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Spatial reciprocity in the evolution of cooperation

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Research

Cite this article: Su Q, Li A, Wang L, Eugene Stanley H. 2019 Spatial reciprocity in the evolution of cooperation. *Proc. R. Soc. B* **286**: 20190041.
http://dx.doi.org/10.1098/rspb.2019.0041

Received: 7 January 2019
Accepted: 11 March 2019

Subject Category:
Evolution

Subject Areas:
evolution, behaviour

Keywords:
evolution of cooperation, spatial reciprocity, evolutionary game theory, population structure, assortment

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Electronic supplementary material is available online at http://dx.doi.org/10.6084/m9.figshare.c.4440278.

Cooperation is key to the survival of all biological systems. The spatial structure of a system constrains who interacts with whom (interaction partner) and who acquires new traits from whom (role model). Understanding when and to what degree a spatial structure affects the evolution of cooperation is an important and challenging topic. Here, we provide an analytical formula to predict when natural selection favours cooperation where the effects of a spatial structure are described by a single parameter. We find that a spatial structure promotes cooperation (spatial reciprocity) when interaction partners overlap role models. When they do not, spatial structure inhibits cooperation even without cooperation dilemmas. Furthermore, a spatial structure in which individuals interact with their role models more often shows stronger reciprocity. Thus, imitating individuals with frequent interactions facilitates cooperation. Our findings are applicable to both pairwise and group interactions and show that strong social ties might hinder, while asymmetric spatial structures for interaction and trait dispersal could promote cooperation.

1. Introduction

Cooperation is ubiquitous in living systems ranging from single cells, multicellular organisms, to groups of animals [1,2]. Understanding the emergence and persistence of this altruistic behaviour in a competitive world has long been a challenge since the time of Darwin [3]. Evolutionary game theory provides a powerful mathematical framework for exploring this conundrum in which two-player and multiplayer games are employed to capture social dilemmas in pairwise and group interactions, respectively [4–6]. During the last two decades, it was found that spatial structures can strongly affect evolutionary dynamics [7–9], and this has elicited much research including numerical simulations [10–12], theoretical analysis [13–20] and empirical studies [21].

Spatial structures constrain the choice of interacting partner and also constrain which player serves as a role model for strategy imitation. Without distinguishing between the two constraints—role models are always interaction partners [15–21]—it is widely accepted that spatial structures can promote cooperation (spatial reciprocity) with respect to the well-mixed settings [22]. However, when spatial structures lead to asymmetric interaction partners and role models, fundamental questions about the interplay between spatial structures and the evolution of cooperation remain unanswered. When does spatial reciprocity emerge? How does spatial structure affect the intensity of reciprocity? Although related studies using two-player games have provided insights [13,14,23,24], they have ignored the increased complexity arising from the transition from pairwise interactions to group interactions, especially when spatial structures are under consideration [25–27]. We thus need to explore whether there are any rules governing spatial reciprocity in both pairwise and group interactions. In addition, many empirical studies have found

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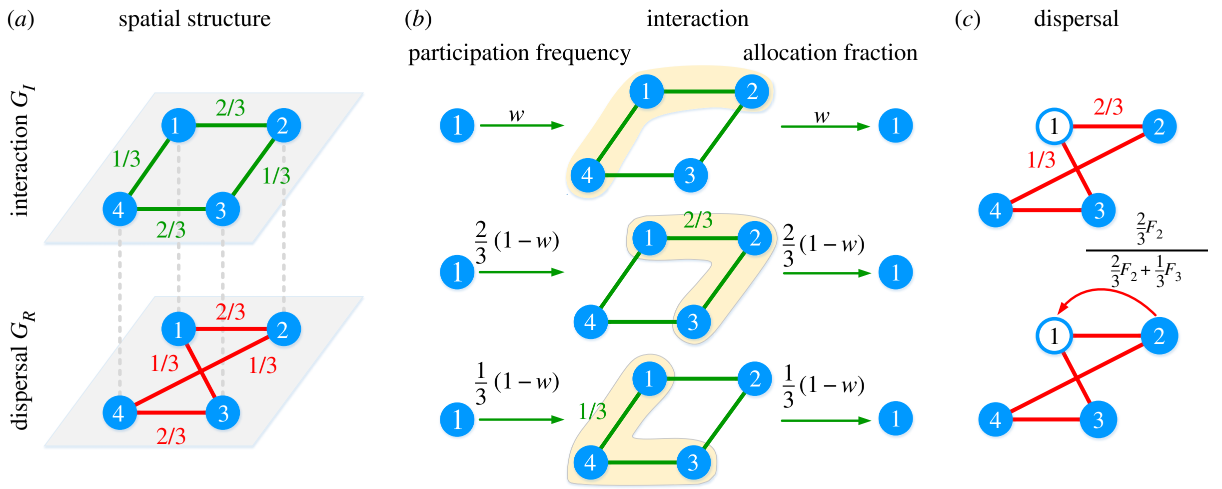

Figure 1. PGGs in spatial structures. (*a*) The spatial structure described by an interaction graph G_I and an dispersal graph G_R. Nodes are labelled by 1, 2, 3, 4, separately. The value alongside each edge corresponds to the edge weight. (*b*) Participation frequencies and pay-off allocation fractions associated with the player occupying node 1 (called player 1) in three games (highlighted). s_i denotes i's strategy ($s_i = 1$ means cooperation and $s_i = 0$ means defection). Player 1 participates in the self-centred game at frequency w and invests ws_1, and correspondingly is allocated a fraction w of the total benefits. Player 1 participates in the game centred on player 2 at frequency proportional to the edge weight d_{12}, i.e. $2(1 - w)/3$, and invests $2(1 - w)s_1/3$. It obtains a fraction $2(1 - w)/3$ of the total benefits from this game. (*c*) Strategy update under death–birth rule. A randomly selected player 1 dies and its neighbour like player 2 competes to replace 1 with probability proportional to $e_{12}F_2$, where F_2 is 2's fitness. (Online version in colour.)

that interactions in real-world networks often differ in their strength and frequency [28,29]. Individuals tend to cluster together and create tightly knit groups, such as communities [30,31]. These findings contradict traditional assumptions that systems have homogeneous social ties and lack structural clusters [16–18]. How these realistic structure characteristics affect spatial reciprocity thus remains as an open question.

We here answer these questions by applying a unifying analytical framework to various population structures, evolution scenarios and to both pairwise and group interactions. We introduce a single parameter that can quantify the effects of a spatial structure on the evolution of cooperation. A unifying formula with such a parameter is provided for predicting when natural selection favours cooperation over defection. Compared with well-mixed settings, a spatial structure only promotes cooperation when there are overlaps between role models and interaction partners. When the overlap is not present, spatial structure inhibits cooperation. Furthermore, choosing players with frequent interactions as role models facilitates cooperation. We design an algorithm in which every player uses only local interaction information to self-organize their social ties. The result is an evolving structure with stronger spatial reciprocity. In addition, our findings provide new insights into a few well-known results. Typically, asymmetric spatial structures for interactions and trait propagation might enhance while strong social ties could weaken spatial reciprocity.

2. Model

(a) Spatial structure

We examine a population of fixed size N with a spatial structure described by two graphs: (i) a graph G_I determining social interactions, and (ii) a graph G_R defining strategy dispersal. The two graphs have the same node set V, where each node is occupied by a player. Edge weight d_{ij} in the interaction graph measures the interaction strength and e_{ij} in the dispersal graph describes patterns of strategy dispersal. Here, we assume that all individuals present the similar pattern of interactions and the similar pattern of strategy dispersal [14,20,24] (technically, G_I and G_R are joint transitive and all nodes look the same, see appendix Aa) and are symmetrical, i.e. $d_{ij} = d_{ji}$, $e_{ij} = e_{ji}$. In addition, in the interaction and strategy dispersal graph, there is no edge that connects a node to itself, i.e. $d_{ii} = 0$ and $e_{ii} = 0$ for $1 \le i \le N$. We rescale edge weights so that $\sum_{j\in V} d_{ij} = 1$, $\sum_{j\in V} e_{ij} = 1$. This category covers most classical population structures (electronic supplementary material, figure S2).

(b) Public goods game

We use the public goods game (PGG) to model group interactions. The PGG depicts an L-player interaction in which cooperation and defection are the only two options. Each cooperator invests an amount c in the common pool and the investment produces benefit b, where $r = b/c$ is the enhancement factor. Defectors do not contribute. Eventually, the total benefits are equally distributed over all L participants. Under the framework of evolutionary games, every player organizes a self-centred PGG. In well-mixed settings, participants in a PGG include the organizer (termed focal player) and $L - 1$ randomly selected players. In the conventional setting of PGGs in structured populations, the player occupying node i (called player i) and all of its neighbours engage in the PGG centred on i.

We further extend PGGs to weighted graphs. Each player participates in different PGGs at frequencies associated with the edge weights (figure 1*a*,*b*). We normalize to 1 the total participation frequency of each player. Every player participates in the self-centred game at a frequency w and all neighbour-centred games at a frequency $1 - w$. Let s_i denote the strategy taken by player i, where $s_i = 1$ means cooperation and $s_i = 0$ defection. In the self-centred game, a player invests ws_i. Then, it obtains a fraction w of total benefits in the self-centred game. Player i participates in the game centred on neighbour j at a frequency $d_{ij}(1 - w)$ and invests $d_{ij}(1-w)s_i$. Then, a fraction $d_{ij}(1-w)$ of the total benefits in the j-centred game is allocated to i. In the game centred on i and j ($i \neq j$), i's pay-offs are, respectively,

$$f_i^i = rw\left[\sum_{l\in V} d_{li}(1-w)s_l + ws_i\right] - ws_i$$

$$f_i^j = rd_{ij}(1-w)\left[\sum_{l\in V} d_{lj}(1-w)s_l + ws_j\right] - d_{ij}(1-w)s_i.$$

We can recover the conventional case if: (i) the interaction and dispersal graphs are identical and unweighted, and (ii) every player participates in the self-centred and each neighbour-centred game at the same frequency [11]. Each player accumulates pay-offs from all interactions and derives pay-off $f_i = \sum_{l\in V} f_i^l$. The pay-off is transformed to the fitness by $F_i = 1 - \delta + \delta f_i$, where δ is the intensity of selection [16,32]. We here focus on weak selection ($\delta \ll 1$).

(c) Strategy update

At the end of each generation, players use the dispersal graph to update strategies or propagate genes. Dispersal can be cultural or genetic. We use the highly studied death–birth update rule [16] (figure 1*c*). A random player i is chosen to die. With a probability proportional to effective fitness $e_{ji}F_j$, a random neighbour j is selected to be the reproducing agent, and its offspring then occupies node i. We also examine three other update rules (electronic supplementary material, S1).

3. Results

We study whether selection favours cooperation over defection by comparing the fixation probability ρ_C with the fixation probability ρ_D. ρ_C (ρ_D) is the probability that a single cooperator (defector) in a random position turns a fully defecting population into a fully cooperating one (one fully cooperating population into a fully defecting one) [32]. Cooperation is more successful than defection if $\rho_C > \rho_D$ [24,32].

(a) A unifying formula to predict cooperators' success

We begin by studying a class of spatial structures that are described by a pair of unweighted but not necessarily symmetric graphs (see appendix Aa for technical details). Each player participates in self- and each neighbour-centred game once in each generation. We introduce two concepts: (i) interaction partner and (ii) role model. If player i and j are likely to participate in the same game, j is i's interaction partner. On the one hand, one's interaction partners are not necessarily connected to this player in the interaction graph because they may encounter in games centred on common neighbours. On the other hand, when having many neighbours in common, two players could interact many times owing to their concurrent participation in these neighbour-centred games. These two cases model well many realistic situations: interactions probably occur between strangers owing to their common acquaintances; frequent interactions often occur between individuals who have many common friends. Let n_I denote the sum of times that a player interacts with each interaction partner. Assuming player i has two interaction partners j_1 and j_2, if in each generation i encounters j_1 in two games and j_2 in one game, we have $n_I = 3$. Given similar interaction patterns, n_Is are identical for all players. Players whose offspring potentially occupies node i or who can disperse strategies to player i serve as i's role models. In the dispersal graph with node degree k_R, each player has k_R role models. We denote the sum of times that a player interacts with each role model by n_R. Analogously, n_Rs are identical for all players. We stress that interactions occur between a player and its role model only if this role model is also an interaction partner. Therefore, $n_R > 0$ means that interaction partners overlap role models and $n_R = 0$ indicates that there is no overlap between them.

We introduce a concept termed as 'assortment coefficient':

$$\theta = \frac{n_R}{n_I}\frac{1}{k_R}. \tag{3.1}$$

Here, θ measures the average frequency of a player interacting with a role model. The larger θ is, the more frequently a player interacts with an individual role model. We illustrate the calculation of θ using figure 1*a*,*b*. If both interaction and dispersal graphs are unweighted, player 1 encounters 2 in 1- and 2-centred games and encounters 4 in 1- and 4-centred games. In addition, although player 3 is not directly connected to 1 in the interaction graph, both of them engage in games centred on their common neighbours such as 2 and 4. We have $n_I = 6$. Only players 2 and 3 are player 1's role models. We have $n_R = 4$ and $\theta = 1/3$. We provide a formula for calculating θ in any unweighted and joint transitive graphs in the electronic supplementary material, S2.

For a given population size N and a game size L, natural selection favours cooperation over defection under weak selection only if the enhancement factor exceeds the threshold (electronic supplementary material, S2)

$$r^* = \frac{(N-2)L}{N(L-1)\theta + N - 2L}. \tag{3.2}$$

Equation (3.2) is applicable to various spatial structures and figure 2*a*–*d* shows a few representative examples. Intriguingly, θ is the only determinant of evolutionary outcomes in different spatial structures. For a well-mixed setting, we have $\theta = 1/(N-1)$ and $r^* = (N-1)L/(N-L)$ (figure 2*a*). When both interaction and dispersal graphs are lattices and fully overlap, we have $\theta = 1/10$ and $r^* = 25(N-2)/(7N-50)$ (figure 2*c*). Equation (3.2) also provides an alternative approach to investigating evolutionary game dynamics in set structures, where calculating the single parameter θ is much easier than analysing the entire system (figure 2*b*).

To further examine the generality of this formula, we develop two variations of spatial PGGs: random PGG and l-order PGG. In a random PGG, the focal player and only a fraction of its nearest neighbours participate (figure 2*e*). Random PGGs describe the case where a collective interaction does not always involve all acquaintances. This variation can cover two-player interactions on graphs by setting $L = 2$, where participants in a game are the organizer and a neighbour. It also enables investigation into the evolutionary dynamics in complex systems with diverse structure characteristics, like biological systems with multiple species, where the intraspecies interactions of individuals are random (well-mixed) but the interspecies interactions are constrained by geographical sites (structured). In l-order PGGs, a player initiates a game and all players within an l-step walk from this player become involved (figure 2*f*). l-order PGGs depict the situation in which participants of a collective interaction are not limited to acquaintances.

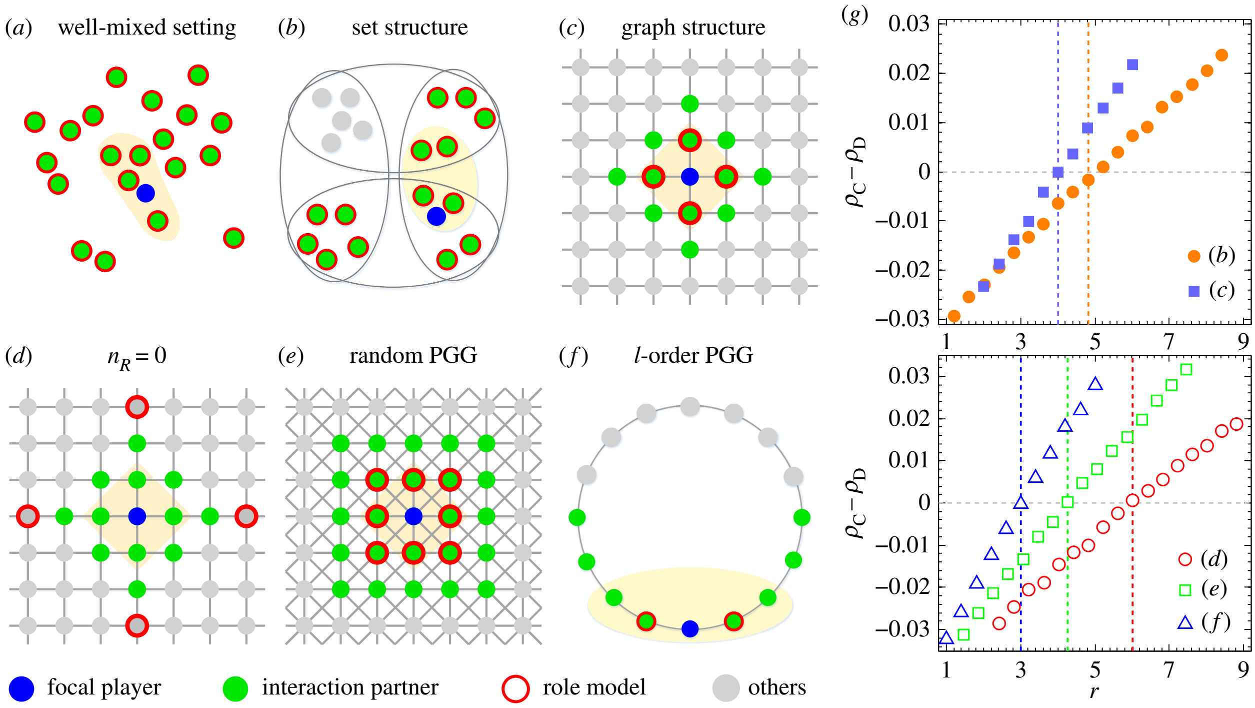

Figure 2. Various spatial structures for which θ is shown. We present interaction partners (green filled nodes) and role models (red framed nodes) only for the focal player (blue filled nodes). Here, the size of a PGG is fixed to $L = 5$ for all spatial structures and interaction scenarios. Players in the highlighted zone are participants of a PGG centred on the focal player. (*a*) In the well-mixed setting, we have $\theta = 1/(N-1)$. (*b*) In set structures, all participants of a game belong to the same set. Each player is situated in two common sets with $M - 1$ players and in one common set with $2M$ players. We have $\theta = 1/(3M-1)$. (*c*) In the lattice satisfying that interaction and dispersal graphs are fully overlapped, we have $\theta = 1/10$. (*d*) When no interaction partner overlaps role models ($n_R = 0$), we have $\theta = 0$. (*e*) In a random PGG, the focal player and $L - 1$ randomly selected neighbours (in the interaction graph) are participants. Here, we have $\theta = 23/280$. (*f*) In an *l*-order PGG, all players within a *l*-step walk from the focal player (in the interaction graph) participate in the game centred on the focal player. Panel (*f*) corresponds to a 2-order PGG and we have $\theta = 1/5$. (*g*) The analytical value of r^* (vertical lines) agrees well with simulation data (cross points of dots and horizontal lines). Population size $N = 49$. ρ_C (ρ_D) is determined by the fraction of runs where a cooperator (defector) reaches fixation out of 10^6 runs under weak selection, $\delta = 0.01$. (Online version in colour.)

We stress that a conventional graphed PGG is actually a random PGG with $L = k_I + 1$ and also an *l*-order PGG with $l = 1$. Despite the increasing complexity arising from these variations, equation (3.2) still accurately predicts the success of cooperation over defection (see the electronic supplementary material, S2, for θs corresponding to the two variations). Figure 2*g* shows that analytical results agree well with Monte Carlo simulations in various spatial structures (see the electronic supplementary material, figure S2, for more examples).

(b) Emergence of spatial reciprocity

Analysing equation (3.2), we find that a spatial structure promotes cooperation with respect to the well-mixed setting only if (electronic supplementary material, S3)

$$\theta > \frac{1}{N-1}.$$

If $\theta = 1/(N-1)$, the evolutionary outcome in structured populations is the same as that in well-mixed populations. If $\theta < 1/(N-1)$, the spatial arrangement of interaction partners and role models inhibits cooperation. To understand the underlying mechanisms, we examine whether a spatial structure facilitates the assortment between cooperators. This assortment contributes to the frequent interactions between cooperators and allows them to make up for the disadvantages when confronting defectors [33]. Essentially, assortment in a spatial structure is determined by how the strategy dispersal between a player and its role models affect the strategy association between this player and its interaction partners. When a cooperative role model *j* disperses cooperation to player *i*, if *j* is *i*'s interaction partner, such strategy dispersal achieves the strategic reciprocity (mutual cooperation) between *i* and *j*. This thus increases the survivability of both cooperator *i* and *j* against neighbouring defectors. Otherwise, isolated cooperator *i* is vulnerable to the invasion of defectors.

θ well quantifies the ability of a spatial structure to assort strategies and achieve reciprocity. In equation (3.1), θ consists of two terms, n_R/n_I and $1/k_R$. $1/k_R$ represents the possibility for a player to reciprocate an individual role model. n_R/n_I measures the reciprocity strength. The two terms together determine how a spatial structure affects the evolution of cooperation. In the well-mixed setting, in spite of a large value of n_R/n_I (=1), $1/k_R$ (=$1/(N-1)$) is extremely low, which thus weakens the strategy reciprocity and makes cooperation hard to evolve. If none of role models overlap interaction partners ($n_R = 0$), $\theta = 0$ and the threshold $r^* = (N-2)L/(N-2L)$. Intriguingly, in this case, the threshold r^* is beyond the parameter range for cooperation dilemmas ($1 < r < L$). For $L \le r \le r^*$ where cooperation dilemmas are relieved, cooperation is still unfavoured owing to local interactions and strategy dispersal. Such a spatial structure thus leads to a more stringent condition for the success of cooperators with respect to well-mixed settings. We find, for a spatial structure that constrains the ranges for interaction and strategy

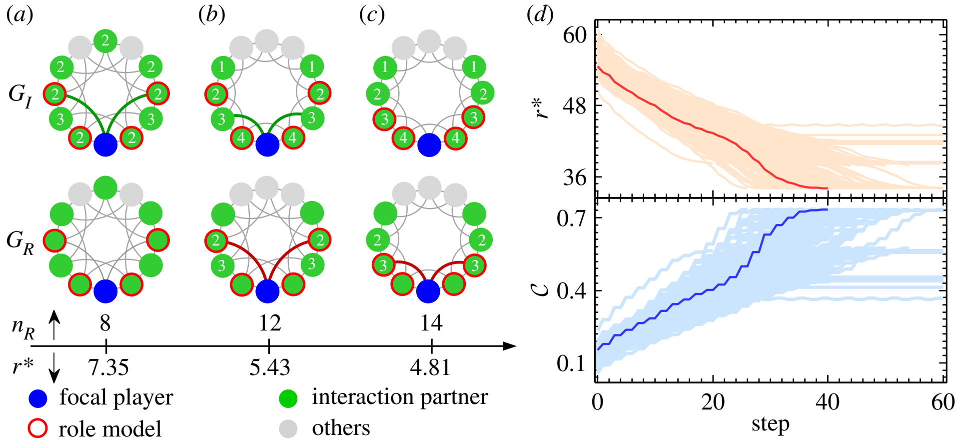

Figure 3. Enhancement of spatial reciprocity. (*a*–*c*) Three spatial structures. We present interaction partners (green filled nodes) and role models (red framed nodes) only for the focal player (blue filled node). The number inside each green node represents interaction times of an interaction partner with the focal player in each generation. The sum of interaction times with each role model (n_R) is the sum of numbers inside each red framed node. In terms of the focal player, (*a*,*b*) differ in interaction graph G_I (marked by green edges) and (*b*,*c*) differ in dispersal graph G_R (marked by red edges). From (*a*) to (*c*), n_R increases and r^* decreases, indicating the enhanced spatial reciprocity. (*d*) Evolving spatial structures based on edge rewiring. Concretely, interaction edges are rewired to players with more interactions (see green edges in G_Is in (*a*,*b*)); dispersal edges are rewired to players with more interactions (see red edges in G_Rs in (*b*,*c*)). Note that rewiring interaction edges probably changes the interaction time of the focal player with each other player (see G_Is in (*a*,*b*)). The algorithm runs in 1000 randomly generated and initially symmetric transitive graphs with $N = 400$ and $k_I = k_R = 50$. r^* and clustering coefficient $\mathcal{C}$ in different steps are separately shown in the upper and lower panels in (*d*). Bright red and blue lines illustrate a representative evolving process. (Online version in colour.)

dispersal, spatial reciprocity emerges only if interaction partners overlap role models (see appendix Ab for details).

(c) Enhancement of spatial reciprocity

Knowing when spatial reciprocity emerges, we now examine how different spatial structures lead to different levels of spatial reciprocity. The goal is to develop new ways of promoting cooperation by altering spatial structures.

We find that when two spatial structures differ only in their connections but have the same population size and node degrees, structure 1 generates a stronger spatial reciprocity than structure 2 if and only if

$$n_{R_1} > n_{R_2}, \tag{3.3}$$

where n_{R_1} (n_{R_2}) is the sum of times that a player interacts with each role model in structure 1 (structure 2). Figure 3*a*–*c* shows an example: more interactions with role models (n_R) result in the lowering threshold r^* for cooperation evolving. In particular, for any player, if interacting more times with player i than with j, this player using i as a role model is more beneficial to cooperation than using j (see G_Rs in figure 3*b*,*c*).

Based on equation (3.3), we develop an algorithm in which every player self-organizes its social ties to strengthen spatial reciprocity. This algorithm begins with a pair of symmetric interaction and dispersal graphs (for a feasibility proof, see the electronic supplementary material, S4):

(i) randomly choose a player i and record the interaction times of i with each interaction partner (see the number inside each green node in figure 3*a*);
(ii) for player j_1 (connected to i in the interaction graph) and j_2 (not connected to i in the interaction graph), if i interacts more times with j_2 than with j_1, i breaks its interaction edge with j_1 and builds an edge to j_2 (see green edges in G_Is in figure 3*a*,*b*). Otherwise, the algorithm terminates; and
(iii) player i rewires the dispersal edge from j_1 to j_2 (see red edges in G_Rs in figure 3*b*,*c*), and the algorithm returns to step (i).

To warrant a pair of joint transitive graphs, all players implement the same rewiring operation synchronously. Figure 3*d* shows that in most cases this algorithm significantly lowers the barrier for cooperators wining defection (see more examples in the electronic supplementary material, figure S4). Especially, when using this algorithm to alter interaction and strategy dispersal edges, players only rely on local information such as interaction partners, interaction times, and role models. To some extent, this algorithm conforms to the pattern of human interactions: individuals, even strangers, are likely to build their interpersonal relationship as frequent contacts, while even friends, may attenuate their relationship if contacting rarely. The promotive effects of this algorithm suggests that a simple principle can also elicit cooperation extensively and the high cognitive ability of individuals may be not necessary to establish a cooperative society. We also find the increasing clustering coefficient $\mathcal{C}$ (the density of structural clusters or triangle loops) [31] in the evolving structures. This indicates that structural clusters act as an effective promotor of the evolution of cooperation (see proof in the electronic supplementary material, S5).

4. Applications

(a) Asymmetric interaction and dispersal graphs

Our findings provide answers to a classic question [23]: how does breaking the symmetry between interaction and dispersal graphs affect the evolution of cooperation? We find that it depends on the interaction times between a player with its nearest and next nearest neighbours in the interaction graph. In two-player interactions, a player interacts with

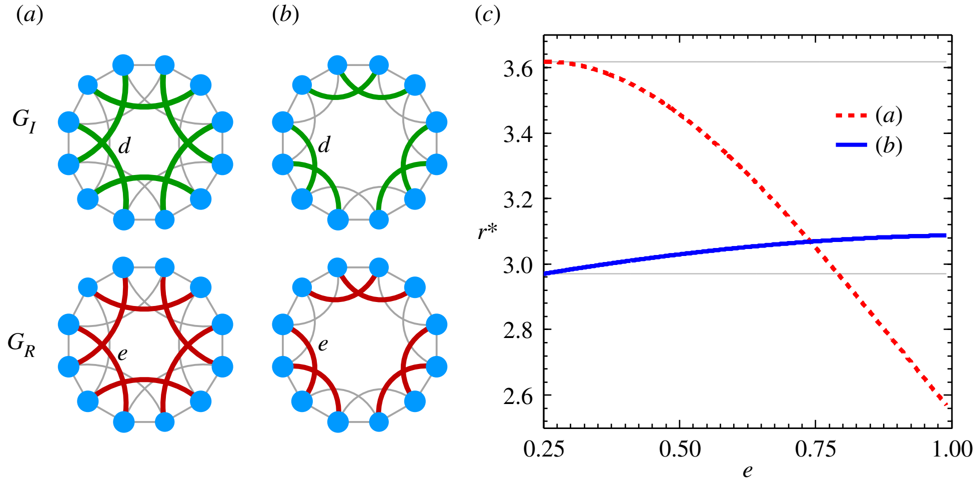

Figure 4. Promotive and inhibitive effects of strong social ties. (*a*) Spatial structure without structural clusters (triangle loops). (*b*) Spatial structure with structural clusters. Edge weights are *d* for green edges in G_I and *e* for red edges in G_R. Node degrees in both graphs are 4. (*c*) r^* as a function of *d* and *e*. We take $d = 0.3e + 0.175$ in case (*a*) and $d = 0.04e + 0.24$ in case (*b*). $w = 1/5$. When *e* increases from 0.25, *d* is greater than 0.25. Edges with $d > 0.25$ in G_I and $e > 0.25$ in G_R are termed strong social ties. In structures with no structural clusters, strong social ties always promote cooperation. In the presence of structural clusters, strong social ties might hinder cooperation. (Online version in colour.)

each nearest neighbour in the interaction graph once and has no interactions with others. All role models overlapping the nearest neighbours in the interaction graph, corresponding to symmetric interaction and dispersal graphs, generates the largest n_R. Breaking the symmetry decreases n_R and thus weakens spatial reciprocity (equation (3.3)), in line with previous studies based on pairwise games [23] and simplified multiplayer games where each player only interacts with their nearest neighbours [17]. However, this does not hold when interaction partners are not limited to the nearest neighbours in the interaction graph. In general multiplayer games, each player interacts with not only its nearest but also next nearest neighbours in the interaction graph. When interacting more times with a next nearest than with a nearest neighbour, the focal player rewiring the dispersal edge from the latter to the former increases n_R and strengthens the spatial reciprocity. Thus, asymmetric spatial structures for interaction and dispersal graphs could provide more advantages to cooperators (see symmetric structures in figure 3*a* and asymmetric structures in figure 3*b*). Our findings hold in both random PGGs and *l*-order PGGs.

(b) Heterogeneous social ties

We examine heterogeneous social ties, i.e. w, $\{d_{ij}\}_{i,j}$, and $\{e_{ij}\}_{i,j}$, by making their strength non-uniform. A sufficiently large w facilitates cooperation regardless of the choice of $\{d_{ij}\}_{i,j}$ and $\{e_{ij}\}_{i,j}$ (electronic supplementary material, S6 and figure S5). This is because cooperators receive more benefits from their investments for large w and defectors exploit less by free-riding behaviours, in agreement with a prior study that reducing the diffusion of public goods facilitates cooperation [34].

How do strong social ties affect spatial reciprocity? Here a strong tie refers to a pair of interaction and dispersal edges between two nodes, and weights of the two edges are larger than the average weight of all edges. We consider a baseline model where the interaction and dispersal graphs are identical and meanwhile weights of all edges are identical. In the baseline model, introducing a strong tie between individual *i* and *j* means that both weights of interaction and dispersal edges between *i* and *j* increase. If the introduction of strong ties reduces the threshold r^*, such strong ties facilitate cooperation. We find that in a spatial structure without structural clusters, regardless of the edge weights of strong ties, introducing strong ties always promotes cooperation (see an example in figure 4*a*,*c* and more details in the electronic supplementary material, S6 and figure S6). Actually, when there is no structural cluster, player *i* encounters *j* only in *i*- and *j*-centred games. Player *i* reciprocates *j* only in the two games. Strong social ties between them enhance their reciprocity and thus facilitate cooperation, but when structural clusters are introduced, in addition in *i*- and *j*-centred games, *i* encounters *j* in games centred on their common neighbours. That is, *i* reciprocates *j* in more games. Strong ties indeed increases reciprocity in self-centred games while possibly decreases reciprocity in games centred on common neighbours. Thus, theoretically, in some cases, strong ties have negative effects on the maintenance of cooperation. We illustrate a representative example in figure 4*b*,*c*: in the baseline model (without strong ties), players interact more times with the nearest neighbours than with the next nearest neighbours; building strong ties between players and their next nearest neighbours increases the barrier for the success of cooperation.

Finally, we investigate a few social networks, including small-world networks where individuals form structural clusters [31] and scale-free networks where individuals have different numbers of social ties [35] (electronic supplementary material, S7 and figures S7, S8). Our findings still hold qualitatively in these networks.

5. Discussion and conclusion

We have studied evolutionary game dynamics in a wide class of spatial structures and provided a unifying formula for predicting when altruistic behaviours are more successful than selfish behaviours. Assortment between individuals carrying cooperative genotypes or helping behaviours is the most fundamental requirement for the evolution of altruism [33]. We introduce 'assortment coefficient' θ which well quantifies the capacity of a spatial structure to assort strategies. A spatial structure with a large value of θ facilitates the assortment between cooperative individuals and the establishment of cooperator clusters [16–18,21], but a spatial structure with a small value of θ blends cooperative and defective players and puts cooperators at a disadvantage compared with their competitors. Recently, Tarnita *et al.* [19] demonstrated that the structure coefficient parameter σ can capture how population structures affect strategy selection and is applicable to any population structure. Despite their innovative insights, calculating the structure coefficient for evolutionary multiplayer games remains intricate, even in well-mixed settings [36]. It becomes more challenging in structured populations [17]. Unlike the structure coefficient, the value of assortment coefficient is accessible in many cases (equation (3.1)). In addition, when both θ and σ are used to described the same system, calculating θ also helps to learn σ.

We find that spatial structure promotes cooperation only when role models and interaction partners overlap. When they do not, the spatial structure inhibits cooperation with respect to well-mixed settings, even in the absence of social dilemmas. Thus, in some cases highly localized interactions and strategy dispersal can help to establish cooperation clusters, but in other cases it may destroy them, which was rarely observed in prior studies [16–18,21]. We also find that the strength of spatial reciprocity is positively correlated with the average interaction frequency of a player with an individual role model. These results suggest that choosing appropriate role models may be more beneficial to the evolution of cooperation than owning a number of role models. When each individual adjusts its social ties based on these simple rules, the evolving population structure shows stronger spatial reciprocity. Our work thus provides a new way of affecting contact networks and promoting the transition to cooperative societies [13].

Our findings provide new insights into many prior results. For example, based on two-player interactions Ohtsuki *et al.* [23] found that cooperation flourishes best when interaction and strategy dispersal graphs are symmetric. Breaking the symmetry between interaction and strategy dispersal graphs impedes the evolution of cooperation. This is not the case in many-player interactions. If players interact more frequently with the nearest than with the other neighbours, symmetry facilitates cooperation, in line with prior studies [17,23], but when players interact more frequently with the other neighbours, a pair of asymmetric interaction and strategy dispersal graphs could facilitate cooperation. In a seminal paper, Allen *et al.* [13,24] found that cooperation thrives most in societies with strong pairwise ties. This is the case in two-player interactions because strong social ties enhance strategy reciprocity between directly connected players [28,29]. When moving to collective interactions, two players encounter and reciprocate each other not only in games initiated by themselves but also in games organized by their common neighbours. Strong social ties indeed strengthen the former but possibly weaken the latter, which possibly makes cooperation harder to evolve. Our finding indicates that the transition from two-player to multiplayer interactions adds much complexity in studying evolutionary dynamics in structured populations.

We use joint transitive graphs to examine linear multiplayer games and check our results in a few complex networks. But we realize that real-world spatial structures are more complicated [37]. The link rewiring in graphed structures [38], the mutation of set memberships in set structures [39], and the variation in inheriting parent phenotypes [40] produce a dynamic population structure that affects strategy assortment. Besides, many realistic collective interactions are often nonlinear and pay-offs are not a linear function of the number of cooperative participants [36]. Investigating nonlinear interactions in any population structure is an enduring challenge, but it is key if we are to understand the collective behaviours present in complex systems [13]. Finally, we point out that the current work is based on theoretical assumptions and we thus expect proceeding experimental studies to these theoretical results.

Data accessibility. No data were collected in order to conduct the research presented in this manuscript.

Authors' contributions. Q.S., A.L. and L.W. designed the research. Q.S. performed analytical calculations and numerical simulations. All authors analysed the results. Q.S. and A.L. wrote the manuscript. L.W. and H.E.S. edited the manuscript.

Competing interests. The authors declare that they have no competing interests.

Funding. This work is supported by the National Natural Science Foundation of China (grant nos. 61751301 and 61533001). Q.S. acknowledges the support from China Scholarship Council (grant no. 201706010277). A.L. acknowledges the generous support from the Chair of Systems Design at ETH Zürich and HFSP postdoctoral fellowship (LT000696/2018-C). The Boston University Center for Polymer Studies is supported by the National Science Foundation (grant nos. PHY-1505000, CMMI-1125290 and CHE-1213217) and by the Defense Threat Reduction Agency (grant no. HDTRA1-14-1-0017).

Acknowledgements. We thank Benjamin Allen and Feng Fu for helpful discussions.

Appendix A

(a) Population structures

The interaction graph G_I and the dispersal graph G_R are joint transitive if for every pair of nodes $i, j \in V$, there is a permutation T of the node set such that $T(i) = j$ and in addition $d_{T(m)T(n)} = d_{mn}$, $e_{T(m)T(n)} = e_{mn}$ for every pair of m, n [14,20,24]. G_I is unweighted when $d_{ij} = 1/k_I$ for $j \in N_I^i$, where k_I is the node degree and N_I^i is the set of i's neighbouring nodes in G_I. An analogous definition can be applied to the unweighted dispersal graph. The setting of an unweighted graph here is essentially in line with the conventional setting where an edge either exists or not and has no edge weight. In our framework, endowing each existing edge with an identical weight $1/k_I$ does not change the evolutionary outcome. We can recover the classical population structure as a special case by employing identical and unweighted G_I and G_R.

(b) Emergence of spatial reciprocity

In a pair of large joint transitive graphs, compared with the well-mixed setting, a spatial structure promotes cooperation if and only if there is overlap between interaction partners and role models. The minimum population size for this rule is $N^* = 2 + k_I(k_I + 1)k_R$ in conventional PGGs and $N^* = 2 + L(L - 1)k_R$ in l-order PGGs. In random PGGs, the minimum population size is $N^* = 2 + k_I k_R$ for $L = 2$ and $N^* = 2 + k_I(k_I - 1)k_R L/(L - 2)$ for $L > 2$. If none of the interaction partners overlaps role models, irrespective of the population size, the spatial structure inhibits cooperation compared with the well-mixed setting.

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