Early exclusion leads to cyclical cooperation in repeated group interactions

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Explaining the emergence and maintenance of cooperation among selfish individuals from an evolutionary perspective remains a grand challenge in biology, economy, and social sciences. Ostracism or social exclusion is believed to be an answer to this conundrum, but related studies often assume one-shot interactions and ignore how free-riding is identified. In this work, we consider repeated interactions where excluders need to pay a monitoring cost to identify free-riders for exclusion and free-riders cannot participate in the following possible game interactions once they are identified and excluded by excluders in the repeated interaction process. We reveal that the introduction of such exclusion can prevent the breakdown of cooperation in repeated group interactions. In particular, we demonstrate that an evolutionary oscillation among cooperators, defectors, and excluders can appear in infinitely large populations when early exclusion is implemented. In addition, we find that the population spends most of the time in states where cooperators dominate for early exclusion when stochastic mutation-selection is considered in finite populations. Our results highlight that immediate exclusion is more successful than late implementation of exclusion in solving the mentioned enigma of cooperation.

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1. Introduction

Cooperative behaviour provides generous benefits for group members, but it is vulnerable to the exploitation of public goods by selfish individuals who contribute nothing to the joint venture [1–5]. In this way, cooperation will eventually collapse [6]. Conversely, cooperation described by providing public goods is universal ranging from microorganism to human society [7–10]. Thus what drives the emergence of cooperative behaviour has attracted widespread attention from broad range of disciplines [11–14].

In past decades, a substantial body of theoretical and experimental investigations have illuminated various solutions including norms and incentive mechanisms that can be used to promote the evolution of cooperation [15–26]. A frequently discussed incentive mechanism is punishment, with which some cooperators pay extra cost to punish selfish individuals [27–31]. As a special form of punishment, social exclusion has been introduced. Indeed this incentive mechanism has been found in realistic human and biological interactions [32–35]. For instance, cooperating groups of bacteria (wild-type Pseudomonas aeruginosa) growing on protein can restrict cheater emergence by producing costly cyanide to exclude LasR-null social cheaters from sharing the provided public goods [32, 33]. Recently, social exclusion has been investigated from the theoretical perspective recently [36]. It is often assumed that free-riders will be expelled from the beneficiaries and cannot get any benefit when exclusion is implemented, which is different from the setting of traditional punishment under which free-riders are imposed with a fixed penalty fine. Social exclusion strategy has been found to be more favourable to the evolution of cooperation compared with the traditional punishment, since its introduction into evolutionary games [37–39].

Although the aforementioned studies have enhanced our understanding about how social exclusion influences cooperative behaviour, they generally build on some limiting and questioning assumptions. To be specific, the evolutionary dynamics of exclusion strategy are always explored in ephemeral one-shot, but not repeated interactions. Furthermore, excluders only need to pay the exclusion cost for excluding defectors. Indeed in previous behavioural experiments about social exclusion, it is often required that excluders in the group must be able to identify "bad apples" before excluding them in repeated public goods games [40–42]. These excluders identify cooperators and defectors by recording players' names and allocation decisions, which could require excluders to pay the extra cost of monitoring and information collecting in the interaction process.

Hence when the above mentioned restrictions are released, it is unclear whether exclusion is still a viable strategy and how it can facilitate cooperation from the theoretical perspective, which are worth investigating.

In this work, we thereby propose a social exclusion strategy and explore its evolutionary consequence in repeated public goods games. We assume that excluders can monitor the decisions of all group members permanently to identify free-riding behaviours in the repeated interaction process by paying a monitoring cost, and subsequently expel these identified free-riders from group benefits. Our results reveal that the exclusion round is crucial for cooperation to thrive, since it determines how much defectors can benefit from previous repeated interactions. In infinite well-mixed populations, we observe evolutionary oscillations among cooperators, defectors, and excluders when free-riders can be expelled at the earliest stage. Similarly, stochastic evolution in finite populations can favour cooperation over defection when implemented exclusion is timely.

2. Model and Methods

We consider a well-mixed population from which N individuals are selected randomly to form an interaction group for playing a repeated public goods game. There are three game strategies: cooperation (C), defection (D), and peer exclusion (E). Both C and E individuals contribute c to the common pool in every round, while D individuals do nothing. In every round the accumulated contributions are multiplied by an enhancement factor F ($1 < F < N$) and subsequently shared equally among all group members, irrespective of whether they contributed or not. In the framework of repeated group interactions, the above game process will be repeated with probability w ($0 < w < 1$), resulting in an average number of $\langle r \rangle = \frac{1}{1-w}$ rounds [43]. Here we assume that peer excluders pay a permanent cost σ to monitor the game process for identifying D individuals and subsequently exclude all identified defectors from the group at the ς-th round by paying an additional cost c_E. The excluded free-riders cannot share the public goods of the ς-th round and will lose the opportunity to participate in the following possible game rounds. It is worth noting that if the average number of rounds is smaller than the round in which defectors are excluded, namely, $\langle r \rangle < \varsigma$, then peer exclusion strategists completely degenerate into pure cooperators except the permanent cost σ of monitoring. Thus in this case defection is a more advantageous strategy than peer exclusion and cooperation [36].

Following the above description of game model, we can write the payoff of a cooperator, defector, and excluder playing the repeated public goods game in a group in which N_C cooperators, N_E

excluders, and N_D defectors are present. Thus the related payoff values for cooperators, defectors, and excluders are respectively give as

$$\pi_C=\begin{cases} \dfrac{Fc(N_C+N_E+1)}{N}(\varsigma-1)+Fc(\langle r\rangle-\varsigma+1)-\langle r\rangle c, & \text{if } \varsigma\leq\langle r\rangle \quad \text{and} \quad N_E\neq 0;\\ \dfrac{Fc(N_C+N_E+1)}{N}\langle r\rangle-\langle r\rangle c, & \text{otherwise.}\end{cases}$$

$$\pi_D=\begin{cases} \dfrac{Fc(N_C+N_E)}{N}(\varsigma-1), & \text{if } \varsigma\leq\langle r\rangle \quad \text{and} \quad N_E\neq 0;\\ \dfrac{Fc(N_C+N_E)}{N}\langle r\rangle, & \text{otherwise.}\end{cases}$$

$$\pi_E=\begin{cases} \dfrac{Fc(N_C+N_E+1)}{N}(\varsigma-1)+Fc(\langle r\rangle-\varsigma+1)-\langle r\rangle c-c_EN_D-\sigma, & \text{if } \varsigma\leq\langle r\rangle;\\ \dfrac{Fc(N_C+N_E+1)}{N}\langle r\rangle-\langle r\rangle c-\sigma, & \text{otherwise.}\end{cases}$$

We then apply evolutionary game theory to investigate the evolution of strategies in our model [55] . To be specific, we will respectively consider our model in infinite and finite well-mixed populations in the following.

(a) Infinite well-mixed populations.

We consider an infinite well-mixed population, in which N individuals are selected randomly to engage in the repeated public goods game. Since random sampling leads to groups with compositions that follow a multivariate binomial distribution, the average payoff P_i of one individual adopting a given strategy i can be calculated as

$$P_i=\sum_{N_C=0}^{N-1}\sum_{N_D=0}^{N-N_C-1}\binom{N-1}{N_C}\binom{N-N_C-1}{N_D}x^{N_C}y^{N_D}z^{N-N_C-N_D-1}\pi_i,$$

where $i=C$, D, or E.

In order to investigate the evolutionary dynamics in infinite well-mixed populations, we use the replicator equation approach [44, 45]. To do that, we use x, y, and z to denote the fraction of C, D, and E players, respectively. Correspondingly, we have $x+y+z=1$ and the replicator equation can be written as

$$\begin{cases} \dot{x}=x(P_C-\bar{P}),\\ \dot{y}=y(P_D-\bar{P}),\\ \dot{z}=z(P_E-\bar{P}),\end{cases} \tag{1}$$

where $\bar{P} = xP_C + yP_D + zP_E$ represents the average payoff of the whole population. More detailed theoretical analysis of the replicator dynamics can be found in Electronic Supplementary Material.

Furthermore, since replication is error-prone [56, 57], we also incorporate mutation into the above deterministic replicator dynamics. The resulting replicator-mutator equation can be written as

$$\begin{cases} \dot{x} = xP_C q_{C\to C} + yP_D q_{D\to C} + zP_E q_{E\to C} - x\bar{P}, \\ \dot{y} = yP_D q_{D\to D} + xP_C q_{C\to D} + zP_E q_{E\to D} - y\bar{P}, \\ \dot{z} = zP_E q_{E\to E} + xP_C q_{C\to E} + yP_D q_{D\to E} - z\bar{P}, \end{cases} \tag{2}$$

where $q_{U\to V}$ denotes the probability that strategy U generates an offspring using strategy V ($U, V = C, D$, or E). A detailed description and analysis of the replicator-mutator equation is present in Electronic Supplementary Material.

(b) Finite well-mixed populations.

We further consider our model in a finite well-mixed population in which the population size is Z. For finite well-mixed populations of size Z with i_C cooperators, i_E excluders, and $Z - i_C - i_E$ defectors, we know that the average payoffs of these three strategies in a configuration $\mathbf{i} = \{i_E, i_C\}$ can be respectively computed by using a hypergeometric sampling [18]. More precisely, the average payoffs of cooperators, defectors, and excluders in the configuration $\mathbf{i} = \{i_E, i_C\}$ can be respectively given as

$$\begin{aligned} f_C &= \sum_{N_C=0}^{N-1} \sum_{N_E=0}^{N-N_C-1} \frac{\binom{i_C-1}{N_C}\binom{i_E}{N_E}\binom{Z-i_C-i_E}{N-N_C-N_E-1}}{\binom{Z-1}{N-1}} \pi_C, \\ f_D &= \sum_{N_C=0}^{N-1} \sum_{N_E=0}^{N-N_C-1} \frac{\binom{i_C}{N_C}\binom{i_E}{N_E}\binom{Z-i_C-i_E-1}{N-N_C-N_E-1}}{\binom{Z-1}{N-1}} \pi_D, \\ f_E &= \sum_{N_C=0}^{N-1} \sum_{N_E=0}^{N-N_C-1} \frac{\binom{i_C}{N_C}\binom{i_E-1}{N_E}\binom{Z-i_C-i_E}{N-N_C-N_E-1}}{\binom{Z-1}{N-1}} \pi_E. \end{aligned} \tag{3}$$

Subsequently, we consider the pairwise comparison rule combined with mutation to describe how the number of individuals adopting a given strategy evolves in finite well-mixed populations [48, 61, 62]. To be specific, with probability μ, mutation occurs and one randomly selected player L picks a new strategy randomly from the remaining available strategies space. With probability $1 - \mu$, player L imitates the strategy of another randomly selected player R as follows. Player L

adopts the strategy of player R with probability

$$\bar{p} = \frac{1}{1 + \exp\left[\beta(f_L - f_R)\right]}, \tag{4}$$

where $\beta \geq 0$, the so-called the intensity of selection, translates into noise associated with errors in the imitation process [60]. In the limit case $\beta \to \infty$, player L always adopts the more successful strategy of player R. While $\beta \to 0$ indicates weak selection limit where strategy adoption becomes random independently of the payoffs difference between these two players. In between these extremes, for a finite value of β, a better performing strategy is more likely to be adopted. With probability $1 - \bar{p}$, player L remains his/her current strategy unchanged.

Based on the above description, we can write the transition probability that an individual selected from i_U players with a given strategy U changes into another different strategy V as [61]

$$T_{U \to V} = (1 - \mu)\left[\frac{i_U}{Z}\frac{i_V}{Z - 1}\frac{1}{1 + \exp\left(\beta(f_U - f_V)\right)}\right] + \mu\frac{i_U}{(d - 1)Z},$$

where $U, V = C, D$, or E, and d is the number of alternative strategies in the strategy space.

We stress that, in the presence of mutation, the population will never fixate in any of the absorbing states. Here we focus on finite populations and consider two different cases: the case of sufficiently small mutation rates and the case of arbitrary mutation rates. For smaller mutation rates, a mutant either goes extinct or takes over the whole population before next mutation occurs [63–65]. Thus the population is homogeneous most of the time and only consists two strategies at a given time. In this case, the dynamics can be described by an embedded Markov chain based on the transition from one homogeneous state to another. The stationary distribution which describes the percentage of time spent by the population can be calculated by searching the eigenvector corresponding to the eigenvalue 1 of the transition matrix. The element of transition matrix, representing the probability of transition from $AllU$ state to $AllV$ state, can be given by $\mu\rho_{UV}/(d - 1)$, where ρ_{UV} denotes the fixation probability and can be written as

$$\rho_{UV} = \frac{1}{1 + \sum_{q=1}^{Z-1} \exp[\beta \sum_{i_V=1}^{q}(f_U - f_V)]}.$$

It is worth noting that the imitation strength β plays a crucial role in the evolutionary dynamics of the system. For theoretical analysis, we shall focus on the two limit cases, i.e., weak selection limit ($\beta \to 0$) and strong imitation strength limit ($\beta \to \infty$). Detailed theoretical analysis can be found in Electronic Supplementary Material.

For arbitrarily mutation rates, the evolutionary dynamics among C, D, and E can be described by an embedded Markov process over a two-dimensional space. Transitions take place between different configurations of the system characterized by the vector $\mathbf{i}(t) = \{i_E, i_C\}$. The study of Markov process is to mainly determine the evolution of its probability density function, $p_{\mathbf{i}}(t)$, which provides information on the prevalence of each configuration at time t [61]. The transition probability and probability density function obey the following discrete time Master Equation [66], described as

$$p_{\mathbf{i}}(t+\tau) - p_{\mathbf{i}}(t) = \sum_{\mathbf{i}'} \{T_{\mathbf{i}\mathbf{i}'} p_{\mathbf{i}'}(t) - T_{\mathbf{i}'\mathbf{i}} p_{\mathbf{i}}(t)\}, \tag{5}$$

where $T_{\mathbf{i}'\mathbf{i}}$ denotes the transition probability from configuration $\mathbf{i}$ to adjacent configuration $\mathbf{i}'$ in the time interval τ. The so-called stationary distribution $\bar{p}_{\mathbf{i}}$ is obtained by making the left side of Eq. (5) zero, which transforms our calculation into an eigenvector search problem. Namely, the eigenvector is associated with the eigenvalue 1 of the transition matrix (see Electronic Supplementary Material for details).

Furthermore, employing the Kramers-Moyal expansion of the above Master Equation, we can obtain the gradient of selection, which provides information on the most likely direction of change of the population configuration with time [49], as

$$g_{\mathbf{i}} = (T_{\mathbf{i}}^{E+} - T_{\mathbf{i}}^{E-})\mathbf{u}_E + (T_{\mathbf{i}}^{C+} - T_{\mathbf{i}}^{C-})\mathbf{u}_C, \tag{6}$$

where $\mathbf{u}_E$ and $\mathbf{u}_C$ are unit vectors defining as a basis of the two dimensional simplex. Besides, $T_{\mathbf{i}}^{E+}$ $(T_{\mathbf{i}}^{E-})$ represents the probability that the number of individuals adopting strategy E to increases (decreases) by one, and $T_{\mathbf{i}}^{C+}$ $(T_{\mathbf{i}}^{C-})$ represents the probability that the number of individuals adopting strategy C increases (decreases) by one, which can be respectively computed as

$$T_{\mathbf{i}}^{E\pm} = T_{\mathbf{i}\{i_E \pm 1, i_C \mp 1, i_D\}} + T_{\mathbf{i}\{i_E \pm 1, i_C, i_D \mp 1\}},$$

and

$$T_{\mathbf{i}}^{C\pm} = T_{\mathbf{i}\{i_E \mp 1, i_C \pm 1, i_D\}} + T_{\mathbf{i}\{i_E, i_C \pm 1, i_D \mp 1\}}.$$

Furthermore, to describe the average abundance of strategy U more intuitively, we provide another important quantity, the so-called average strategy level $\bar{\rho}_U$, averaging over all possible configurations, weighted with the corresponding stationary distribution. Accordingly, it can be computed as

$$\bar{\rho}_U = \sum_{\mathbf{i}} \mathbf{i}_{i_U} \bar{p}_{\mathbf{i}} / Z, \tag{7}$$

where $\mathbf{i}_{i_U}$ denotes the number of U strategists in the configuration $\mathbf{i}$ and $U = C, D$ or E.

By means of individual-based simulations, we also investigate social learning dynamics with an arbitrary exploration rate μ in finite populations [64]. Each individual obtains an average payoff calculated by Eq. (3) based on the random sampling of the interaction groups. Strategies evolve via a mutation-selection process that can be used to describe the evolution of strategies in discrete time. At each time step, one player L is randomly selected to update its strategy in the following way: with probability μ, player L undergoes a mutation and randomly adopts one of the available strategies. With probability $1-\mu$, another player R is selected randomly to be a role model for player L. Then player L imitates the strategy of player R according to Eq. (4).

3. Results

In the following, we respectively present our results of evolutionary dynamics of cooperators, defectors, and excluders in infinite and finite well-mixed populations.

(a) Evolutionary dynamics in infinite well-mixed populations.

Let us first focus on the evolutionary dynamics of the three strategies C, D, and E described by Eq. (1) in infinite well-mixed populations. According to the theoretical analysis, we distinguish three different cases where the outcome changes with increasing exclusion round ς. For small exclusion round satisfying $\varsigma < \frac{N[(F-1)\langle r\rangle c-\sigma-(N-1)c_E]}{(N-1)Fc} + 1$, cooperation, defection, and exclusion can form a cyclic dominance that resembles a rock-scissors-paper cycle on the boundary of S_3, as shown in Fig. 1A and B. Here the evolution on the CD edge is unidirectional from C to D. It goes from D to E on the DE edge and goes from E to C on the EC edge. In Electronic Supplementary Material, we theoretically prove that there is an asymptotically stable heteroclinic cycle on the boundary of S_3. We show that there exists a limit cycle in the interior of the simplex, in which all interior trajectories of the state space form evolutionary oscillations around the interior equilibrium when ς is small (see Fig. 1A, B, D, and E). As ς increases and satisfies $\frac{N[(F-1)\langle r\rangle c-\sigma-(N-1)c_E]}{(N-1)Fc} + 1 < \varsigma < \frac{N[(F-1)\langle r\rangle c-\sigma]}{(N-1)Fc} + 1$, an unstable equilibrium appears on the DE edge and the state where each individuals choose to defect is the only stable equilibrium. Numerical calculations confirm that all trajectories started in the state space converge to a state where all D players appear (see Fig. 1C and F). As ς further increases and exceeds $\langle r\rangle$, defectors have more advantages over both cooperators and excluders, so that the sate of full D is globally stable.

Next, we study the effects of other parameters on the replicator dynamics of cooperators, defectors, and excluders, as shown in Electronic Supplementary Material. We find that cooperative behaviours can be maintained in the population when the exclusion round ς is not too large. Particularly, in the specific case of $\varsigma = 1$ we can reproduce previous findings that excluders can emerge in a sea of defectors and dominate them [36]. Furthermore, we provide some numerical examples to show the effects of different observation cost σ (Fig. S2) and discount factor w (Fig. S4) on replicator dynamics. We find that our main results remain valid if the value of σ is approximately changed. Besides, the cyclic dominance among cooperators, defectors, and excluders can still appear when the value of w is not too small.

In order to shed light on the details of the evolutionary oscillations dynamics shown in the Fig. 1A and B, we depict the average levels of the mentioned three strategies over an approximate periodic orbit for different exclusion rounds ς. Fig. 2 illustrates that the highest cooperation rates can be obtained for immediate exclusion. The intuitive explanation is that the maximal cooperation level arises if excluders can quickly expel free-riders from the beneficiaries. Interestingly, although the average level of pure cooperators decreases with the increase of ς, it is always higher than that of excluders and free-riders, as long as the exclusion is executed not too late.

Furthermore, we extend the replicator equation and consider the “replicator-mutator equation” for frequency-dependent selection with mutation in infinite well-mixed populations. For small mutation rate, we find that there is also an unstable interior equilibrium containing all three strategies, and an evolutionary oscillation forms around this equilibrium (Fig. S5A in Electronic Supplementary Material). If the mutation rate exceeds a critical value, the evolutionary oscillation disappears and all interior trajectories converge to a stable fixed point. With the increase of μ, the interior equilibrium point moves towards the inner part of simplex gradually (Fig. S5B-E in Electronic Supplementary Material).

(b) Evolutionary dynamics in finite well-mixed populations.

We note that replicator equations cannot be used directly to describe the dynamics of a more realistic system where the population size is finite. In the latter case, stochastic effects including behavioural mutations or errors of imitation may play important roles in the evolutionary dynamics

[47, 48]. In the following, we investigate the stochastic dynamics of finite populations when mutation rates are sufficiently small and arbitrarily large.

When mutation rate is arbitrarily large, the stochastic effects can drive the system from the vicinity of one configuration of the state space to the other. The stochastic dynamics associated with these three strategies are best characterized by the gradient of selection and the full stationary distributions, as shown in Fig. 3A-C and Figs. S8-S10. Each triangular simplex contains all possible configurations of the finite population where each configuration is represented by a small circle. The magnitude of stationary distributions is shown by using a grey scale where darker areas indicate more often visited configurations. The arrows show the so-called gradient of selection, which provides the most likely direction of evolution from a given configuration, which can be calculated from the drift term of the Fokker-Planck equation [49].

Similarly to the evolutionary outcomes in infinite well-mixed populations, the qualitative behavioral dynamics in the finite population change with the exclusion round ς. As shown in Fig. 3A-C, three representative examples of the behavioural dynamics among C, D, and E players for different exclusion rounds ς are presented when mutation is not negligible. For small exclusion rounds, if most players of the population are C players, it is better to be a D player due to social dilemma. If D players are prevalent, E players can rapidly outcompete D players, leading the population to the configuration that contains all-E players. In the latter case, behavioural mutations allow the emergence of C players in the population and E players have less advantage than C players since C players do not need to bear additional monitoring costs. Accordingly, C players spread. As a result, a cyclical evolutionary scenario can be formed (see the direction of arrow flow). This outcome is also verified by individual-based simulations (see Fig. 3D and E). Besides, as shown by the stationary distributions, the population will spend most of the time in configurations comprising a sizable amount of C players together with E players, which can prevent D players from invading (see Fig. 3A and B).

For high values of exclusion round ($\varsigma = 9$), the behavioural dynamics are quite different. As shown in Fig. 3C, the population spends a significant amount of time in configurations in which defectors spread. Fig. 3E also reveals that the whole population is taken over completely by defectors. It is not surprising that such outcome occurs when the value of exclusion rounds is too large because D players have obtained a higher payoff before they are excluded from the repeated group interactions by E players. Furthermore, exclusion strategy will be completely ineffective in resisting defection when exclusion round exceeds the average game rounds, allowing the population to spend longer periods of time in configurations with many defectors.

Finally, we present theoretical and numerical results for the stationary distribution when the mutation rate is sufficiently small. In this case, the time scales of mutation and imitation are separated, thus the population is homogeneous most of the time. The evolutionary dynamics are determined by an embedded Markov chain where the state space is composed of homogeneous states (more details can be found in Electronic Supplementary Material). Both theoretical and numerical results underline that exclusion strategy can have more evolutionary advantages over the other two strategies for weak imitation strength when the exclusion round is small (Fig. S10A). For strong imitation strength, however, the long-run frequencies of the three competing strategies are identical (Fig. S11A). A detailed analytical approximations of the transition matrix among these three homogeneous states shows that the long-run frequencies in the (C, D, E) subpopulations are $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$ in the strong selection (see Electronic Supplementary Material).

Similarly to the above described cases, when exclusion round is high, defectors can have more advantages than the two other strategies for weak imitation strength (Fig. S10B). With the increase of imitation strength, the advantage of defectors increases gradually. In the strong imitation limit, defection is the most advantaged strategy, yielding $(0, 0, 1)$ fractions for C, E, and D strategies, respectively (Fig. S11B). A detailed theoretical analysis of the transition matrix of the system and the linear approximation of the stationary distribution in the weak imitation strength can be found in Electronic Supplementary Material.

In Fig.4, we further show the average levels of cooperation, exclusion, and defection for different values of ς when mutation cannot be ignored. Interestingly, the average cooperation level slightly increases first then decreases with the increase of the exclusion round ς. The changing trend about the cooperation level is opposite to that about the average level of excluders. Besides, the level of defection increases with the increase of ς. Altogether, Fig. 4 confirms that cooperation can be maintained at a high level as long as free-riders can be executed in the early rounds. Indeed, in the presence of mutation, the population will never fixate in any of the absorbing states. In addition, the intensity of selection incorporates noise associated with errors into the process of strategy updates. Accordingly, we can find that there exists evolutionary oscillations for the frequencies of cooperators, defectors, excluders, as shown in Fig. 3D and E. Since the cooperation levle shown in Fig.4 averaging over all possible configurations are weighted with the corresponding strategy distribution, the oscillation effects has been involved and we can see that the cooperation level slightly increases with the number of rounds even when the values of intensity of selection and mutation rate are changed appropriately. However, we stress that our main conclusion that immediate exclusion is favourable to the evolution of cooperation is still valid in finite well-mixed populations.

4. Discussion

In modern societies, it has been widely observed that ostracism or the exclusion of disapproved members from groups, teams, and communities can enforce norm conformity and cooperation [33, 50]. However, it still needs further theoretical efforts to understand its evolutionary advantage. In this work, we have developed an evolutionary game model to explore the dynamical consequences of social exclusion strategy in the public goods game where group members are engaged in repeated interactions. We assume that excluders need to monitor the whole group interactions for collecting relevant information before excluding free-riders. If the exclusion is executed, then free-riders cannot obtain the benefits of common pool anymore, but they can have the incomes originated from previous rounds. We have found that the actual round at which defectors are excluded plays a decisive and highly non-trivial role in the general well-being. Interestingly, the evolutionary oscillation among the competing strategies can be detected if the exclusion is executed at an early stage in repeated interactions. More surprisingly, the time averages of the temporary fractions of strategies display the outcome of the dominance of cooperators. We have also investigated the stochastic dynamics of a finite population in the presence of behavioural mutations and found that immediate exclusion can lead to a high level of cooperation.

In this work, we investigate the effects of ostracism on cooperation in the multi-period public goods game by comparing the treatments with and without exclusion, mainly inspired by some interesting behavioural experiments [40–42, 51]. In the former experiments, subjects are given the opportunity to exclude each other after they are informed about the individual contributions of other group members, and player who is ostracized cannot take part in the subsequent interactions. The experimental results show that subjects exhibit a willingness to exclude other members of their group and the threat of social exclusion for uncooperative behaviour can significantly improve the level of contribution [40]. It is worth emphasizing that two hypotheses have been considered to identify uncooperative “bad apples” in previous experiment: cooperation decisions are not anonymous; group members can be identified by name [42]. Inspired by the above-mentioned behavioural experiments, our mathematical model considers that excluders need to pay a permanent cost of monitoring to identify other players’ behaviours during the repeated group interaction process. This realistic set-up makes our model more reasonable and brings a step closer towards understanding how social exclusion strategy works in the realistic case. Accordingly, our work is essentially different from the previously reported incidental ostracism [50]. First, the ways of implementing social exclusion and incidental ostracism are different. Previous study assumes that individuals can select partners and those who are not selected are excluded from social interactions [50]. However, in our work we regard social exclusion as instrumental punishment of free-riders. In addition, participants play an iterated prisoners dilemma or coordination game with partner choice in the previous study [50]. While in our model, we explore the evolutionary dynamics of social exclusion strategy in repeated group interactions. Our results underline that cooperative behaviour cannot be promoted when implementing exclusion on free-riders is too late, which is consistent with the experimental results that the introduction of ostracism increases contribution levels except in the last period [51]. Our calculation also reveals that too early exclusion could be a source of modest cooperation.

The positive role of peer exclusion in the evolution of cooperation has already been reported in previous theoretical model developed in large well-mixed populations [36]. However, the mentioned work mainly examined the dynamics of the system when interaction among group members is one-shot and defectors can be detected in a cost-free manner. In our model, we release these limitations. In addition, in our model we assume that social exclusion are implemented simultaneously and faultlessly in all groups and we do not consider the case in which defectors will be excluded from the group probabilistically. The main reason is that our model takes into account that the social excluders have paid the observation cost in advance to identify all the free-riders during the repeated group interaction process. Interestingly, we explore new dynamical behaviours, such as evolutionary oscillations, as summarized in Fig. 1. It is worth noting that evolutionary oscillations can be also observed from the interactions of Pseudomonas aeruginosa when Pseudomonas aeruginosa uses the strategy of social exclusion by using cooperator-released toxic cyanide to exclude lasR mutant defectors lacking the LasR regulon for detoxification [32, 33]. Besides, we can reproduce previous findings that rare excluders can emerge in a sea of defectors and subvert them [36] (also see Fig. S1). Our work may unveil the effects of social exclusion on the evolution of cooperation in a realistic manner.

As we have found, the application of different exclusion rounds can induce rather distinct dynamical behaviours. We stress that the actual number of exclusion rounds is not the only factor that affects evolutionary dynamics. As Fig. S2 in Electronic Supplementary Material demonstrates clearly, the cost of monitoring can modify the amplitude of oscillation significantly, thus altering the evolutionary advantage of this incentive. Further important parameter is the discount factor of repeated games, which strongly influences the cooperation level. Our results highlight that cooperative behaviours cannot emerge when the mentioned discount factor is lower than an intermediate value (Fig. S4). Here, we show that it is beneficial for excluders to manage to expel free-riders from the beginning even in situations complicated with high monitoring cost or intermediate discount factor. Our model thus predicts that quickly excluding of free-riders can maintain a high level of cooperation over a wide range of parameters. Our observations may offer a potential way for how to use exclusion strategy efficiently in real and complicated situations.

In this work, we stress that once defectors are excluded from the interaction group, they cannot participate in the interactions any more in our model. In reality, it is a frequently applied practice that individuals who violate social rules can regain their qualification to participate in activities after a certain period of time. For example, a drunk driver whose driver's license has been revoked can take a driving license again after some time. Also, this scenario has been applied to a behavioural experiment in which one player who is ostracized can re-enter the next round unless ostracized again [52]. For future study, thus a potential extension of our present work could be to explore the possible consequence in the realistic scenario where the finite-time effect is considered for exclusion of free-riders in repeated interactions. Furthermore, it is also worth exploring the effect of different social structures on the dynamics of social exclusion in repeated group interactions. Previous experimental evidences underlined that free choice of interaction links drastically increases cooperation in social networks. In experimental treatments, cooperators who refuse interacting with defectors on the basis of past behaviour account for most of social exclusion [53]. Besides, it is worth noting that in structured populations excluders may be separated from simple cooperators, hence they can fight against defectors more efficiently than those who behave as second-order free-riders [54]. In this way, there is an indirect territorial competition between excluders and pure cooperators, but the competitive outcome is intrinsically unpredictable, which is worth investigating for future study. Furthermore, we stress that in our present model the existence of a single excluder can purge any number of defectors in the group. Thus, the larger the interaction group is, the more effective the exclusion strategy is in keeping defectors at check. Such an advantage provided to large groups contrasts the usually found benefit from small groups, which may lead to an nonlinear effect of the group size on the evolutionary dynamics, as found in previous studies [67–69]. In particular, the group size for players undergoing group interactions in structured populations could be variable and diverse [70–72] , which can lead to more complicated effects on the evolution of cooperation. Thus, the effects of group size would deserve to be considered in our model for future study.

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Author contributions

X.C., L.L., and A. S. designed the research, L.L. and Z.X. performed the research, X.C., L.L., and A. S. wrote the manuscript, and all authors discussed the results and commented on and improved the manuscript.

Competing financial interests

The authors declare no competing financial interests.

Data availability

The raw data generated with these computer calculations is available from the corresponding author upon reasonable request.

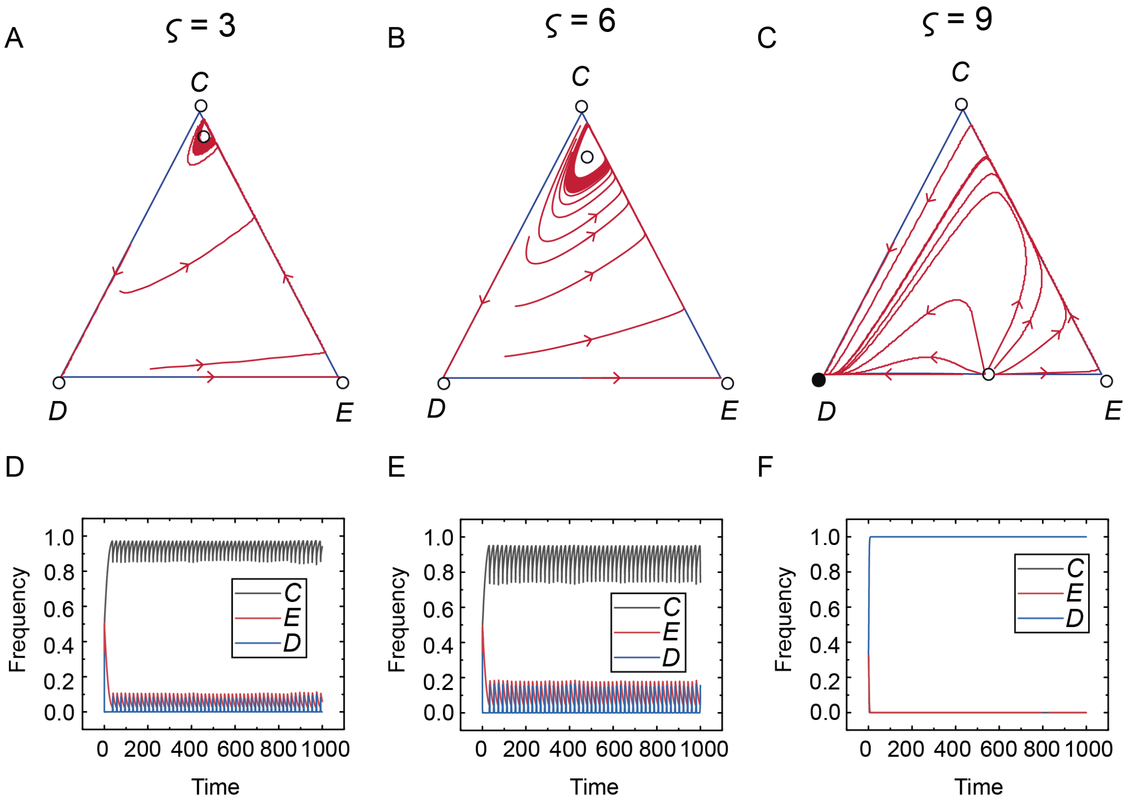

FIG. 1: Deterministic replicator dynamics among cooperators, defectors, and excluders in an infinite well-mixed population with different exclusion rounds ς. The triangle represents the state space $S_3 = \{(x, y, z) : x, y, z \geq 0, x + y + z = 1\}$, where x, y, and z denote the frequencies of cooperators, defectors, and excluders, respectively. The three vertices C, D, and E correspond to the three homogeneous states in which the population exclusively consists of cooperators $(x = 1)$, defectors $(y = 1)$, or excluders $(z = 1)$. The open circles represent unstable equilibria, and the filled circles denote stable equilibria. Panels D-F show the time evolution of fractions of three strategies C (black line), E (red line), and D (blue line) for three different ς values. Parameter values are: $N = 5, F = 3, c = 1, c_E = 0.4, w = 0.9$, and $\sigma = 0.1$.

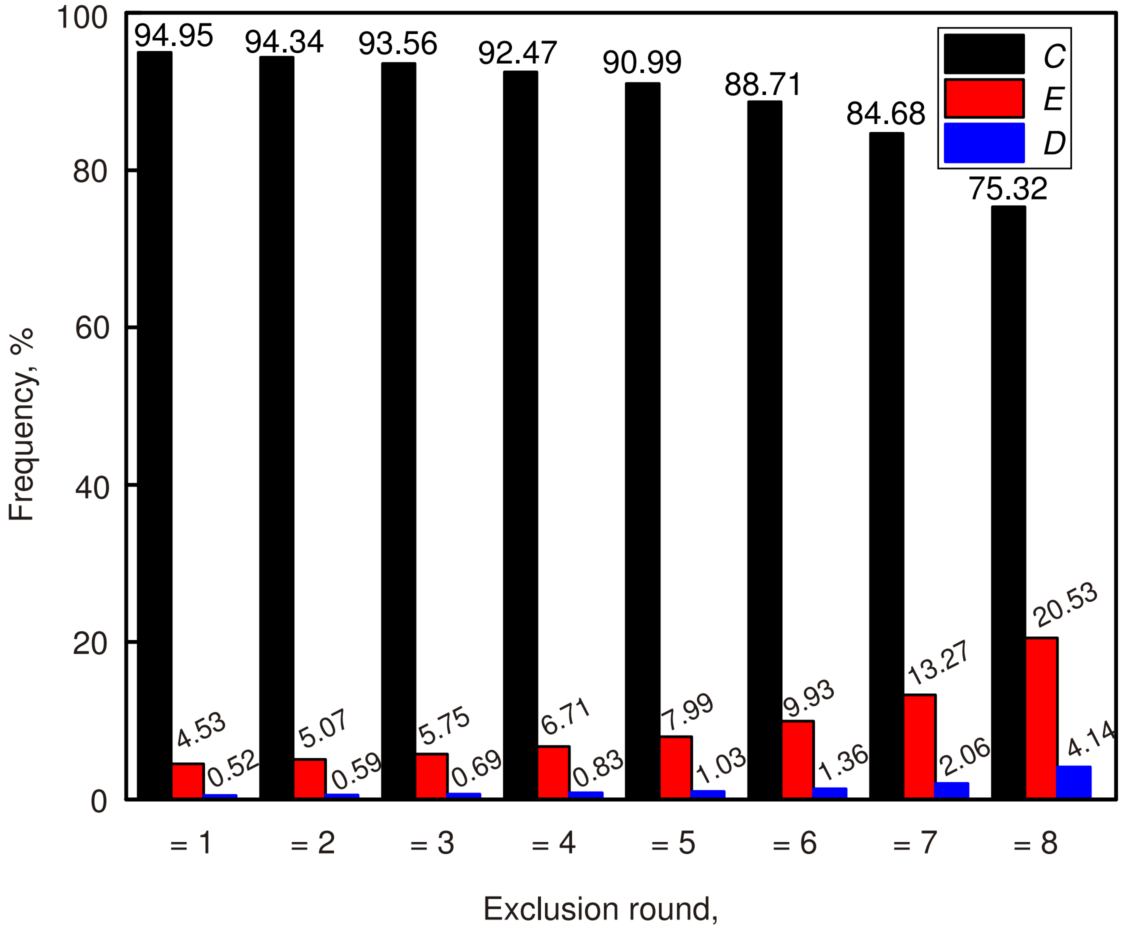

FIG. 2: Average levels of cooperation, defection, and exclusion for different ς values. When C, D, and E can form an evolutionary oscillation, the average level of each strategy can be calculated over an approximate periodic orbit. These frequencies of C, D, and E strategies vary with different exclusion round values ς, as indicated on the horizontal axis. Parameter values are: $N = 5, F = 3, c = 1, c_E = 0.4, w = 0.9$, and $\sigma = 0.1$.

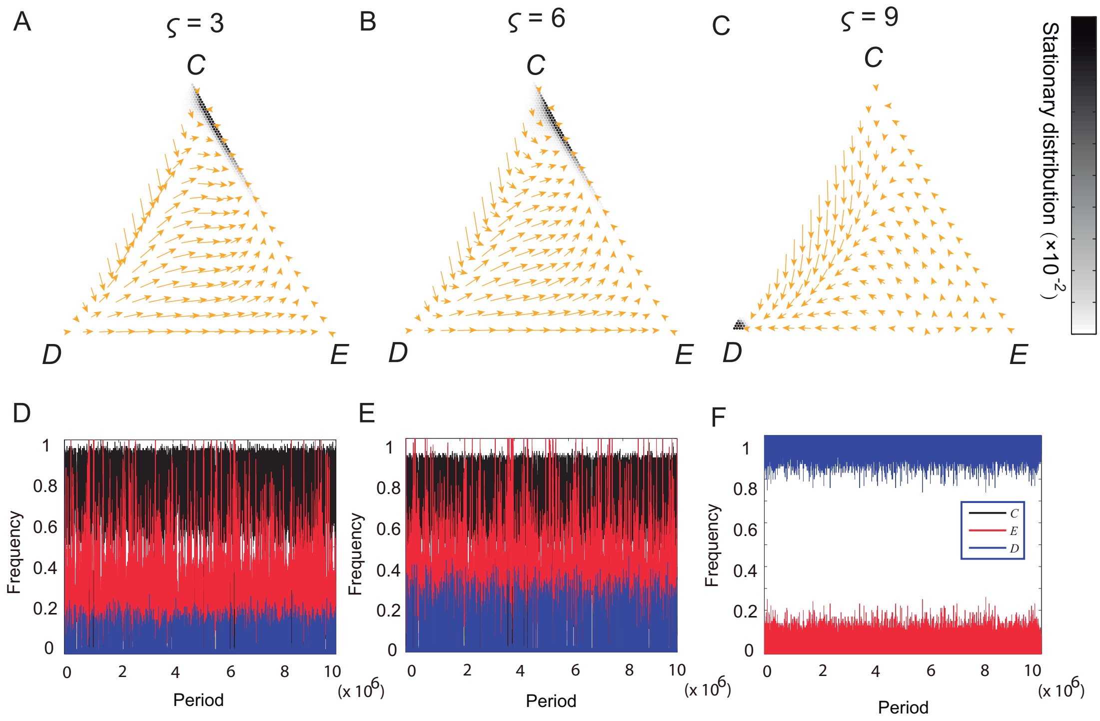

FIG. 3: Evolutionary dynamics of cooperation, defection, and exclusion in finite well-mixed populations for different exclusion round ς values. The dynamics are best characterized by the full stationary distribution, which is mapped onto the triangular simplex. Each simplex contains all possible configurations of the population, and each state is denoted by a small cycle. The value of the stationary distribution at each configuration is shown using a grey scale, where darker dots denote those configurations in which the population spends more time. The red arrows depict the so-called gradient of selection, which provide the most probable directions of evolution. Panels D-F show the time evolution of strategies by individual-based simulations for different ς values. Parameter values are: $Z = 100, N = 5$, $F = 3$, $c = 1$, $c_E = 0.4, \beta = 2, \sigma = 0.1, \mu = 0.01$, and $w = 0.9$.

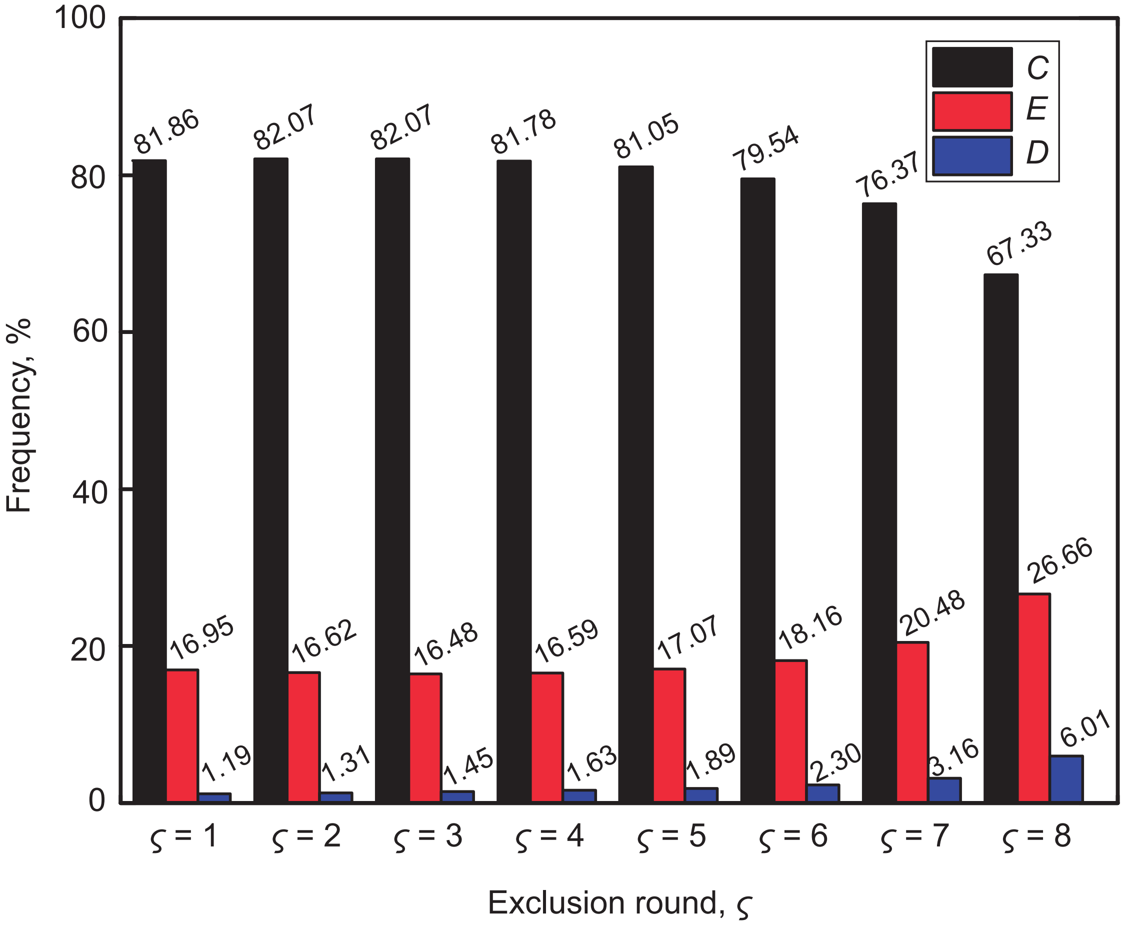

FIG. 4: The average levels of cooperation, defection, and exclusion in finite populations for different exclusion round values ς. These frequencies of C, D, and E strategies vary with different exclusion round values ς, as indicated on the horizontal axis. Parameter values are: $Z = 100, N = 5$, $F = 3$, $c = 1$, $c_E = 0.4, \beta = 2, \sigma = 0.1, \mu = 0.01$, and $w = 0.9$.