Evolutionary dynamics of general group interactions in structured populations

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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 guaranteeing 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
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,
where the vacant site, gaining it with probability proportional to their
evolutionary step, and then all of its neighbors compete for
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 princi-
ple, the population structures are represented by regular
graphs [19,46,55,56]. The notations \( p_{XY} \) and \( q_X \) 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 \( q'_X \). Hence based on the above
definitions, we have the relations between these notations as
\[
p_X + p_Y = 1, \quad q_{X|X} + q_{Y|X} = 1, \\
p_{XY} = p_Y q_{X|Y}, \quad p_X = p_{XY},
\]
where in this physical system, all variables could be repre-
sented by \( p_X \) and \( q_{X|Y} \).

After long calculations with the evolutionary process of the
whole population captured by \( p_X \) and \( q_{X|Y} \), 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
\[
q_{X|X} = \frac{k - 2}{k - 1} p_X + \frac{1}{k - 1}
\]
at evolutionary equilibrium based on the separation of two
time scales [57]. According to the above relation between \( p_X \)
and \( q_{X|Y} \), 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
\[
\dot{x} = \frac{w(k - 2)}{k(k - 1)} x(1 - x) f(x),
\]
where \( f(x) = k(\pi^X_X - \pi^Y_Y) + [(k - 2)x + 1][(\pi^X_X - \pi^Y_Y) - (\pi^X_Y - \pi^Y_Y)] \), and \( \pi^Y_Y \) 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

<table>
<thead>
<tr>
<th>Opposing X players</th>
<th>0</th>
<th>1</th>
<th>…</th>
<th>( i )</th>
<th>…</th>
<th>( k - 1 )</th>
<th>( k )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( X )</td>
<td>( a_0 )</td>
<td>( a_1 )</td>
<td>…</td>
<td>( a_i )</td>
<td>…</td>
<td>( a_{k-1} )</td>
<td>( a_k )</td>
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<tr>
<td>( Y )</td>
<td>( b_0 )</td>
<td>( b_1 )</td>
<td>…</td>
<td>( b_i )</td>
<td>…</td>
<td>( b_{k-1} )</td>
<td>( b_k )</td>
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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.
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

$$
\pi_X^X = a_{k_X} + \sum_{i=0}^{k-1} \frac{p(i)}{i!(k-1-i)!} q_{X|X}^{k-1-i},
$$

and

$$
\pi_X^Y = b_{k_X+1} + \sum_{i=0}^{k-1} \frac{p(i)}{i!(k-1-i)!} q_{Y|Y}^{k-1-i},
$$

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

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

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

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

in structured populations where every individual has $k$ neighbors ($n = k + 1$ here). Considering $n > \frac{n^2}{(n+1)}$, 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 $b$ and cost $c$ for a cooperator. We have the relations

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

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

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

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.

### 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 $0 \leq i \leq n-1$. For the replicator dynamics in well-mixed populations [6], we have

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

where $x$ is the proportion of cooperators in the population.
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 \( x^*_c = \sqrt[n]{c/b} \), 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

\[
\dot{x} = \frac{w(n-3)}{(n-1)(n-2)} \frac{x(1-x)}{\left(\frac{n-3}{n-2}\right)^{n-1}} - n(n-1)c.
\]

(7)

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

\[
\frac{b}{c} > \frac{n-1}{n-2}.
\]

(8)

For defectors, the criterion is

\[
\frac{b}{c} > \frac{n-1}{n-2}^{n-2}.
\]

(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 \( x^*_c = \sqrt[n]{(n-1)(n-2)^{n-2}c/b} \) emerges [see Fig. 2(g)]. However, we should not miss the case of \( b/c < (n-1)(n-2) \) where cooperators become extinct [see Fig. 2(f)], which will never happen for well-mixed populations accompanied by the cooperative attraction interval \((\sqrt[n]{(n-2)/(n-1)},1]\) [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 would merely consist of cooperators.
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 cooperators, then we have
\[ q_{X(k+1)} = 2/(k+1) \]
and
\[ p_X = (k-3)/(k+1)(k-2) \]
for the structured population according to Eq. (1). For the well-mixed
case, \( q_{X(k+1)} = p_X \), and \( q_{X(k+1)} \) 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.

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**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

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

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

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

and

\[
\sum_{i=0}^{k-1} p(i) b_{i+1} = \sum_{i=0}^{k-1} \frac{(k-1)!}{i!(k-1-i)!} q_{C|D}^{k-1-i} q_{D|D}^{i} \left[ \frac{(i+1)b}{k+1} \right] = \frac{b}{k+1} [1 + (k-1)q_{C|C}].
\]
Hence we obtain

\[
\pi_C^D - \pi_D^D = a_{c_{k-1}} - b_{c_{k}} + \sum_{i=0}^{k-1} p(i)a_i - \sum_{i=0}^{k-1} q(i)b_i + \sum_{i=0}^{k-1} p(i) \left[ \sum_{i=0}^{k-1} p(l)a_{i+1} + (k - 1 - i) \sum_{l=0}^{k-1} q(l)a_l \right] \\
- \sum_{i=0}^{k-1} q(i) \left[ i \sum_{l=0}^{k-1} p(l)b_{i+1} + (k - 1 - i) \sum_{l=0}^{k-1} q(l)b_l \right] \\
= -c - c + \frac{b}{k+1} [1 + (k - 1)q_C|C|] - \frac{b}{k+1} (k - 1)q_C|D| + \sum_{i=0}^{k-1} p(i) \left\{ \left( -c + \frac{b}{k+1} [2 + (k - 1)q_C|C|] \right) \\
+ (k - 1 - i) \left\{ -c + \frac{b}{k+1} [1 + (k - 1)q_C|D|] \right\} \right\} \\
- \sum_{i=0}^{k-1} q(i) \left\{ i \sum_{l=0}^{k-1} p(l)[1 + (k - 1)q_C|C|] + (k - 1 - i) \frac{b}{k+1} (k - 1)q_C|D| \right\} \\
= -2c + \frac{b}{k+1} [1 + (k - 1)(q_C|C| - q_C|D|)] + \sum_{i=0}^{k-1} p(i) \left\{ -(k - 1)c + \frac{b}{k+1} [2i + k - 1 + (k^2 - 3k + 2)p_C] \right\} \\
- \sum_{i=0}^{k-1} q(i) \frac{b}{k+1} [2i + (k^2 - 3k + 2)p_C] \\
= -2c + \frac{2b}{k+1} - (k - 1)c + \frac{b}{k+1} (k - 1) + \frac{2b}{k+1} \sum_{i=0}^{k-1} i[p(i) - q(i)] \\
= -(k + 1)c + b + \frac{2b}{k+1} = \frac{(k + 3)b}{k+1} - (k + 1)c \tag{A1}
\]

and

\[
\pi_C^C - \pi_D^C - (\pi_C^D - \pi_D^D) = a_{c_{k}} - b_{c_{k+1}} - (a_{c_{k-1}} - b_{c_{k-1}}) + \sum_{i=0}^{k-1} p(i)(a_{i+1} - a_i) + \sum_{i=0}^{k-1} q(i)(b_i - b_{i+1}) \\
= \frac{b}{k+1} \sum_{i=0}^{k-1} [p(i) - q(i)] = 0. \tag{A2}
\]

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

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

and

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

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

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

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

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

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

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