Evolution of cooperation in multilevel public goods games with community structures

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Abstract – In a community-structured population, public goods games (PGG) occur both within and between communities. Such type of PGG is referred as multilevel public goods games (MPGG). We propose a minimalist evolutionary model of the MPGG and analytically study the evolution of cooperation. We demonstrate that in the case of sufficiently large community size and community number, if the imitation strength within community is weak, i.e., an individual imitates another one in the same community almost randomly, cooperation as well as punishment are more abundant than defection in the long run; if the imitation strength between communities is strong, i.e., the more successful strategy in two individuals from distinct communities is always imitated, cooperation and punishment are also more abundant. However, when both of the two imitation intensities are strong, defection becomes the most abundant strategy in the population. Our model provides insight into the investigation of the large-scale cooperation in public social dilemma among contemporary communities.

Introduction. – How cooperation emerges and prevails in a selfish population poses a challenging problem in evolutionary biology as well as behavioral science [1,2]. A powerful paradigm for investigating this problem in groups of interacting players of arbitrary size is public goods game (PGG) [3,4]. In a PGG, each cooperator invests into a common pool while each defector attempts to exploit the public goods without any contributions. Thus, the payoff of a cooperator is always less than that of a defector. It is better off defecting than cooperating.

During the past few years, a number of mechanisms have been demonstrated analytically or experimentally to promote cooperation [3–11]. As an important mechanism, how spatial structure affects the evolution of cooperation has attracted much attention recently [12–14]. In structured populations, cooperators may form clusters to resist exploitation by defectors, resulting in the maintenance of cooperation. So far, most previous works of PGG in structured populations are based on lattice, small-world networks and scale-free networks. However, the study of PGG in populations with community structure, which is a signature of the hierarchical nature of real social and biological systems [15,16], has received little attention.

The so-called community structure consists of many groups, where the interaction rate within a group is higher than that between groups [15,16]. Due to the community structure, it is straightforward to consider that games are not only played among community members, but also played among different communities. Each individual engages in not only the “local” PGG in its community, but also the “global” PGG played among distinct communities. Hence, individuals are simultaneously involved in multiple PGGs on different hierarchical levels [17–19]. These simultaneous local and global PGGs in a community-structured population constitute a multilevel PGG (MPGG).

Based on the MPGG, several straightforward questions arise: how to maintain cooperation in a large-scale among multiple communities? What is the effect of community structures on the evolution of cooperation? Some recent works have investigated the large-scale cooperation in PGG among contemporary societies by behavioral experiments [17–19] and simulation [20]. Some theoretical models are proposed to study the cooperation and punishment in infinite group-structured populations by deterministic analysis [21]. However, finite population size is proved to bring internal noise which drives the
population dynamics off the deterministic trajectory in the infinite situations [22,23]. Thus, a mathematical model of how community structures affect the evolution of cooperation in finite populations is still lacking.

Motivated by these, we propose a minimalist evolutionary model of MPGG and analytically study the evolution of cooperation in finite populations with such community structures where the interaction within community is far more frequent than that between communities. We adopt the imitation updating rule and explore how the imitation strength within community and that between communities influence the evolutionary of cooperation. We demonstrate that under the condition of sufficiently large community size and community number, if the imitation strength within community is weak, or that between communities is strong, cooperation can prevail in the population. Nevertheless, if both of the imitation strengths are strong, defection is the unique favorable strategy. Furthermore, when the imitation within community is moderate, small imitation between communities may favor punishers prevailing while cooperators nearly disappear.

Model. – Consider a finite population with community structures in which individuals take part in an n-level PGG. In this population, every $m_1$ individuals form a community, and any two such communities have no common member. Denote this type of communities by $G_1$. Moreover, every $m_2$ $G_1$-communities constitute a larger community denoted by $G_2$. This similar formation process repeats until $m_n$ $G_{n-1}$-communities make up a $G_n$-community which is the entire population. According to the above formation rule, this population is characterized by a hierarchical structure (see fig. 1).

We first study the simplest case with only two strategies: cooperation and defection (the case with punishment will be added and described later). A MPGG is played as follows: on the first level, in each $G_1$-community, $m_1$ individuals play a PGG together. Each cooperator contributes $c$ into the public pool in the $G_1$-community to which this player belongs, and every defector donates nothing. The total amount in this public pool is separated into two parts: one portion, whose proportion is $k_1$, is allocated to the local PGG in this $G_1$-community, and the other portion, whose proportion is $1 - k_1$, is contributed into a higher public pool in the larger $G_2$-community which contains this $G_1$-community. The total contribution in this local PGG is multiplied by an enhancement factor $r_1$, and the product is distributed equally among all players in this $G_1$-community no matter whether they contribute or not.

On the second level, in each $G_2$-community, $m_2$ $G_1$-communities engage in a larger PGG. Each $G_1$-community contributes a fraction of the total amount (the proportion is $1 - k_1$), which is collected in the PGG among its members, into the public pool in $G_2$-community which contains this $G_1$-community. Then, the total amount in this public pool in $G_2$-community is also divided into two parts: one part whose proportion is $k_2$ is contributed to the PGG in this $G_2$-community and the other part is submitted to the higher public pool in the $G_3$-community on the third level. The first part is multiplied by an enhancement factor $r_2$, and the product is distributed among all individuals in this $G_2$-community.

Such type of PGG repeats until the highest level. On the highest level, the total amount in the public pool in $G_n$-community is contributed into the global PGG. This amount is multiplied by an enhancement factor $r_n$, then the product is distributed among the entire population. Although cooperators only contribute in the $G_1$-community on the lowest level, their contributions are allocated in $n$ different PGGs at hierarchical levels. The payoff of each individual, irrespective of cooperators and defectors, is derived from $n$ PGGs.

Individuals in the population adjust their strategies through imitation. At each time step, two players $i$ and $j$ are randomly chosen. These two players belong to the same $G_1$-community with the interaction rate $q_1$. The probability that individual $i$ adopts the strategy of $j$ is given by $1/(1 + \exp[-w_1(F_j - F_i)])$, where $w_1 \geq 0$ denotes the imitation strength between two players in the same $G_1$-community, $F_i$ and $F_j$ are the payoff of individual $i$ and $j$ [7]. The imitation strength measures the dependence of decision making on the payoff comparison. For $w_1 \rightarrow 0$, individual $i$ imitates the strategy of $j$ almost randomly, which is referred as “weak imitation”. For $w_1 \rightarrow \infty$, a more successful player is always imitated, which is referred as “strong imitation”.

Moreover, if the two players do not belong to the same $G_1$-community, but they are part of the same $G_2$-community, the interaction rate for these two players is $q_2$. In this case, player $i$ imitates the strategy of $j$ with the probability $1/(1 + \exp[-w_2(F_j - F_i)])$, where $w_2$ is the imitation strength between two players from different $G_1$-communities but in the same $G_2$-community. In general, the interaction rate for two players belonging to different $G_1$-communities ($l = 1, \ldots, n-1$) but in the same $G_{l+1}$-community is $q_{l+1}$. The relationship $\sum_{i=1}^{n} q_i = 1$ needs to be satisfied. In this
by \( \rho_{BA}^2 \). Suppose there are \( i \) \( G_1 \)-communities consisting of only \( A \) players and \( m_2 - i \) \( G_1 \)-communities of only \( B \) players. In this focal \( G_2 \)-community, the payoff of each \( A \) player is denoted by \( F_A^2(i) \) and that of each \( B \) player is \( F_B^2(m_2 - i) \). A new \( G_1 \)-community full of \( A \) players arises when two players with different strategies from different \( G_1 \)-communities are chosen, and the \( B \) player alters its strategy through imitation, then it takes over its \( G_1 \)-community. Thus, the probability to increase the number of \( G_1 \)-communities full of \( A \) players by one is given by

\[
\Gamma_A(i) = q_2 \frac{i \cdot m_2 - i}{m_2} \frac{1}{1 + \exp\{-w_2[F_A^2(i) - F_B^2(m_2 - i)]\}}.
\]

Similarly, the probability to decrease the number of \( G_1 \)-communities full of \( A \) players by one is

\[
\Gamma_A(i) = q_2 \frac{i \cdot m_2 - i}{m_2} \frac{1}{1 + \exp\{-w_2[F_B^2(m_2 - i) - F_A^2(i)]\}}.
\]

The fixation probability of a \( G_1 \)-community full of \( A \) players in a \( G_2 \)-community is obtained as follows:

\[
\rho_{BA}^2 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp\{w_2 \sum_{i=1}^{j-1} [F_B^2(m_2 - i) - F_A^2(i)]\} (\rho_{AB}/\rho_{BA})^{j-1}}.
\]

In general, denote the fixation probability of a single \( A \) mutant in a \( G_1 \)-community consisting of only \( B \) players \( (l = 2, \ldots, n) \) by \( \Phi_{BA}^l \). Accordingly, we have

\[
\Phi_{BA}^l = \rho_{BA}^l \times \rho_{BA}^{2-\ell} \times \cdots \times \rho_{BA}^1.
\]

where

\[
\rho_{BA}^1 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp\{w_1 \sum_{i=1}^{j-1} [F_B^1(m_1 - i) - F_A^1(i)]\} (\rho_{AB}/\rho_{BA})^{j-1}}.
\]

Two-level PGG with punishment. – We now consider two-level PGG. Suppose three available strategies in this PGG: cooperation, defection and punishment. Punishers are such type of players which contribute as cooperators but reduce the payoff of defectors with a cost to themselves. We focus on the situation without second-order punishment which does not punish cooperators [7].

In each \( G_1 \)-community, punishment acts as a personal behavior. Its object is defectors. Each punisher imposes a fine \( \beta_1 \) on each defector at a cost \( \gamma_1 \) \( (\gamma_1 < \beta_1) \) to itself. The total fine for a defector relies on the number of punishers in this \( G_1 \)-community, whereas the total cost for a punisher is determined by the number of defectors.

Furthermore, for the separation of time scales, communities always stay in homogeneous states. If a homogeneous community is composed of punishers, they act as an institute of punishment. This institute of punishment punishes those communities consisting of defectors even also containing cooperators or punishers since such communities free-ride on the global public.

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Fig. 2: (Color online) Fixation process of a single mutant in a population. (a) A single mutant is produced in the population. (b) This mutant successfully takes over its \( G_1 \)-community, and another individual from other \( G_1 \)-communities imitates the mutant’s strategy. (c) The mutant successfully invades its \( G_2 \)-community, and another one from other \( G_2 \)-communities imitates the strategy of the mutant. This type of fixation and imitation repeat until the population is full of one type of players.

For finite populations, we analyze the advantage of a strategy through fixation probability, which measures the probability for a single mutant using such focal strategy to successfully take over the resident population. In order to obtain a general expression, we suppose there are two types of strategies, \( A \) and \( B \). Imagine that a mutant adopting strategy \( A \) is produced in a population of \( B \) players. Since \( q_1 \gg q_2 \), the time that this mutant takes over the \( G_1 \)-community to which it belongs or disappears is shorter than that two individuals from different \( G_1 \) communities meet. The time scales of fixation in a \( G_1 \)-community and imitation between two individuals from different \( G_1 \)-communities are separated. Thus, fixation of this mutant \( A \) in the population goes through several stages described by fig. 2.

Actually, the fixation process of a single \( A \) mutant in a population is equivalent to only \( n \) steps: the fixation of this \( A \) mutant in its \( G_1 \)-community; the fixation of this \( G_1 \)-community composed entirely of \( A \) players in its \( G_2 \)-community; \( \ldots \); the fixation of the \( G_{n-1} \)-community invaded by the \( A \) mutant in the whole population.

Denote the fixation probability of a single \( A \) mutant invading a \( G_1 \)-community of \( B \) players by \( \rho_{BA}^1 \). This fixation probability is given by

\[
\rho_{BA}^1 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp\{w_1 \sum_{i=1}^{j-1} [F_B^1(m_1 - i) - F_A^1(i)]\} (\rho_{AB}/\rho_{BA})^{j-1}}.
\]

where \( F_A^1(i) \) and \( F_B^1(m_1 - i) \) are the payoff of each \( A \) player and each \( B \) player in the focal \( G_1 \)-community, respectively, when there are \( i \) \( A \) players and \( m_1 - i \) \( B \) players in this \( G_1 \)-community [24].

Denote the fixation probability of a \( G_1 \)-community full of \( A \) players in its \( G_2 \)-community of only \( B \) individuals by \( \rho_{BA}^2 \). Suppose there are \( i \) \( G_1 \)-communities consisting of only \( A \) players and \( m_2 - i \) \( G_1 \)-communities of only \( B \) players. In this focal \( G_2 \)-community, the payoff of each \( A \) player is denoted by \( F_A^2(i) \) and that of each \( B \) player is \( F_B^2(m_2 - i) \). A new \( G_1 \)-community full of \( A \) players arises when two players with different strategies from different \( G_1 \)-communities are chosen, and the \( B \) player alters its strategy through imitation, then it takes over its \( G_1 \)-community. Thus, the probability to increase the number of \( G_1 \)-communities full of \( A \) players by one is given by

\[
\Gamma_A(i) = q_2 \frac{i \cdot m_2 - i}{m_2} \frac{1}{1 + \exp\{-w_2[F_A^2(i) - F_B^2(m_2 - i)]\}}.
\]

Similarly, the probability to decrease the number of \( G_1 \)-communities full of \( A \) players by one is

\[
\Gamma_A(i) = q_2 \frac{i \cdot m_2 - i}{m_2} \frac{1}{1 + \exp\{-w_2[F_B^2(m_2 - i) - F_A^2(i)]\}}.
\]

The fixation probability of a \( G_1 \)-community full of \( A \) players in a \( G_2 \)-community is obtained as follows:

\[
\rho_{BA}^2 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp\{w_2 \sum_{i=1}^{j-1} [F_B^2(m_2 - i) - F_A^2(i)]\} (\rho_{AB}/\rho_{BA})^{j-1}}.
\]

In general, denote the fixation probability of a single \( A \) mutant in a \( G_1 \)-community consisting of only \( B \) players \( (l = 2, \ldots, n) \) by \( \Phi_{BA}^l \). Accordingly, we have

\[
\Phi_{BA}^l = \rho_{BA}^l \times \rho_{BA}^{2-\ell} \times \cdots \times \rho_{BA}^1.
\]

where

\[
\rho_{BA}^1 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp\{w_1 \sum_{i=1}^{j-1} [F_B^1(m_1 - i) - F_A^1(i)]\} (\rho_{AB}/\rho_{BA})^{j-1}}.
\]
goods. Specifically, a community full of punishers punishes those communities where defectors exist. Each punishing community reduces the total payoff of each punished community by \( m_1 \beta_2 \), at a total cost \( m_1 \gamma_2 \) (\( \gamma_2 < \beta_2 \)). Then, the cost of punishing is shared by all punishers in this punishing community, whereas the fine on the punished community is distributed among its members. Hence, the total fine for each individual in the punished communities depends on the number of the punishing communities, while the total cost for each punisher in the punishing communities is determined by the number of the punished communities.

Although the strategy updating is mainly dependent on imitation, mutation of strategies may happen sometimes. At each time step, every individual may mistakenly switch its strategy to a different and random strategy with the probability \( \mu \). Suppose the mutation rate \( \mu \to 0 \). Sufficiently small \( \mu \) assures that a single mutant vanishes or fixes in a population before the next mutant appears.

The population is homogeneous most of the time \([5,24,25]\). Therefore, in the limit of rare mutations, the evolutionary process of consideration can be approximated by a Markov chain where the state space is composed of homogeneous states of the population consisting entirely of cooperators, defectors, and punishers, respectively, the probability of cooperators, defectors, and punishers, respectively, the probability of cooperators, defectors, and punishers, respectively, the probability of cooperators, defectors, and punishers. The corresponding transition probability matrix is

\[
\Lambda = \begin{pmatrix}
1 - \Phi_{DC}^n - \Phi_{CP}^n & \Phi_{CP}^n & \Phi_{CP}^n \\
\Phi_{CD}^n & 1 - \Phi_{DC}^n - \Phi_{DP}^n & \Phi_{DP}^n \\
\Phi_{PC}^n & \Phi_{PD}^n & 1 - \Phi_{PC}^n - \Phi_{PD}^n
\end{pmatrix}.
\]

The normalized left eigenvector corresponding to the eigenvalue 1 of the matrix \( \Lambda \) determines the stationary distribution, which describes in the long run, the percentage of time spent by the population in each homogeneous state. The stationary distribution for the above transition matrix eq. (3) can be calculated as follows:

\[
X_C = \frac{\Phi_{PC}^n \Phi_{DP}^n + \Phi_{PC}^n \Phi_{DC}^n + \Phi_{DC}^n \Phi_{PD}^n}{\Delta},
\]

\[
X_D = \frac{\Phi_{PC}^n \Phi_{CD}^n + \Phi_{CD}^n \Phi_{PD}^n + \Phi_{PD}^n \Phi_{PC}^n}{\Delta}.
\]

\[
X_P = \frac{\Phi_{PC}^n \Phi_{DC}^n + \Phi_{CD}^n \Phi_{DP}^n + \Phi_{DP}^n \Phi_{PC}^n}{\Delta},
\]

where \( X_C \), \( X_D \), and \( X_P \) denote the probability to find the population in the homogeneous state consisting entirely of cooperators, defectors, and punishers, respectively, the normalization factor \( \Delta \) insures \( X_C + X_D + X_P = 1 \).

We only discuss the situation of a two-level PGG in detail. In the case of no defectors, since punishers do the same as cooperators under the condition of no second-order punishment, these two types of players are of no difference. This situation can be viewed as “neutral case”, where the fixation probability of a neutral mutant equals the reciprocal of the population size \([26]\), that is, \( \Phi_{CP}^2 = 1/(m_1 m_2) \) and \( \Phi_{DC}^2 = 1/(m_1 m_2) \).

The fixation probabilities \( \Phi_{DC}^2 \), \( \Phi_{CD}^2 \), \( \Phi_{DP}^2 \) and \( \Phi_{PD}^2 \) are given as follows:

\[
\Phi_{DP}^2 = \rho_{DP}^4 \times \Phi_{DP}^2,
\]

\[
\frac{1}{\rho_{DP}^2} = 1 + \sum_{j=1}^{m_2-1} \exp\left\{ \sum_{i=1}^{m_2-1} [c + \gamma_2 m_2 - c k_1 r_1 - (\beta_2 + \gamma_2) i] \right\}
\times \left( \frac{\rho_{DP}^1}{\rho_{DP}^2} \right)^j,
\]

\[
\Phi_{DC}^2 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp(-\Theta j)} \times \frac{1}{1 + \sum_{j=1}^{m_1-1} \exp(w_1 j)},
\]

\[
\Phi_{CD}^2 = \frac{1}{1 + \sum_{j=1}^{m_2-1} \exp(\Theta j)} \times \frac{1}{1 + \sum_{j=1}^{m_1-1} \exp(w_1 j)},
\]

\[
\Phi_{PD}^2 = \rho_{PD}^2 \times \Phi_{PD}^2 = \frac{1}{1 + \sum_{j=1}^{m_1-1} \exp\{w_1 \sum_{i=1}^{m_2-1} [(m_1 - i) \beta_1 - c - i \gamma_1]\}}
\times \left( \frac{\rho_{PD}^1}{\rho_{PD}^2} \right)^j,
\]

where \( \Theta = c[w_2 (1 - k_1 r_1) + w_1 (m_1 - 1)] \).

Note that when \( w_1 \to 0 \) and \( w_2 \) is not weak, the relationship \( \Phi_{DC}^2 < \frac{1}{\rho_{DC}^2} < \Phi_{CD}^2 \) is always satisfied in the case of \( k_1 r_1 > 1 \). Besides, when \( w_2 \to \infty \) and \( w_1 \) is limited, there is \( \Phi_{DC}^2 > \Phi_{CD}^2 \) in the case of \( k_1 r_1 > 1 \). It indicates that in these two situations, cooperation is more abundant than defection \([27]\). Except for these two conditions, defection is always more abundant than cooperation. In addition, when \( m_1 \gamma_1 \gg c \) and \( m_1 \beta_1 \gg c \), the inequality \( \Phi_{DP}^2 > \Phi_{PD}^2 \) is always satisfied. Furthermore, when \( m_2 \gamma_2 \gg c - c k_1 r_1 \) and \( m_2 \beta_2 \gg c k_1 r_1 - c \), the relationship \( \Phi_{DP}^2 > \Phi_{PD}^2 \) always holds, regardless of the imitation strengths \( w_1 \) and \( w_2 \). Hence, if \( m_1 \) and \( m_2 \) are sufficiently large, punishers are always more abundant than defectors.

Based on the stationary distribution, we find that when \( m_1 \) and \( m_2 \) are sufficiently large, weak imitation within \( G_1 \)-community or strong imitation between \( G_1 \)-communities is of great benefit to cooperators and punishers (see fig. 3). In these two cases, cooperators do as well as punishers, they are both more abundant than defectors. However, if these two imitation strengths are both strong, it is harmful to the evolution of cooperation and punishment. Moreover, in the case of moderate imitation strength \( w_1 \), small \( w_2 \) may favor punishers prevailing but has a little effect on the emergence of cooperation (see fig. 4(a)). Furthermore, when \( w_2 \) is moderate, the preservation of cooperators and punishers is hindered. When \( w_2 \) is large enough, cooperation and punishment are still more abundant than defection.
The rising of cooperation and punishment. Parameters: prevalence of cooperators as well as punishers. However, if both imitation strengths are strong, it is harmful to the emergence of cooperation and punishment. Parameters: $c = 0.8$, $k_1 = 0.5$, $r_1 = 3$, $\beta_1 = 1$, $\gamma_1 = 0.5$, $\beta_2 = 1$, $\gamma_2 = 0.5$, $m_1 = 20$, and $m_2 = 20$.

The reason for the above phenomenon is that under the condition $k_1 r_1 > 1$, weak $w_1$ incurs $\Phi_{DC}^2 > \Phi_{PD}^2$, and the inequality $\Phi_{DP}^2 > \Phi_{PD}^2$ always holds for sufficiently large $m_1$ and $m_2$. Based on eq. (4), we obtain $X_C > X_D$ and $X_P > X_D$ for weak $w_1$. In this case, the population spends most time in the homogeneous state of cooperators or punishers. We state that our below results are all based on the assumption of sufficiently large $m_1$ and $m_2$. Note that $k_1 r_1$ denotes effective enhancement factor within the community. Only when the effective enhancement factor is larger than unity, cooperation may be favored in the long run. This condition $k_1 r_1 > 1$ is consistent with that in [3]. Moreover, when $w_1$ is moderate ($w_1 = 0.1$ in fig. 4(a)), small $w_2$ leads to the inequality $\Phi_{DC}^2 < \Phi_{PD}^2$ and the increase of $X_D$ leads to the decrease of $X_P$ as well as $X_C$, but increasing $X_D$. When the gap between $\Phi_{DC}^2$ and $\Phi_{PD}^2$ is sufficiently small, the population spends its most time staying in the homogeneous state of punishers. With the increase in this gap, the advantage of defection over cooperation is enhanced, or that of punishment over defection is weakened. Consequently, defectors become more and more frequent than cooperators and punishers. However, when the imitation strength $w_2$ reaches so large that makes the inequality $\Phi_{PD}^2 > \Phi_{DC}^2$ satisfied, defectors perform the worst, the population is most likely to be found in the homogenous state full of cooperators or punishers with nearly equal probabilities.

Large imitation strength $w_2$ can also be viewed as positive out-group attitude which shows preference for individuals from other communities, while weak $w_2$ can be seen as neutral out-group attitude. From fig. 4(a), the neutral out-group attitude is of great benefit to punishment but harmful to the evolution of cooperation.

The impact of positive out-group attitude on the evolution of punishment is complicated. With an enhanced positive out-group attitude, punishment is favored at first, then its amount shrinks and rises finally. When the preference of individuals for those in other communities is sufficiently large, cooperation is also greatly favored.

Discussions and conclusions. – We have proposed a minimalist theoretical model of MPG in finite populations with community structures and explored under what circumstances the assortment of cooperation can be achieved in community-structured populations. We found that if the community size and the community number are both sufficiently large, weak imitation within community or strong imitation between communities promotes the prevalence of cooperation. This can be attributed to the principle that weak imitation within community may lead to assortment of cooperators, while strong imitation between communities assures the prevalence of cooperative behavior once a cluster of cooperators appears. However, if the imitation strengths within and between communities are both strong, cooperation as well as punishment are eliminated from the population. In addition, it is interesting that when the imitation within community is moderate, small imitation between communities makes punishers extraordinarily abundant in the population but cooperators nearly disappear.

A model relevant to ours is from ref. [28], where Traulsen and Nowak studied the effect of multilevel selection on the evolution of cooperation in Prisoner’s Dilemma (PD) which is a two-person game. Compared with this model, we focus on PGG, a multiperson game, which has different ingredients and background from PD. Moreover, in [28], the game only occurs in each group, and there is no interaction between any two individuals from different groups. However, in our model, game exists not only in each community but among different communities. Besides, interactions always happen between individuals.
from distinct communities. It incurs the prevalence of a strategy across community. For the strategy updating rule, Moran process is applied in [28] while we adopted imitation process. Although the approximate expressions of fixation probability in these two different processes in the limit of weak selection are almost identical [29], those in the case of a moderate selection are extraordinarily different from each other. In addition, according to the evolution process, we obtain the essential difference between the model in [28] and ours as the mechanism to promote cooperation: the former is group selection whereas the latter is spatial selection. Group selection is suitable for the situation where individuals compete within groups and groups also compete with each other. Spatial selection is valid when there is only assortment of cooperators and no group level of selection [30].

In our model, there is no competition among communities and no selection at group level. Thus, this is not group selection but spatial selection. Another similar concept to the community-structured population in biology is metapopulation [31]. Although both metapopulation and the community-structured population can be viewed as group-structured population, the mechanisms for the evolution of populations in these two types of models are different. The evolution of species in metapopulation is driven by recolonization and extinction, i.e., birth and death process in biology, while the evolution of cooperation in our work is inspired by imitation which is a behavior in sociology. In addition, we consider a simple type of punishment in this paper, which solely punishes defectors. In this case, cooperators become second-order free-riders since they exploit the sacrifice of punishers. Thus, cooperation should also be punished. Sigmund et al. showed that incorporating second-order punishment, which punishes both defectors and cooperators, the evolutionary dynamics can be drastically altered [7]. Besides, amount of empirical evidences reveal that defectors sometimes punish cooperators [32]. The corresponding population dynamics can be qualitatively changed by this “anti-social punishment” [33]. Therefore, to explore the effects of second-order punishment and anti-social punishment on the evolution of cooperation deserves more attention in future studies.

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