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Tag-mediated cooperation with non-deterministic genotype-phenotype mapping

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Abstract – Tag-mediated cooperation provides a helpful framework for resolving evolutionary social dilemmas. However, most of the previous studies have not taken into account genotype-phenotype distinction in tags, which may play an important role in the process of evolution. To take this into consideration, we introduce non-deterministic genotype-phenotype mapping into a tag-based model with spatial prisoner's dilemma. By our definition, the similarity between genotypic tags does not directly imply the similarity between phenotypic tags. We find that the non-deterministic mapping from genotypic tag to phenotypic tag has non-trivial effects on tag-mediated cooperation. Although we observe that high levels of cooperation can be established under a wide variety of conditions especially when the decisiveness is moderate, the uncertainty in the determination of phenotypic tags may have a detrimental effect on the tag mechanism by disturbing the homophilic interaction structure which can explain the promotion of cooperation in tag systems. Furthermore, the non-deterministic mapping may undermine the robustness of the tag mechanism with respect to various factors such as the structure of the tag space and the tag flexibility. This observation warns us about the danger of applying the classical tag-based models to the analysis of empirical phenomena if genotype-phenotype distinction is significant in real world. Non-deterministic genotype-phenotype mapping thus provides a new perspective to the understanding of tag-mediated cooperation.

Evolution of cooperation in social dilemmas is a central problem in both natural science and social science [1–3]. The individuals who cooperate reduce their fitness to contribute to the welfare of others, while defectors pay no costs but may benefit from the cooperative behavior. The process of evolution, therefore, always favors defectors due to the fact that cooperators are vulnerable to exploitation by defectors. In contrast to the theoretical prediction, the successful evolution of cooperation is widely observed in real world, and thus makes it fascinating to investigate why and how cooperation can emerge and be maintained among selfish individuals.

To reconcile the theoretical prediction and the observations, the researchers in many disciplines have proposed and identified a wide variety of mechanisms that favor cooperation in social dilemmas [2–6]. As a remarkable example, Hamilton [7] has put forward a hypothesis that if a cooperator can recognize other cooperators, by the so-called "green beard", and only help them but not the defectors, cooperators can proliferate and finally dominate the population. This hypothesis can be supported if a perceivable tag such as green beard and the predisposition to recognize this tag and help the individuals who own this tag are encoded simultaneously in a single gene. However, this mechanism will no longer be robust when facing the invasion by cheaters who also have the green beard as

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cooperators but defect. In spite of the troubles with the explanation by "green-beard effect", Hamilton's work has generated a growing body of research on tag-mediated cooperation, which highlights the importance of phenotypic tags in the promotion of cooperation [8–27], under the framework of evolutionary game theory [28,29].

An important assumption behind the existing research of tag mechanism, however, is that there is no genotype-phenotype distinction so the tags are deterministically perceived and are fixed if the genotypes (and also the phenotypes, by definition) are not changed. In this letter, in contrast, we study tag-mediated cooperation with genotype-phenotype distinction by explicitly introducing non-deterministic genotype-phenotype mapping into a tag-based model. By our definition of this mapping, two agents with quite different genotypes may regard each other as similar. Meanwhile, even two agents with identical genotypes may resist interactions between them because they are different in their phenotypes. As we will show, this non-deterministic mapping may significantly change the effects of tag mechanism on the evolutionary prisoner's dilemma in various perspectives. Consequently, some classical results in the previous studies of tag systems may need reconsideration and further research if genotype-phenotype distinction is salient in reality [30].

Formally, we consider a population of N agents located on a L^2 square lattice with periodic boundary condition. We assume $N = L^2$ so the lattice is fully occupied and the agents cannot move away from their initial sites. The agents engage in pairwise interactions and may play a Prisoner's dilemma game (PDG) with their neighbors based on von Neumann Neighborhood. Each agent i has an inheritable trait s_i representing its unconditional strategy (C or D) in the PDG. At the initiation step, cooperators (C) and defectors (D) are uniformly distributed on the lattice at random. Unless stated differently, the initial fraction of cooperators is 50%. Here we use the single parameter rescaled payoff matrix [31,32], where $R = 1$, $P = u$, $S = 0$, and $T = 1 + u$. The parameter u measures the temptation to defect or the cost-to-benefit ratio (if the matrix is interpreted as a donor-recipient game).

In addition to the strategy trait, each agent i has an inheritable genotypic tag which determines its perceivable phenotypic tag. The representations of genotypic tag and phenotypic tag are different, and the mapping from genotypic tag to phenotypic tag is non-deterministic. Specifically, a genotypic tag g_i is a real number which is initially randomized uniformly in $[0, 1)$. A phenotypic tag t_i has n possible values in $\{0, 1, 2, \ldots, n-1\}$. Each of these possible tags has a corresponding position $p_k = k/n$ evenly distributed in $[0, 1)$ and specifies how the genotypic tag determines the phenotypic tag at each time step. We assume that if a genotypic tag is close to a corresponding position for a possible phenotypic tag, this tag has more chances to be chosen as the phenotypic tag of the agent. The two edges at 0 and 1 for the genotypic tag are looped so the distance between a genotypic tag and a position, $d_{i,k}$, is defined as $\min\{|g_i - p_k|, 1 - |g_i - p_k|\}$. Note that the maximum possible distance is thus $1/2$. We assume that the probability that a phenotypic tag is chosen is given by the following rule:

$$Prob(t_i = k) = \frac{(\frac{1}{2} - d_{i,k})^c}{\sum_j (\frac{1}{2} - d_{i,j})^c}.$$

The parameter $c \geq 0$ characterizes the decisiveness of the distances in controlling the determination of phenotypic tag. As extreme cases, if $c = 0$, all phenotypic tags become indistinguishable and the agents always have random tags at each time step; if $c \to \infty$, the phenotypic tag that owns the position closest to the genotypic tag will be chosen deterministically. Note that, in the latter case, the tag system will degenerate to those in conventional tag-based models where an agents has a simple tag without genotype-phenotype distinction [14,15,33].

The simulations of the evolutionary process is carried out in accordance with the standard Monte Carlo simulation procedure consisting of the following steps. First, a randomly selected agent i perceives the phenotypic tags of itself and the neighbors to decide the interaction partners. If the tag of the focal agent is identical to that of a neighbor, they interact and play the PDG, otherwise they do not interact. The focal agent i obtains its total payoff U_i by playing the corresponding PDGs with all its interaction partners. Next, all the neighbors of agent i also obtain its total payoff U_j in the same way. Finally, agent i will try to update both strategy and genotypic tag with the Imitation Max (IM) rule [34]: if the richest neighbor's payoff is larger than that of the focal agent, the focal agent imitates both the richest neighbor's strategy and genotypic tag, otherwise the focal agent's traits remain unchanged. To quantify the uncertainty related to the imitation process, we assume that the two traits of each agent both have a chance to mutate. With probability m_s, the strategy s_i has a chance to be replaced by a randomly picked strategy. With probability m_g, the genotypic tag g_i has a chance to be randomly reset with the uniform distribution on $[0, 1)$. Note that the mutation procedure of each trait is defined independently. The agents are updated asynchronously and every agent has a chance to update both its strategy and tag in each full Monte Carlo step (MCS). All simulation results are averaged over 20 or more independent runs and are obtained until a stationary state of the average fraction of cooperators f_C has been reached.

We begin our exploration by showing how the fraction of cooperators, f_C, changes in dependence on the temptation u for different decisiveness c. As shown in fig. 1, there are several discontinuous transitions from high cooperation levels to low cooperation levels as the temptation is increased. Interestingly, although the change of decisiveness c does not affect the positions of the transition points, it will change the performance of the tag mechanism in a non-trivial way. First, when the temptation is relatively low ($u \leq 0.32$, see the left half in fig. 1), the highest levels

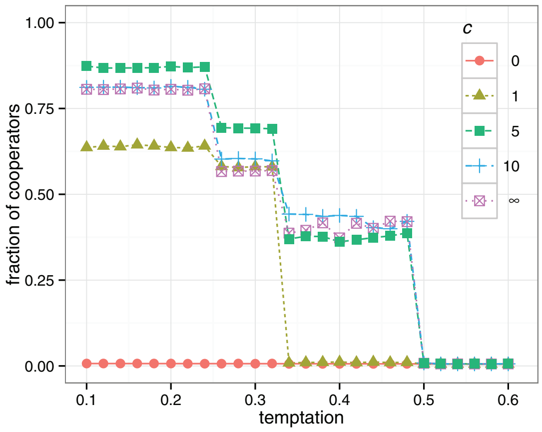

Fig. 1: (Color online) Fraction of cooperators f_C as a function of temptation u for different decisiveness c (see legend). Several discontinuous transitions are depicted, reflecting an important nature of Imitation Max rule. Varying decisiveness does not alter the transition points, but controls the relative performance of the tag mechanism for supporting cooperation. Other parameters: $m_g = 0.01$, $m_s = 0.01$, $n = 4$, $L = 100$.

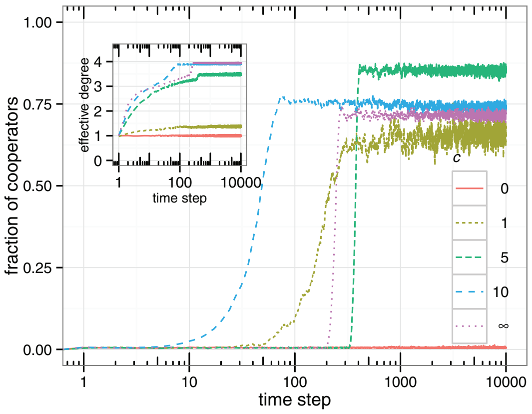

Fig. 2: (Color online) Representative time evolution, initiated with full defection, of the fraction of cooperators f_C for different decisiveness c (see legend). The inset shows the corresponding time evolution of the effective degree defined as the average number of interaction partners of the agents. Other parameters: $u = 0.2$, $m_g = 0.01$, $m_s = 0.01$, $n = 4$, $L = 100$.

of cooperation can be attained under a moderate degree of decisiveness ($c = 5$). Second, if the tags are deterministic or approximately deterministic ($c = 10$, $c \to \infty$), the classical results of tag-mediated cooperation can be recovered and the performance may be better than that under low decisiveness (for example, $c = 1$). However, as we have seen in the case under moderate decisiveness, the introduction of non-deterministic genotype-phenotype mapping has the chance to improve the performance of tag mechanism.

The above observation is based on the assumption that cooperators and defectors have an equal initial fraction (50%). However, this assumption may become empirically implausible if we consider biological or sociological applications, because it is a crucial problem whether a new cooperator or a small cluster of mutant cooperators can invade a full defective population [34]. To address this problem, we examine whether cooperators can invade the population with $f_C = 0\%$ through mutation and imitation. The evolution of cooperation with 0% initial fraction of cooperators is plotted in fig. 2 for different decisiveness c. We find that the cooperation levels have a takeoff within 1000 time steps and finally reach a dynamical equilibrium except in the pure random tag case ($c = 0$). We have observed, in fact, that the takeoffs of cooperation are often started with an expansion of cooperative cluster with single phenotypic tag if the degree of decisiveness is high ($c \geq 5$). The reason cooperators can spread into the territory of defectors is that most boundary cooperators can avoid interactions with dissimilar others so as to resist being exploited by defectors. To demonstrate the relation between interaction structure and the promotion of cooperation more clearly, we show in the inset of fig. 2 the evolution of effective degree which we defined as the average number of interaction partners of all the agents. Note that this measure always starts with value 1 on average and can vary from 0 to 4 according to the coevolutionary process. We find that if the degree of decisiveness is high ($c \geq 5$), the agents will increase the number of interaction partners, indicating the emergence of local homophily and approximately deterministic interactions. However, this homophilic interaction does not directly result in the takeoff of cooperation. The initial emergence of cooperation can be fulfilled purely by the help of spatial reciprocity, but the boundaries between homophilic clusters create a better environment for the expansion of cooperators. Furthermore, we can observe that the effective degree has a drastic increase during the establishment of cooperation. This is because the full interaction state is favored within a cooperative cluster.

As we have shown, a homophilic interaction can coevolve with tag-mediated cooperation, but we have not yet examined the formation of such structure in a microscopic view to understand the source of the approximately deterministic interactions. The representative snapshots and distributions of genotype values at different time steps are simultaneously shown in fig. 3. It can be observed that numerous homophilic clusters with small sizes appear in the population after initiation. The clusters have clear boundaries between them thus help the population to resist the invasion of defectors. The sizes of the clusters become larger and their number is reduced, indicating the enhancement of homophilic interactions. Cooperators can benefit from such enhancement, because they become wealthier if full interaction can be achieved. The distribution of genotypes is also subject to evolution. At the beginning, the genotypes are uniformly distributed, but the distribution will gradually change into homophilic structure so that the approximately deterministic tag mapping itself can emerge. In other words, although we assume the mapping from genotype to phenotype is not deterministic,

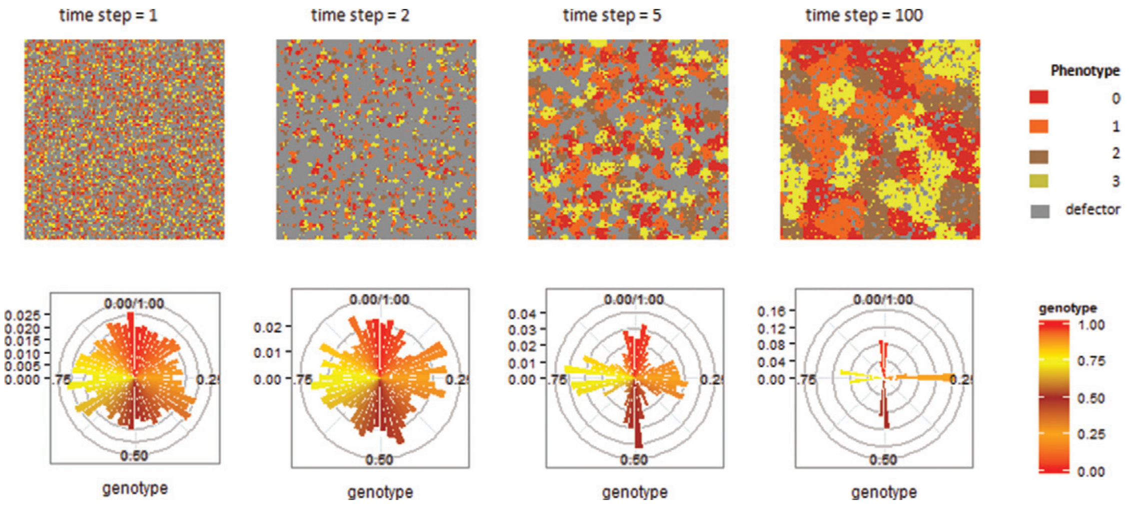

Fig. 3: (Color online) Representative snapshots and distributions of genotype values at different time steps. Cooperators are represented by patches with different colors (see legend). Defectors are represented by gray patches. It is clear that the agents with more deterministic relation between genotype and phenotype are favored by natural selection. Parameters: $u = 0.2$, $c = 5$, $m_g = 0.01$, $m_s = 0.01$, $n = 4$, $L = 100$.

the agents can gain a more direct relation between their genotype and phenotype if such homophilic structure can evolve. If the value of a genotypic tag is close enough to the corresponding position for a phenotype, the agent who owns it will permanently have the phenotypic tag and thus will constantly interact with the partners who owns similar genotypes.

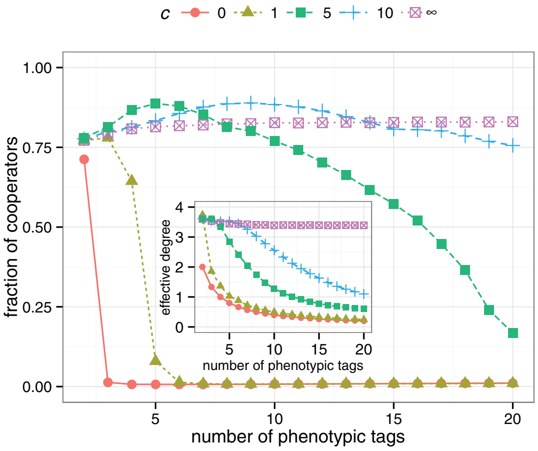

Fig. 4: (Color online) Fraction of cooperators f_C as a function of the number of phenotypic tags n for different decisiveness c (see legend). The relation between f_C and n shows different patterns for different decisiveness c. Large phenotypic tag space has a detrimental effect on the survival of cooperators under low decisiveness ($c = 0$, and $c = 1$), while the cooperation level depends non-monotonically on the number of phenotypic tags under moderate decisiveness ($c = 5$, and $c = 10$). Only when the model degenerates to the deterministic case ($c \to \infty$), extending the tag space can further enhance cooperation. The inset shows the effective degree in dependence on the number of phenotypic tags. The effective degree is defined as the average number of interaction partners of the agents. Other parameters: $m_g = 0.01$, $m_s = 0.01$, $u = 0.2$, $L = 100$.

The previous investigations have suggested that enlarging the tag space often exhibits a beneficial influence on cooperation in tag systems [14,16,35]. Does this proposition remain valid under the complex relation between genotype and phenotype? The results presented in fig. 4 reveal how the number of available phenotypic tags affects the cooperation levels. We see that only the deterministic case replicates the observation found in the previous models. That is, increasing the available tags can improve the performance of the tag mechanism. This, however, may no longer be true if the non-deterministic mapping is introduced. When the decisiveness is very low ($c = 0$ and $c = 1$), cooperators can dominate if n is small, but cooperators can no longer survive as n is increased slightly. To understand this, we also depict the effect of varying tag number n on the effective degree. We see that, in the cases with low decisiveness, as the tag number is increased the effective degree will reach very low levels, which are considered as a detrimental factor in the promotion of cooperation [36–38]. When the decisiveness is higher ($n = 5$ and $n = 10$), there will be a moderate value of n which promotes cooperation most significantly. As n exceeds this moderate value and is increased further, the cooperation level will gradually decrease along with the decrease of the effective degree. We find that the corresponding effective degrees of the optimal cooperation for the two cases have similar values close to 3 (2.850 for $c = 5$ and 2.777 for $c = 10$), indicating that the promotion of cooperation in our model can be explained by the interaction structure created by the tag mechanism. Another interesting observation is that the relative performance of different decisiveness can be changed by varying the number of tags. For example, although a moderate decisiveness ($c = 5$)

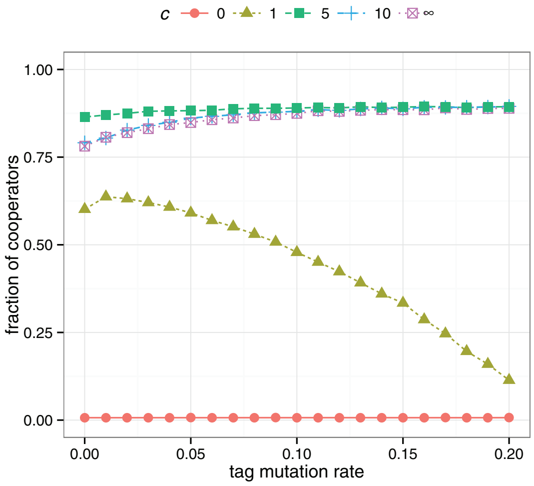

Fig. 5: (Color online) Fraction of cooperators f_C as a function of (genotypic) tag mutation rate m_g for different decisiveness c (see legend). Varying the decisiveness may alter the effect of the tag mutation rate on the cooperation level. It is clear that high decisiveness ($c \geq 5$) recovers the classical results found in deterministic tag-based models, but the results are no longer robust under low decisiveness ($c = 1$). Other parameters: $m_s = 0.01$, $u = 0.2$, $n = 4$, $L = 100$.

outperforms higher decisiveness if the number of phenotypic tags n is sufficiently small, the cooperation level under this decisiveness will be reduced more significantly by the increase of n which leads to a significant reduction of the effective degree.

It is still controversial how the tag flexibility (controlled by the tag mutation rate) affects the performance of the tag mechanism. Is "change your tags fast" [15] always beneficial to the promotion of cooperation? The results presented in fig. 5 demonstrate that the outcome of increasing tag mutation rate depends on the significance of the role played by the non-deterministic mapping. We find that if the decisiveness is sufficiently high ($c \geq 5$), the classical observation that a high tag mutation rate enhances cooperation can be replicated in our simulations. In the classical tag-based models with selective interaction [8,14,15], cooperators may benefit from high flexibility because it allows more opportunities to escape from the defectors and create new tag clusters. The reason why this observation can be replicated under high decisiveness is that the genotype-phenotype mapping can become approximately deterministic thus recovering the effect of increasing flexibility found in the previous research. If the decisiveness c is very low, in contrast, varying the tag mutation rate has an additional influence with the non-deterministic mapping: the existing homophilic clusters will soon collapse if the agents change their (genotypic) tags too fast; as a consequence, cooperators cannot enjoy the benefit of the homophilic interaction structure. Thus we see that the cooperation level is reduced as the tag mutation rate is increased under low decisiveness ($c = 1$).

Summarizing, we have shown that the introduction of non-deterministic mapping from genotypic tag to phenotypic tag has non-trivial effects on tag-mediated cooperation in the evolutionary prisoner's dilemma. The non-deterministic mapping can significantly weaken the promotion of cooperation driven by the tag mechanism if the decisiveness for the determination from genotype to phenotype is sufficiently low. However, tag-mediated cooperation remains effective with relatively high decisiveness. Especially when the decisiveness is moderate, the tag mechanism in our model can establish high levels of cooperation even more effective than those under the deterministic tag system.

We also note that although cooperation can be established under low decisiveness (for example, when $c = 1$), the effective degree only reaches a level that allow very few interactions between the agents. If the payoffs gained by the agents are interpreted as the welfare, we doubt whether the system is in its efficient state. This warns us that it may be misleading to use the selective interaction approach to explain the resolution of social dilemmas. A more reasonable measure, rather than the fraction of a particular strategy, may need to be devised in future research to evaluate the efficiency of the system.

In the discussion of tag space and tag flexibility, we have seen that the introduction of non-deterministic mapping may undermine the robustness of tag mechanism with respect to the change of (phenotypic) tag space and the change of tag flexibility. In our model, enlarging the tag space or enhancing the tag flexibility creates more uncertainty which cannot be found in the classical tag systems, thus it makes the system unable to establish an optimal interaction structure to support cooperation. Due to the existence of genotype-phenotype distinction in real world [30], our work reveals the importance of examining the applicability of tag-based models in biological science or social science by explicitly taking into account the complex relation between genotype and phenotype.

The evolution of homophilic interaction in our model is analogous to the coarsening processes in evolutionary systems with species competition [39] or spatial games [40–42]. For example, refs. [41] and [42] have found that if the originally continuous strategy space is constrained to be discrete and finite in the spatial ultimatum game, the self-organizing pattern and cyclic dominance of the strategy distribution emerge and promote the evolution of fairness. In our study, we have shown that the hybrid tag system with both continuous and discrete values also shapes the characteristics of the evolutionary system. Interestingly, the "discreteness" itself can emerge by the enhancement of certainty, thus the importance of discreteness is highlighted in the research of evolutionary systems.

Finally, we have confirmed that our results are robust with respect to different types of payoff matrix, to different updating fashions (synchronous, asynchronous), to different imitation rules (such as Fermi-like rule), and at least to some different manners of genotype-phenotype mapping. This means that the qualitative results do not change under a wide range of variations to our model. However, we have not examined the effects of different network topologies on the efficiency of the tag mechanism, which may also be an important problem as suggested in the previous studies [20,27]. Furthermore, it is also possible to introduce uncertainty in the determination of the actual strategy which may deviate from the genotypic strategy. Further research is needed to address these problems.

* * *

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