THE ROYAL SOCIETY
PUBLISHING

Evolution of conditional cooperation in collective-risk social dilemma with repeated group interactions

Shijia Hua, Zitong Hui and Linjie Liu

College of Science, Northwest A & F University, Yangling 712100, People's Republic of China

(iD) LL, 0000-0003-0286-8885

The evolution and long-term sustenance of cooperation has consistently piqued scholarly interest across the disciplines of evolutionary biology and social sciences. Previous theoretical and experimental studies on collective risk social dilemma games have revealed that the risk of collective failure will affect the evolution of cooperation. In the real world, individuals usually adjust their decisions based on environmental factors such as risk intensity and cooperation level. However, it is still not well understood how such conditional behaviours affect the evolution of cooperation in repeated group interactions scenario from a theoretical perspective. Here, we construct an evolutionary game model with repeated interactions, in which defectors decide whether to cooperate in subsequent rounds of the game based on whether the risk exceeds their tolerance threshold and whether the number of cooperators exceeds the collective goal in the early rounds of the game. We find that the introduction of conditional cooperation strategy can effectively promote the emergence of cooperation, especially when the risk is low. In addition, the risk threshold significantly affects the evolutionary outcomes, with a high risk promoting the emergence of cooperation. Importantly, when the risk of failure to reach collective goals exceeds a certain threshold, the timely transition from a defective strategy to a cooperative strategy by conditional cooperators is beneficial for maintaining high-level cooperation.

1. Introduction

Cooperation is a fundamental aspect of both natural systems and human societies [1–4]. In the natural world, many species engage in cooperative behaviours such as hunting [5], foraging [6] and caring for offspring [7]. Similarly, in human societies, cooperation is essential for achieving common goals such as preventing the spread of infectious diseases [8,9], mitigating climate change [10,11] and maintaining public resources [12]. However, maintaining effective public cooperation among genetically unrelated individuals can be challenging due to various factors. The failure of cooperation can often be attributed to the inherent conflict between the maximization of self-interest and the maximization of group interest. Individuals tend to prioritize their own interests, often at the expense of the group's overall interests [13].

Evolutionary game theory offers a theoretical scaffold to probe the rise of cooperation, especially when kin selection is non-functional, as observed among genetically unrelated individuals [14–23]. In recent years, various theoretical models such as the prisoner's dilemma game, snowdrift game, stag hunt game and public goods game have been proposed to study the evolution of cooperation in real-world scenarios [24–26]. In addition to these models, the collective-risk social dilemma game, as a nonlinear public goods game, is gaining recognition due to its potential for application in climate change and migration [27–35]. In this model framework, all participants in the game have an initial endowment, and cooperators contribute a fraction of their initial endowment, while defectors do not contribute. If the number of cooperators in the game group does not reach the collective goal, all individuals will lose

all their remaining endowments with a probability of r, otherwise each individual will retain their own endowment [33,36]. Previous experimental and theoretical studies have revealed that high risk stimulates individuals' willingness to cooperate, thereby promoting the achievement of collective goals [32,37–40]. Recent studies have incorporated factors such as costly punishment [41] and communication [42] into the collective-risk social dilemma game model and also applied it to address carbon emissions.

Although a considerable amount of research has been conducted on the collective-risk social dilemma game, there are still many questions that warrant further exploration. One key issue to consider is how conditional cooperation strategies influence the evolution of cooperation in repeated group interactions. Previous studies have primarily focused on one-shot game scenarios [27–31], whereas in reality, interactions between individuals often occur repeatedly [14,43,44]. In such repeated interactions, where the game is played over many rounds, individuals are able to adjust their behavioural decisions based on the game environment they find themselves in. Hilbe *et al.* [45] employed evolutionary game theory to investigate the impact of strategic timing on the evolutionary outcomes in collective-risk social dilemmas. In their model, individuals were given the choice to wait for others' decisions or influence others by taking the lead. The findings suggest that the timing of participants' contributions significantly increased the probability of moving towards efficient equilibrium. Furthermore, in the study by Abou Chakra and Traulsen [46], each participant determined their contribution (a or b) based on whether the total sum exceeded their threshold. Under the all-or-nothing piecewise risk function, they saw the players who delayed their contributions were favoured in a high-risk setting.

In addition to the theoretical studies mentioned earlier, conditional behaviour in repeated interactions scenarios is also very common in real-life situations. Taking the example of climate summits, countries also decide whether to take cooperative action based on their own interests and risk preferences [47]. If a country perceives significant risks to its national security and economic development from climate change and believes that taking action can mitigate these risks, it may be inclined to take cooperative action such as signing a climate agreement and committing to reducing greenhouse gas emissions. However, if a country believes that taking action would have negative impacts on its economic interests or does not trust that other countries will also take action, it may choose not to cooperate. Therefore, a country's decision to cooperate is often based on its perception and expectation of risks and cooperative actions. Along these lines, prior studies have incorporated wealth inequalities [35,40,48] and heterogeneity in risks [35] into the collective-risk social dilemma, revealing the importance of capturing real-life scenarios for individual decision-making. For example, Abou Chakra & Traulsen [48] found that the poor contribute only when early contributions are made by the rich players. Abou Chakra *et al.* [35] found that 'wait and see' strategy is effective only when players are aware of the critical time to contribute to avert danger and if their contributions can effectively mitigate the risks.

In this work, our aim is to construct a game-theoretic model based on the collective-risk social dilemma. We investigate the evolutionary dynamics of conditional cooperation strategy in a scenario of repeated group interactions. In this

Table 1. Model parameters and their corresponding definitions.

parameter	meaning
b	initial endowment
c	cost of cooperation
r	risk
n_{pg}	collective goal
N	group size
N_C	number of cooperators in the group
T	tolerance threshold
w	repeated game probability
ξ	rounds for conditional cooperators to switch strategies
F	expected total number of game rounds
σ	observation cost

scenario, defectors observe the game environment to assess the level of risk and cooperation within the group during the early rounds of the game. On the basis of this assessment, they make decisions in subsequent rounds on whether to cooperate. These decisions are influenced by factors such as whether the risk exceeds their tolerance threshold and whether the group has achieved the desired level of cooperation in relation to the collective goal.

2. Model and methods

We consider a well-mixed population from which N individuals are randomly selected to participate in a collective-risk social dilemma game [33]. Each player has an initial endowment of b and can decide whether to contribute towards achieving collective goals. Cooperators (C) incur a cost of c, while defectors (D) contribute nothing. If the number of cooperators in the game group is less than the collective goal n_{pg}, all individuals will lose their endowments with probability r. Otherwise, all individuals maintain their endowments. We further introduce repeated group interactions, where the game is repeated with probability w, which leads to an expected number of game rounds $F = 1/(1-w)$ [14,49].

Under the framework of repeated collective-risk social dilemma game, we introduce conditional cooperation strategy, where all individuals engage in collective-risk social dilemma game in the first $\xi - 1$ rounds. During these periods, defectors incur a cost of σ to observe the game environment; specifically, they can know about the risk level and cooperation level of the group in the first $\xi - 1$ rounds. Defectors then evaluate the situation by comparing the risk level of the game with their own tolerance threshold T, and the number of cooperators in the group with the collective target n_{pg}, and decide whether to cooperate. Only when both conditions are met, will defectors choose to cooperate in subsequent rounds of the game. To provide a clearer understanding of our model configuration, we present our model parameters and their meanings in table 1.

Firstly, we consider a population composed of cooperators and conditional cooperators. According to the aforementioned description, we can write the payoffs for cooperators and conditional cooperators as follows:

$$\pi_C = \begin{cases} [-c + (1-r)b](\xi-1) + (b-c)(F-\xi+1), & \text{if } N_C + 1 < n_{pg} \qquad r \geq T \\ \{-c + b\theta(N_C + 1 - n_{pg}) + (1-r)b[1 - \theta(N_C + 1 - n_{pg})]\}F, & \text{otherwise} \end{cases}$$

and

$$\pi_{DC} = \begin{cases} (1-r)b(\xi-1) + (b-c)(F-\xi+1) - \sigma, & \text{if } N_C < n_{pg} \qquad r \geq T \\ \{b\theta(N_C - n_{pg}) + (1-r)b[1 - \theta(N_C - n_{pg})]\}F - \sigma, & \text{otherwise,} \end{cases}$$

where the terms $[-c + (1-r)b](\xi-1)$ and $(1-r)b(\xi-1)$ denote the payoffs of cooperators and conditional cooperators (defectors) in the first $\xi-1$ rounds of the game when the number of cooperators in the group is below the collective target and the risk is not below the tolerance threshold. $(b-c)(F-\xi+1)$ represents the payoffs of cooperators and conditional cooperators in the subsequent $F-\xi+1$ rounds of the game when the number of cooperators in the group is

below the collective target and the risk is not below the tolerance threshold. Otherwise, the payoffs of cooperators and conditional cooperators (defectors) are the payoffs of F rounds repeated collective-risk social dilemma game.

Next, we consider a population consisting of cooperators, defectors and conditional cooperators. Accordingly, we can express the payoffs of cooperators, defectors and conditional cooperators as follows:

$$\pi_C = \begin{cases} [-c + (1-r)b](\xi-1) + [b\theta(N_C + N_{DC} + 1 - n_{pg}) - c + \\ (1-r)b(1 - \theta(N_C + N_{DC} + 1 - n_{pg}))](F-\xi+1), & \text{if } N_C + 1 < n_{pg} \qquad r \geq T \\ \{-c + b\theta(N_C + 1 - n_{pg}) + (1-r)b[1 - \theta(N_C + 1 - n_{pg})]\}F, & \text{otherwise} \end{cases}$$

$$\pi_D = \begin{cases} (1-r)b(\xi-1) + [b\theta(N_C + N_{DC} - n_{pg}) + \\ (1-r)b(1 - \theta(N_C + N_{DC} - n_{pg}))](F-\xi+1), & \text{if } N_C < n_{pg} \qquad r \geq T \\ \{b\theta(N_C - n_{pg}) + (1-r)b[1 - \theta(N_C - n_{pg})]\}F, & \text{otherwise} \end{cases}$$

and $\quad \pi_{DC} = \begin{cases} (1-r)b(\xi-1) + [b\theta(N_C + N_{DC} + 1 - n_{pg}) - c + \\ (1-r)b(1 - \theta(N_C + N_{DC} + 1 - n_{pg}))](F-\xi+1) - \sigma, & \text{if } N_C < n_{pg} \qquad r \geq T \\ \{b\theta(N_C - n_{pg}) + (1-r)b[1 - \theta(N_C - n_{pg})]\}F - \sigma, & \text{otherwise,} \end{cases}$

where N_{DC} denotes the number of conditional cooperators in the group.

In the following, we investigate the evolutionary dynamics of the system in an infinite well-mixed population by analysing replicator equations [49–51]. Subsequently, we employ the Markov decision process to address the stochastic effects and population dynamics in a finite well-mixed population [52,53].

3. Replicator equation

In an infinite population, we consider a population state as $\mathbf{x} = (x_1, x_2, \ldots, x_n)$ where x_i denotes the frequency of adoption of i strategy by individuals in the population. The rate of change of the frequency of a strategy in a population is proportional to the difference between the average payoff of that strategy and the average payoff of the population as a whole. Accordingly, the replicator equation can be written as follows:

$$\dot{x}_i = x_i(\Pi_i(\mathbf{x}) - \bar{\Pi}(\mathbf{x})), \tag{3.1}$$

where $\Pi_i(\mathbf{x})$ denotes the average payoff of an individual using strategy i and $\bar{\Pi}(\mathbf{x}) = \sum_{j=1}^{n} x_j \Pi_j(\mathbf{x})$ denotes the average payoff of the whole population. The direction of change for each strategy can be represented by the aforementioned differential equations, which allows for a

complete characterization of the strategic variations in the population.

4. Markov decision process

When individuals interact in finite populations, stochastic effects including behavioural mutations and imitation errors become non-negligible. The stochastic dynamics in such finite populations can be described by the gradient of selection, defined as the difference between the probabilities of increasing and decreasing the number of given strategies, and the stationary distribution of the associated Markov chain, which characterizes the pervasiveness in time of a given composition of the population [54].

We adopt a pairwise comparison rule to describe the process of strategy selection. Specifically, at each time step, an individual A is randomly selected to update its strategy, and with probability $1/(1 + \exp[\beta(f_A - f_B)])$, A imitates the strategy of another randomly selected individual B, where β is referred to as the intensity of selection [55] and f_A and f_B represent the average payoffs of individuals A and B, respectively. Furthermore, we introduce behavioural mutation, where with probability μ, individual A randomly selects a strategy from the remaining strategy space to use, and with probability $1 - \mu$, A updates its strategy using the
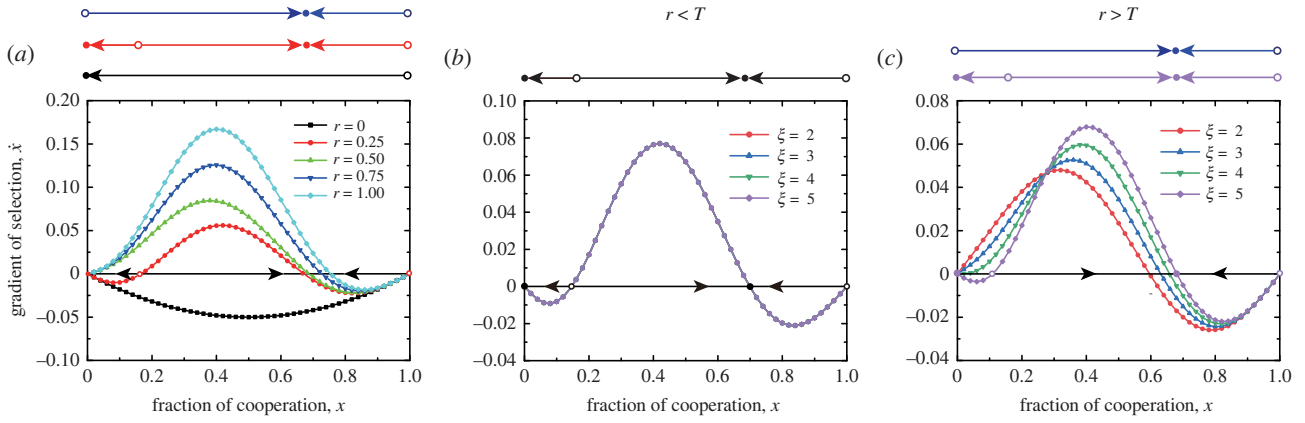
Figure 1. Gradient of selection of the replicator dynamics. (*a*) It is shown that high risk can promote high-level cooperation. (*b*) It is shown that the number of rounds in which the conditional cooperator adjusts its strategy does not affect the outcome when the risk is below the tolerance threshold. (*c*) It is revealed that timely adjustment of the strategy is advantageous for maintaining cooperation when risk exceeds the tolerance threshold. Parameters used are as follows: (*a*) $N = 6$, $n_{pg} = 3$, $\xi = 3$, $T = 0.5$, $w = 0.8$ and $\sigma = 0.3$; (*b*) $N = 6$, $n_{pg} = 3$, $r = 0.3$, $T = 0.5$, $w = 0.8$ and $\sigma = 0.3$; and (*c*) $N = 6$, $n_{pg} = 3$, $r = 0.3$, $T = 0.2$, $w = 0.8$ and $\sigma = 0.3$.

pairwise comparison rule described earlier. Concretely, in a population with n strategies, the probability that individual A adopts the strategy of individual B can be written as follows:

$$T_{A \to B} = (1 - \mu) \frac{i_A}{Z} \frac{i_B}{Z - 1} \frac{1}{1 + \exp[\beta(f_A - f_B)]} + \mu \frac{i_A}{(n-1)Z}, \quad (4.1)$$

where i_A and i_B denote the numbers of A and B individuals in finite populations, respectively.

Therefore, in a tri-strategy population, the gradient of selection [54] used to characterize the most probable direction of system evolution after leaving the current configuration $\mathbf{i} = (i_A, i_B)$ can be expressed as follows: $\nabla_{\mathbf{i}} = (T_{\mathbf{i}}^{A+} - T_{\mathbf{i}}^{A-})\mathbf{u_A} + (T_{\mathbf{i}}^{B+} - T_{\mathbf{i}}^{B-})\mathbf{u_B}$, where $\mathbf{u_A}$ and $\mathbf{u_B}$ are basis vectors. $T_{\mathbf{i}}^{A+}(T_{\mathbf{i}}^{A-})$ and $T_{\mathbf{i}}^{B+}(T_{\mathbf{i}}^{B-})$, respectively, denote the probabilities that the numbers of A and B individuals increase (decrease) one. In a bi-strategy population, the gradient of selection is defined as the difference between the probabilities of increasing and decreasing the number of individuals adopting a given strategy, namely, $G(i_A) = T^+(i_A) - T^-(i_A)$.

On the basis of equation (4.1), we can derive the transition probability from state $\mathbf{i}$ to an adjacent state $\mathbf{i}'$. Thus, the transition matrix $T = [T_{\mathbf{i},\mathbf{i}'}]$, which fully characterizes the stochastic process dynamics. The stationary distribution of the system, representing the amount of time the population spends at each state, can be analytically computed by normalizing the eigenvector associated with the eigenvalue 1 of the transition matrix T of the Markov chain [54].

5. Results

(a) Evolutionary dynamics in infinite populations

We first consider a population consisting only of cooperators and conditional cooperators, where the fraction of cooperators is x and the fraction of conditional cooperators is $1 - x$. In an infinite well-mixed population, we use the gradient of selection to characterize the evolution of strategies. Concretely, the replicator equation can be expressed as $\dot{x} = x(1 - x)(\Pi_C - \Pi_{DC})$, where Π_C and Π_{DC}, respectively, denote the expected payoffs of cooperators and conditional cooperators, and $\dot{x}$ means the rate of change in x over time.

According to the replicator equation, when $\dot{x} > 0$, the frequency of cooperators in the population will increase. In

figure 1*a*, we present the result that the gradient of selection changes with the fraction of cooperators in the population for different risk values. In the absence of risk, the gradient value $\dot{x}$ is always negative, resulting in conditional cooperators occupying the entire population regardless of the initial conditions. However, with a slight increase in the risk value ($r = 0.25$), we observe the emergence of two internal equilibrium points, one of which is stable and the other is unstable. This risk value was previously considered unable to promote the emergence of cooperation in the theoretical study [36]. When the risk value is high ($r \geq 0.5$), the unstable equilibrium point disappears, and sustained cooperation at a significant level can be maintained. This means that an increase in risk is conducive to the emergence of a high percentage of cooperation ($x > 0.6$). Furthermore, we investigate the impact of the game round ξ that conditional cooperators adjust their strategy on the evolutionary outcomes when the risk value is below the tolerance threshold ($r < T$) and above the tolerance threshold ($r > T$). We find that when the risk value is below the tolerance threshold, different values of ξ do not affect the evolutionary outcome, where the system exhibits an unstable equilibrium point and a stable equilibrium point (figure 1*b*). When the risk exceeds the tolerance threshold, we find that an intermediate value of ξ can sustain a high level of cooperation. However, when ξ is particularly high ($\xi = 5$), the system exhibits bistability, where depending on the initial conditions, the system either converges to a high-level cooperation state or the D state (figure 1*c*). This means that an individual choosing a free-riding strategy can also be favoured by natural selection.

In figure 2, we show the location of internal equilibria as a function of observation cost σ for different values of ξ and n_{pg} when the risk value is lower than the tolerance threshold and is higher than the tolerance threshold, respectively. We observe that as the value of σ increases, the value of the unstable internal equilibrium point gradually decreases until it reaches zero, while the stable equilibrium point gradually increases until it reaches one. This indicates that the increase in observation cost expands the basin of attraction of stable equilibrium point, thereby enabling the maintenance of high-level cooperation. Besides, the increase in collective goals leads to an increase in the values of existing internal equilibrium points, regardless of whether the collective risk exceeds the tolerance threshold of conditional
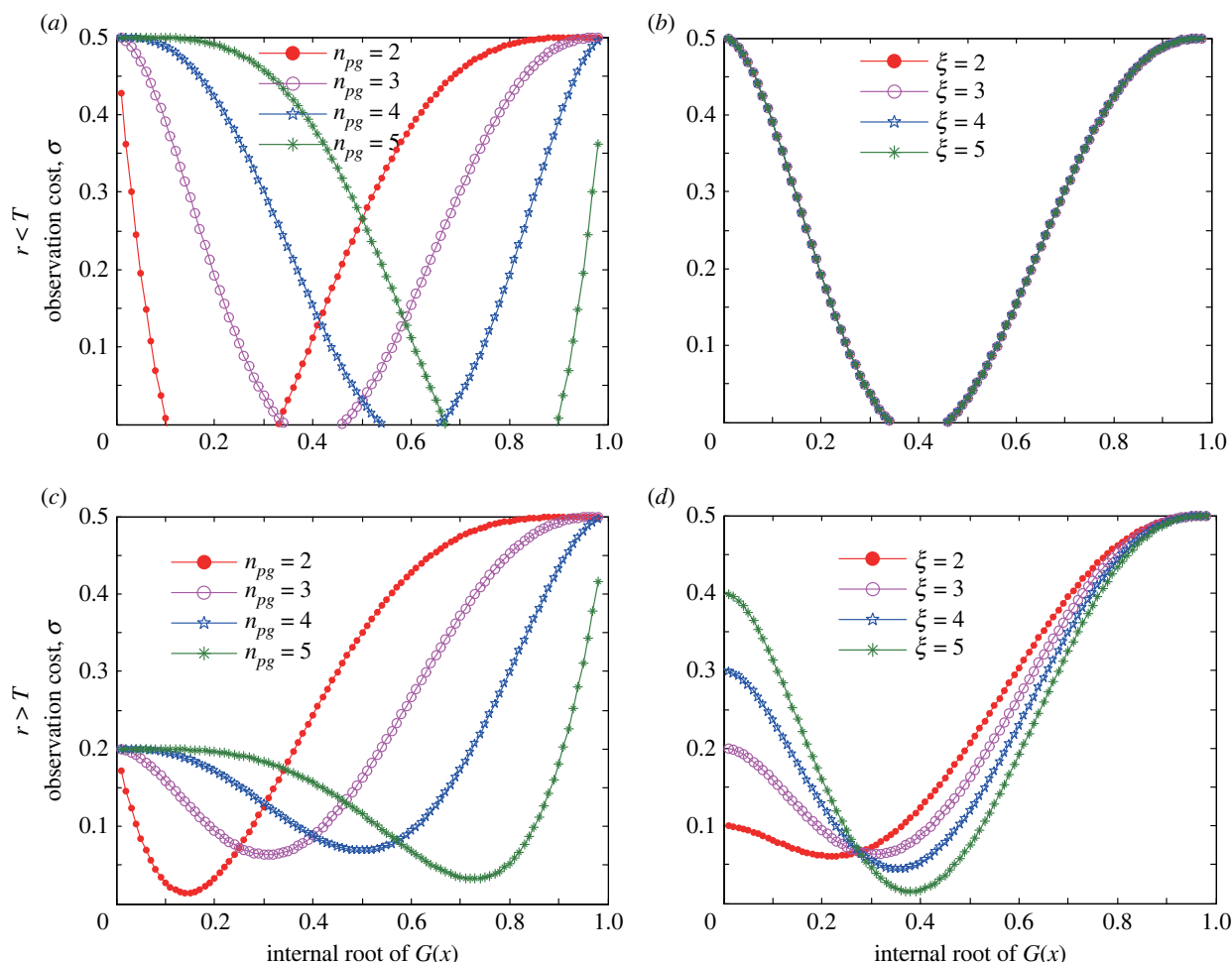
Figure 2. Internal roots of the gradient of selection as a function of observation cost for different n_{pg} and ξ values. Expanding the observation cost will enhance the evolutionary advantage of cooperation. Parameters used are as follows: (a) $N = 6$, $\xi = 3$, $T = 0.5$, $w = 0.8$ and $r = 0.3$; (b) $N = 6$, $n_{pg} = 3$, $r = 0.3$, $T = 0.5$ and $w = 0.8$; (c) $N = 6$, $r = 0.3$, $T = 0.2$, $w = 0.8$ and $\xi = 3$; and (d) $N = 6$, $r = 0.3$, $T = 0.2$, $w = 0.8$ and $n_{pg} = 3$.

cooperators (figure 2a,c). In addition, the increase of collective goals reduces the attraction domain of stable internal equilibrium point, which is therefore detrimental to the maintenance of high-level cooperation. Furthermore, we find that when the risk is below the tolerance threshold, the increase in the value of ξ has no effect on the internal equilibrium points (figure 2b). However, when the risk exceeds the tolerance threshold, we observe that an increase in the value of ξ leads to an increase in the values of internal equilibrium points (figure 2d), which implies that the attraction domain of stable equilibrium points decreases, thereby detrimental to the maintenance of cooperation.

Next, we consider a population consisting of cooperators, defectors and conditional cooperators, where the frequency of cooperators is x, the frequency of defectors is y and the frequency of conditional cooperators is z. In figure 3, we numerically investigate the impact of different values of ξ on the evolutionary dynamics of cooperators, defectors and conditional cooperators. The top row shows evolutionary results of the system when the risk is lower than the tolerance threshold. There exist seven equilibrium points, among which the vertex equilibrium point $(x, y, z) = (0, 1, 0)$ and the D–C boundary equilibrium point K_1 are stable. Therefore, when the initial fraction of cooperation is not particularly low, cooperators can stably coexist with defectors in the population. Moreover, as the value of ξ increases, the evolutionary outcomes of the system remain unchanged (figure 3a–d). The

reason for this phenomenon is that the risk has not reached the tolerance threshold of conditional cooperators, and therefore, they will not change their own strategies.

When the risk exceeds the tolerance threshold, the system could generate new evolutionary dynamics. Specifically, when the value of ξ is small ($\xi = 2$), we find that there are nine equilibrium points in the system, among which the interior equilibrium point Q_1, vertex D and equilibrium point K_6 on the D–DC boundary are stable (figure 3e). The majority of interior trajectories converge to the interior stable point, thus cooperators, defectors and conditional cooperators can stably coexist in the population. As the value of ξ increases, we observe that the interior equilibrium point moves closer to the boundary D–C, and two new interior equilibrium points, Q_2 and Q_3, can emerge, which results in a reduction of the basin of attraction of the interior equilibrium point Q_1 (figure 3f,g). When the value of ξ is extremely large ($\xi = 5$), we observe the disappearance of the interior equilibrium point, resulting in the existence of seven equilibrium points in the system (figure 3h). Among them, stable equilibrium is achieved at point K_1 on the boundary of D–C and at vertex D. It should be noted that the basin of attraction of K_1 exceeds that of vertex D, indicating that high-level cooperation can still be sustained, attributed to the high-risk level. It should be noted that the attraction domain of D is also the largest compared with the previous situations.
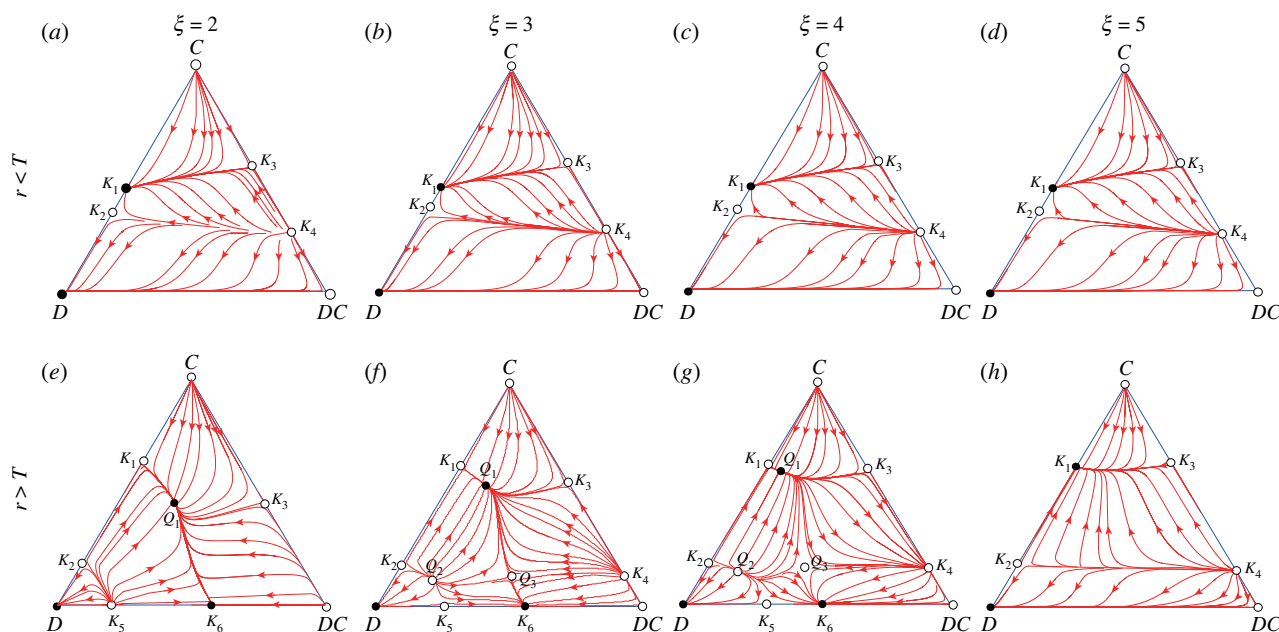
Figure 3. Evolutionary dynamics of cooperation, defection and conditional cooperation strategies in the simplex S_3. Empty circles represent unstable equilibrium points, while solid dots represent stable equilibrium points. Arrows represent the direction of evolution. Cooperators are able to stably coexist with defectors and conditional cooperators in a population when the risk exceeds the threshold of tolerance. Parameters are expressed as follows: (a) $N = 6$, $n_{pg} = 3$, $c = 0.1$, $b = 1$, $T = 0.5$, $r = 0.3$, $w = 0.8$, $\sigma = 0.1$ and $\xi = 2$; (b) $\xi = 3$; (c) $\xi = 4$; (d) $\xi = 5$; (e) $N = 6$, $n_{pg} = 3$, $c = 0.1$, $b = 1$, $T = 0.2$, $r = 0.5$, $w = 0.8$, $\sigma = 0.1$ and $\xi = 2$; (f) $\xi = 3$; (g) $\xi = 4$; and (h) $\xi = 5$.

We further investigate the impact of other model parameters on the evolutionary outcomes. In electronic supplementary material, figure A1, we show the role of different levels of risk in the evolution of cooperation and find that cooperation cannot emerge in scenario with low risk, while increasing risk can effectively promote the emergence of cooperation. Specifically, when the risk level exceeds the tolerance threshold, there exists a stable interior equilibrium point, where the three types of strategists can stably coexist in the population. Moreover, we find that increasing the collective target value (n_{pg}) expands the attraction domain of full defection (electronic supplementary material, figure A2). It is worth emphasizing that when the risk exceeds the tolerance threshold, the system still exhibits a stable interior equilibrium point, although its attraction domain decreases with increasing values of n_{pg}, it is still larger than the attraction domain of D, thus enabling the maintenance of high-level cooperation. We are further interested in the impact of observation cost σ on the evolutionary outcomes. As shown in electronic supplementary material, figure A3, we present the effects of different observation costs on the evolution of cooperation in scenarios where the risk is lower than the tolerance threshold ($r < T$) and higher than the tolerance threshold ($r > T$). We find that when $r < T$, the system exhibits bistability, where the trajectory of the system converges to either the vertex D or the point K_1 on the $C–DC$ boundary, depending on the initial conditions. Besides, increasing the observation cost σ alters the distribution of equilibrium points on the $C–DC$ boundary. When $r > T$, the system can exhibit a stable interior equilibrium point when observation cost is low. As observation cost increases, the interior equilibrium point disappears and most system trajectories converge to the equilibrium point K_1 on the $D–C$ boundary. This implies that cooperators and defectors can stably coexist in the population. We also further investigate the impact of the repeated

probability of game on the evolutionary results. As shown in electronic supplementary material, figure A4, when the risk is below the tolerance threshold, we find that depending on the initial proportion of each strategy, the system will converge to a state of coexistence between cooperators and defectors or a state where defectors dominate. The repeated probability of game does not have a significant impact on the evolutionary outcome (electronic supplementary material, figure A4a–d). When the risk is above the tolerance threshold, cooperators, defectors and conditional cooperators can stably coexist in the population. The increase of repeated probability promotes the emergence of this stable coexistence state (electronic supplementary material, figure A4e–h).

(b) Evolutionary dynamics in finite well-mixed populations

When the population size is finite, we employ the Markov process to analyse the evolutionary dynamics of the system. In figure 4, we present the results of the gradient of selection and stationary distribution when the population is composed of cooperators and conditional cooperators. Due to the existence of behavioural mutation, we find that in the absence of risk, the gradient equation $G(i_C) = 0$ has a stable internal root, in which cooperators and conditional cooperators can coexist stably within the population (figure 4a). As the level of risk increases, we observe that the proportion of cooperators at the stable equilibrium further increases. Importantly, higher levels of risk ensure a higher fraction of cooperators at the stable equilibrium. In figure 4b, we show the stationary distributions for different values of risk. In the absence of risk, the population spends most of its time in the state of defection. However, as the level of risk increases, the population spends a significant amount of time in the configuration where
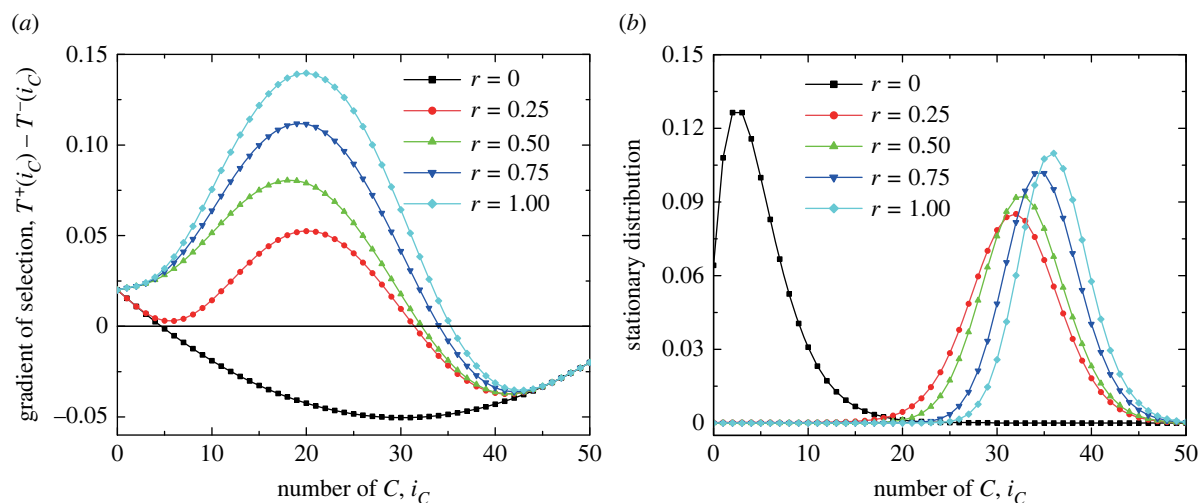
Figure 4. Evolutionary dynamics of cooperation and conditional cooperation in finite populations. (a) The gradient of selection as a function of the number of cooperators for different risk. (b) The stationary distribution for a finite population to describe the prevalence of each state. High risk promotes the emergence of cooperation. Parameters used are as follows: $Z = 50$, $N = 6$, $n_{pg} = 3$, $\xi = 3$, $T = 0.5$, $w = 0.8$, $\mu = 1/Z$, $\beta = 2$ and $\sigma = 0.3$.

cooperation prevails, regardless of initial conditions. Similarly, higher levels of risk ensure a high level of cooperation.

In figure 5, we present the impact of ξ values on the evolutionary outcomes in finite populations. We find that for four different ξ values, the gradient equation always exhibits a stable internal equilibrium point. Moreover, as the ξ value increases, the equilibrium point moves towards the right axis, indicating higher levels of cooperation (figure 5a). This deviation from the results in infinite populations is fundamentally attributed to stochastic effects. Results from the stationary distributions show that the population spends most of the time in configurations where cooperators prevail (figure 5b). A higher value of ξ ensures a higher level of cooperation.

When the population consists of cooperators, defectors and conditional cooperators, we present in figure 6 the stationary distribution and gradient of selection for different values of ξ, when the risk is below the tolerance threshold and when the risk is above the tolerance threshold, respectively. We find that the population spends the most of the time in configurations where defectors prevail when $r < T$. In addition, an increase in ξ does not alter the stochastic dynamics (figure 6a–d). This implies that defection is always favoured by natural selection. When the risk is above the tolerance threshold, the stochastic dynamics of cooperation, defection and conditional cooperation strategies will undergo significant changes. Specifically, when the value of ξ is low, we find that the population spends a considerable amount of time in configurations in the centre of the simplex, which means that the three strategies can stably coexist in the population (figure 6e). Most of the interior trajectories converge to this region, while a small number of trajectories converge to vertex D. As the value of ξ increases, we observe that the shaded region moves towards the D–C boundary, indicating a gradual decrease in the proportion of conditional cooperators in the steady state (figure 6e–h).

We further investigate the impact of different model parameters on the stochastic dynamics of finite populations. In electronic supplementary material, figure A5, we present outcomes from stationary distribution and gradient of selection for four different risk values. We find that when the risk is low, the population spends the majority of time in configurations where defectors prevail (electronic supplementary

material, figure A5a), and a slight increase in risk does not significantly alter the stationary distribution results but does affect the gradient of selection (two equilibrium states will appear on the D–C boundary (electronic supplementary material, figure A5b). A continued increase in risk drives the emergence of interior steady states. As shown in electronic supplementary material, figure A5c, most of the interior trajectories flow towards the interior equilibrium states, a small portion flows towards vertex D and the remaining trajectories converge to the middle portion of the D–DC boundary. Such dynamical outcome persists until relatively large risk values (electronic supplementary material, figure A5d), which implies that high levels of risk can effectively enhance cooperation.

We are also interested in investigating the impact of different collective target values on the evolutionary dynamics when stochastic factors are taken into account. In the top row of electronic supplementary material, figure A6, we study the effects of different collective targets on the evolutionary dynamics of cooperation, defection and conditional cooperation when the risk is below the tolerance threshold. When the collective target value is small ($n_{pg} = 2$), we observe there exists bistability, where the population spends time in both configurations where defectors win and configurations near the D–C boundary (implying stable coexistence of cooperators and defectors within the population) (electronic supplementary material, figure A6a). As the collective target value increases, we observe that the population spends most of the time in the configuration where the defectors prevail (electronic supplementary material, figure A6b–d). When the risk exceeds the tolerance threshold, we observe that for lower collective targets, the population spends more time inside the simplex where three strategies can coexist (electronic supplementary material, figure A6e). The increase in collective target values drives the shadow area to move towards configurations that favour cooperation (see electronic supplementary material, figure A6f–h).

Furthermore, we are highly interested in conducting further research to examine the effects of observation costs on evolutionary outcomes in finite populations. We find that when the risk is below the tolerance threshold, for different observation cost values, the population spends most of the time in the configuration dominated by defectors (electronic supplementary material, figure A7a–d). However, when the
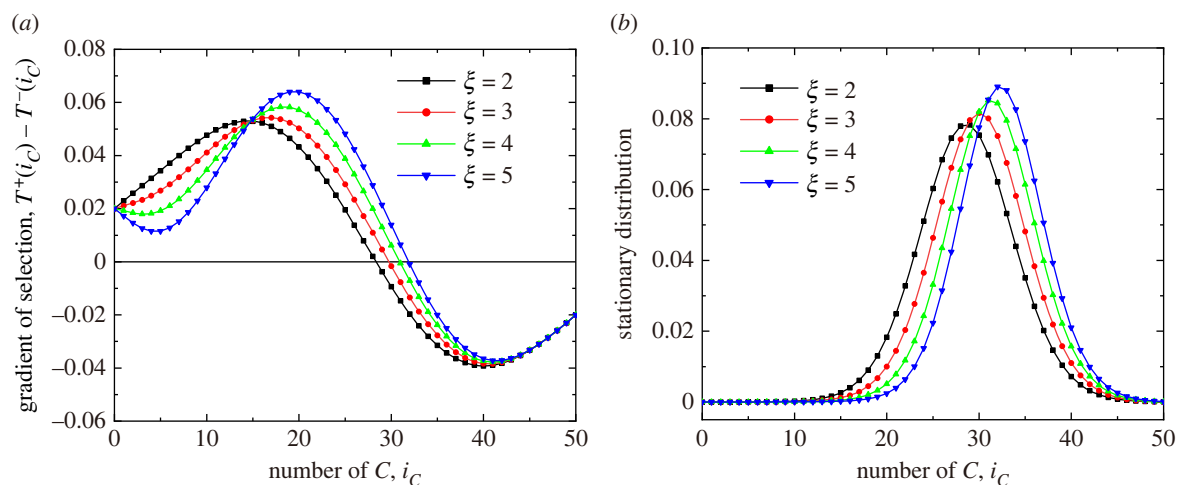
Figure 5. Gradient of selection and stationary distributions for different values of ξ in finite populations. The presence of behavioural mutations makes it more advantageous to delay the adjustment of strategies for the emergence of high-level cooperation. Parameters used are as follows: $Z = 50$, $N = 6$, $n_{pg} = 3$, $T = 0.2$, $r = 0.3$, $w = 0.8$, $\mu = 1/Z$, $\beta = 2$ and $\sigma = 0.3$.
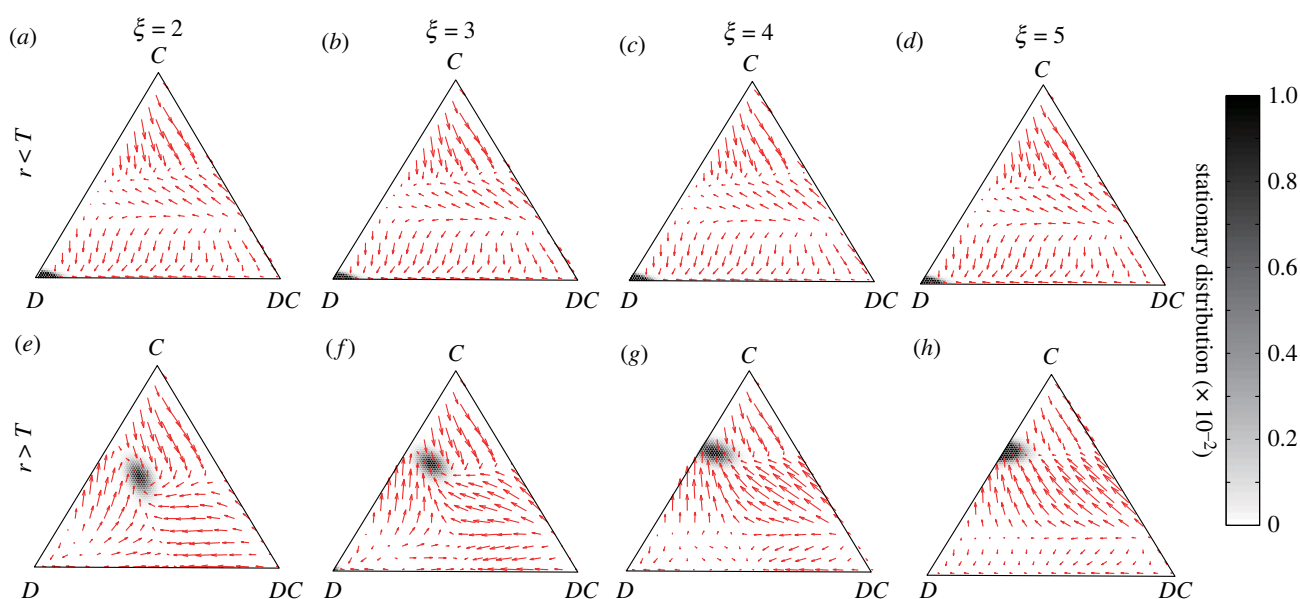
Figure 6. The evolutionary dynamics of cooperation, defection and conditional cooperation strategies in finite populations for different values of ξ. The simplex S_3 contains all possible configurations, where each small dot represents one state. The colourbar indicates the magnitude of the stationary distribution value, and darker dots indicate those configurations visited more often. The red arrow is derived from the gradient equation solution and is used to describe the most likely evolutionary direction when leaving the current configuration. When the risk is below the tolerance threshold, defectors dominate the entire population, while when the risk exceeds the tolerance threshold, cooperators, defectors and conditional cooperators can stably coexist in the population. Parameters used are as follows: (a) $Z = 100$, $\mu = 1/Z$, $\beta = 5$, $N = 6$, $n_{pg} = 3$, $c = 0.1$, $b = 1$, $T = 0.5$, $r = 0.3$, $w = 0.8$, $\sigma = 0.1$ and $\xi = 2$; (b) $\xi = 3$; (c) $\xi = 4$; (d) $\xi = 5$; (e) $Z = 100$, $\mu = 1/Z$, $\beta = 5$, $N = 6$, $n_{pg} = 3$, $c = 0.1$, $b = 1$, $T = 0.2$, $r = 0.5$, $w = 0.8$, $\sigma = 0.1$ and $\xi = 2$; (f) $\xi = 3$; (g) $\xi = 4$; and (h) $\xi = 5$.

risk is higher than the tolerance threshold, an interior coexistence state can emerge and gradually approach the $D–C$ boundary with the increase of observation costs (electronic supplementary material, figure A7e–h). This indicates that an increase in risk can facilitate the maintenance of high levels of cooperation. Finally, we aim to investigate the impact of the repeated probability of the game in finite populations on evolutionary outcomes (electronic supplementary material, figure A8). Similar to the results in infinite populations, we find that when the risk is below the tolerance threshold, defectors are favoured by natural selection (electronic supplementary material, figure A8a–d); while when the risk is above the threshold, the system exhibits an interior steady state where cooperators, defectors and conditional cooperators can coexist (electronic supplementary material, figure A8e–h).

Therefore, the increase in the repeated probability does not significantly alter the dynamics of the system.

6. Conclusion

In collective-risk social dilemma games, conflicts of interest among individuals often hinder cooperation, leading to a loss of overall benefits. To address this issue, we explored the collective-risk social dilemma through a theoretical model incorporating repeated group interactions and a conditional cooperation strategy. This strategy allows defectors to assess the game's risk level and the number of cooperators before deciding whether to contribute in later rounds. Our key findings reveal that introducing a conditional cooperation

strategy can foster cooperation, even in situations of relatively low collective risk.

Conditional cooperation strategies are widely observed in the framework of evolutionary game theory. Such strategies allow individuals to adjust their actions based on the behaviour of others in the group and the game environment they are in. For example, in the context of emissions reduction actions, major carbon-emitting countries including the United States, the European Union, Japan, China and India have stated in a series of declarations that they will only significantly reduce emissions if other countries take corresponding actions [47]. Besides, previous experimental and theoretical studies based on collective-risk social dilemma games have demonstrated that individuals tend to contribute based on the previous decisions made by other group members [56,57]. The findings indicate that conditional behaviour, also called trigger strategies in [57], is more successful than those adopting fixed strategies. Previous studies on collective-risk social dilemma games have considered conditional strategies (individuals make decisions based on the total contributions) and different perceived risk factors [35,48]. The results indicate that by adding loss parameters, one can shift the system from late to early contributors. Inspired by these studies, we introduce DC strategists who only switch in the last rounds, but it is not clear if it will happen, which adds another level of uncertainty compared with previous studies.

The emergence of conditional cooperation strategies depends on the repeated group interactions scenario. In repeated games, players have the opportunity to observe each other's behaviour in multiple interactions and adjust their strategies based on their observations. Previous theoretical studies on collective-risk social dilemmas primarily relies on one-shot game interaction scenarios where participants are only able to make a single decision [27,29,33]. As a result, participants often opt for selfish strategies, leading to the breakdown of cooperation and the emergence of social dilemmas. In this work, we consider the repeated group interactions where individuals can adjust their behaviour based on the game environment, including the risk level and group cooperation level. Our findings demonstrate that the risk level and the number of game rounds for strategy adjustment have a significant impact on the evolutionary outcomes. Specifically, when the risk level exceeds the tolerance threshold of conditional cooperators, timely strategy adjustment by conditional cooperators can promote the stable coexistence of cooperators, defectors and conditional cooperators in the population. Moreover, an increase in the number of rounds for strategy adjustment expands the prevalence of free-riders in the population.

In our work, we assume that conditional cooperators decide whether to cooperate based on their assessment of the cooperation level within the group and game risk level. It should be noted that both the cooperation level and risk level are evaluated by the conditional cooperators based on the initial rounds of the game, and there may be errors in the evaluation [58]. Therefore, it is worthwhile to investigate the impact of overestimation and underestimation on the evolutionary outcome. Furthermore, decision-making by individuals often involves decision cost, and it is worth further exploring how the introduction of decision cost affects the evolutionary outcomes of the system. Risk can affect cooperative behaviour in various ways [59,60], and in our model, the risk value of the game is constant. However, in reality, the shape of the risk curve may be diverse. Abou Chakra et al. [35] manipulated the shape of the risk curve and investigated how risk curve characteristics affect individual contributions. Therefore, future research could investigate the impact of different risk equations on the evolutionary outcomes. Finally, it is important to emphasize that the study of cooperation is just one type of moral behaviour that can be studied using these models [61]. To better understand selfless human behaviour and adjust policies accordingly, future research could focus on mathematical modelling of moral preferences. This represents a promising avenue for advancing our understanding of moral decision-making and promoting socially responsible behaviour.

Individual decision-making, oscillating between cooperative and defective strategies, is often governed by the balance of risk against personal tolerance thresholds and the achievement of collective objectives. This is a ubiquitous phenomenon observed across various domains. Taking climate change as an illustrative example, if the collective objective of mitigating climate change has not yet been achieved and the perceived risk surpasses a nation's tolerance level, the country is more likely to adopt cooperative strategies. These may include reducing greenhouse gas emissions, investing in renewable energy and supporting international climate agreements. By constructing a theoretical model, our work reveals that timely transition from defective strategy to cooperative strategy is beneficial for the construction of a cooperative society.

References

1. Perc M, Jordan JJ, Rand DG, Wang Z, Boccaletti S, Szolnoki A. 2017 Statistical physics of human cooperation. *Phys. Rep.* **687**, 1–51. (doi:10.1016/j.physrep.2017.05.004)

2. Lie-Panis J, André JB. 2022 Cooperation as a signal of time preferences. *Proc. R. Soc. B* **289**, 20212266. (doi:10.1098/rspb.2021.2266)

3. Stockley P, Bro-Jørgensen J. 2011 Female competition and its evolutionary consequences in mammals. *Biol. Rev.* **86**, 341–366. (doi:10.1111/j.1469-185X.2010.00149.x)

4. Thomas CD et al. 2004 Extinction risk from climate change. Nature 427, 145–148. (doi:10.1038/nature02121)

5. Boesch C. 1994 Cooperative hunting in wild chimpanzees. Anim. Behav. 48, 653–667. (doi:10.1006/anbe.1994.1285)

6. Ranta E, Rita H, Lindstrom K. 1993 Competition versus cooperation: success of individuals foraging alone and in groups. Am. Nat. 142, 42–58. (doi:10.1086/285528)

7. Wilkinson GS, Carter GG, Bohn KM, Adams DM. 2016 Non-kin cooperation in bats. Phil. Trans. R. Soc. B 371, 20150095. (doi:10.1098/rstb.2015.0095)

8. Chen X, Fu F. 2022 Highly coordinated nationwide massive travel restrictions are central to effective mitigation and control of COVID-19 outbreaks in China. Proc. R. Soc. A: Math. Phys. Eng. Sci. 478, 20220040. (doi:10.1098/rspa.2022.0040)

9. Chen X, Fu F. 2019 Imperfect vaccine and hysteresis. Proc. R. Soc. B 286, 20182406. (doi:10.1098/rspb.2018.2406)

10. Andrews TM, Delton AW, Kline R. 2018 High-risk high-reward investments to mitigate climate change. Nat. Clim. Change 8, 890–894. (doi:10.1038/s41558-018-0266-y)

11. Grimalda G, Belianin A, Hennig-Schmidt H, Requate T, Ryzhkova MV. 2022 Sanctions and international interaction improve cooperation to avert climate change. Proc. R. Soc. B 289, 20212174. (doi:10.1098/rspb.2021.2174)

12. Schlüter M, Tavoni A, Levin S. 2016 Robustness of norm-driven cooperation in the commons. Proc. R. Soc. B 283, 20152431. (doi:10.1098/rspb.2015.2431)

13. Bornstein G, Ben-Yossef M. 1994 Cooperation in intergroup and single-group social dilemmas. J. Exp. Soc. Psychol. 30, 52–67. (doi:10.1006/jesp.1994.1003)

14. Liu L, Xiao Z, Chen X, Szolnoki A. 2022 Early exclusion leads to cyclical cooperation in repeated group interactions. J. R. Soc. Interface 19, 20210755. (doi:10.1098/rsif.2021.0755)

15. Han TA, Perret C, Powers ST. 2021 When to (or not to) trust intelligent machines: insights from an evolutionary game theory analysis of trust in repeated games. Cogn. Syst. Res. 68, 111–124. (doi:10.1016/j.cogsys.2021.02.003)

16. Han TA, Pereira LM, Lenaerts T, Santos FC. 2021 Mediating artificial intelligence developments through negative and positive incentives. PLoS ONE 16, e0244592. (doi:10.1162/isal_a_00385)

17. Han TA. 2022 Emergent behaviours in multi-agent systems with evolutionary game theory. AI Commun. 35, 327–337. (doi:10.3233/AIC-220104)

18. Han TA. 2022 Institutional incentives for the evolution of committed cooperation: ensuring participation is as important as enhancing compliance. J. R. Soc. Interface 19, 20220036. (doi:10.1098/rsif.2022.0036)

19. Tanimoto J. 2017 How does resolution of strategy affect network reciprocity in spatial prisoner's dilemma games? Appl. Math. Comput. 301, 36–42.

20. Tanimoto J. 2015 Fundamentals of evolutionary game theory and its applications. Tokyo, Japan: Springer.

21. Tanimoto J 2021 Sociophysics approach to epidemics. Singapore: Springer.

22. Szolnoki A, Mobilia M, Jiang LL, Szczesny B, Rucklidge AM, Perc M. 2014 Cyclic dominance in evolutionary games: a review. J. R. Soc. Interface 11, 20140735. (doi:10.1098/rsif.2014.0735)

23. Szolnoki A, Perc M, Danku Z. 2008 Making new connections towards cooperation in the prisoner's dilemma game. EPL 84, 50007. (doi:10.1209/0295-5075/84/50007)

24. Xia C, Li X, Wang Z, Perc M. 2018 Doubly effects of information sharing on interdependent network reciprocity. New J. Phys. 20, 075005. (doi:10.1088/1367-2630/aad140)

25. Zhu Y, Xia C, Wang Z, Chen Z. 2022 Networked decision-making dynamics based on fair, extortionate and generous strategies in iterated public goods games. IEEE Trans. Netw. Sci. Eng. 9, 2450–2462. (doi:10.1109/TNSE.2022.3164094)

26. Xia C, Hu Z, Zhao D. 2022 Costly reputation building still promotes the collective trust within the networked population. New J. Phys. 24, 083041. (doi:10.1088/1367-2630/ac8898)

27. Chen X, Szolnoki A, Perc M. 2012 Risk-driven migration and the collective-risk social dilemma. Phys. Rev. E 86, 036101. (doi:10.1103/PhysRevE.86.036101)

28. He N, Chen X, Szolnoki A. 2019 Central governance based on monitoring and reporting solves the collective-risk social dilemma. Appl. Math. Comput. 347, 334–341.

29. Chen X, Zhang Y, Huang TZ, Perc M. 2014 Solving the collective-risk social dilemma with risky assets in well-mixed and structured populations. Phys. Rev. E 90, 052823. (doi:10.1103/PhysRevE.90.052823)

30. Chen X, Szolnoki A, Perc M. 2012 Averting group failures in collective-risk social dilemmas. EPL 99, 68003. (doi:10.1209/0295-5075/99/68003)

31. Wang J, Fu F, Wu T, Wang L. 2009 Emergence of social cooperation in threshold public goods games with collective risk. Phys. Rev. E 80, 016101. (doi:10.1103/PhysRevE.80.016101)

32. Milinski M, Sommerfeld RD, Krambeck HJ, Reed FA, Marotzke J. 2008 The collective-risk social dilemma and the prevention of simulated dangerous climate change. Proc. Natl Acad. Sci. USA 105, 2291–2294. (doi:10.1073/pnas.0709546105)

33. Santos FC, Vasconcelos VV, Santos MD, Neves PNB, Pacheco JM. 2012 Evolutionary dynamics of climate change under collective-risk dilemmas. Math. Models Methods Appl. Sci. 22, 1140004. (doi:10.1142/S0218202511400045)

34. Szekely A, Lipari F, Antonioni A, Paolucci M, Sánchez A, Tummolini L, Andrighetto G. 2021 Evidence from a long-term experiment that collective risks change social norms and promote cooperation. Nat. Commun. 12, 5452. (doi:10.1038/s41467-021-25734-w)

35. Abou Chakra M, Bumann S, Schenk H, Oschlies A, Traulsen A. 2018 Immediate action is the best strategy when facing uncertain climate change. Nat. Commun. 9, 2566. (doi:10.1038/s41467-018-04968-1)

36. Santos FC, Pacheco JM. 2011 Risk of collective failure provides an escape from the tragedy of the commons. Proc. Natl Acad. Sci. USA 108, 10 421–10 425. (doi:10.1073/pnas.1015648108)

37. Liu L, Chen X. 2018 Evolution of public cooperation in a risky society with heterogeneous assets. Front. Phys. 5, 67. (doi:10.3389/fphy.2017.00067)

38. Sun W, Liu L, Chen X, Szolnoki A, Vasconcelos VV. 2021 Combination of institutional incentives for cooperative governance of risky commons. iScience 24, 102844. (doi:10.1016/j.isci.2021.102844)

39. Góis AR, Santos FP, Pacheco JM, Santos FC. 2019 Reward and punishment in climate change dilemmas. Sci. Rep. 9, 16193.

40. Vasconcelos VV, Santos FC, Pacheco JM, Levin SA. 2014 Climate policies under wealth inequality. Proc. Natl Acad. Sci. USA 111, 2212–2216. (doi:10.1073/pnas.1323479111)

41. Jiang LL, Chen Z, Perc M, Wang Z, Kurths J, Moreno Y. 2023 Deterrence through punishment can resolve collective risk dilemmas in carbon emission games. Chaos 33, 043127. (doi:10.1063/5.0147226)

42. Wang Z et al. 2020 Communicating sentiment and outlook reverses inaction against collective risks. Proc. Natl Acad. Sci. USA 117, 17 650–17 655. (doi:10.1073/pnas.1922345117)

43. Van Segbroeck S, Pacheco JM, Lenaerts T, Santos FC. 2012 Emergence of fairness in repeated group interactions. Phys. Rev. Lett. 108, 158104. (doi:10.1103/PhysRevLett.108.158104)

44. Liu L, Chen X. 2022 Indirect exclusion can promote cooperation in repeated group interactions. Proc. R. Soc. A: Math. Phys. Eng. Sci. 478, 20220290. (doi:10.1098/rspa.2022.0290)

45. Hilbe C, Abou Chakra M, Altrock PM, Traulsen A. 2013 The evolution of strategic timing in collective-risk dilemmas. PLoS ONE 8, e66490. (doi:10.1371/journal.pone.0066490)

46. Abou Chakra M, Traulsen A. 2012 Evolutionary dynamics of strategic behavior in a collective-risk dilemma. PLoS Comput. Biol. 8, e1002652. (doi:10.1371/journal.pcbi.1002652)

47. Tingley D, Tomz M. 2014 Conditional cooperation and climate change. Comp. Polit. Stud. 47, 344–368. (doi:10.1177/0010414013509571)

48. Abou Chakra M, Traulsen A. 2014 Under high stakes and uncertainty the rich should lend the poor a helping hand. J. Theor. Biol. 341, 123–130. (doi:10.1016/j.jtbi.2013.10.004)

49. Sigmund K 2010 The calculus of selfishness. Princeton, NJ: Princeton University Press.

50. Schuster P, Sigmund K. 1983 Replicator dynamics. J. Theor. Biol. 100, 533–538. (doi:10.1016/0022-5193(83)90445-9)

51. Hofbauer J, Sigmund K 1998 Evolutionary games and population dynamics. Cambridge, UK: Cambridge University Press.

52. Imhof LA, Fudenberg D, Nowak MA. 2005 Evolutionary cycles of cooperation and defection. Proc. Natl Acad. Sci. USA 102, 10 797–10 800. (doi:10.1073/pnas.0502589102)

53. Van Kampen NG 2007 *Stochastic processes in physics and chemistry*. Amsterdam, The Netherlands: NorthHolland Personal Library.

54. Vasconcelos VV, Santos FC, Pacheco JM. 2013 A bottom-up institutional approach to cooperative governance of risky commons. *Nat. Clim. Change* **3**, 797–801. (doi:10.1038/nclimate1927)

55. Szabó G, Toke C. 1998 Evolutionary prisoner's dilemma game on a square lattice. *Phys. Rev. E* **58**, 69.

56. Domingos EF, Grujic J, Burguillo JC, Kirchsteiger G, Santos FC, Lenaerts T. 2020 Timing uncertainty in collective risk dilemmas encourages group reciprocation and polarization. *iScience* **23**, 101752. (doi:10.1016/j.isci.2020.101752)

57. Greenwood G. 2011 Evolution of strategies for the collective-risk social dilemma relating to climate change. *EPL* **95**, 40006. (doi:10.1209/0295-5075/95/40006)

58. Santos FP, Levin SA, Vasconcelos VV. 2021 Biased perceptions explain collective action deadlocks and suggest new mechanisms to prompt cooperation. *iScience* **24**, 102375. (doi:10.1016/j.isci.2021.102375)

59. Liu L, Chen X, Szolnoki A. 2023 Coevolutionary dynamics via adaptive feedback in collective-risk social dilemma game. *eLife* **12**, e82954. (doi:10.7554/eLife.82954)

60. Hagel K, Abou Chakra M, Bauer B, Traulsen A. 2016 Which risk scenarios can drive the emergence of costly cooperation? *Sci. Rep.* **6**, 19269. (doi:10.1038/srep19269)

61. Capraro V, Perc M. 2021 Mathematical foundations of moral preferences. *J. R. Soc. Interface* **18**, 20200880. (doi:10.1098/rsif.2020.0880)

62. Hua S, Hui Z, Liu L. 2023 Data from: Evolution of conditional cooperation in collective-risk social dilemma with repeated group interactions. Dryad, Dataset. (doi:10.5061/dryad.80gb5mkw0)

63. Hua S, Hui Z, Liu L. 2023 Evolution of conditional cooperation in collective-risk social dilemma with repeated group interactions. Figshare. (doi:10.6084/m9.figshare.c.6806534)

11