploring the evolution of cooperation under the metaphor of multiplayer games; thus Monte Carlo numerical simulations are frequently employed to investigate this issue. Here we theoretically address the evolutionary dynamics of general group interactions in structured populations represented by regular graphs, where the payoff functions are not necessarily continuous. Two popular examples, linear and threshold public goods games, are adopted to illustrate the dynamics. We find that the threshold public goods game could give the possibility of the emergence of cooperation with the maximum threshold even when the benefit to cost ratio b/c is small in well-mixed populations, which is impossible for the linear case. Counterintuitively, we find that population structure is not always helpful for the evolution of cooperation under simple nonlinear group interactions (for example, the public goods game with maximum threshold). Our results give another case demonstrating that spatial reciprocity sometimes cannot facilitate the evolution of cooperation under nonlinear group interactions, in addition to the sole preceding one under the metaphor of the snowdrift game [18].

As we explore the effects of population structure on the evolution of cooperation for group interactions, the concept of total payoffs [46,50] is adopted to capture the interactions, where each individual acquires payoffs from the game organized by itself as well as its neighbors. However for well-mixed populations, the average payoff for each individual is usually considered; i.e., it is the average payoff from one group interaction for individuals with different strategies. We have retained these conventions, since they do not affect our substantive results; if we had used the total payoff for our well-mixed populations, for example, the rate of change in the replicator dynamics would be increased, but the phase space and equilibria would be completely unchanged.

At first sight it is puzzling that, following Eq. (1), structured populations are more favorable for cooperation (strategy X) than the well-mixed population, given that the conditional probability clearly means that neighbors are more likely than random to be of their own type. For the threshold public goods game, a tightly clustered group of defectors would score zero, but this would be better than their cooperator neighbors, as any such neighbor would likely have contributions from games involving at least one defector, giving a negative reward. In the well-mixed case, this would not be true and cooperators would be more likely to receive benefits. In particular for the structured game, one of the contributions to an individual's reward is the game centered on an individual that it might replace. Thus if we consider the possibility of a cooperator replacing a defector, the defector will have a contribution from the cooperator-centered game, and the cooperator will have a contribution from the defector-centred game. In the well-mixed game this is not the case as it involves a (or several) random group(s) including the given individual. From the perspective of theory, we could consider an example like this: assuming there are $k+1$ cooperators (strategy X) in a structured population with the configuration of a cooperator surrounded by k cooperator neighbors, then we have $q_{X|X} = 2/(k+1)$ and $p_X = (k-3)/[(k+1)(k-2)]$ for the structured population according to Eq. (1). For the well-mixed case, $q_{X|X} = p_X$, and $q_{X|X}$ could be smaller than that for its structured counterpart; however, it is possible for well-mixed populations to have more cooperators than structured ones when $(k-3)/[(k+1)(k-2)] < p_X < 2/(k+1)$. Thus it is possible for well-mixed populations sometimes to be better for cooperation (X) than structured populations. We note that the same relationship as Eq. (1) also occurs for pairwise interactions [19] as well as group interactions with synergy and discounting [46], and it shows that, in probability, population structure could favor the evolution of cooperation [17].

Furthermore, the coevolution of population structure and strategy is explored analytically using linking dynamics, where the evolutionary dynamics derived from well-mixed populations [12] could give good approximations for that [22]. For general group interactions, it is worth exploring the validation of general evolutionary dynamics on situations where the population structure (not well-mixed) is allowed to switch during evolution (also known as coevolutionary dynamics [58]). Here our result may provide a theoretical approximation for more complicated evolutionary scenarios with the evolution of enormous configurations of population structures.

ACKNOWLEDGMENTS

The authors thank the members of Barabási laboratory for helpful discussions. A.L., J.D., and L.W. are supported by NSFC (Grants No. 61375120 and No. 61533001). A.L. also acknowledges the support from China Scholarship Council (201406010195). M.B. is supported by funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie Grant Agreement No. 690817.

APPENDIX A: THE DERIVATION PROCESS OF EVOLUTIONARY DYNAMICS FOR THE PUBLIC GOODS GAME

For the public goods game, using X and Y to represent cooperation represented by C) and defection (represented by D), we have

$$\sum_{i=0}^{k-1} p(i)a_i = \sum_{i=0}^{k-1} \frac{(k-1)!}{i!(k-1-i)!} q_{C|C}^{i} q_{D|C}^{k-1-i}\left[\frac{(i+1)b}{k+1} - c\right]$$

$$= -c + \frac{b}{k+1}\left[1 + \sum_{i=1}^{k-1} \frac{(k-1)!}{(i-1)!(k-1-i)!} q_{C|C}^{i} q_{D|C}^{k-1-i}\right] = -c + \frac{b}{k+1}[1+(k-1)q_{C|C}],$$

$$\sum_{l=0}^{k-1} p(l)a_{l+1} = \sum_{l=0}^{k-1} \frac{(k-1)!}{l!(k-1-l)!} q_{C|C}^{l} q_{D|C}^{k-1-l}\left[\frac{(l+2)b}{k+1} - c\right] = -c + \frac{b}{k+1}[2+(k-1)q_{C|C}],$$

$$\sum_{l=0}^{k-1} q(l)a_l = \sum_{l=0}^{k-1} \frac{(k-1)!}{l!(k-1-l)!} q_{C|D}^{l} q_{D|D}^{k-1-l}\left[\frac{(l+1)b}{k+1} - c\right] = -c + \frac{b}{k+1}[1+(k-1)q_{C|D}],$$

$$\sum_{i=0}^{k-1} q(i)b_i = \sum_{i=0}^{k-1} \frac{(k-1)!}{i!(k-1-i)!} q_{C|D}^{i} q_{D|D}^{k-1-i} \frac{ib}{k+1} = \frac{b}{k+1}(k-1)q_{C|D} = \sum_{l=0}^{k-1} q(l)b_l,$$

and

$$\sum_{l=0}^{k-1} p(l)b_{l+1} = \sum_{l=0}^{k-1} \frac{(k-1)!}{l!(k-1-l)!} q_{C|D}^{l} q_{D|D}^{k-1-l} \frac{(l+1)b}{k+1} = \frac{b}{k+1}[1+(k-1)q_{C|C}].$$

Hence we obtain

$$\begin{aligned}
\pi_C^D - \pi_D^D &= a_{k_C-1} - b_{k_C} + \sum_{i=0}^{k-1} p(i)a_i - \sum_{i=0}^{k-1} q(i)b_i + \sum_{i=0}^{k-1} p(i)*\left[i\sum_{l=0}^{k-1} p(l)a_{l+1} + (k-1-i)\sum_{l=0}^{k-1} q(l)a_l\right] \\
&\quad - \sum_{i=0}^{k-1} q(i)*\left[i\sum_{l=0}^{k-1} p(l)b_{l+1} + (k-1-i)\sum_{l=0}^{k-1} q(l)b_l\right] \\
&= -c - c + \frac{b}{k+1}[1+(k-1)q_{C|C}] - \frac{b}{k+1}(k-1)q_{C|D} + \sum_{i=0}^{k-1} p(i)*\left(i*\left\{-c+\frac{b}{k+1}[2+(k-1)q_{C|C}]\right\}\right. \\
&\quad \left.+(k-1-i)\left\{-c+\frac{b}{k+1}[1+(k-1)q_{C|D}]\right)\right\} \\
&\quad - \sum_{i=0}^{k-1} q(i)*\left\{i*\frac{b}{k+1}[1+(k-1)q_{C|C}] + (k-1-i)\frac{b}{k+1}(k-1)q_{C|D}\right\} \\
&= -2c + \frac{b}{k+1}[1+(k-1)(q_{C|C}-q_{C|D})] + \sum_{i=0}^{k-1} p(i)*\left\{-(k-1)c + \frac{b}{k+1}[2i+k-1+(k^2-3k+2)p_C]\right\} \\
&\quad - \sum_{i=0}^{k-1} q(i)\frac{b}{k+1}[2i+(k^2-3k+2)p_C] \\
&= -2c + \frac{2b}{k+1} - (k-1)c + \frac{b}{k+1}(k-1) + \frac{2b}{k+1}\sum_{i=0}^{k-1} i[p(i)-q(i)] \\
&= -(k+1)c + b + \frac{2b}{k+1} = \frac{(k+3)b}{k+1} - (k+1)c
\end{aligned} \tag{A1}$$

and

$$\begin{aligned}
\pi_C^C - \pi_D^C - \left(\pi_C^D - \pi_D^D\right) &= a_{k_C} - b_{k_C+1} - \left(a_{k_C-1} - b_{k_C}\right) + \sum_{i=0}^{k-1} p(i)(a_{i+1}-a_i) + \sum_{i=0}^{k-1} q(i)(b_i - b_{i+1}) \\
&= \frac{b}{k+1}\sum_{i=0}^{k-1}[p(i)-q(i)] = 0.
\end{aligned} \tag{A2}$$

Therefore, substituting Eqs. (A1) and (A2) into Eq. (2), we get the evolutionary dynamics (4) for the public goods game.

APPENDIX B: THE DERIVATION PROCESS OF EVOLUTIONARY DYNAMICS FOR THE THRESHOLD PUBLIC GOODS GAME

For the threshold public goods game shown in Eq. (6) with $M = k+1$, we have

$$\left(\pi_C^C - \pi_D^C\right) - \left(\pi_C^D - \pi_D^D\right) = p(k-1)(a_k - a_{k-1}) = b\left(\frac{k-2}{k-1}x + \frac{1}{k-1}\right)^{k-1}$$

and

$$\begin{aligned}
\pi_C^D - \pi_D^D &= -c - \sum_{i=0}^{k-1} p(i)\,c + \sum_{i=0}^{k-1} p(i)\left[i\sum_{l=0}^{k-1} p(l)\,(-c) + i\;p\,(k-1)\,b + (k-1-i)\sum_{l=0}^{k-1} q(l)\,(-c)\right] \\
&= b\,(k-1)\left(\frac{k-2}{k-1}x + \frac{1}{k-1}\right)^k - (k+1)c.
\end{aligned}$$

Hence we obtain the evolutionary dynamics (7) for the threshold public goods game with $n = k+1$.

Denoting $\dot{x} = F(x)$, we have $F(0) = F(1) = 0$, and

$$F'(x) = \frac{w\,(k-2)}{k\,(k-1)}\,[(1-x)\,f(x) - x\,f(x) + x\,(1-x)\,f'(x)].$$

If $F^{'}(1) < 0$, it means that $x = 1$ is stable, and we have

$$F'(1) < 0 \Longleftrightarrow f(1) > 0 \Longleftrightarrow \frac{b}{c} > \frac{k}{k-1}.$$

If $F^{'}(0) > 0$, it means that $x = 0$ is unstable, and we have

$$F'(0) > 0 \Longleftrightarrow f(0) > 0 \Longleftrightarrow \frac{b}{c} > k\,(k-1)^{k-1}.$$

Thus the criteria (8) and (9) are obtained for $n = k + 1$.

---

[1] C. Darwin, *On the Origin of Species* (John Murray, London, 1859).
[2] J. von Neumann and O. Morgenstern, *Theory of Games and Economic Behavior* (Princeton University Press, Princeton, 1944).
[3] W. D. Hamilton, Am. Nat. **97**, 354 (1963).
[4] P. D. Taylor and L. B. Jonker, Math. Biosci. **40**, 145 (1978).
[5] J. Smith, *Evolution and the Theory of Games* (Cambridge University Press, Cambridge, 1982).
[6] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics* (Cambridge University Press, Cambridge, 1998).
[7] M. A. Nowak, Science **314**, 1560 (2006).
[8] J. M. Smith and G. R. Price, Nature (London) **246**, 15 (1973).
[9] M. A. Nowak and K. Sigmund, Science **303**, 793 (2004).
[10] M. Broom and J. Rychtář, J. Theor. Bio. **302**, 70 (2012).
[11] M. A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg, Nature (London) **428**, 646 (2004).
[12] A. Traulsen, J. C. Claussen, and C. Hauert, Phys. Rev. Lett. **95**, 238701 (2005).
[13] A. Traulsen, M. A. Nowak, and J. M. Pacheco, Phys. Rev. E **74**, 011909 (2006).
[14] A. Rapoport and A. Chammah, *Prisoner's Dilemma: A Study in Conflict and Cooperation* (University of Michigan Press, Ann Arbor, 1965).
[15] R. Sugden, *The Economics of Rights, Co-operation and Welfare* (Blackwell, Oxford, 1986).
[16] B. Skyrms, *The Stag Hunt and the Evolution of Social Structure* (Cambridge University Press, Cambridge, 2004).
[17] M. A. Nowak and R. May, Nature (London) **359**, 826 (1992).
[18] C. Hauert and M. Doebeli, Nature (London) **428**, 643 (2004).
[19] H. Ohtsuki, C. Hauert, E. Lieberman, and M. A. Nowak, Nature (London) **441**, 502 (2006).
[20] F. Fu, C. Hauert, M. A. Nowak, and L. Wang, Phys. Rev. E **78**, 026117 (2008).
[21] W.-X. Wang, J. Ren, G. Chen, and B.-H. Wang, Phys. Rev. E **74**, 056113 (2006).
[22] B. Wu, D. Zhou, F. Fu, Q. Luo, L. Wang, and A. Traulsen, PLoS ONE **5**, e11187 (2010).
[23] B. Allen and M. A. Nowak, EMS Surv. Math. Sci. **1**, 113 (2014).
[24] P. Shakarian, P. Roos, and A. Johnson, Biosystems **107**, 66 (2012).
[25] M. Broom and J. Rychtar, *Game-Theoretical Models in Biology*, Chapman & Hall/CRC Mathematical and Computational Biology (Taylor & Francis, Philadelphia, 2013).
[26] J. Zhang and C. Zhang, Eur. Phys. J. B **88**, 136 (2015).
[27] M. Broom, C. Cannings, and G. Vickers, B. Math. Biol. **59**, 931 (1997).
[28] C. Gokhale and A. Traulsen, Proc. Natl. Acad. Sci. USA **107**, 5500 (2010).
[29] M. Archetti and I. Scheuring, J. Theor. Bio. **299**, 9 (2012).
[30] C. Hauert, S. Monte, J. Hofbauer, and K. Sigmund, J. Theor. Bio. **218**, 187 (2002).
[31] D. F. Zheng, H. P. Yin, C. H. Chan, and P. M. Hui, Europhys. Lett. **80**, 18002 (2007).
[32] M. O. Souza, J. M. Pacheco, and F. C. Santos, J. Theor. Bio. **260**, 581 (2009).
[33] M. Perc, J. Gómez-Gardeñes, A. Szolnoki, L. M. Floría, and Y. Moreno, J. R. Soc. Interface **10**, 20120997 (2013).
[34] B. Wu, A. Traulsen, and C. S. Gokhale, Games **4**, 182 (2013).
[35] A. Li, T. Wu, R. Cong, and L. Wang, Europhys. Lett. **103**, 30007 (2013).
[36] J. Du, B. Wu, and L. Wang, Phys. Rev. E **85**, 056117 (2012).
[37] J. Du, B. Wu, P. M. Altrock, and L. Wang, J. R. Soc. Interface **11**, 20140077 (2014).
[38] M. Archetti and I. Scheuring, Evolution **65**, 1140 (2011).
[39] J. M. Pacheco, F. C. Santos, M. O. Souza, and B. Skyrms, Proc. R. Soc. London, Ser. B **276**, 315 (2009).
[40] F. P. Santos, F. C. Santos, A. Paiva, and J. M. Pacheco, J. Theor. Bio. **378**, 96 (2015).
[41] A. Szolnoki, M. Perc, and G. Szabó, Phys. Rev. E **80**, 056109 (2009).
[42] S. Kurokawa and Y. Ihara, Proc. R. Soc. London, Ser. B **276**, 1379 (2009).
[43] C. S. Gokhale and A. Traulsen, J. Theor. Bio. **283**, 180 (2011).
[44] M. van Veelen and M. A. Nowak, J. Theor. Bio. **292**, 116 (2012).
[45] B. Allen, J. Gore, and M. A. Nowak, eLife **2**, e01169 (2013).
[46] A. Li, B. Wu, and L. Wang, Sci. Rep. **4**, 5536 (2014).
[47] L. Zhou, A. Li, and L. Wang, Europhys. Lett. **110**, 60006 (2015).
[48] A. Li and L. Wang, J. Theor. Bio. **377**, 57 (2015).
[49] F. C. Santos and J. M. Pacheco, Phys. Rev. Lett. **95**, 098104 (2005).
[50] F. C. Santos, M. D. Santos, and J. M. Pacheco, Nature (London) **454**, 213 (2008).
[51] M. Perc and A. Szolnoki, Phys. Rev. E **77**, 011904 (2008).
[52] D. G. Rand, M. A. Nowak, J. H. Fowler, and N. A. Christakis, Proc. Natl. Acad. Sci. USA **111**, 17093 (2014).
[53] F. C. Santos and J. M. Pacheco, Proc. Natl. Acad. Sci. USA **108**, 10421 (2011).
[54] M. D. Santos, F. L. Pinheiro, F. C. Santos, and J. M. Pacheco, J. Theor. Bio. **315**, 81 (2012).
[55] H. Matsuda, N. Ogita, A. Sasaki, and K. Sato, Prog. Theor. Phys. **88**, 1035 (1992).
[56] T. Konno, J. Theor. Bio. **269**, 224 (2011).
[57] H. Khalil, *Nonlinear Systems* (Prentice Hall, Upper Saddle River, NJ, 2002).
[58] M. Perc and A. Szolnoki, Biosystems **99**, 109 (2010).