

Robust cooperation against mutations via costly expulsion

XIAOFENG WANG^{1,2}, MAJA DUH³ and MATJAŽ PERC^{3,4,5} 

¹ Department of Automation, School of Information Science & Technology, Donghua University - Shanghai, China

² Engineering Research Center of Digitized Textile & Apparel Technology, Donghua University - Shanghai, China

³ Faculty of Natural Sciences and Mathematics, University of Maribor - Koroška cesta 160, 2000 Maribor, Slovenia

⁴ Dept. of Medical Research, China Medical University Hospital, China Medical University Taichung, Taiwan

⁵ Complexity Science Hub Vienna - Josefstädterstraße 39, 1080 Vienna, Austria

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Abstract – Research has shown that spatial selection can lead to the evolution of cooperation in social dilemmas. However, the effectiveness of spatial reciprocity among cooperative players is often diminished by mutations. Here, we report the evolution of robust cooperation against mutations, which is brought about by costly expulsion in the spatial public goods game. We find that costly expulsion is able to enhance the robustness of positive assortment among cooperators against mutations. Moreover, we also show that moderate mutation rates are beneficial for the expansion of spatial clusters among cooperative individuals once the spontaneous formation of segregation patterns is completed by costly expulsion. Our results thus communicate the counterintuitive conclusions that mutations are not always detrimental for the evolution of cooperation in spatial social dilemma games, and what is more, can even be beneficial for faster spreading of cooperator clusters.

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Introduction. – Mutation and natural selection are the two fundamental principles of evolution in order to reproduce information [1]: i) mutation means errors in information transfer leading to different types of messages; ii) selection refers to competition among diverse types of information if they reproduce at different speeds. In the context of evolutionary game theory, the information of intra- or inter-generational transmission are strategies that are available for individuals to adopt [2]. Traditionally, the mutation-selection dynamics describing how the state of a population changes driven by the coupled interplay between mutation and frequency-dependent selection of strategies can be classified into two categories: i) deterministic mutation-selection dynamics in the infinitely well-mixed populations [3,4]; ii) stochastic mutation-selection dynamics in the finitely well-mixed populations [3–6]. Later on, the mutation-selection dynamics has been extended to the study of evolutionary games in structured populations [7,8]. Particularly, the impacts of mutation in the evolutionary games on graphs have also attracted much attention from physicists due to the fascinating physical phenomena such

as phase transition, pattern formation, equilibrium selection and self-organization, exhibited by the complex systems that usually consist of a large number of interacting agents [9–15].

For example, Allen *et al.* have derived the critical conditions for the evolution of cooperation on graphs in the limit of weak selection by analyzing coalescing random walks via generating functions, and have found that the increment of mutation rates diminishes the clusters of cooperators [16]. Helbing *et al.* have used Monte Carlo simulations to investigate the effects of mutations on the evolution of cooperation in the spatial public goods game with punishment, and have revealed that rare mutations can largely accelerate the spreading of costly punishers by breaking the balance of power between both cooperative strategies due to the permanent presence of defectors [17]. Recently, Ichinose *et al.* have systematically studied how mutation alters the evolutionary dynamics of cooperation on networks, and have shown that mutation always has a negative effect on the evolution of cooperation regardless of the payoff functions, initial fraction of cooperators, and network structures [18].

In this letter, we aim to study the evolution of robust cooperation against mutations by comparing the mutation-selection dynamics of the spatial public goods game with costly expulsion [19,20] and defection as the two competing strategies with that of the traditionally spatial public goods game. In the spatial public goods game with costly expulsion, we intentionally leave out cooperators who do not pay a cost to expel defectors from their neighborhoods so as to avoid the second-order free-riding problem [21–23], and thus to be able to concentrate solely on the effectiveness of costly expulsion against mutations. In what follows, we will show that costly expulsion does help the construction of robust cooperation against mutations and that mutations can even play a beneficial role in the evolution of cooperation in the spatial public goods game with costly expulsion.

Model. – Consider a square lattice of $L \times L$ sites with von Neumann neighborhood (*i.e.*, the degree $k = 4$) and periodic boundary conditions where $N (\leq L^2)$ individuals are randomly placed. Accordingly, each site can be either empty or occupied by an individual who is randomly assigned with one of the two competing strategies (*i.e.*, costly expulsion *vs.* defection in the public goods game with costly expulsion as well as cooperation *vs.* defection in the traditional public goods game) with equal probability initially. During the whole evolutionary process, the density of vacant sites is kept constant and is given by $\rho_v = (L^2 - N)/L^2$. Each time step in our model includes two successive phases, *i.e.*, the game interaction phase and the strategy update phase.

Game interaction phase. All individuals engage in group interactions with, if any, the von Neumann neighbors synchronously. If not all the neighboring sites of an individual are empty, the individual can play the games that centered on both its neighbors and itself. Otherwise, the individual has no chance to play the game, and thus obtains no payoff. For the public goods game with costly expulsion, the payoffs of expellers and defectors are respectively given by

$$\begin{cases} P_E = rG_E/G - 1 - c_E G_D, \\ P_D = rG_E/G, \end{cases} \quad (1)$$

where G_E and G_D respectively denote the number of expellers and defectors in a group of size $G \in \{2, 3, \dots, k+1\}$ for a particular game. $r \in (1, k+1)$ represents the enhancement factor applied to group investment, while $c_E > 0$ the cost paid by the expellers to banish each defector, if any, in their group. Here we assume that expellers in the same group cannot coordinate their expulsive behavior [24]. In our model, each defector is selected, in a random sequence manner, exactly once to be unilaterally expelled to any other vacant sites, if any, on the spatial network, if there is at least one expeller in any one of the public goods games with costly expulsion the defector participates in. For the traditional version

of the public goods game, the payoff of cooperators and defectors are respectively given by

$$\begin{cases} P_C = rG_C/G - 1, \\ P_D = rG_C/G, \end{cases} \quad (2)$$

where G_C denotes the number of cooperators in a group of size $G \in \{2, 3, \dots, k+1\}$ for a particular game.

Strategy update phase. The strategy update phase is governed by a coupled mutation-selection process. All individuals synchronously update their strategies either by imitation or by mutation. With probability $1 - \mu$, an individual (*e.g.*, the one at site i) imitates the strategy of another randomly chosen neighbor (*e.g.*, the one at site j), if any, with a probability given by the Fermi function,

$$F(P_j - P_i) = \frac{1}{1 + \exp[-(P_j - P_i)/K]}, \quad (3)$$

where $K = 0.1$ denotes the amplitude of noise, implying that better performing players are readily adopted though it is also possible to adopt the strategy of players performing worse [25]. With probability μ , an individual (*e.g.*, the one at site i) randomly adopts any available strategy. Obviously, the mutation rate $\mu \in [0, 1]$ governs the time scale between the mutation process and the natural selection process (or the imitation process). When $\mu \rightarrow 0$, the imitation process proceeds much faster than the mutation process, which means the strategy update dynamics are largely controlled by the imitation process. In the other limit, *i.e.*, $\mu \rightarrow 1$, the strategy update dynamics are mainly governed by the mutation process, which typically leads to dynamics of neutral evolution. Whenever $0 < \mu < 1$, the strategy update dynamics are driven by a coupled interplay between these two processes.

The simulations are performed on a square lattice of $L \times L$ sites with periodic boundary conditions. The average fractions of players $\rho_X (X \in \{E, C\})$, which are normalized by the population density $1 - \rho_v$, on the square lattice are determined in the stationary state after a sufficiently long relaxation time. Depending on the typical size of emerging spatial patterns, the linear size of the system is varied from $L = 200$ to 500, and the relaxation time is varied from $t = 10^4$ to 10^6 time steps.

Results. – Before presenting the main results, let us briefly summarize the evolutionary outcomes in a well-mixed population. Whenever the enhancement factor r is smaller than the group size $G = 5$, the cooperative strategies (*i.e.*, cooperation in the traditional version of public goods game and costly expulsion in the public goods game with costly expulsion) are sustained solely by mutations in the absence of a limited interaction range, and thus their densities in the mutation-selection equilibrium can be given by $\mu/2$.

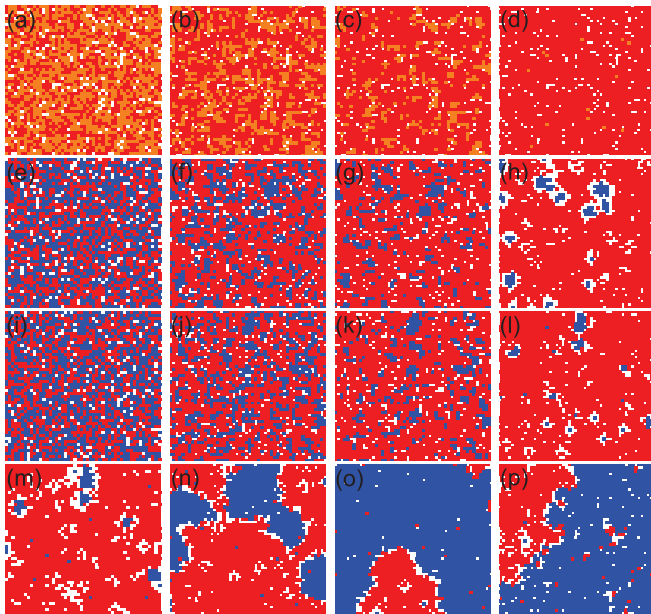


Fig. 1: Typical formation processes of spatial patterns started from the random initial condition in the spatial public goods game. The sites in the square lattice that are occupied by expellers, cooperators and defectors are respectively depicted in blue, orange and red, while the vacant sites are depicted in white. Here we show a 50×50 portion of a larger 200×200 square lattice. Other parameter settings: enhancement factor $r = 2.5$ and density of vacant sites $\rho_v = 0.1$. (a)–(d) Representative spatial evolution in the traditional version of public goods game for the mutation rate $\mu = 0.01$. The snapshots were taken at time steps: (a) $t = 1$ ($\rho_C = 0.5$); (b) $t = 2$ ($\rho_C \approx 0.259$); (c) $t = 3$ ($\rho_C \approx 0.111$) and (d) $t = 20001$ ($\rho_C \approx 0.005$) (see the hollow squares in fig. 2 marking when the snapshots were recorded in figs. 1(a)–(d)). (e)–(h) Representative spatial evolution in the public goods game with costly expulsion for the mutation rate $\mu = 0$ and the expulsion cost $c_E = 0.5$. The snapshots were taken at time steps: (e) $t = 1$ ($\rho_E = 0.5$); (f) $t = 2$ ($\rho_E \approx 0.258$); (g) $t = 3$ ($\rho_E \approx 0.115$) and (h) $t \in \{9, 10, \dots, 20001\}$ ($\rho_E \approx 0.013$) (see the hollow circles in fig. 2 marking when the snapshots were recorded in figs. 1(e)–(h)). (i)–(p) Representative spatial evolution in the public goods game with costly expulsion for the mutation rate $\mu = 0.01$ and the expulsion cost $c_E = 0.5$. The snapshots were taken at time steps: (i) $t = 1$ ($\rho_E = 0.5$); (j) $t = 2$ ($\rho_E \approx 0.262$); (k) $t = 3$ ($\rho_E \approx 0.123$); (l) $t = 9$ ($\rho_E \approx 0.014$); (m) $t = 14$ ($\rho_E \approx 0.016$); (n) $t = 57$ ($\rho_E \approx 0.1$); (o) $t = 126$ ($\rho_E \approx 0.368$) and (p) $t = 20001$ ($\rho_E \approx 0.728$) (see the hollow triangles in fig. 2 marking when the snapshots were recorded in figs. 1(i)–(p)).

Pattern formation dynamics. The dynamics of pattern formation in the spatial public goods game for the density of vacant sites $\rho_v = 0.1$ and the enhancement factor $r = 2.5$ are presented in figs. 1 and 2. For such a low enhancement factor (*i.e.*, $r = 2.5$), cooperators in the traditional version of spatial public goods game cannot survive solely due to spatial reciprocity [26]. In this case, the clusters of cooperators are quickly destroyed because

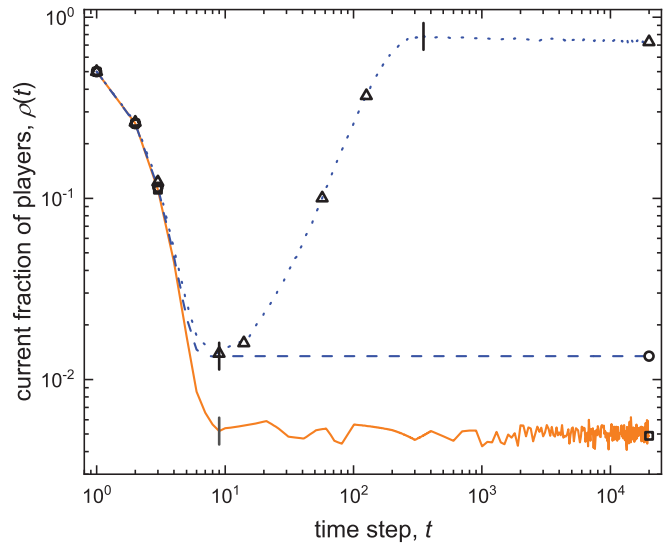


Fig. 2: Time evolution of the fraction of cooperative players (solid orange line: the current fraction of cooperators $\rho_C(t)$ in the traditional version of spatial public goods game for the mutation rate $\mu = 0.01$; dashed blue line: the current fraction of expellers $\rho_E(t)$ in the spatial public goods game with costly expulsion for the mutation rate $\mu = 0$ and the expulsion cost $c_E = 0.5$; dotted blue line: the current fraction of expellers $\rho_E(t)$ in the spatial public goods game with costly expulsion for the mutation rate $\mu = 0.01$ and the expulsion cost $c_E = 0.5$) for the enhancement factor $r = 2.5$ and the density of vacant sites $\rho_v = 0.1$. Note that both the horizontal and vertical axes are logarithmic. The hollow symbols mark the time steps when the snapshots were recorded in fig. 1 for each case, while the short vertical lines the time steps when the respective system enters into the stationary state.

of the severe social dilemma, and finally very few cooperators in the stationary state are randomly scattered around the structured population (see figs. 1(a)–(d)). Indeed, the resulting fraction of cooperators ρ_C in the traditional version of spatial public goods game tends to be very low, and it approximately equals $\mu/2$ as a result of mutations (see fig. 2). In the spatial public goods game with costly expulsion but without mutations, the clusters of expellers still cannot be maintained initially, but a certain number of expellers can survive in small clusters by completely expelling defectors from their neighborhoods (see figs. 1(e)–(h)). Here, the spatial patterns become frozen (*i.e.*, without any further strategy changes) after the initial relaxation time (*i.e.*, $t = 9$), and thus the resulting level of expellers is constant in the stationary state (see fig. 2). Quite surprisingly, in the spatial public goods game with both costly expulsion and mutations, although the initial relaxation process is very similar to that of the spatial public goods game with costly expulsion but without mutations (compare figs. 1(i)–(l) with figs. 1(e)–(h); see also fig. 2), the residual clusters of expellers continue to expand by being imitated by defectors with comparatively lower payoffs at their boundaries, who are expelled from

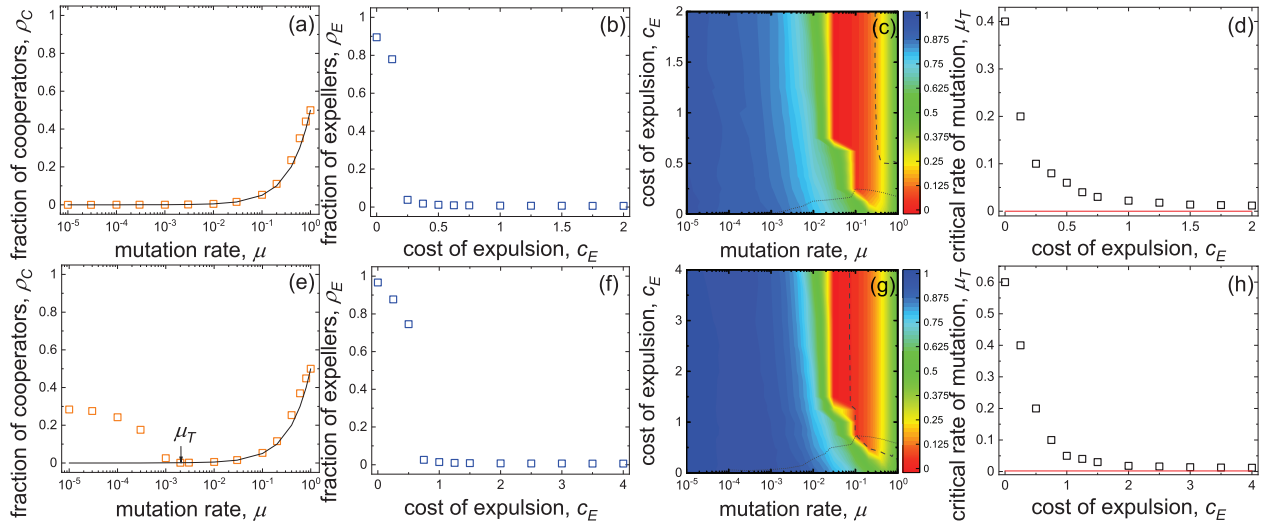


Fig. 3: Mutation-selection equilibria in the spatial public goods game for two representative enhancement factors (upper row: $r = 2.5$; bottom row: $r = 3.5$). (a), (e): stationary fraction of cooperators ρ_C as a function of the mutation rate μ in the traditional version of spatial public goods game. Note that the horizontal axes are logarithmic. The solid lines are predicted by $\rho_C = \mu/2$, which is expected to be accurate in the spatial public goods game when cooperators cannot be maintained by spatial reciprocity [26] but are solely sustained by mutations [4]. The critical mutation rate μ_T represents the threshold value, above which the spatial reciprocity between cooperative players is almost completely destroyed by mutations [16]: (a) $\mu_T = 0$; (e) $\mu_T = 2 \times 10^{-3}$. (b), (f): stationary frequency of expellers ρ_E in dependence on the expulsion cost c_E in the spatial public goods game with costly expulsion for the mutation rate $\mu = 0$. (c), (g): contour graphs of the stationary fraction of expellers ρ_E on the μ - c_E two-dimensional parameter space in the spatial public goods game with costly expulsion. Note that the horizontal axes are logarithmic. The dashed lines separate the μ - c_E parameter space into two areas: the upper-right regions satisfying $\rho_E < \rho_C$ (note that ρ_C is larger than ρ_E only to a marginal degree, *i.e.*, $0 < \rho_C - \rho_E < 10^{-2}$ in this parameter region) and the remaining regions satisfying $\rho_E > \rho_C$ under the condition of the same mutation rate, whereas the dotted lines also divide the μ - c_E parameter space into two areas: the bottom-right regions satisfying $\rho_E(\mu > 0) < \rho_E(\mu = 0)$ and the remaining regions satisfying $\rho_E(\mu > 0) > \rho_E(\mu = 0)$ under the condition of the same cost of expulsion. (d), (h): critical rate of mutation μ_T as a function of the expulsion cost c_E in the spatial public goods game with costly expulsion. The red lines mark the critical rates of mutation μ_T in the traditional version of spatial public goods game: (d) $\mu_T = 0$; (h) $\mu_T = 2 \times 10^{-3}$. The critical rate of mutation μ_T in the spatial public goods game with costly expulsion is strictly larger than that in the traditional version of spatial public goods game across the reasonable range of the expulsion cost c_E . Other parameter settings: number of sites $L \times L$ varying from 200×200 to 500×500 and density of vacant sites $\rho_v = 0.1$.

the clusters of defectors by the mutant expellers inside them (see figs. 1(m)–(p) and fig. 2). Note that the clusters of expellers in this case are robust against the invasion of mutant defectors inside them because these defectors with comparatively higher payoffs would no longer stay in their original sites due to the costly expulsion by their formerly neighboring expellers (see figs. 1(i)–(p)).

Mutation-selection equilibria. To systematically investigate the evolution of robust cooperation against mutations by costly expulsion, we focus on the mutation-selection equilibria as obtained for two representative values of the enhancement factor that cover two relevantly different scenarios of the spatial public goods game. Specifically, we use the enhancement factor $r = 3.5$, where the spatial selection allows cooperators to survive by forming clusters in the absence of mutations, besides the enhancement factor is $r = 2.5$ for the density of vacant sites $\rho_v = 0.1$ (see figs. 3(a) and (e)). Previous studies show that the introduction of mutations leads to the decrease of stationary cooperation level in the social dilemma game

on graphs [18]. Here we find that this result is dependent on a critical value of mutation rate μ_T (figs. 3(a) and (e)): i) below the critical mutation rate μ_T , the stationary fraction of cooperators ρ_C is decreased with the mutation rate μ mainly due to the destructive effect of mutations on the clustering of cooperators [16]; ii) above the critical mutation rate μ_T , the stationary fraction of cooperators ρ_C is increased with the mutation rate μ largely because cooperators are maintained in the structured population by virtue of mutations. For the enhancement factor $r = 2.5$, since the critical mutation rate $\mu_T = 0$, the stationary fraction of cooperators ρ_C is increased with the whole applicable range of the mutation rate μ in the traditional version of spatial public goods game (see fig. 3(a)). For the enhancement factor $r = 3.5$, as the critical mutation rate $\mu_T = 2 \times 10^{-3}$, the stationary frequency of cooperators ρ_C is decreased with the mutation rate $\mu \in (0, \mu_T)$ and then is increased with the mutation rate $\mu \in (\mu_T, 1)$ in the traditional version of spatial public goods game (see fig. 3(e)).

In principle, the critical mutation rate μ_T can be used to measure the resistance ability of positive assortment among cooperative individuals against mutations for social dilemma games on networks. Figures 3(d) and (h) demonstrate that costly expulsion enhances the resistance ability of cooperator clusters against mutations in comparison with that in the traditional version of spatial public goods game, though the destructive effect towards the assortment among cooperative individuals by mutations is increased with the expulsion cost c_E . Indeed, the construction of robust cooperation against mutations can be realized by costly expulsion (see figs. 3(c) and (g)). For reasonable values of expulsion cost c_E , cooperative expellers are even able to dominate the whole structured population as long as the mutation rate μ is not too large, which is not realized in the traditional version of spatial public goods game (see the first and the third columns of fig. 3). Furthermore, the stationary frequency of cooperative expellers ρ_E is no less than that of cooperators ρ_C unless the expulsion cost c_E is larger than a threshold value and the mutation rate μ is considerably large. All above results clearly indicate the constructive impact of costly expulsion in the evolution of cooperation even if the expulsive behavior is costly and the mutation rate is non-negligible.

Figures 3(b) and (f) show that the stationary frequency of cooperative expellers ρ_E decreases with the cost of expulsion c_E for the mutation rate $\mu = 0$ in the spatial public goods game with costly expulsion. Moreover, we have found that the presence of mutations can always enhance the stationary fraction of cooperative expellers ρ_E if only the expulsion cost c_E is not small and the mutation rate μ is not too large (see the third column of fig. 3). Consequently, there is a considerably large μ - c_E parameter region where mutations lead to a higher stationary level of cooperation in the spatial public goods game with costly expulsion in comparison with that in the spatial public goods game with costly expulsion but without mutations.

Conclusion. – In this letter, we have shown that the evolution of cooperation by costly expulsion is robust against and can even benefit from mutations in the spatial public goods game, which is in sharp contrast with the recent findings for social dilemma games on graphs that the evolutionary success of cooperators is hindered by mutations [16,18] and that mutations, at most, can speed up the spreading of cooperative strategies, but are not able to enhance the stationary level of cooperation [17]. It is interesting that costly expulsion alone cannot achieve a larger final cooperation level than the combination of costly expulsion and mutations does (see fig. 3), considering that mutations alone are detrimental for the evolution of cooperation in the spatial public goods game. The analysis of pattern formation dynamics reveals the key mechanism that explains how costly expulsion can promote the evolution of cooperation in the presence of the opposing mutation effects. In the spatial public goods game with both

costly expulsion and mutations, the typical process of evolution can be divided into two stages: the separation stage and the expansion stage (see fig. 2). In the separation stage, a small number of expeller clusters can survive by expelling defectors from their boundaries so as to avoid the invasion of cheaters (see figs. 1(i)–(l)). In the expansion stage, the residual clusters of expellers can recover the formerly lost territories and even expand into other spaces by assimilating defectors in their boundaries that were previously expelled by the mutant expellers from the interior of the defector clusters (see figs. 1(m)–(p)). In future works, it will be worthwhile to systematically consider how the mutation-selection dynamics of the public goods game with costly expulsion varies with, *e.g.*, different population structures (*e.g.*, small-world networks [27–32] or scale-free networks [33–46]) or different degrees of noise [47–49]. We expect further intriguing collective phenomena to emerge from the systematic investigation of the interplay between costly expulsion and mutations in evolutionary games.

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