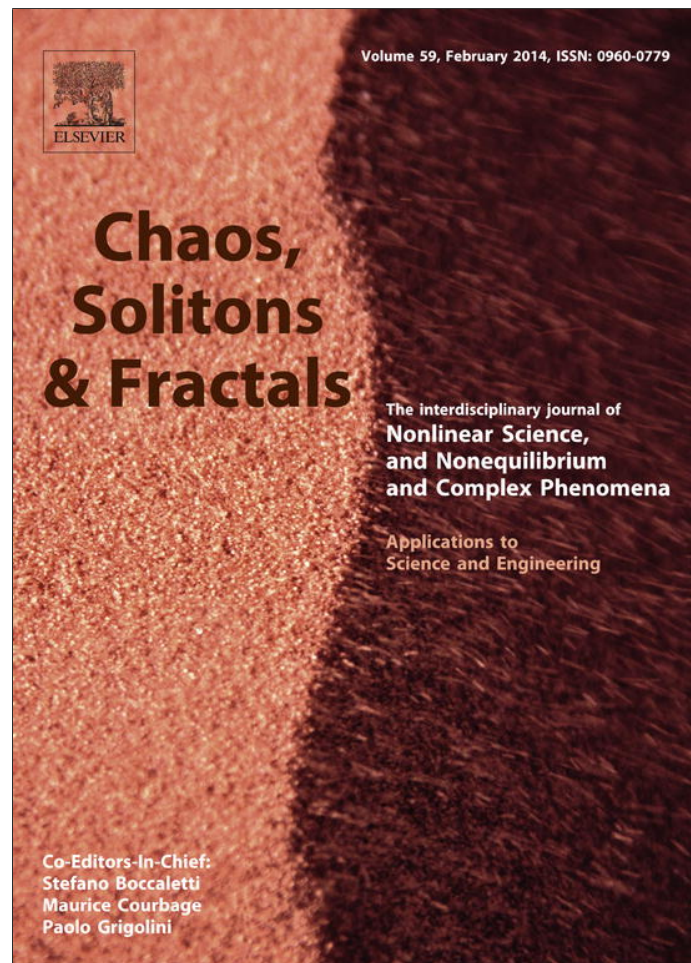


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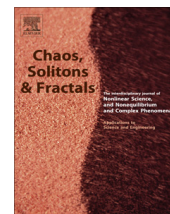
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Evolution of cooperation among game players with non-uniform migration scopes

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ABSTRACT

In social dilemmas, cooperation among randomly interacting individuals is often hard to achieve. The situation changes if migration takes place, where game structure jointly evolves with the migration from adverse neighborhoods. Here we introduce a framework combining migration with the individual heterogeneity of migration scopes. When faced with a gloomy outlook, some players prefer vacant sites within their adjacent neighborhoods, while others may migrate within the whole network, provided the sites are empty. Thus, we can make a thorough inquiry of the sustainability of cooperation in a spatially distributed population divided by these two groups, and all possible mixtures between them. Our main result is that small-scope migration and suitable population density can gear up high cooperation levels in the midst of dense populations structured by scale-free networks, while large-scope migration and sparsity favor the cooperator clustering among lattice-structured populations. In this sense, the conditions for the emergence of cooperation are prevalently created by the spatial reciprocity, and migration also has enough potential to help cooperation to prevail in suitable combination of game parameters in dynamics (e.g., population density, the type of interaction structure and also the migration scope).

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1. Introduction

Why and under what circumstances, presumptively selfish individuals take cooperative action is, in many fields, still a perennial enigma. Revelation of mechanisms supporting cooperation, which is against the fundamental principles of Darwinian selection, is of key interest. In the investigation of this plight the most prevailing framework is the game theory together with its extensions involving evolutionary context [1–12]. Particularly, perhaps one of the best suited (and most used) two-player-two-strategies models to describe the confusion of how cooperation arises is: the Prisoner's Dilemma game [13–19]. It is generally

studied as an archetypical model for reciprocal altruism, and has attracted most attention in theoretical and experiment research.

A variety of studies have suggested that, the integration of the microscopic patterns of interactions among the individuals composing a large population into the evolutionary setting, affords a way out for cooperation to exist in paradigmatic scenarios. A standard hypothesis is that each site in the graph carries one player and, edges determine who plays with whom [20–32]. Recent advances point towards that, while spatial interaction and heterogeneity have been recognized as potent promoters of cooperation, coevolutionary rules can extend the potentials of such entities further. A significant avenue of research having its roots in coevolutionary games is the study of migration, which has recently drawn a large amount of attention [33–41]. When faced with a gloomy outlook, players can migrate to another location and establish new links in the new local neighborhood. Here, as noted by Vainstein et al. [34],

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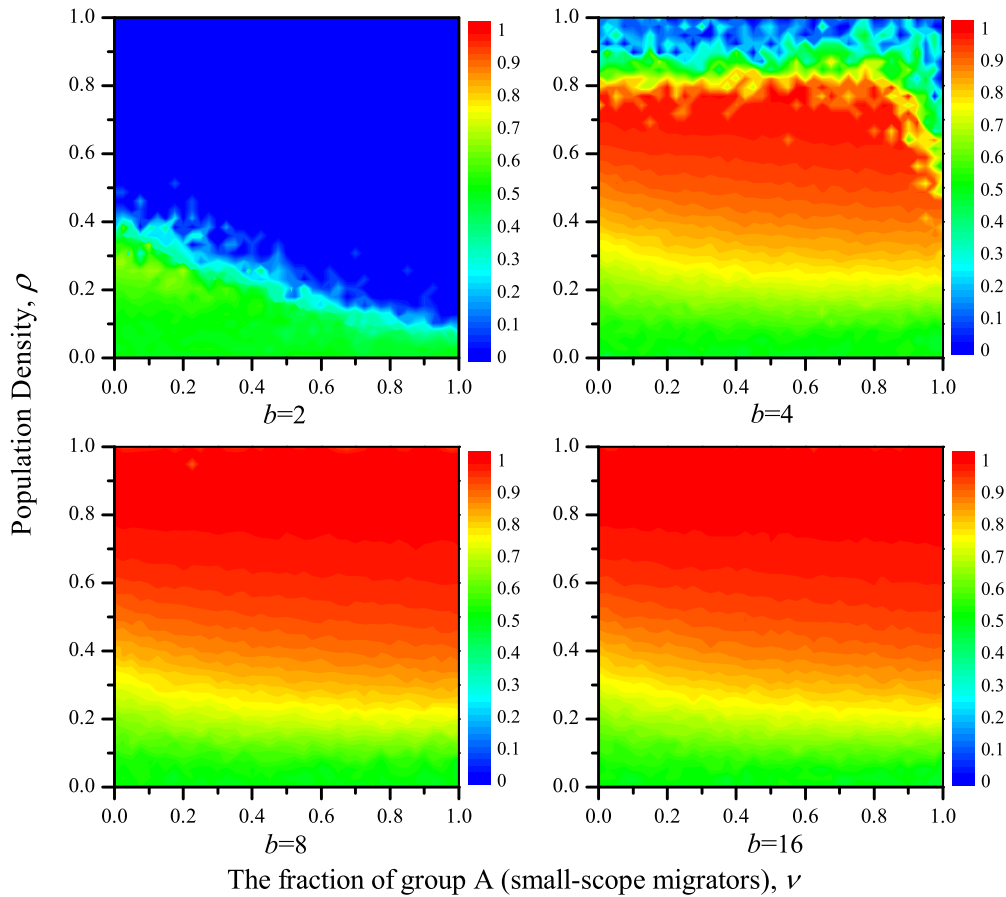


Fig. 1. Color maps of the fraction of cooperators on BASF network in dependence on the fraction ν of group A (small-scope migrators) and the population density ρ , for different values of the PD game parameter b . The horizontal axis denotes the fraction ν of group A in the population, and the vertical axis is the population density. In this figure, the employed size of nodes is $N = 2500$, and accordingly, the population size is ρN . The PD payoff matrix takes the following shape using the parameter b : $T = b, R = b - 1, P = 0$, and $S = -1$, where $b > 1$. The b used in panels are $b = 2, b = 4, b = 8$ and $b = 16$, respectively. The color mapping depicts the stationary fraction of cooperators in BASF-structured population.

migration may also be subject to more deliberate coevolutionary rules, taking into account personal preferences of players, their strategies, as well as aims. In this regard, many complicated representations, in which an entanglement between agents migration and evolutionary dynamics is put forward, have been studied [42–51]. For example, Helbing et al. [36,37] introduced success-driven migration as a possible mediator leading towards cooperation in selfish populations even under noisy conditions. In their framework, the focal individual could explore all the adjacent empty sites within an assigned distance, and move to the one which potentially brings it the highest payoff. Further, Helbing et al. [47] investigated the effectiveness of success-driven migration on the enhancement of cooperation confronted with individual decision-making mistakes. Moreover, Droz et al. [46] studied the improvement of cooperation with two types of players, if the influential players are allowed to walk randomly through the whole square lattice. However, herein it is worth mentioning that, to our knowledge, previous investigations paid little attention to the heterogeneity of migration scopes in response to adverse conditions, and thoroughly validate the possible effectiveness of it in promoting cooperation.

In fact, everyday experience tells us that individual migration may be restricted by many subsistent factors

(e.g., personal preferences, migration cost, distance or time), which will stir up a heterogeneous scenario of migration behaviors. For instance, players may show heterogeneity in risk preferences. Broadly, risk-averse players have conservative bias towards staying at or near their present locations. They perceive their present or close-by locations as relatively stable safe bet, whereas large-scope migrations may bring unknown and risky or costly hazard. Oppositely, risk-seeking actors are inclined towards seeking new profitable partners, irrespective of the migration scopes. By building on this fact, we break with the general assumption of letting individuals be bound by homogeneous migration scopes, and allow them to retain heterogeneous ones. In this paper we formulate a simplified setup, by dividing populations into two groups, i.e., group A (small-scope migration) and B (large-scope migration), in line with the migration scopes. If unhappy with the current one, players from group A prefer vacant sites within their nearby neighborhoods, while members from group B migrate within the whole network, provided the sites are empty. This is the starting point of our work.

The following is a summary of the rest of the paper. First we describe the model. Next, we present and discuss the main findings, whereas in the final section we sum up our findings and provide concluding comments based on them.

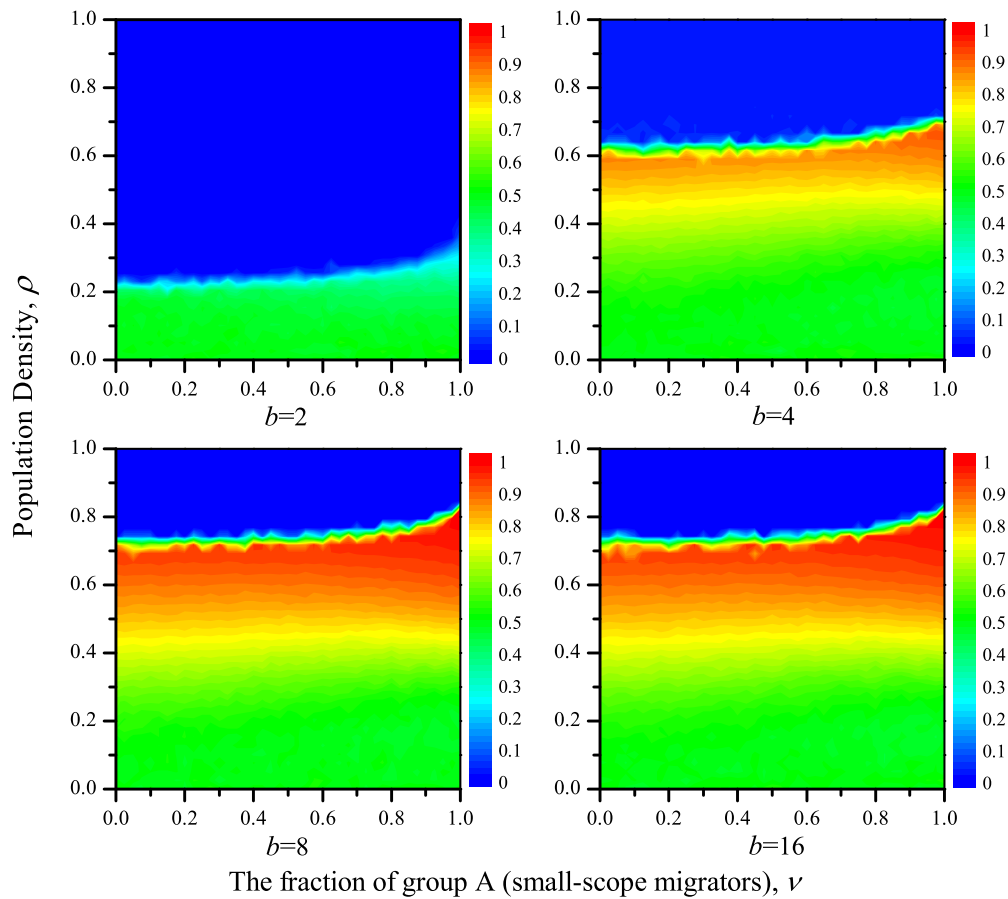


Fig. 2. Color maps of the fraction of cooperators on lattice network in dependence on the fraction ν of group A (small-scale migrators) and the population density ρ , for different values of the PD game parameter b . The horizontal axis denotes the fraction ν of group A in the population, and the vertical axis is the population density. For the simulations, the employed size of nodes is $N = 2500$, and accordingly, the population size is ρN . The PD payoff matrix takes the following shape using the parameter b : $T = b$, $R = b - 1$, $P = 0$, and $S = -1$, where $b > 1$. The b used in panels are $b = 2$, $b = 4$, $b = 8$ and $b = 16$, respectively. The color mapping depicts the stationary fraction of cooperators in lattice-structured population. See main text for details.

2. The model

Our analysis is based on the Prisoner's Dilemma (PD) game, a paradigm to study the evolution of costly cooperation among selfish individuals, since it highlights the potential differences between individual interests and the social optimum. One way to construct a PD game is by assuming that cooperation implies paying a cost for the other player to receive a benefit, whereas defection implies taking something away from the other person. We label the payoff parameters in line with the conventions for the PD game [3]: a cooperator receives the reward R in case of mutual cooperation and the sucker payoff S in case of being defected; a defector receives the temptation to defect T when the other player cooperates and the punishment P in case of mutual defection. The PD game is characterized by the payoff relationships $T > R > P > S$ and, in addition, $2R > T + S$ for repeated games. When played as a one-shot game in a well-mixed population, defection is the only evolutionarily stable strategy; despite of the fact that the payoff P to both players can be considerably smaller than the payoff R for mutual cooperation. In an evolutionary setting, the higher payoff of defectors implies more reproductive success, thus, cooperation should not evolve. In this simplified framework, the payoff matrix

takes the following shape using the parameter b : $T = b$, $R = b - 1$, $P = 0$, and $S = -1$, where $b > 1$.

In each simulation, ρN players are located on the nodes of employed networks and the links between them define the network of contacts, i.e., who can interact with whom. The random dilution is performed only once at the outset of the game. Here, a fraction $(1 - \rho)$ of vacant sites serve as the accommodation of migration. Individuals play PD games with their adjacent neighbors and acquire the accumulated payoffs from these interactions, whereby self-interactions are excluded. Accordingly, the game played with an empty site always yields zero payoff per iteration. In each encounter, players have to choose simultaneously whether to defect or cooperate. In the remainder of the paper we will focus on two representative cases of interactions, lattice and Barabási–Albert scale-free network (BASF) [20], in order to unveil the possible effects that social heterogeneity has on the final results. Notably, the BASF network is adopted to represent interpersonal interactions, since many natural networks share much in common with this network model. Starting with a small number ($m_0 = 3$ here) of nodes, at each time step we add a new node with m ($m \leq m_0$, $m = 2$ here) edges that link the new node to m different nodes already present in the instantaneous network following the preferential attachment rule, i.e. the

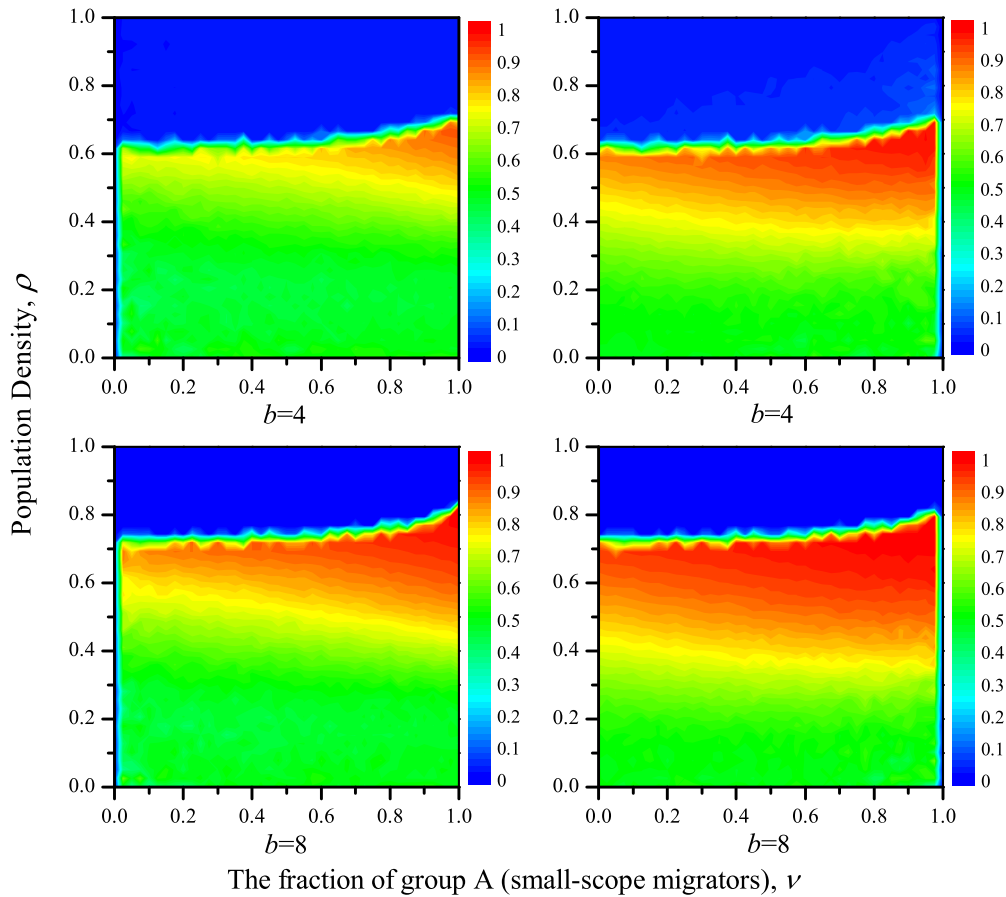


Fig. 3. Color maps of the fraction of cooperators in group A (small-scope migrants, left panels) and B (large-scope migrants, right panels), respectively in dependence on the fraction ν of group A (small-scope migrants) and the population density ρ , for different values of the PD game parameter b . Both groups are situated on lattice networks. The horizontal axis denotes the fraction ν of group A in the population, and the vertical axis is the population density. The PD payoff matrix takes the following shape using the parameter b : $T = b$, $R = b - 1$, $P = 0$, and $S = -1$, where $b > 1$. The b used in panels are $b = 4$ (upper panels) and $b = 8$ (lower panels), respectively. The color mapping depicts the stationary fraction of cooperators in investigated groups.

probability of an existing node attracting a new link is proportional to its current degree. The process is repeated until N nodes are present in the network. A model based on these ingredients leads to the stationary scale-free distributions with an average degree 4 accordingly. Since we intend to acquire legible snapshots of spatial patterns on lattice, here we adopt the moderate network size $N = 2500$ throughout this work for a fair comparison between BASF and lattice. However, we have checked that the results remain qualitatively unaffected for larger sizes, e.g., $N = 100 \times 100$.

Throughout a simulation, each player has the fixed status of either adopting small-scope migration (group A) or large-scope migration (group B) when confronted with adverse conditions. This status is randomly assigned to players at the start of a simulation, with ν being the fraction of small-scope migrants (group A) in the population, irrespective of their initial strategies and remains invariable during the evolution process.

To simulate evolution, we employ the asynchronous updating where interaction and migration occur on the same time scale. Thus, during the simulation procedure a focal player and one of its neighbors are chosen randomly, whereby each player is selected once on average during ρN (population size) such elementary steps. Here, the Fermi function [52] is a viable option. When this occurs, a ran-

domly chosen player, say i , will imitate one of its randomly chosen neighbors s_j depending on the payoffs p_i and p_j of both players in the light of

$$f(s_i \leftarrow s_j) = \frac{1}{1 + \exp[(p_i - p_j)/K]} \quad (1)$$

where the magnitude of K characterizes the uncertainty related to the strategy update. For finite positive values of K , strategies performing worse may also be adopted based on unpredictable variations in payoffs or errors in the decision making. To focus on the key issue at hand, we assume in the main body of the paper that K is set to 0.1, but this assumption can be relaxed. In fact, we have checked that the main conclusions still hold for other positive K values as long as they are not too high (e.g., $K = 1$). As mentioned above, the game played with an vacant site engenders zero payoff per iteration, thus strategy updating is meaningless for isolated players.

Following the game interactions and the strategy change phase, the focal player reconsiders its interaction structure when finding itself in an adverse neighborhood. If the focal individual belongs to group A, it may migrate to empty sites within its restricted neighborhood, provided that there are available positions. The player will stay in its

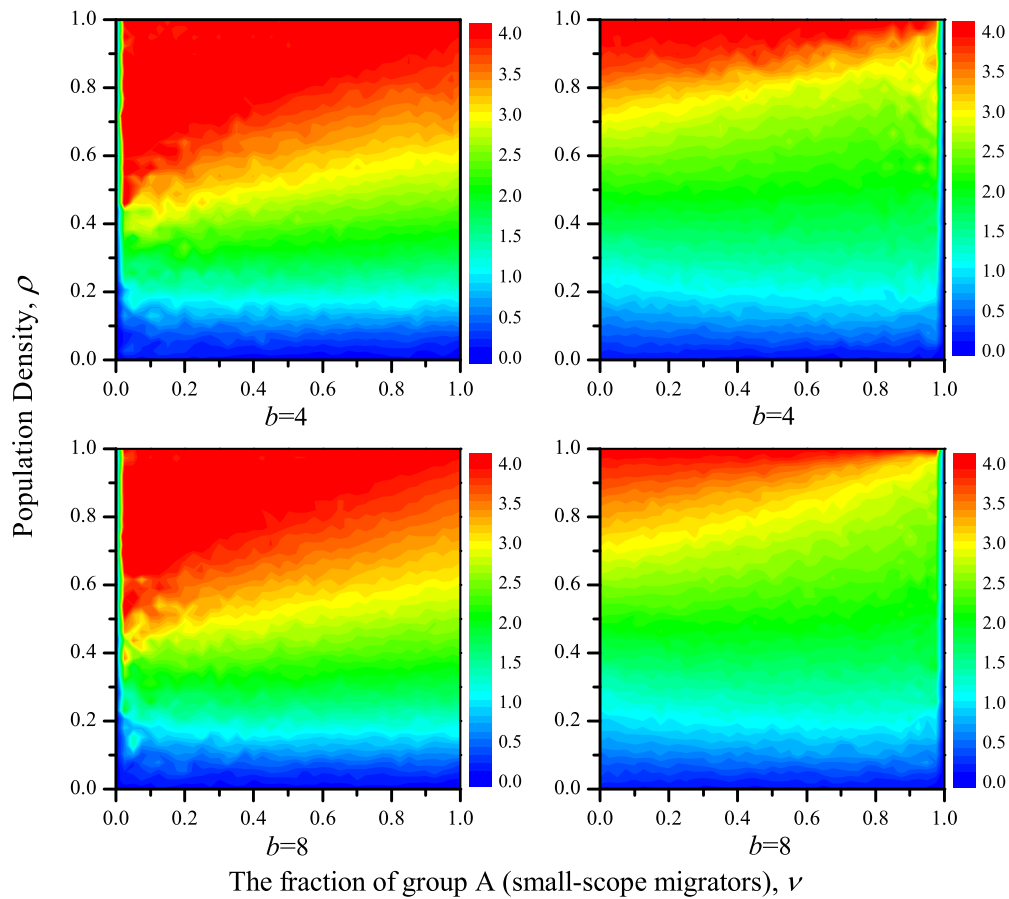


Fig. 4. Color maps of the average degree of group A (small-scope migrators, left panels) and group B (large-scope migrators, right panels) as a function of the fraction ν of group A and the population density ρ , for different values of the PD game parameter b . The underlying network employed is BASF networks. At the outset of the game, both strategies (cooperation and defection) were homogeneously distributed over the whole population. The PD payoff matrix takes the following shape using the parameter b : $T = b$, $R = b - 1$, $P = 0$, and $S = -1$, where $b > 1$. The b used in panels are $b = 4$ (upper panels) and $b = 8$ (lower panels), respectively. The color mapping depicts the average degree of investigated groups on BASF networks.

original position if its neighboring sites are fully occupied. If the focal player belongs to group B, it will implement global migration to favorable and unoccupied sites on the whole grid, provided that the action occurs. Further, we assume that players migrate with a probability proportional to the fraction of defectors in their neighborhoods. Those who fail to migrate play games with their present neighbors, while those who succeed will move to favorable sites and then play the first iteration of games with adjacent partners.

Note that a favorable position purports to a higher cooperation level than that in the current location. Players migrate to the sites with higher cooperation levels, in case of several sites with the same cooperation level, to the closest among them. Otherwise, if the current location offers the highest cooperation level among all the empty sites within the limits of the migration scope, players will not move.

Results are obtained by performing extensive computer simulations starting from random initial conditions of strategies. The evolution process is repeated until a stationary state is reached, where the distribution of strategies and the characteristics of neighborhoods do not change any more. Once the employed system enters into a steady state, we let the dynamics evolve for 10^4 addi-

tional time steps. Each datum shown below is an ensemble average over 100 independent realizations of both the networks and initial conditions to warrant appropriate accuracy. All the numerical experiments in this paper can be replicated using the available computational model.

3. Simulations and discussion

Figs. 1 and 2 show how for four values of the Prisoner's Dilemma (PD) game parameter b the cooperation level evolves in relation to the population density ρ and the relative fraction ν of group A, on networks with BASF and lattice social patterns respectively. Darwinian evolution, through selection by individuals' fitness, points to the rational state of only defectors, while cooperators survive in our system. Cooperation is more difficult to achieve for harder dilemma situations, but the outcome here is also dominated by the non-uniform migration scopes.

Let us firstly focus on the results when the community structure is described by the BA scale-free network. Clearly, for severe dilemma situations this mechanism is not sufficient to ensure cooperator dominance (see Fig. 1). Large disadvantage of a cooperator when facing a defector benefits the dominance of defectors, and the

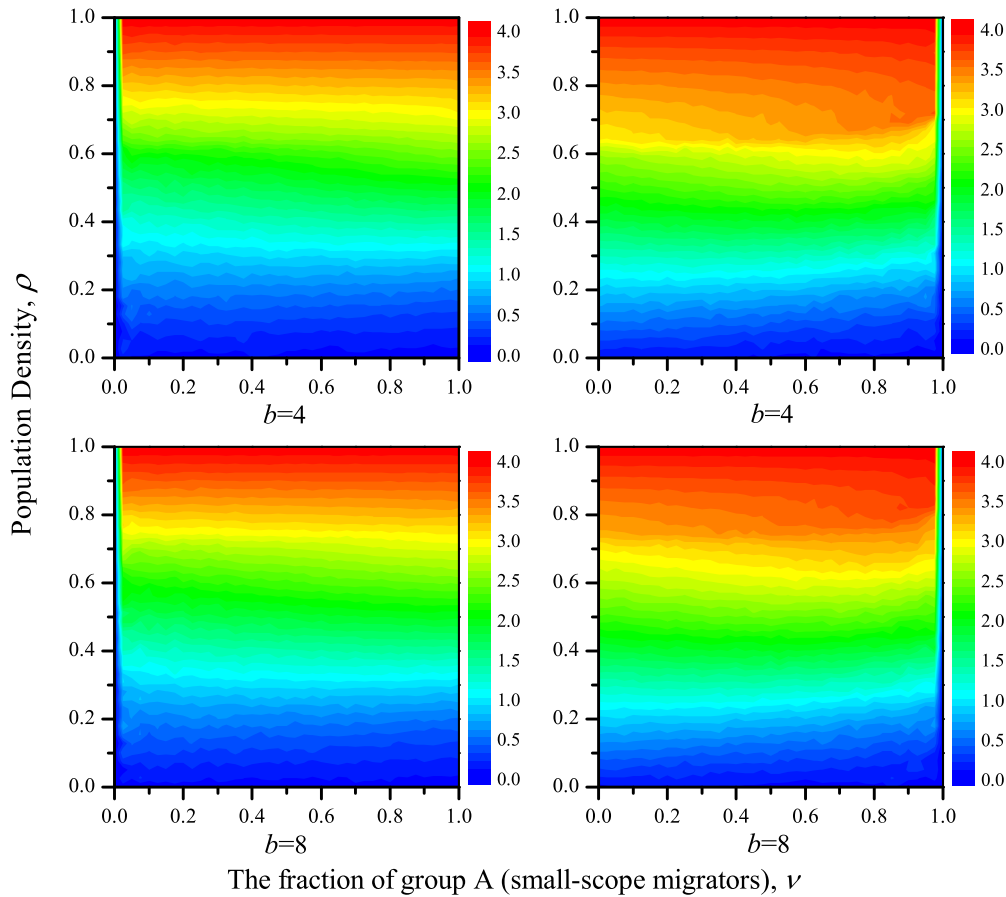


Fig. 5. Color maps of the average degree of group A (small-scope migrators, left panels) and group B (large-scope migrators, right panels) as a function of the fraction ν of group A and the population density ρ , for different values of the PD game parameter b . The underlying network employed is lattice networks. At the outset of the game, both strategies (cooperation and defection) were homogeneously distributed over the whole population. The PD payoff matrix takes the following shape using the parameter b : $T = b$, $R = b - 1$, $P = 0$, and $S = -1$, where $b > 1$. The b used in panels are $b = 4$ (upper panels) and $b = 8$ (lower panels), respectively. The color mapping depicts the average degree of investigated groups on lattice networks.

dense population may finish in an overall defector state. However, for sparse population, many players, as well as large portions of the graph as a whole, will still be disconnected, hence utilizing spatial reciprocity to protect cooperators against invading defectors. Thus, the observation that cooperators can still survive in low population density (large sparsity), is not surprising.

Then, the situation changes considerably in the case of mild dilemma situations (larger b here), where cooperation level increases as ρ (the fraction of occupied nodes) increases. The low cooperation level at lower ρ is also related to the fact that: more unoccupied positions mainly serve the benefits of defecting strategy by allowing an ever increasing efficiency of local exploitation and fleeing. However, as ρ increases, it becomes clear that the increase of heterogeneity when clustering is enlarged on BASF networks. Thus for example, in the $\rho \rightarrow 1$ limit, vacuous position does not exist. This said, the traditional model on BASF networks without migration is recovered. Hence, players are connected enough to transfer the more advantageous mutually beneficial cooperative strategy, while simultaneously the graph is dense enough for the defectors to be unable to escape retaliation from former partners effectively. Accordingly, crucial for this scenario to be valid is thus the combinatorial effect of population density and migration scope.

It is to be stressed that, we observe a rise of cooperation when the fraction of small-scope migrators increases from very small values. And, the increase of cooperation stemming from this is trivial by comparing with the outcomes led by denser population, where fully cooperating populations may finally emerge.

Refer to Fig. 2, in lattice-structured population the situation is strikingly different. The maxima of cooperation level f_c occur at different ρ (i.e., the fraction of occupied nodes) with that on BASF networks. As Fig. 2 highlights, compared with BASF, the lattice requires lower population density (large sparsity) for the cooperation evolution to be optimally promoted. In the $\rho \rightarrow 0$ limit the majority of population are isolated, and hence f_c simply mirrors back to the initial state where $f_c = 0.5$. For small ρ , a gradual rise in the average cooperation level occurs as ρ increases. The increment, however, is significantly lower than that reported in Fig. 1 for BASF networks. In this case, large-scope migration can help individuals to join better-performing groups regardless of distance, hence lower ν marks the advent of cooperator clusters. Then, as soon as ρ increases above a critical value which depends on the heterogeneity of the network, the population composition and the game parameter, the window of opportunity for cooperators no longer exists and defectors dominate finally, as shown in Fig. 2. The reason again lies in the spatial structures of

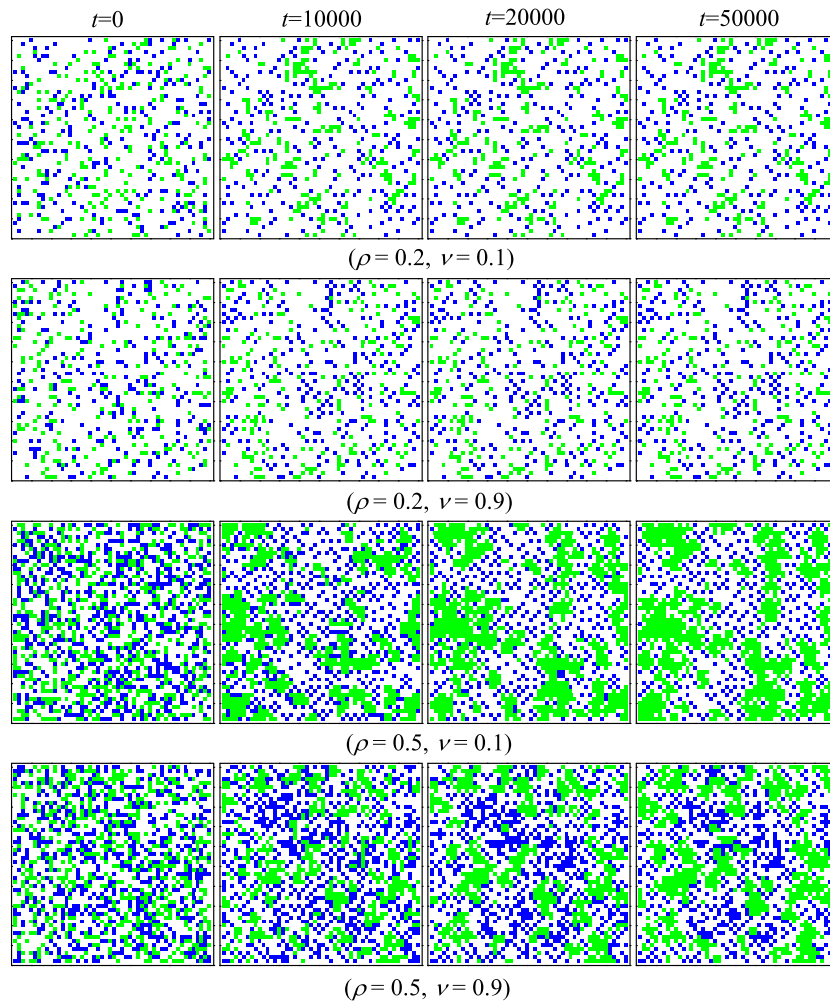


Fig. 6. Typical snapshots of spatial patterns of cooperators and defectors in PD game on a 50×50 square lattice at different time step t , for different values of the fraction ν of group A and the population density ρ . Upper panels correspond to case of $(\rho = 0.2, \nu = 0.1)$ and $(\rho = 0.2, \nu = 0.9)$, and lower panels correspond to situation of $(\rho = 0.5, \nu = 0.1)$ and $(\rho = 0.5, \nu = 0.9)$, respectively. Here, The b used here is $b = 4$. At the outset of the PD game, both strategies (cooperation and defection) were homogeneously distributed over the whole population. Notably, the gained conclusions are still valid for a population situated on larger (e.g., $N = 100 \times 100$) square lattice, while $N = 50 \times 50$ is employed here for providing snapshots with greater image clarity and readability than larger ones. The color coding is as follows: green denotes a cooperator; blue stands for a defector; and white represents an empty site. (For interpretation of the references to colour in this figure caption, the reader is referred to the web version of this article.)

game players. As ρ increases, fewer empty positions on lattice network enable defectors to exploit cooperators without having to fear the consequences of spatial reciprocity. Thus the average level of cooperative acts decreases, even sharply, in the dense lattice-structured population.

Next, Fig. 3 summarizes the evolutionary results of two groups (group A and B) in the lattice models. Consistent with Fig. 2, large-scope migrators (right panels in Fig. 3) perform better than small-scope ones, especially in non-viscous population. We can interpret the observed difference between the two groups as follows. Large-scope migration provides players with more chances to interact with large-hubs regardless of distance, which will allow a promotion of the important ingredients for cooperator clusters to form and resist the invasion of defectors. Thus, large-scope migration plays a key role in the resolution of social dilemmas by elevating the effectiveness of spatial reciprocity. However, the cooperator clustering can only limitedly elevate the heterogeneity of the population situated on lattice network, and thus there cooperation level

remains practically constant regardless of the value of ν . This indicates, the adopted population structure still plays a crucial role in the final outcomes.

To see how the migration scopes impinge on degree distributions, further investigations are required. Figs. 4 and 5 provide the degree distributions of two actors (group A and B) obtained on BASF and lattice, respectively. As evidenced in Fig. 4, small-scope migration is markedly more effective in raising the average degree than large-scope migration, through the whole value span of parameter ν . For BASF networks, the regions in parameter space where high levels of cooperation are evolved (as shown in Fig. 1) correspond to those regions where some nodes are tightly connected in dense population (i.e., where some nodes have high degrees, Fig. 4). Though migration may induce a certain mixing of the population due to increased interaction ranges of migrators, the aggregation of cooperators will eventually lead to a cooperative dominance under suitable population density and dilemma situations. Further, compared with the marked degree differences of the

two groups, their differences of cooperation levels are significantly lower. This still indicates, the heterogeneous final state is crucial for the fortified facilitative effect on cooperation, in particular since it incubates cooperative clusters.

However, refer to the lattice-structured models, the outcomes of degree distribution (described in Fig. 5) differ considerably with Fig. 4, especially in dense population. For a broad span of population density, large-scope migrators gain more interactions than those small-scope ones. For small-scope ones, their choices are limited to their sparse neighboring positions, rendering them easy preys to be exploited by nearby defectors. Hence, it is easy to see that small-scope migration decreases the potentially clustering chances of cooperators. However, the sparse population allows large-scope cooperators to escape the traps in connection with defectors, and seek better neighborhoods. As a result, large-scope migration will promote the emergence of cooperative community. The increment of the hub's payoff gives rise to a positive feedback which reinforces the position of the hub-cooperators. This means, the positive feedback here will increase the average degree of large-scope ones in lattice models. In the high-density scenario, scarce empty positions reduce the migration chances and the connectivity degree of the majority stays around the average degree of underlying networks (here, the employed degree is 4). As a result, the degrees of the two groups show unobvious differences in scenario of dense population.

Lastly, we examine the typical snapshots of spatial patterns of cooperators and defectors (as depicted with green and blue respectively in Fig. 6) in lattice-structured population. The Monte Carlo simulations starting from a random spatial pattern show that, after a relatively short transient, clusters of cooperators are finally formed. From numerical inspection of the population, another noticeable result concerns the number and size of cooperator clusters, which are closely related to the parameter ρ . In sparse population (e.g., $\rho = 0.2$), cooperators aggregate into a few clusters and defectors scatter among the ocean of vacant sites. This scenario is markedly notable as increasing values of population density ρ . Compared with results in Fig. 2, it is clear that there exist suitable population density values at which cooperation can be best promoted. Moreover, our statistical data have shown that, the likelihood of aggregation of more cooperators will turn larger, when the preferred option of the majority (e.g., $v = 0.1$) is large-scope migration. In this case, cooperators will have payoff advantages compared to defectors, then high cooperation levels supported by clusters are naturally achieved. Small-scope migration may decrease the gathering chances of cooperators, who are far away from each other on the grid. Clearly, suitably scattered population opens a window of opportunity, where cooperation is facilitated due to the large-scope migration. However, the game outcomes still depend quite significantly on the topology of population structure. And, the cooperator clustering could hardly elevate the heterogeneity of the population evenly distributed over the lattice network, and therefore fail in boosting the cooperation level to high values in lattice-structured population. Notably, the conclusions still hold in a popula-

tion situated on larger (e.g., $N = 100 \times 100$) square lattice, while $N = 50 \times 50$ is employed here for providing snapshots with greater image clarity and readability than larger ones.

Overall, the visualization of the strategy evolution indicates clearly that the evolutionary process is primarily controlled by the heterogeneity of population structure. Besides it, migration provides a main influencing factor in the fluctuating neighborhood of individuals, which is controlled by the competition between two potential processes. Migration may increase the ability of cooperator clusters to invade and overtake isolated defectors, however, it can also induce a certain mixing of the population due to increased interaction ranges of the migrating players. All these processes together yield a complex competition result dependent on the model parameters (e.g., population density, the type of interaction structure and also the migration scope).

4. Conclusions

Migration rules are receiving growing attention as a potent agonist in the evolution of cooperation. Herein we deliberate a situation where the migration scopes of players to free sites are heterogeneous. To gain a stark and systematic understanding of the problem, we focus on a simplified model, where two groups are distributed over the employed networks (lattice and BA scale-free network used for comparison here), and one prefers the small-scope migration (i.e., closest empty positions), while the other prefers large-scope migration (i.e., the whole grid).

In this context, our main finding is the existence of optimal values of migration scope and population density for cooperation to be maximized, and this property appears to be closely related to the type of population structures. With the support of suitable combination of model parameters, large-scope migration can help cooperators cluster together and reach its full potential in sparse lattice-structured population. However, small-scope migration can help leading the dense population into cooperation in BA scale-free networks. We have also gained a qualitative understanding of conclusions by examining the evolution of spatial patterns of strategies. Our results starkly show that, the key factor underlying the high level and eventual predominance of cooperation is the aggregation of cooperators. They are led by an appropriate combination of the population density, migration scope and interaction structure, which amplifies the effect of spatial reciprocity associated with flushing cooperative states. In this sense, cooperation can be found not only to be possible but often enhanced under suitable combination of model parameters.

The research reported here lends itself to multiple extensions. An immediate one, for example, would be to allow for the possibility of leader–follower patterns among migrating population. Other generalizations would include costs of leaving. Up to now we have limited our study where the costs of migration are zero, while migration will often be more costly in natural settings. Thus, investigating

what happens when varying the costs of migration seems a promising continuation of the results presented here.

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References

- [1] Hamilton WD. The evolution of altruistic behavior. *Am Nat* 1963;97:354–6.
- [2] Doebeli M, Hauert C, Killingback T. The evolutionary origin of cooperators and defectors. *Science* 2004;306:859–62.
- [3] Axelrod R. *The Evolution of Cooperation*. New York: Basic Books; 1984.
- [4] Axelrod R, Dion D. The further evolution of cooperation. *Science* 1988;242:1385–90.
- [5] Nowak MA, Bonhoeffer S, May RM. Robustness of cooperation. *Nature* 1996;379:125–6.
- [6] Sigmund K, Nowak MA. Evolutionary game theory. *Curr Biol* 1999;9:R503–5.
- [7] Fehr E, Fischbacher U. The nature of human altruism. *Nature* 2003;425:785–91.
- [8] Sigmund K, De Silva H, Traulsen A, Hauert C. Social learning promotes institutions for governing the commons. *Nature* 2010;466(7308):861–3.
- [9] Conradt L. When it pays to share decisions. *Nature* 2011;471:40–1.
- [10] Nowak MA, Sigmund K. Bacterial game dynamics. *Nature* 2002;418:138–9.
- [11] Li Q, Iqbal A, Chen M, Abbott D. Evolution of quantum and classical strategies on networks by group interactions. *New J Phys* 2012;14(10):103034.
- [12] Li Q, Chen M, Perc M, Iqbal A, Abbott D. Effects of adaptive degrees of trust on coevolution of quantum strategies on scale-free networks. *Sci Rep* 2013;3:2949.
- [13] Nowak MA, Sigmund K. Evolution of indirect reciprocity by image scoring. *Nature* 1998;393:573–7.
- [14] Perc M. Double resonance in cooperation induced by noise and network variation for an evolutionary prisoner's dilemma. *New J Phys* 2006;8:183.
- [15] Nowak MA, Sigmund K. Evolutionary dynamics of biological games. *Science* 2004;303:793–9.
- [16] Zhang J, Zhang C, Chu T, Perc M. Resolution of the stochastic strategy spatial prisoner's dilemma by means of particle swarm optimization. *PLoS ONE* 2011;6(7):e21787.
- [17] Nowak MA. Prisoners of the dilemma. *Nature* 2004;427:491.
- [18] Perc M. Coherence resonance in spatial prisoner's dilemma game. *New J Phys* 2006;8:22.
- [19] Nowak MA, Ohtsuki H. Prevolutionary dynamics and the origin of evolution. *Proc Natl Acad Sci USA* 2008;105:14924–7.
- [20] Barabási A-L, Albert R. Emergence of scaling in random networks. *Science* 1999;286:509–12.
- [21] Perc M. Chaos promotes cooperation in the spatial prisoner's dilemma game. *EPL* 2006;75:841–6.
- [22] Nowak MA, Sigmund K. Tit for tat in heterogeneous population. *Nature* 1992;355:250–3.
- [23] Nowak MA. Five rules for the evolution of cooperation. *Science* 2006;314:1560–3.
- [24] Perc M, Szolnoki A. Coevolutionary games: a mini review. *BioSystems* 2010;99(2):109–25.
- [25] Zhang J, Chen X, Zhang C, Wang L, Chu T. Elimination mechanism promotes cooperation in coevolutionary prisoners dilemma games. *Physica A* 2010;389(19):4081–6.
- [26] Perc M, Szolnoki A. Self-organization of punishment in structured populations. *New J Phys* 2012;14(4):043013.
- [27] Zhang J, Zhang C, Chu T. The evolution of cooperation in spatial groups. *Chaos Solitons Fract* 2011;44(1):131–6.
- [28] Perc M, Wang Z. Heterogeneous aspirations promote cooperation in the prisoner's dilemma game. *PLoS ONE* 2010;5(12):e15117.
- [29] Szolnoki A, Wang Z, Perc M. Wisdom of groups promotes cooperation in evolutionary social dilemmas. *Sci Rep* 2012;2:576.
- [30] Wang Z, Szolnoki A, Perc M. Interdependent network reciprocity in evolutionary games. *Sci Rep* 2013;3:1183.
- [31] Wang Z, Xia C-Y, Meloni S, Zhou C-S, Moreno Y. Impact of social punishment on cooperative behavior in complex networks. *Sci Rep* 2013;3:3055.
- [32] Yang D-P, Lin H, Shuai J. Coevolution of cooperation and network structure under natural selection. *EPL* 2011;93(4):48001.
- [33] Majeski SJ, Linden G, Linden C, Spitzer A. Agent mobility and the evolution of cooperative communities. *Complexity* 1999;5:16–24.
- [34] Vainstein MH, Silva ATC, Arenzon JJ. Does mobility decrease cooperation? *J Theor Biol* 2007;244:722–8.
- [35] Vainstein MH, Arenzon JJ. Disordered environments in spatial games. *Phys Rev E* 2001;64:051905.
- [36] Helbing D, Yu W. Migration as a mechanism to promote cooperation. *Adv Complex Syst* 2008;11:641–52.
- [37] Helbing D, Yu W. The outbreak of cooperation among success-driven individuals under noisy conditions. *Proc Natl Acad Sci USA* 2009;106:3680–5.
- [38] Ichinose G, Arita T. The role of migration and founder effect for the evolution of cooperation in a multilevel selection context. *Ecol Model* 2008;210:221–30.
- [39] Hamilton IM, Taborsky M. Contingent movement and cooperation evolve under generalized reciprocity. *Proc R Soc B* 2005;272:2259–67.
- [40] Wang Z, Szolnoki A, Perc M. If players are sparse social dilemmas are too: Importance of percolation for evolution of cooperation. *Sci Rep* 2012;2:369.
- [41] Wang Z, Szolnoki A, Perc M. Percolation threshold determines the optimal population density for public cooperation. *Phys Rev E* 2012;85(3):037101.
- [42] Wang J, Chen X, Wang L. Effects of migration on the evolutionary game dynamics in finite populations with community structures. *Physica A* 2010;389:67–78.
- [43] Boyd R, Richerson PJ. Voting with your feet: payoff biased migration and the evolution of group beneficial behavior. *J Theor Biol* 2009;257:331–9.
- [44] Wu Z-X, Holme P. Effects of strategy-migration direction and noise in the evolutionary spatial prisoner's dilemma. *Phys Rev E* 2009;80:026108.
- [45] Yang H-X, Wu Z-X, Wang B-H. Role of aspiration-induced migration in cooperation. *Phys Rev E* 2010;81(6):065101.
- [46] Droz M, Szwabinski J, Szabó G. Motion of influential players can support cooperation in prisoner's dilemma. *Eur Phys J B* 2009;71:579–85.
- [47] Yu W. Mobility enhances cooperation in the presence of decision-making mistakes on complex networks. *Phys Rev E* 2011;83:026105.
- [48] Sicardi EA, Fort H, Vainstein MH, Arenzon JJ. Random mobility and spatial structure often enhance cooperation. *J Theor Biol* 2009;256:240–6.
- [49] Cheng H, Dai Q, Li H, Zhu Y, Zhang M, Yang J. Payoff-related migration enhances cooperation in the prisoner's dilemma game. *New J Phys* 2011;13(4):043032.
- [50] Meloni S, Buscarino A, Fortuna L, Frasca M, Gomez-Gardenes J, Latora V, Moreno Y. Effects of mobility in a population of prisoner's dilemma players. *Phys Rev E* 2009;79:067101.
- [51] Roca CP, Helbing D. Emergence of social cohesion in a model society of greedy, mobile individuals. *Proc Natl Acad Sci USA* 2011;108:11370–4.
- [52] Szabó G, Töke C. Evolutionary prisoner's dilemma game on a square lattice. *Phys Rev E* 1998;58:69–73.