PROCEEDINGS OF
THE ROYAL SOCIETY B
BIOLOGICAL SCIENCES

Parent-preferred dispersal promotes cooperation in structured populations

Journal:	*Proceedings B*
Manuscript ID	Draft
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Chen, Xiaojie; University of Electronic Science and Technology of China; International Institute for Applied Systems Analysis Brännström, Åke; Umeå University; International Institute for Applied Systems Analysis Dieckmann, Ulf; International Institute for Applied Systems Analysis
Subject:	Theoretical biology < BIOLOGY, Evolution < BIOLOGY
Keywords:	prisoner's dilemma, cooperation, population structures, dispersal, update rule
Proceedings B category:	Evolution

Parent-preferred dispersal promotes cooperation in structured populations

Xiaojie Chen[1,2], Åke Brännström[3,2], and Ulf Dieckmann[2]

Author affiliations

[1]School of Mathematical Sciences, University of Electronic Science and Technology of China, Chengdu 611731, China

[2]Evolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), Schlossplatz 1, A-2361 Laxenburg, Austria

[3]Department of Mathematics and Mathematical Statistics, Umeå University, Umeå 90187, Sweden

Author for correspondence:

Xiaojie Chen

e-mail: xiaojiechen@uestc.edu.cn

Abstract

Dispersal is a key process for the emergence of social and biological behaviours. Yet far less attention has been paid to the dispersal effects on the evolution of cooperative behaviour in structured populations. To address this issue, we propose two dispersal modes, parent-preferred and offspring-preferred dispersal, into the birth-death update rule, and then consider the update rule with parent-preferred and offspring-preferred dispersal into evolutionary prisoner's dilemma on random-regular, small-world, and scale-free networks, respectively. We find that parent-preferred dispersal favours the evolution of cooperation in these different types of population structures and offspring-preferred dispersal inhibits the evolution of cooperation in homogeneous populations. But in scale-free networks when the parent-preferred dispersal strength is weak, cooperation is greatly enhanced for intermediate offspring-preferred dispersal strength, and cooperators can coexist with defectors for strong offspring-preferred dispersal strength. Moreover, our theoretical analysis precisely predicts the evolutionary outcomes in random-regular networks. We also incorporate these two dispersal modes into other three update rules, that is, death-birth, imitation, and pairwise comparison update rules, respectively, and find that similar results about effects of parent-preferred and offspring-preferred dispersal can be observed in different types of population structures. Our work, thus, unveil robust effects of individual preferential dispersal on the evolution of cooperation in different interactive environments.

Keywords

prisoner's dilemma, cooperation, population structures, dispersal, update rule

1. Introduction

How to understand the emergence of cooperation among rational individuals is a central challenge in evolutionary biology as well as social sciences. Evolutionary game theory provides a common mathematical framework to interpret the evolution of cooperation [1-3]. In particular, the prisoner's dilemma game, as a typical example, has attracted considerable attention [4,5]. The prisoner's dilemma is traditionally studied in an infinite, well-mixed population, where all individuals are equally likely to interact with each other. However, the well-mixed population typically opposes the evolution of cooperation [6].

In the past few years, it has been increasingly realized that real populations are not well-mixed, but structured, which can be well described by some network models, e.g., small-world [7] and scale-free networks [8]. Many studies show that population structures can promote cooperation via network reciprocity [9-18]. In particular, network heterogeneity is identified as the main driving force behind the flourishing cooperative behavior in scale-free networks [11,12]. However, such positive effects from network reciprocity do not always hold well for the evolution of cooperation, even in heterogeneous networks. For example, the advantage of heterogeneous networks in the evolution of cooperation can be greatly weakened by participation costs [19] or normalizing the accumulative payoff [20]. The update rule also plays an important role in the evolution of cooperation in social networks [9,21-23]. Remarkably, it is found that death-birth update in social networks allows the evolution of cooperation if the benefit-to-cost ratio in the prisoner's dilemma exceeds the average degree of the graph [13]. But surprisingly, under the birth-death update rule [24] cooperation can be never favoured in different types of network structures [13]. These findings show that the birth-death update rule can strongly suppress the favouring factors of network reciprocity for the evolution of cooperation.

Under the original birth-death update rule, a player is chosen for reproduction from the entire population proportional to fitness, and then the offspring replaces a random neighbour of the parental player. Such dispersal behaviour of offspring for the new site will influence the parent'fitness in the game framework, even if the dispersal model is random and local. Thus how to replace the neighbour site of parental player may cause the competition between the offspring and the parent when only local interaction is allowed [25]. Under this competitive scheme, when an individual is selected from the entire population proportional to fitness and then engenders an offspring, the offspring may replace a site of the neighbours according to some preferential dispersal modes, rather than the random dispersal mode. In this work, we thereby consider two different local dispersal modes driven by the parent and offspring respectively [26], that is, parent-preferred dispersal and offspring-preferred dispersal, and assume that the new location for the offspring under the birth-death update rule is determined by parent-preferred dispersal and offspring-preferred dispersal together. On the one hand, under the offspring-preferred dispersal the offspring prefers to have a favourable interactive environment after leaving for the new site [27]. Whereas, on the other hand, under the parent-preferred dispersal the parent prefers to improve or maintain its own interactive environment through the offspring's replacing. This may correspond to the phenomenon that, for example, in the animal world young and male lions are abandoned or ostracized from the group, in order to hold the predominance and reduce the competition from future generations [28].

In this paper, we incorporate such two preferential dispersal modes simultaneously into the birth-death update rule in structured populations, where individuals can have some information about their surrounding environments. We assume that individuals can not only easily observe the information about their nearest neighbours, but also obtain the information about other individuals through their close friends in a social manner since most of individuals can only have local information about others in realistic networked systems [29,30]. Based on the local information the parent and identical offspring can inspect the environments around the new locations. And the potential gains of the parent and offspring after the offspring's replacing could thus be set as two quantities for parent-preferred and offspring-preferred dispersal, which can characterize the surrounding interaction environments for the parent and offspring, respectively. Accordingly, the new location for the offspring can be determined in combination with these quantities.

In this work, we then study how the dispersal rule based on parent-preferred and offspring-preferred dispersal affects the evolution of cooperation in different types of population structures including random-regular [31], small-world, and scale-free networks. Also, we develop the pair-approximation method for some theoretical analysis on regular networks. We find that parent-preferred dispersal can always favour the evolution of cooperation in different types of social networks. In addition, offspring-preferred dispersal inhibits the evolution of cooperation in homogeneous networks, whereas in heterogeneous networks there exists an intermediate offspring-preferred dispersal strength at which cooperators can be promoted for weak parent-preferred dispersal strength. We also explicitly incorporate parent-preferred and offspring-preferred dispersal modes into other three strategy update rules including death-birth, imitation, and pairwise comparison update rules [32-37], and find that our main results about effects of parent-preferred and offspring-preferred dispersal hold against the changes of the update rules.

2. Model

We consider the evolutionary prisoner's dilemma game in structured populations. Following previous study [5], we adopt the game's payoff matrix as

$$M = \begin{bmatrix} b-c & -c \\ b & 0 \end{bmatrix},$$

where b represents the benefit of cooperation, and c $(0 < c < b)$ represents the cost of cooperation.

Initially, each player x is designated to play either as a cooperator (C) or as defector (D), and occupies one node of the network. At each time step, each player x engages in pairwise interactions with all its adjacent neighbours, and then collects its payoff P_x based on the payoff matrix parameters. Furthermore, player x obtains its fitness associated with the payoff information, given as [38]

$$f_x = e^{wP_x},$$

where $w > 0$ is the intensity of selection. In our present study, we adopt the exponential function of fitness so that each individual's fitness is always positive. In order to avoid amplifying the fitness difference among the population under this exponential function, in the main context we simply set $w = 0.01$.

After playing the games, individual x is chosen for reproduction proportional to its fitness. In other words, individual x is selected with probability f_x/T for reproduction, where $T = \sum_j f_j$ denotes the total amount of fitness in the population. We assume that individual x reproduces an identical offspring x_o, and only has local information about its nearest and next-nearest neighbours. Hence, parent x can obtain its expected fitness and its offspring's expected fitness when one site in its neighbourhood is chosen for its offspring x_o. In combination with these expected fitness information, the selection probability of offspring x_o replacing one of the neighbours y is set as

$$P_{x_o \to y} = \frac{(f_{x_{o_{x_o \to y}}})^{\alpha}(f_{x_{x_o \to y}})^{\beta}}{\sum_{z \in \Omega_x}(f_{x_{o_{x_o \to z}}})^{\alpha}(f_{x_{x_o \to z}})^{\beta}},$$

where the sum is over all the neighbours of x, $f_{x_{o_{x_o \to y}}}$ denotes the expected fitness of offspring x_o when x_o occupies the site of player y, $f_{x_{x_o \to y}}$ denotes the expected fitness of parent x when x_o occupies the site of player y, $\alpha > 0$ denotes the offspring-preferred dispersal strength, and $\beta > 0$ denotes the parent-preferred dispersal strength. In particular, for $\alpha = 0$ and $\beta = 0$ the offspring will replace a random neighbour of player x, and in this case the original birth-death rule is considered [13].

In this study, we focus on the effects of α and β on the evolution of cooperation in three different types of population structures, including random-regular, small-world, and scale-free networks. Instead of the fixation probability of cooperation, the key quantity for characterizing the cooperative behaviour of the population is the density of cooperators, which is defined as the fraction of cooperators in the population. We use individual-based simulations as well as the pair-approximation method to perform this study.

Simulations are carried out in a population with the size $N = 1000$. The average number of neighbours in each network model (including random-regular, small-world, and scale-free networks) is set to 4. We implement the simulation with asynchronous update [14,39]. Initially, the two strategies of C and D are randomly distributed among the population with an equal probability 0.5. Under stochastic dynamics, the population will converge to one of the two possible absorbing states: full cooperation or full defection [29]. We run 10^2 independent realizations for each set of parameter values, and compute the fraction of times that the system evolves to full cooperation as the density of cooperators [27,32]. However, if the population does not converge to an absorbing state after 5×10^6 generations, the cooperation level is determined by the average fraction of cooperators in the population over the last 2×10^4 generations.

3. Results

First, we incorporate the proposed offspring-preferred and parent-preferred dispersal modes into the birth-death update rule, and respectively show the fraction of cooperators depending on α and β together in random-regular, small-world, and scale-free networks, as plotted in figure 1. We see that in random-regular and small-world networks the cooperation level dramatically decreases as the offspring-preferred dispersal α increases, whereas intensively increases as the parent-preferred dispersal β increases (figure 1a and 1b). Moreover, full defection can be easily achieved for strong offspring-preferred dispersal strength and weak parent-preferred dispersal strength, whereas full cooperation can be easily achieved for weak offspring-preferred dispersal strength and strong parent-preferred dispersal strength. However, in scale-free networks, the cooperation level monotonically increases with increasing the parent-preferred dispersal strength β for fixed α (figure 1c). For larger fixed values of β, the cooperation level gradually decreases with increasing the offspring-preferred dispersal α. Surprisingly, for smaller fixed values of β (e.g., $\beta = 1$), the cooperation level first increases from zero until reaching the maximum value, and then decreases with increasing α. It means that for small values of β, there exists an intermediate value of α, which can results in the optimal cooperation level in scale-free networks. In addition, the cooperation level is not very low when the value of α becomes large, indicating that cooperators can coexist with defectors.

In figure 2, we provide the theoretical results by pair-approximation method in regular networks (for details see electronic supplementary material). By comparison, we find that theoretical analysis agrees well with numerical simulations in random-regular networks, as shown in figure 1a. However, this theoretical method cannot well predict simulation results in other types of networks, especially in scale-free networks. Here, we do not provide the theoretical results by the extended pair-approximation method considering the clustering effect and degree fluctuation [13,40]. Despite this point, our present theoretical analysis qualitatively reflects the roles of parent-preferred dispersal and offspring-preferred dispersal in the evolution of cooperation in structured populations.

What is the origin of such a boost of cooperation by the parent-preferred dispersal mode in different types of networks? In fact, when a defector is chosen for reproduction, it implies that this defector has a higher fitness and is surrounded by some cooperators. Under the parent-preferred dispersal, the defective parent prefers to let the offspring replace a defective neighbour's site, rather than a cooperative neighbour's. In this situation, although the parent can keep having a higher fitness, the spreading of defective behaviour is inhibited in the population (figure 3*a*). Moreover, in the initial conditions of 50% cooperators and for weak selection, cooperators can also have the opportunity to be chosen for reproduction in these types of population structures, especially in scale-free networks. When a cooperator is chosen for reproduction, it implies that the cooperator should directly connect more cooperative neighbours than others. Under the parent-preferred dispersal, if the cooperative parent also directly connects some defectors, the offspring prefers to replace the defective site so that the parent can have a higher fitness. On the one hand, such replacement can expand the cooperators' clusters, and the cooperative behaviour is spreading (figure 3*a*). On the other hand, it leads to a positive feedback mechanism, so that cooperators in the population can have more opportunities to be chosen for reproduction. Consequently, cooperative behaviour can evolve and prevail in structured populations.

Why does the offspring-preferred dispersal inhibit the evolution of cooperation in random-regular and small-world networks? In fact, under the offspring-preferred dispersal, when a defector is chosen for reproduction, the offspring prefers to choose a neighbour who is connecting more cooperators. Accordingly, this defective offspring replaces a cooperative neighbour of the parent. This is because that the cooperative neighbour often connects other cooperators under the birth-death rule without mutation, and it has the same (similar) number of interacting neighbours to others' in random-regular (small-world) networks. Correspondingly, the defective offspring can have a higher fitness, but the defective behaviour is spreading in the population (figure 3*b*). On the other hand, when a cooperator is chosen for reproduction, the offspring prefers to take over a cooperative neighbour of its parent so that the offspring can have a higher fitness in random-regular and small-world networks. However, such replacing for its offspring is unfavourable to the expansion of cooperators' cluster, and hence the spreading of the cooperative behaviour in the population is slow and stagnated (figure 3*b*).

It still remains to explain why cooperators can survive in scale-free networks under the strong offspring-preferred dispersal. To do this, we investigate the time evolution of bias in distribution of cooperators across degree number in scale-free networks. as shown in figure 4. We define the distribution bias for each time step t

as $\mathrm{sign}[b_k(t)]1/(1+1/|b_k(t)|)$, where $b_k(t)=[\rho_{ck}(t)-\rho_c(t)]/\rho_c(t)$. Here, $\rho_c(t)$ represents the total fraction of cooperation at time t, and $\rho_{ck}(t)$ represents the fraction of cooperators on nodes with degree k at time t.

We find that for weak offspring-preferred strength, as time increases the fractions of cooperators on high-degree and middle-degree nodes first becomes smaller than the total fraction of cooperation in the whole population (figure 4*a*). Thus, cooperation cannot evolve in this situation. For moderate offspring-preferred dispersal strength, as time increases the fractions of cooperators on high-degree and middle-degree nodes becomes higher than the total fraction of cooperation in the whole population, which induces a positive feedback mechanism for the evolution of cooperation (figure 4*b*). For strong offspring-preferred dispersal strength, as time increases there are always some fluctuations of distribution bias of cooperators on high-degree and middle-degree nodes (figure 4*c*). Hence, cooperators cannot stably dominate the high-degree nodes, which indeed play a crucial role in the emergence of cooperation in scale-free networks [11]. However, in this situation cooperators can coexist with defectors for a long time. This is because that in scale-free networks individuals occupying high-degree nodes can be easily chosen for reproduction. When a D-hub is chosen, its offspring prefers to move the site of one nearest neighbour with high-degree number for strong offspring-preferred dispersal strength. This induces a negative feedback mechanism that reduces their fitness and the opportunity of being chosen for reproduction. When a C-hub is chosen, its offspring prefers to move the site of one nearest neighbour with high-degree number for strong offspring-preferred dispersal strength. Moreover, for strong offspring-preferred dispersal strength the cooperative offspring always prefers to choose the high-degree nodes for replacing. This does not facilitate the expanding of cooperator clusters in the networks. However, cooperators can still coexist with defectors in this situation. On the contrary, under relatively weaker offspring-preferred dispersal strength the cooperative offspring may prefer to choose the site with other degree classes for replacing, which is helpful to the spreading of cooperative strategy. Consequently, cooperative behaviour can dominate the whole population.

Finally, it is of interest to elaborate on the generality of the effectiveness of offspring-preferred and parent-preferred dispersal for the evolution of cooperation. To do so, we further incorporate explicitly the offspring-preferred and parent-preferred dispersal modes into other three update rules, that is, death-birth, imitation, and pairwise comparison update rules, respectively (for detailed description see electronic supplementary material). We still find that under these three different update rules the parent-preferred dispersal approach can promote the evolution of cooperation in different types of population structures, and in scale-free networks cooperation can be still enhanced by an intermediate value of offspring-preferred dispersal strength when the parent-preferred dispersal strength is not high (electronic supplementary material, figure S2). However, together with figure 1, we can further find that under the birth-death update rule a favourable cooperation level can be achieved in a wider parameter range in comparison with the results for other three update rules. Noticeably, full cooperation can only be realized in a relatively narrow parameter range under the pairwise comparison update rule, since the intensity of selection also influences the evolutionary outcome of cooperation [14].

4. Discussion

In this work, we have proposed two dispersal modes simultaneously into the birth-death update rule, and shown that parent-preferred dispersal favours cooperation to evolve in different types of population structures. Thus, our results indicate that when some competition exists between the parent and its offspring in structured populations, cooperative behaviour can thrive if the parent is more self-interested. Moreover, we have found that offspring-preferred dispersal often inhibits the evolution of cooperation in homogeneous networks. While for strong offspring-preferred dispersal cooperators can coexist with defectors for a long time in a heterogeneous population. And, compared with the case without offspring-preferred dispersal or parent-preferred dispersal in scale-free networks cooperation is still promoted by the introduction of offspring-preferred dispersal in scale-free networks (electronic supplementary material, figure S1). Our work highlights the importance of dispersal rule to the evolution of cooperation in structured populations.

Our dispersal rule is one mode of local migration or mobility for individuals, but is different from the ones often studied on a square lattice [41-46]. In the traditional framework of migration, only the focal individual moves into an empty site from an occupied one if needed, so that the spatial interactions and the number of interactive individuals are both influenced, and even individuals can become isolated.

Such spatial dispersal has been considered into evolutionary games for studying the evolution of cooperation [41-44] and the evolving biodiversity [45,46]. Whereas in our study we propose two different dispersal modes and simultaneously incorporate them into different types of population structures. Under our dispersal rule, only the offspring individual replaces the site of the neighbouring individual who is chosen to be dead. Hence the empty site in our study is temporary. Moreover, previous study found that when individuals move into a favourable environment for cooperation, cooperation can prevail even in a noise condition [44]. However, in our framework we find that when an offspring individual moves into a favourable interactive environment for itself, cooperation cannot evolve in homogeneous populations. Instead, when the offspring individual moves into a favourable interaction environment for its parent, cooperation can flourish in structured populations. In fact, under the birth-death update rule with random dispersal, cooperation can be never favoured in structured populations [13]. Thus, in a sense our work extends the local dispersal rule into different types of structured populations from the spatially structured populations, and enriches the knowledge of local dispersal's effects on the evolution of cooperation in structured populations.

Our dispersal approach is simultaneously driven by both the parent's and offspring's preferences. And, dispersal competition exists between them, and such kin-like competition works as the driver determining the final dispersal site of the offspring. Here, we compare the relative contribution of parent-preferred and offspring-preferred dispersal to the evolution of cooperation. Intuitively, cooperation could be favourable under the strong offspring-preferred dispersal. This is because that the parental individual may sacrifice its own interests for maximizing its offspring's benefit in structured populations, leading to the emergence of kin selection [6]. However, surprisingly we find that the parent-preferred dispersal can favour the evolution of cooperation in different types of population structures, compared with the offspring-preferred dispersal. Although cooperators can coexist with defectors in scale-free networks for strong offspring-preferred dispersal strength, this result depends on the topology features of scale-free networks.

We set that initially cooperators randomly occupy 50% of the sites of individuals in the population, rather than only one cooperator like Ref. [13]. In fact, in that harsh initial condition, the only one cooperator is chosen for reproduction with an extremely small probability in scale-free network with large population size (e.g.,

$N = 1000$) in some simulation realizations. Conversely, the cooperator could be replaced by the defective offspring with a higher probability even under strong parent-preferred dispersal. Hence this initial condition can greatly diminish the positive effects induced by strong parent-preferred dispersal. Correspondingly, we consider that cooperators and defectors are equally distributed on the population structure as the initial condition in our study as previous works did [11,12]. In addition, we use the fraction of cooperators as the key quantity instead of the fixation probability of cooperation. This is because that we find that cooperators can coexist with defectors for a long time in scale-free network under some parameter settings (figure 1*c*), even if initially half the players are cooperators. Furthermore, we only provide the theoretical results by the pair-approximation method for regular graphs in this work. In fact, there are some improved pair-approximation approaches by considering the clustering effect and degree fluctuation [40,47], which can be used to predict our evolutionary outcomes in scale-free networks. Thus, it is worth using these approaches or further developing precise analytical tools to confirm our simulation results in scale-free networks in the future [48].

In this work, we consider that the parent only has the local information of its nearest and next-nearest neighbours, and the offspring can only replace one site of the parent's nearest neighbours. That is to say, nearest-neighbour dispersal mode is used. In fact, individuals may have the information of more neighbours in the population, and they can move into distant sites in the population. If there are more placements for dispersal, both the defective parent and offspring do not prefer that the offspring moves to the nearest sites. And both cooperators and defectors prefer that they are surrounded by more layers of cooperators when the distant dispersal mode is considered. In this extended framework, it is worth studying how the non-local parent-preferred and offspring-preferred dispersal modes are implemented in structured populations and how they influence the evolution of cooperation in structured populations. In addition, we do not include the effects of behavioural mutation [37] or imitation errors [49] in the present study. For example, when an individual is chosen for reproduction, mutation may occur on the offspring with a probability. And stochastic effects arising from different sorts of errors may play an important role in the cooperative behaviour at a population level. Thus, an interesting extension is to examine the robustness of our results in the presence of mutation errors.

Acknowledgments

X. C. acknowledges the National Natural Science Foundation of China (Grants No. 61503062). U. D. gratefully acknowledges financial support by the Austrian Science Fund, through a grant for the research project *The Adaptive Evolution of Mutualistic Interactions* as part of the multinational collaborative research project *Mutualisms, Contracts, Space, and Dispersal (BIOCONTRACT)* selected by the European Science Foundation as part of the European Collaborative Research (EUROCORES) Programme *The Evolution of Cooperation and Trading (TECT)*. Additional funding to UD was provided by the European Commission, the European Science Foundation, the Austrian Ministry of Science and Research, and the Vienna Science and Technology Fund.

References

[1] Maynard Smith J. Evolution and the Theory of Games. (Cambridge University Press, Cambridge, 1982).

[2] Hofbauer J, Sigmund K. Evolutionary Games and Population Dynamics. (Cambridge University Press, Cambridge, UK, 1998).

[3] Nowak MA. Evolutionary dynamics. (Harvard University Press, Cambridge, MA, 2006).

[4] Axelrod R. The Evolution of Cooperation. (Basic Books, New York, 1984).

[5] Doebeli M, Hauert C. 2005 Models of cooperation based on the prisoner's dilemma and the snowdrift game. *Ecol. Lett.* **8**, 748-766 . (doi:10.1111/j.1461-0248.2005.00773.x)

[6] Nowak MA. 2006 Five rules for the evolution of cooperation. *Science* 314, 1560-1563. (doi: 10.1126/science.1133755)

[7] Newman MEJ, Watts DJ. 1999 Scaling and percolation in the small-world network model. *Phys. Rev. E* 60, 7332-7342. (doi: 10.1103/PhysRevE.60.7332)

[8] Barabási AL, Albert R. 1999 Emergence of scaling in random networks. *Science* 286, 509-512. (doi: 10.1126/science.286.5439.509)

[9] Nowak MA, May RM. 1992 Evolutionary games and spatial chaos. *Nature* **359**, 826-829. (doi:10.1038/359826a0)

[10] Lieberman E, Hauert C, Nowak MA. 2005 Evolutionary dynamics on graphs. *Nature* 433, 312. (doi:10.1038/nature03204)

[11] Santos FC, Pacheco, JM. 2005 Scale-free networks provide a unifying framework for the emergence of cooperation. *Phys. Rev. Lett.* 95, 098104. (doi: 10.1103/PhysRevLett.95.098104)

[12] Santos FC, Pacheco JM, Lenaerts T. 2006 Evolutionary dynamics of social dilemmas in structured heterogeneous populations. *Proc. Natl. Acad. Sci. U.S.A.* 103, 3490-3494. (doi: doi:10.1073/pnas.0508201103)

[13] Ohtsuki H, Hauert C, Lieberman E, Nowak MA. 2006 A simple rule for the evolution of cooperation on graphs and social networks. *Nature* 441, 502-505. (doi:10.1038/nature04605)

[14] Szabó G, Fáth G. 2007 Evolutionary games on graphs. *Phys. Rep.* 446, 97 -216. (doi: 10.1016/j.physrep.2007.04.004)

[15] Nowak MA, Tarnita CE, Antal T. 2010 Evolutionary dynamics in structured populations. *Phil. Trans. R. Soc. B* **365**, 19-30. (doi: doi:10.1098/rstb.2009.0215)

[16] Rand DG, Nowak MA, Fowler JH, Christakis NA. 2014 Static network structure can stabilize human cooperation. *Proc. Natl. Acad. Sci. U.S.A.* 111, 17093-17098. (doi: 10.1073/pnas.1400406111)

[17] Maciejewski W, Fu F, Hauert C. 2014 Evolutionary game dynamics in populations with heterogenous structures. *PLOS Comp. Biol.* 10, e1003567 (doi: 10.1371/journal.pcbi.1003567)

[18] Tanimoto J, Kishimoto N. 2015 Network reciprocity created in prisoner's dilemma games by coupling two mechanisms. *Phys. Rev. E* 91, 042106. (doi: 10.1103/PhysRevE.91.042106)

[19] Masuda N. 2007 Participation costs dismiss the advantage of heterogeneous networks in evolution of cooperaiton. *Proc. R. Soc. B* 274, 1815-1821. (doi: doi:10.1098/rspb.2007.0294)

[20] Szolnoki A, Perc M, Danku Z. 2008 Towards effective payoffs in the prisoner’s dilemma game on scale-free networks. *Physica A* **387**, 2075-2082. (doi:10.1016/j.physa.2007.11.021)

[21] Huberman BA, Glance NS. 1993 Evolutionary games and computer simulations. *Proc. Natl. Acad. Sci. U.S.A*. **90**, 7716-7718. (doi: 10.1073/pnas.90.16.7716)

[22] Roca CP, Sánchez A, Cuesta JA. 2012 Individual strategy update and emergence of cooperation in social networks. *J. Mathe. Socio.* 36, 1-21. (doi: 10.1080/0022250X.2010.520830)

[23] Szolnoki A, Perc M. 2015 Conformity enhances network reciprocity in

evolutionary social dilemmas. *J. R. Soc. Interface* 12, 20141299. (doi:10.1098/rsif.2014.1299)

[24] Ohtsuki H, Nowak MA. 2006 The replicator equation on graphs, *J. Theor. Boil.* 243, 86-97. (doi:10.1016/j.jtbi.2006.06.004)

[25] Huang ZG, Wu ZX, Xu XJ, Guan JY, Wang YH. 2007 Coevolutionary dynamics of networks and games under birth-death and birth mechanisms. *Eur. Phys. J. B* **58**, 493-498. (doi: 10.1140/epjb/e2007-00241-1)

[26] Poethke HJ, Pfenning B, Hovestadt T. 2007 The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. *Evol. Ecol. Res.* **9**, 41-50.

[27] Chen X, Fu F, Wang L. 2009 Social tolerance allows cooperation to prevail in an adaptive environment. *Phys. Rev. E* 80, 051104. (doi: 10.1103/PhysRevE.80.051104)

[28] Violle C, Nemergut DR, Pu Z, Jiang L. 2011 Phylogenetic limiting similarity and competitive exclusion. *Ecol. Lett.* 14, 782-787. (doi: 10.1111/j.1461-0248.2011.01644.x)

[29] Santos FC, Pacheco JM, Lenaerts T. 2006 Cooperation prevails when individuals adjust their social ties. *PLoS Comput. Boil.* 2, e140. (doi: 10.1371/journal.pcbi.0020140)

[30] Kossinets G, Watts DJ. 2006 Empirical analysis of an evolving social network. *Science* 311, 88-90. (doi: 10.1126/science.1116869)

[31] Bollobás B. Random Graphs (Academic Press, New York, 1995).

[32] Ohtsuki H, Nowak MA. 2006 Evolutionary games on cycles. *Proc. R. Soc. B* 273, 2249-2256. (doi: 10.1098/rspb.2006.3576)

[33] Ohtsuki H, Nowak MA, Pacheco JM. 2007 Breaking the symmetry between interaction and replacement in evolutionary dynamics on graphs. *Phys. Rev. Lett.* 98, 108106. (doi: 10.1103/PhysRevLett.98.108106)

[34] Ohtsuki H, Nowak MA. 2008 Evolutionary stability on graphs. *J. Theor. Biol.* 251, 698-707. (doi: 10.1016/j.jtbi.2008.01.005)

[35] Perc M, Gómez-Gardeñes J, Szolnoki A, Floría LM, Moreno Y. 2013 Evolutionary dynamics of group interactions on structured populations: a review. *J. R. Soc. Interface* 10, 20120997. (doi: 10.1098/rsif.2012.0997)

[36] Szolnoki A, Antonioni A, Tomassini M, Perc M. 2014 Binary birth-death dynamics and the expansion of cooperation by means of self-organized growth.

EPL 105, 48001. (doi: 10.1209/0295-5075/105/48001)

[37] Chen X, Sasaki T, Brännström Å, Dieckmann U. 2015 First carrot, then stick: how the adaptive hybridization of incentives promotes cooperation. *J. R. Soc. Interface* 12, 20140935. (doi: 10.1098/rsif.2014.0935)

[38] Traulsen A, Shoresh N, Nowak MA. 2008 Analytical results for individual and group selection of any intensity. *Bull. Math. Biol.* 70, 1410-1424. (doi: 10.1007/s11538-008-9305-6)

[39] Adami C, Schossau J, Hintze A. 2016 Evolutionary game theory using agent-based methods. *Phys. Life Rev.* 19, 1-26 (doi: 10.1016/j.plrev.2016.08.015).

[40] Konno T. A condition for cooperation in a game on complex networks. 2011 *J. Theor. Boil.* 269, 224-233. (doi: 10.1016/j.jtbi.2010.10.033)

[41] Vainstein MH, Silva ATC, Arenzon JJ. 2007 Does mobility decrease cooperation? *J. Theor. Biol.* 244, 722-728. (doi: 10.1016/j.jtbi.2006.09.012)

[42] Sicardi EA, Fort H, Vainstein MH, Arenzon JJ. 2009 Random mobility and spatial structure often enhance cooperation. *J. Theor. Biol.* **256**, 240-246. (doi: 10.1016/j.jtbi.2008.09.022)

[43] Meloni S, Buscarino A, Fortuna L, Frasca M, Gómez-Gardeñes J, Latora V, Moreno Y. 2009 Effects of mobility in a population of prisoner's dilemma players. *Phys. Rev. E* 79, 067101. (doi: 10.1103/PhysRevE.79.067101)

[44] Helbing D, Yu W. 2009 The outbreak of cooperation among success-driven individuals under noisy conditions. *Proc. Natl. Acad. Sci. U.S.A.* 106, 3680-3685. (doi: 10.1073pnas.0811503106)

[45] Reichenbach T, Mobilia M, Frey E. 2007 Mobility promotes and jeopardizes biodiversity in rock-paper-scissors games. *Nature* 448, 1046-1049. (doi: :10.1038/nature06095)

[46] Kerr B, Riley MA, Feldman MW, Bohannan BJM. 2002 Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418, 171-174. (doi: 10.1038/nature00823)

[47] Antal T, Redner S, Sood V. 2006 Evolutionary dynamics on degree-heterogeneous graphs. *Phys. Rev. Lett.* 96, 188104. (doi: 10.1103/PhysRevLett.96.188104)

[48] Allen B, Lippner G, Chen YT, Fotouhi B, Momeni N, Yau ST, Nowak MA. 2017 Evolutionary dynamics on any population structure.. *Nature* 544, 227230. (doi: 10.1038/nature21723)

[49] Santos FC, Pacheco JM. 2011 Risk of collective failure provides an escape from the tragedy of the commons. *Proc. Natl. Acad. Sci. U.S.A.* 108, 10421-10425. (doi: 10.1073/pnas.1015648108)

Figures and Captions

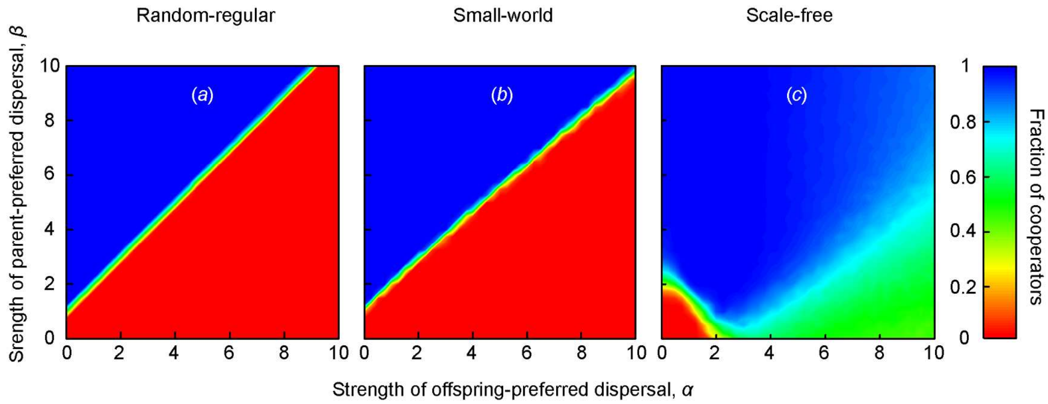

Figure 1: Fraction of cooperators depending on offspring-preferred dispersal strength α and parent-preferred dispersal strength β in a contour plot form in random-regular (a), small-world (b), and scale-free (c) networks, respectively. Parent-preferred dispersal favours the evolution of cooperation in different types of population structures. In scale-free networks, cooperators can coexist with defectors under strong offspring-preferred dispersal strength. Here, $w = 0.01$ and $b/c = 4$.

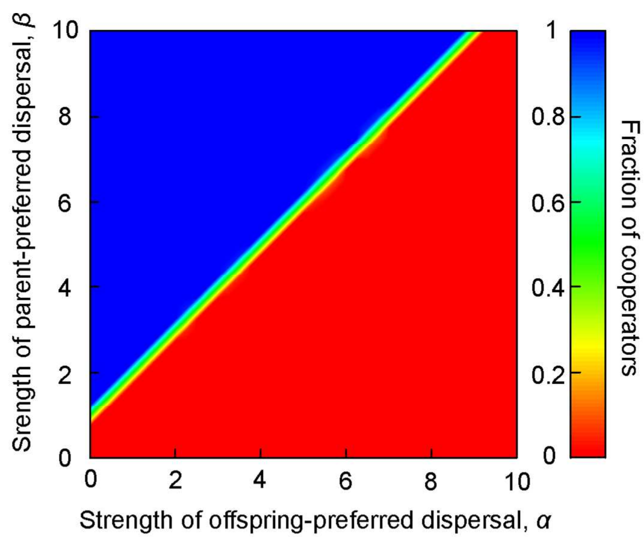

Figure 2: Theoretical analysis by pair-approximation method in regular networks depending on the offspring-preferred dispersal strength α and parent-preferred dispersal strength β in a contour plot. The analysis precisely predicts the evolutionary outcomes in random-regular networks.

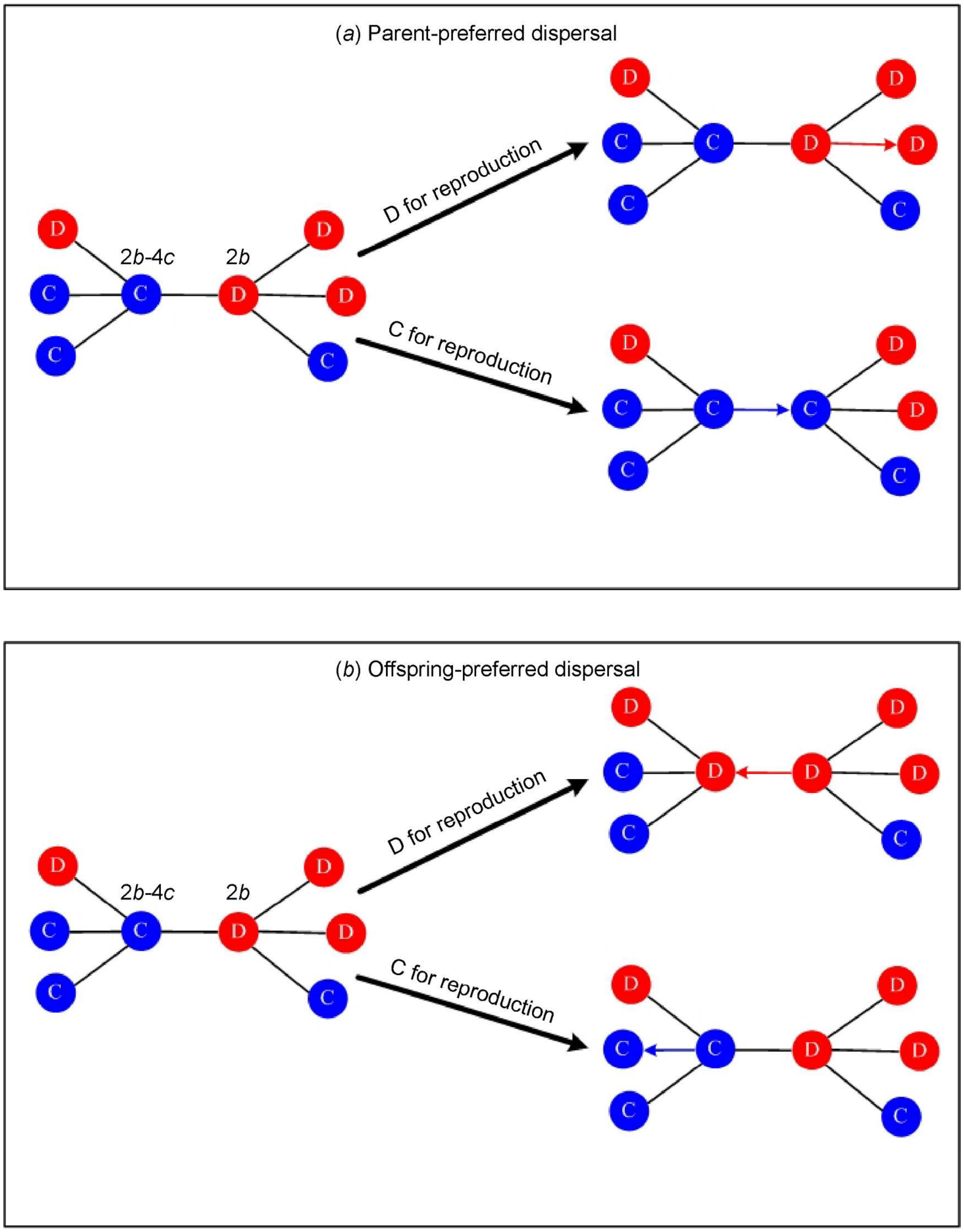

Figure 3: Intuitive illustrations for microscopic evolution in homogeneous networks. We consider a cooperator-defector pair competing for the next reproduction event. The defector with payoff $2b$ has a great advantage to be chosen for reproduction. However, its left cooperative neighbour with payoff $2b-4c$ can have the opportunity to be chosen for reproduction under the proportional birth rule and for weak selection. (a) Under the parent-preferred dispersal, the offspring of the focal defector prefers to replace a neighbouring defector; which induces a positive feedback

mechanism for the expanding of cooperator clusters. (b) Under the offspring-preferred dispersal, the offspring of the focal defector prefers to replace the site of the focal cooperator, leading to the expanding of defectors, whereas the offspring of the focal cooperator prefers to replace a cooperative neighbour.

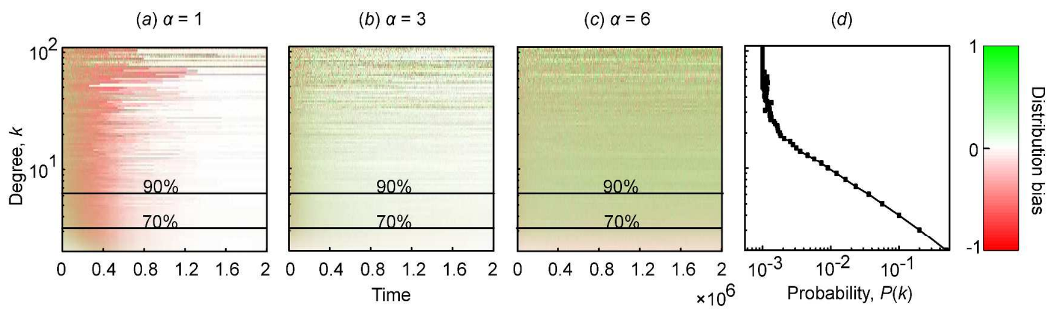

Figure 4: Time evolution of bias in distribution of cooperators across degree number in scale-free networks for weak parent-preferred dispersal strength $\beta = 1$ and different values of offspring-preferred dispersal strength: (a) $\alpha = 1$, (b) $\alpha = 3$, and (c) $\alpha = 6$. The distribution bias for each time step t is computed as $\mathrm{sign}[b_k(t)]1/(1 + 1/|b_k(t)|)$, where $b_k(t) = \left[\rho_{ck}(t) - \rho_{c}(t)\right]/\rho_{c}(t)$. Here, $\rho_{c}(t)$ represents the total fraction of cooperation at time t, and $\rho_{ck}(t)$ represents the fraction of cooperators on nodes with degree k at time t. (d) describes the degree distribution of scale-free with average degree number $k = 4$ and population size $N = 1000$. In the networks, there are 70% nodes whose degree number is not larger than 3, and 90% nodes whose degree number is not larger than 6. Here, $w = 0.01$ and $b = 4$.