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Cooperation with both synergistic and local interactions can be worse than each alone

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Cooperation is ubiquitous ranging from multicellular organisms to human societies. Population structures indicating individuals' limited interaction ranges are crucial to understand this issue. But it remains unknown to what extent multiple interactions involving nonlinearity in payoff influence the cooperation in structured populations. Here we show a rule, which determines the emergence and stabilization of cooperation, under multiple discounted, linear, and synergistic interactions. The rule is validated by simulations in homogenous and heterogenous structured populations. We find that the more neighbours there are the harder for cooperation to evolve for multiple interactions with linearity and discounting. For synergistic scenario, however, distinct from its pairwise counterpart, moderate number of neighbours can be the worst, indicating that synergistic interactions work with strangers but not with neighbours. Our results suggest that the combination of different factors which promotes cooperation alone can be worse than that with every single factor.

The particulars of why and how cooperation evolves have perplexed evolutionary biologists and sociologists enduringly^{1–4}. A cooperator takes an altruistic action which supplies a benefit, b , for another individual at a cost, c , while a defector does nothing. One of the main tasks of evolutionary theory is to explain why and how cooperation is present. Evolutionary game theory provides a powerful platform to understand the evolution of cooperation in unstructured populations, with the replicator equation in infinite populations³ and stochastic dynamics in finite populations^{5–7}. Recently the assumption of a well mixed population is removed, and the population allows individuals to interact locally^{8,9}. Typically networks are adopted to depict such population structure, since it is simple in definition, while complex in property^{8,10}. The nodes of the network represent individuals, while the edges denote connections in between^{11,12}. In this way, a network paves the way to capture the intrinsic idea of local interaction^{13,14}. Individuals interact with their neighbours only. In particular, the degree of a node represents the number of neighbours of the focal individual, which indicates the interaction range. These network structures are widespread in human organizations^{15,16}, scientific collaboration among researchers¹⁷, and even somatic evolution within multicellular organisms¹⁸. However, for structured populations, in contrast with that in the well mixed case^{5,6}, it becomes challenging to analyze the evolutionary dynamics theoretically. This is because enormous possible topological configurations arise during the process of evolution^{19–21}. In spite of being challenging, there are advances in the analytical methods^{12,22–26}. The main result is that local interactions can pave the way for the emergence of cooperation.

The conflict between cooperation and defection is captured by the prisoner's dilemma in the beginning^{2,27}, a pairwise game. Though the "Tragedy of Commons", a multi-player game, was introduced to depict this dilemma long before²⁸, it has not been popular until recently owing to its complexity^{29–38}. This is also true in structured populations: For pairwise interactions, conditions for cooperators to be selected over defectors have been theoretically investigated in general structured populations^{12,22,24}. For multiple interactions, however, only two extreme types of network structure with cycle³⁹ and well mixed populations^{32,34,35,40} have been addressed. For the network degree in between the minimum (the cycle) and the maximum (well-mixed population), it is unclear under what conditions cooperation outperforms defection. Besides, we introduce nonlinearity in the public goods, which is intrinsic to the fitness of multi-player games. For simplicity, the synergistic and discountable effects of the public goods are adopted: These effects are wide spread in microbes^{41–43}. As a cluster of microbes secretes enzymes to digest the extracellular resource, the benefit of the secreted enzyme (public goods) provided

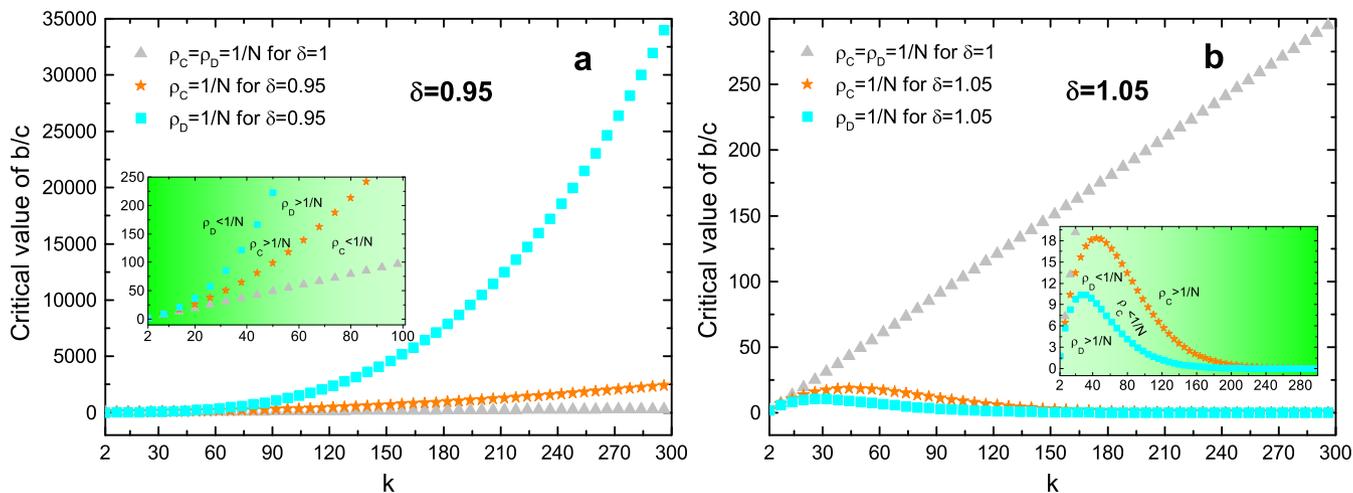


Figure 2 | The critical value of the benefit-to-cost ratio for natural selection favoring emergence and stabilization of cooperation (defection). We set $\delta = 0.95$ (a) and 1.05 (b) to represent respectively the weak discounting and synergy in structured populations with $N = 5 \times 10^3$ numerically. For discounting effect $\delta < 1$, both the critical values for $\rho_C = 1/N$ and $\rho_D = 1/N$ increase rapidly with average degree k . Yet the critical value for $\rho_D = 1/N$ is greater than that of $\rho_C = 1/N$, and it also increases much faster. This shows that in the discounting public goods game, with the increase in the number of neighbours, it is easier for a cooperator to be invasive ($\rho_C > 1/N$) than to be stabilized ($\rho_D < 1/N$). For synergy effect $\delta > 1$, the critical value for $\rho_C = 1/N$ is greater than that of $\rho_D = 1/N$ for any neighbour size. This shows that it is easier for cooperation to be stabilized ($\rho_D < 1/N$) than to be invasive ($\rho_C > 1/N$). Interestingly, both the critical values for $\rho_C = 1/N$ and $\rho_D = 1/N$ are non-monotonic and is a one-hump function of k for weak synergy. This shows for both the emergence and the stabilization of cooperation in the public goods game with weak synergy, a moderate number of neighbours is the worst. Further, for the strong synergy case, we will see that the one-hump degenerates to a decreasing function of k .

$$b/c > \begin{cases} \frac{(k+1)^2}{k+3} & \text{for } \delta = 1 \\ \frac{18}{3\delta^2 + 4\delta + 3} & \text{for } k = 2 \\ \frac{(N-1)(k+1)Q_1}{2Ng(\delta)} & \text{otherwise} \end{cases} \quad (4)$$

where the notations Q_1 , $f(\delta)$, and $g(\delta)$ can be found in Methods.

For the linear public goods game ($\delta = 1$), natural selection favors not only the emergence of cooperation but also its stabilization if and only if

$$b/c > (k+1)^2 / (k+3). \quad (5)$$

On this occasion, the rule is equivalent to $r > n^2 / (n+2)$ where r is the multiplication factor of the common pool. Since $n^2 / (n+2) < n$, it implies theoretically that cooperative dilemma can be relaxed in structured populations compared with that in the well mixed case, without invoking any other additional mechanisms. For the linear public goods game on the cycle ($\delta = 1$ and $k = 2$), $\rho_C > \rho_D$ is equivalent to $b/c > 9/5$, which coincides with³⁹ (Supplementary Note 2.4).

What's more is that the general rule to determine the emergence of cooperation is found to be in good agreement with computer numerical simulations (the first row of Supplementary Fig. S1). And it also approximately applies to heterogeneous structured populations (the second row of Supplementary Fig. S1).

Based on equation (5), we find that $\rho_C > \rho_D$ is also equivalent with the emergence $\rho_C > 1/N$ and stabilization $\rho_D < 1/N$ of cooperation. Furthermore, the following equivalence holds

$$\rho_C > \frac{1}{N} \Leftrightarrow \rho_C > \rho_D \Leftrightarrow \rho_D < \frac{1}{N} \quad (6)$$

for the public goods game which is either linear $\delta = 1$ or on a cycle $k = 2$. That is to say, for large structured population under linear public goods game or public goods game with nonlinearity in individual payoff on cycle, we have that natural selection favors emergence of cooperation if and only if it favors stabilization of cooperation. Further, we show that the critical value, both for the emergence and the stabilization of cooperation, is continuous with

the discounting or synergy factor δ (Supplementary Note 3.1). Hence the equivalent proposition (6) applies for infinitesimal nonlinearity (Supplementary Note 3.2).

Nonlinearity on the evolution of cooperation. From the rule (inequalities (3) and (4) in Methods), we theoretically get the critical benefit-to-cost ratio b/c for the emergence and stabilization of cooperation (defection) with the two factors combined, saying the spatial reciprocity and nonlinearity in payoff induced by multiple interactions. Fig. 2 shows that weak discounting significantly inhibits both the emergence and stabilization of cooperation, whereas the weak synergy favors them greatly. In contrast with the linear public goods game, the critical ratios b/c for $\rho_C = 1/N$ and $\rho_D = 1/N$ are no longer overlapping for nonlinear payoff effects (Fig. 2). In other words, taking into account either discounting or synergy, a particular form of nonlinearity in payoff, the emergence and the stabilization of cooperation are no longer equivalent as in the linear public goods case (equivalent proposition (6)).

For multiple interactions such as linear public goods, similar to pairwise interactions¹², cooperation will also be impeded with an increase of the number of neighbours (light gray up triangle in Fig. 2). Discounting in payoff significantly inhibits cooperation (Fig. 2a). In particular, in this case, with the increase in the size of neighbourhood, it will become even harder for the emergence and stabilization of cooperation. The critical benefit-to-cost ratio is increasing much rapidly than its linear public goods game counterpart.

For weak synergy, the critical benefit-to-cost ratio b/c for emergence or stabilization of cooperation still first increases as the growth of every player's number of neighbours (Fig. 2b). But it decreases as neighbour size is big enough and tends towards zero. This illustrates that for small size of neighbour, increasing interaction range, i.e. k , is detrimental for cooperation, which is consistent with linear public goods game; yet the interesting story comes along when the interaction range is relatively large, in this case, increasing the interaction range is beneficial for cooperation, which is seldom observed in cooperative dilemmas. An intuitive understanding can be: for small neighbour size, the local competition plays a key role. Even though



the public goods are exponentially increasing with additional cooperator in a group, the group is small in size generally, thus the defector would reproduce more efficiently with the increase of size. This leads to the increase of the critical benefit-to-cost ratio. For large size of neighbours, however, the exponential increase in the accumulation of public goods with an additional cooperator outperforms the reproduction of defectors. For example, with the j^{th} ($0 \leq j \leq k + 1$) cooperator's benefit $b\delta^{j-1}$ to common pool, big j induces large payoff $b\delta^{j-1}/(k + 1)$ to every player in the same group with weak synergistically enhanced effect δ as well as the baseline benefit b . This rather large payoff paves the way for emergence and stabilization of cooperation for large neighbour size. Therefore, it is the worst for emergence of cooperation when the number of neighbours is moderate. Another intuitive explanation is that for weak synergy effect, the replicator dynamics allows the coexistence of cooperators and defectors⁴¹, which is quite similar to the snowdrift game. For the snowdrift game, however, local interaction can inhibit cooperation⁴⁹ in contrast with the prisoner's dilemma⁵⁰. Here, we explicitly show up to how many numbers would be the worst for cooperation in such scenario. It shows that synergistic interactions work with strangers in well mixed populations⁴¹. Furthermore, we also find that the synergistic interactions do not work with neighbours in structured populations.

For stronger synergy, the critical benefit-to-cost ratio always decreases with the neighbour size (Fig. 3). Thus in this case cooperation could be promoted significantly with the increase of every player's number of neighbours under strong synergy, which intrinsically differs from effect of linearity, discounting, or weak synergy. This is because the synergy effect is so great that it effectively is a

coexistence game where best relies should be of the population minority. In this case, enlarging the interaction range paves the way for cooperator mutants to be more like an minority yielding an enhancement of cooperation level.

Our results show that the intrinsic multiple interactions, where payoffs are nonlinear in general, can lead to a one-hump function of the critical benefit-to-cost ratio to facilitate cooperation, which never happens in pairwise interactions, or even linear multiple interactions. This echoes partly Hamilton's metaphor of novelty of multiple interactions, though he also pointed out that the investigation will be challenging, which is mirrored as sea-sickness⁵¹.

Discussion

Over the past two decades, structured populations depicted by networks have been taken into consideration to study the evolution of cooperation by virtue of evolutionary graph theory^{11,20,24,52}. It has been shown that cooperation can flourish in both static network and dynamic network^{8,12,20,25,52,53} (for an exception, please see⁴⁹). The main reason is that these population structures can lead to a clustering of cooperative individuals^{8,12,21,24}, within which cooperators can survive by enjoying the benefits from mutual cooperation even though some cooperators are exploited by defectors along cluster boundaries. We indicate that in a non-additive public goods game, where nonlinearity in payoff arises, this clustering (equations (S20) and (S21) in Supplementary Note 1.2) is not always beneficial when the neighbours are few in number: in a synergy public goods scenario, where the latter cooperators in the group contribute significantly much more than the previous cooperators, the worst case for cooperation emerges when the number of neighbours is mod-

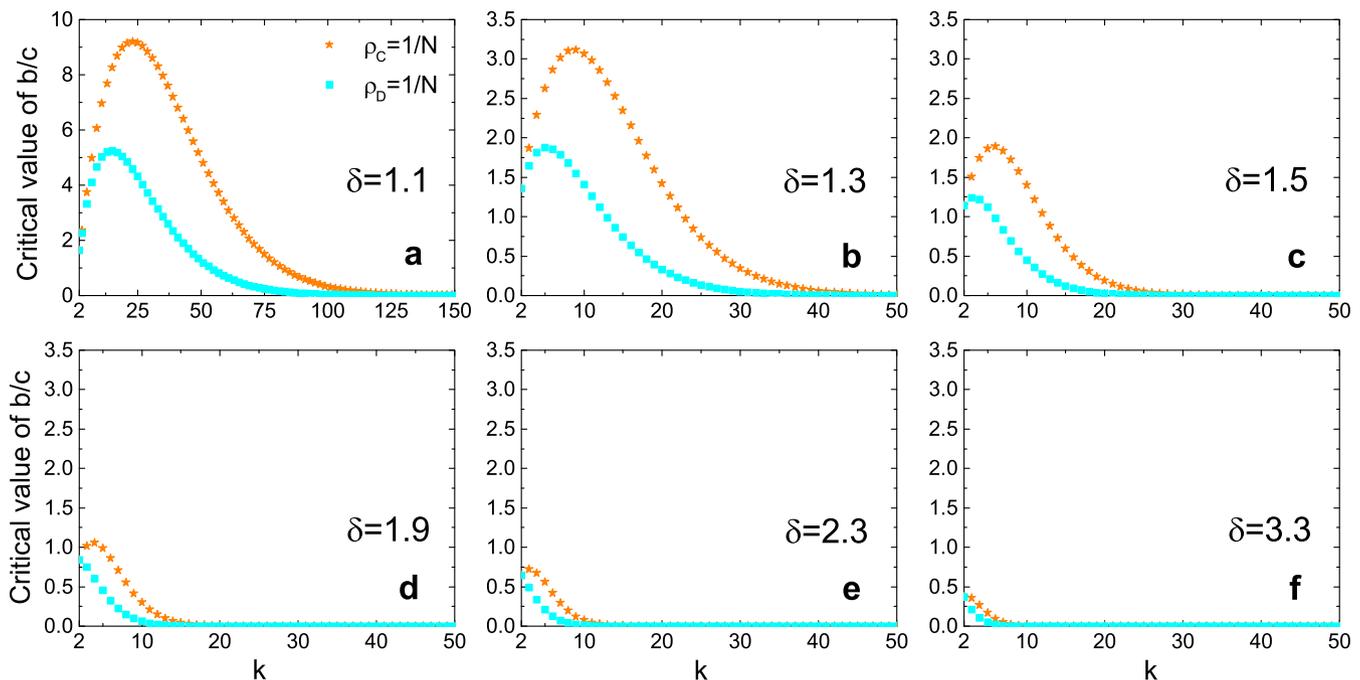


Figure 3 | Critical value of benefit-to-cost ratio degenerates to a monotonic function of average degree k from one-hump function with the enhancement of synergy. We set different synergy factors to investigate its effects on the critical value of b/c with population size $N = 5 \times 10^3$. Specific values of δ are marked on each panel. Orange star and cyan square are used to indicate $\rho_C = 1/N$ and $\rho_D = 1/N$ respectively. The critical value decreases with the increase of δ . And it is a parabolic function of k when synergy is weak ((a), (b), (c), (d), and (e)), whereas monotonic when synergy is strong (f). Under the synergistic effect, big k or δ can drive the critical value to approach 0. The intuitive understanding behind this is the competition between the two factors. For large k , the population is approximately well mixed, thus the local interaction diminishes by the replicator equation⁴¹, and cooperation with synergy thrives, leading to a decrease of the critical value with increasing k . For small k , the local interaction plays an important role if the synergy effect is not strong. That is to say for δ slightly more than the unit, increasing k does inhibit the fixation for both strategies as in the pairwise prisoner's dilemma¹². To sum up, for small $\delta > 1$, there is a hump for the critical value with the increase of neighbours. For large δ , however, even for small k , the synergy effect is strong enough to outperform the locality of the population structure. By the same argument, the critical value is monotonically decreasing with the neighbours.



erate, not too big nor too small. This means that synergistic interactions work with strangers but not with neighbours. The technical part is challenging for a general multi-player game⁵⁴. Here we adopt synergistic and discounted effects as an example to indicate the nonlinearity in public goods for mathematical convenience. Synergy and discounting can be used to unify typical social dilemmas such as the prisoner's dilemma and snowdrift game⁴¹, thus it also does not lose much of the generality. Our results show that the interaction between different mechanisms⁵⁵ might trigger novel unexpected results. The combination of different factors with each promoting cooperation alone can be worse than every factor alone in promoting cooperation. Thus, it may be promising to investigate the combination of previous mechanisms promoting cooperation.

We find that the rules governing the emergence and stabilization of cooperation are equivalent for linear public goods games, which is validated by numerical simulations on homogenous as well as heterogeneous structured populations. The rule simply asks the benefit to cost ratio b/c to exceed a critical value $(k + 1)^2/(k + 3)$, where k is the average number of neighbours in the population.

In fact, for any number of neighbours k , the numerator of the critical value is $(k + 1)^2$, which suggests the number of individuals relevant to the payoff of the focal individual with recounting (Fig. 1), i.e., the product of the group size $k + 1$ and the average number of the public goods game every player involved in, $k + 1$. Therefore, in this case, as in a well mixed population, multiple interactions significantly inhibit the cooperation than its pairwise counterpart. For public goods games on a cycle, with either linearity, discounting, or synergy, the equivalence still holds between the rules facilitating the emergence of cooperation and that governing the stabilization. Therefore the same criterion applies to determine under what condition the average abundance of cooperation exceeds that of defection in the mutation-selection equilibrium under small mutation^{56,57}.

The equivalence falls down for general population structures and nonlinear public goods game. For the synergy effect, the emergence and the stabilization of cooperation are facilitated significantly for any number of neighbours compared with the linear public goods game. Being stabilized, in this case, is much easier than the emergence. For the discounting effect, both the emergence and the stabilization of cooperation are inhibited significantly for any number of neighbours compared with the linear public goods game. Being stabilized, in this case, is much harder than the emergence. Therefore, both synergy and discounting has a more significant role in the stabilization compared with the emergence.

We find that our theoretical results can be approximated well by simulations as the synergy or discounting effect is weak, i.e., when δ is close 1 (Supplementary Fig. S1). However, for δ deviating from 1, the pair approximation leads to a large deviation from simulations (Supplementary Fig. S1). The reason for such deviation is mainly in two folds^{52,58}: The first is that pair approximation is formulated for the regular graph without any loops. For our graphs, however, they are not always in this case (Fig. 1); The second is that the approximation is precise for large population size and weak selection, whereas the simulations bear finite population size, which generates the prediction error. In fact, triplet correlations are a more natural and more precise choice for calculating payoffs from group interactions, since one's payoff is not merely related with his or her neighbors but also with the neighbors' neighbors in our model. But the triplet approximation introduces more independent variables, leading to a tedious analysis. Another limitation of our work is the weak selection assumption. In general, results obtained under the weak selection can not be extrapolated to the strong selection directly for multi-player games even in well mixed populations⁵⁹. Thus we do not expect that our theoretical results stay robust for the strong selection.

As applications, for microbes with either synergy and discounting public goods, in particular, if the public goods are diffusive⁶⁰, the average degree of the network suggests the diffusion rate of the public

goods. Our result suggests that for the discounting public goods game, only a low diffusion rate of public goods can make the cooperator cells thrive; For the synergy public goods game, however, it is always better than the discounting case. The interesting result lies in the fact that cooperation is better off for both very low and very high diffusion, whereas is worst off for moderate diffusion rate. Experimental validation along this line might be interesting.

Methods

Notations in inequalities (3) and (4) are

$$f(\delta) = (NQ_2 + Q_3)\delta^{\frac{k-2}{N}} - (Q_2 + Q_3)\delta^{k-2} - (N-1)Q_2, \quad (7)$$

$$g(\delta) = [NQ_2 + (N-1)Q_3]\delta^{\frac{(k-2)(N-1)}{N}} - (N-1)(Q_2 + Q_3)\delta^{k-2} - Q_2, \quad (8)$$

and

$$Q_1 = k(k+1)(k-2)^3 \ln^3 \delta, \quad (9)$$

$$Q_2 = 2(\delta^2 - 1)(k-2)(k+1) - [(k-2)(k+1)\delta^2 + 2k(k-2)\delta + (k-2)(k^2 - 1)] \ln \delta, \quad (10)$$

$$Q_3 = (1 - \delta^2)(k+1)(k-2)^2 \ln \delta. \quad (11)$$

The precise process of the calculation can be found in Supplementary Notes 1 and 2. Expanding $f(\delta)$ and $g(\delta)$ in Taylor series around $\delta = 1$ leads to

$$f(\delta) = \frac{k(k+3)(k-2)^3(N-1)}{2N}(\delta-1)^3 + \frac{(4-3k^2)(N^2-3N+2) - k(19N^2-3N-16) + 2k^3(N^2-1)}{12N^2}(k-2)^3(\delta-1)^4 + o((\delta-1)^4) \quad (12)$$

$$g(\delta) = \frac{k(k+3)(k-2)^3(N-1)}{2N}(\delta-1)^3 + \frac{(3k^2-4)(N^2-3N+2) - k(35N^2-51N+16) + k^3(4N^2-6N+2)}{12N^2}(k-2)^3(\delta-1)^4 + o((\delta-1)^4) \quad (13)$$

where $o((\delta-1)^4)$ shows the error is the high order infinitesimal of $(\delta-1)^4$. Further analysis can be found in Supplementary Notes 2.4 and 3.

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Author contributions

A.L., B.W. and L.W. devised and analysed the model. A.L. performed theoretical derivation and numerical simulations. A.L., B.W. and L.W. analysed the results and wrote the paper.

Additional information

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