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Supplementary Information for

Evolution of cooperation with asymmetric social interactions

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Supporting Information Text

The Supplementary Information is structured as follows. In Section 1, we describe the model of evolutionary dynamics with general asymmetric interactions. In Section 2, we derive an analytical condition for one strategy to be favored over the other. A further analysis gives the mathematical formula for the critical benefit-to-cost ratio for cooperation to be favored by selection. In Section 3, we introduce three network motifs in directed networks, which are shown to correlate with evolutionary outcomes. In Section 4, we provide a description of empirical networks and analyses of evolutionary dynamics on these networks..

1. Model

The population structure is described by a directed network with N nodes (labelled by $\mathcal{N} = \{1, 2, \cdots, N\}$) and directed edges w_{ij}, where $w_{ij} > 0$ means a directed edge from source node i to target node j. To ensure absorption of one type of strategy or another, the directed network is required to be strongly-connected. That is, for all pairs of $i, j \in \mathcal{N}$, there is a path from i to j. The payoff structure for the interaction in directed edge w_{ij} is

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a_1, a_2 & b_1, b_2 \\ c_1, c_2 & d_1, d_2 \end{pmatrix} \end{array}. \qquad [1]$$

The entry (X, Y) in the payoff matrix means that when the player at the source node (i.e. i) uses the strategy in the row and the player in the target node (i.e. j) uses the strategy in the column, the former obtains payoff X and the later obtains payoff Y. Let s_i denote player i's strategy ($s_i = 1$ means A-strategy and $s_i = 0$ means B-strategy). The accumulated payoff for player i is

$$\begin{aligned} \pi_i = &\sum_j w_{ij} \left[a_1 s_i s_j + b_1 s_i (1 - s_j) + c_1 (1 - s_i) s_j + d_1 (1 - s_i)(1 - s_j) \right] \\ &+ \sum_j w_{ji} \left[a_2 s_i s_j + b_2 (1 - s_i) s_j + c_2 s_i (1 - s_j) + d_2 (1 - s_i)(1 - s_j) \right], \end{aligned} \qquad [2]$$

which is then transformed to a reproductive rate by $F_i = 1 + \delta \pi_i$. At the end of each generation, a random player i is selected to "die" uniformly. Then all players that occupy source nodes of i's incoming edges complete to reproduce an offspring and replace the vacancy at i, with probability proportional to their reproductive rate. Therefore, player j successfully sends an "offspring" to i with probability

$$e_{j \to i} = \frac{1}{N} \frac{w_{ji} F_j}{\sum_{\ell \in \mathcal{N}} w_{\ell i} F_\ell}. \qquad [3]$$

The process described above corresponds to the 'downstream' dispersal in the main text. The equations for 'upstream' dispersal can be easily modified from the 'downstream' case.

2. Methods

A. Analysis for random regular networks. We begin with a partly directional and unweighted random regular network, in which each node has $k^{(I)}$ incoming edges, $k^{(O)}$ outgoing edges, and $k^{(U)}$ bi-directional edges. We have $k^{(I)} = k^{(O)}$ and node degree $k = k^{(I)} + k^{(O)} + k^{(U)}$. Let p_A (resp. p_B) denote the frequency of A-players (resp. B-players). Each player therefore has three types of neighbors, namely incoming neighbors (I, source nodes of incoming edges), outgoing neighbors (O, target nodes of outgoing edges), and bi-directed neighbors (U, neighboring nodes of bi-directed edges). Let $p_{XY}^{(I)}$ denote the frequency of incoming edges $X \leftarrow Y$ (taking the first subscript as the focal player); $p_{XY}^{(O)}$ the frequency of outgoing edges $X \rightarrow Y$; $p_{XY}^{(U)}$ the frequency of bi-directed edges $X \leftrightarrow Y$. Let $q_{Y|X}^{(I)}$ denote the probability that given the focal player is an X-player, the incoming neighbor is a Y-player; $q_{Y|X}^{(O)}$ the probability that given the focal player is an X-player, the outgoing neighbor is a Y-player; $q_{Y|X}^{(U)}$ the probability that given the focal player is an X-player, the bi-directed neighbor is a Y-player. We have the following identities

$$p_A + p_B = 1, \tag{4a}$$

$$p_{AB}^{(Z)} = p_{BA}^{(Z)}, \tag{4b}$$

$$q_{X|Y}^{(Z)} = \frac{p_{XY}^{(Z)}}{p_Y}, \tag{4c}$$

$$q_{A|Y}^{(Z)} + q_{B|Y}^{(Z)} = 1, \tag{4d}$$

where $X, Y \in \{A, B\}$ and $Z \in \{I, O, U\}$. Furthermore, we have

$$p_{AA}^{(I)} = p_A q_{A|A}^{(I)} = p_{AA}^{(O)} = p_A q_{A|A}^{(O)}, \tag{5}$$

which gives $q_{A|A}^{(I)} = q_{A|A}^{(O)}$ and

$$p_{AB}^{(I)} = p_A q_{B|A}^{(I)} = p_A \left(1 - q_{A|A}^{(I)}\right) = p_A \left(1 - q_{A|A}^{(O)}\right) = p_A q_{B|A}^{(O)} = p_{AB}^{(O)} = p_{BA}^{(O)}. \tag{6}$$

Overall, the whole system can be described by three variables, i.e. p_A, $q_{A|A}^{(I)}$, and $q_{A|A}^{(U)}$.

A.1. Updating a B-player. We first investigate the case where a B-player is replaced by a neighboring A-player. Let $k_A^{(Z)}$ and $k_B^{(Z)}$ denote the numbers of A- and B-players among three types of neighbors, $Z \in \{I, O, U\}$. We have $k_A^{(Z)} + k_B^{(Z)} = k^{(Z)}$ and $\sum_{Z \in \{I,O,U\}} \left(k_A^{(Z)} + k_B^{(Z)}\right) = k$. Such a neighborhood configuration occurs with probability

$$\mathcal{B}\left(k_A^{(I)}, k_A^{(O)}, k_A^{(U)}\right) = \prod_{Z \in \{I,O,U\}} \binom{k^{(Z)}}{k_A^{(Z)}} \left(q_{A|B}^{(Z)}\right)^{k_A^{(Z)}} \left(q_{B|B}^{(Z)}\right)^{k_B^{(Z)}}. \tag{7}$$

We introduce two quantities

$$\begin{aligned} \pi_A &= \left(k^{(I)} q_{A|A}^{(I)} + k^{(U)} q_{A|A}^{(U)}\right)(a_1 + a_2) + \left(k^{(I)} q_{B|A}^{(I)} + k^{(U)} q_{B|A}^{(U)}\right)(b_1 + c_2), \\ \pi_B &= \left(k^{(I)} q_{A|B}^{(I)} + k^{(U)} q_{A|B}^{(U)}\right)(c_1 + b_2) + \left(k^{(I)} q_{B|B}^{(I)} + k^{(U)} q_{B|B}^{(U)}\right)(d_1 + d_2). \end{aligned} \tag{8}$$

The average fitness of each A- and B-player neighbor of type Z is

$$F_{A|B}^{(Z)} = 1 + \delta \pi_{A|B}^{(Z)}, \tag{9a}$$

$$F_{B|B}^{(Z)} = 1 + \delta \pi_{B|B}^{(Z)}, \tag{9b}$$

where

$$\pi_{A|B}^{(I)} = \pi_A - q_{A|A}^{(O)} a_1 - q_{B|A}^{(O)} b_1 + b_1, \tag{10a}$$

$$\pi_{B|B}^{(I)} = \pi_B - q_{A|B}^{(O)} c_1 - q_{B|B}^{(O)} d_1 + d_1, \tag{10b}$$

$$\pi_{A|B}^{(U)} = \pi_A - q_{A|A}^{(U)}(a_1 + a_2) - q_{B|A}^{(U)}(b_1 + c_2) + b_1 + c_2, \tag{10c}$$

$$\pi_{B|B}^{(U)} = \pi_B - q_{A|B}^{(U)}(c_1 + b_2) - q_{B|B}^{(U)}(d_1 + d_2) + d_1 + d_2. \tag{10d}$$

Under such a neighborhood configuration, the probability that an A-player takes over the empty site is

$$\frac{k_A^{(I)} F_{A|B}^{(I)} + k_A^{(U)} F_{A|B}^{(U)}}{k_A^{(I)} F_{A|B}^{(I)} + k_B^{(I)} F_{B|B}^{(I)} + k_A^{(U)} F_{A|B}^{(U)} + k_B^{(U)} F_{B|B}^{(U)}}. \tag{11}$$

Therefore, p_A increases by $1/N$ with probability

$$\text{Prob}\left(\Delta p_A = \frac{1}{N}\right) = p_B \sum_{k_A^{(I)},k_A^{(O)},k_A^{(U)}} \mathcal{B}\left(k_A^{(I)},k_A^{(O)},k_A^{(U)}\right) \frac{k_A^{(I)}F_{A|B}^{(I)} + k_A^{(U)}F_{A|B}^{(U)}}{k_A^{(I)}F_{A|B}^{(I)} + k_B^{(I)}F_{B|B}^{(I)} + k_A^{(U)}F_{A|B}^{(U)} + k_B^{(U)}F_{B|B}^{(U)}}.$$

The number of incoming edge $A \leftarrow A$ increases by $k_A^{(I)} + k_A^{(O)}$. Therefore $p_{AA}^{(I)}$ increases by $\left(k_A^{(I)} + k_A^{(O)}\right)/\left(k^{(I)}N\right)$ with probability

$$\text{Prob}\left(\Delta p_{AA}^{(I)} = \frac{k_A^{(I)} + k_A^{(O)}}{k^{(I)}N}\right) = p_B \mathcal{B}\left(k_A^{(I)},k_A^{(O)},k_A^{(U)}\right) \frac{k_A^{(I)}F_{A|B}^{(I)} + k_A^{(U)}F_{A|B}^{(U)}}{k_A^{(I)}F_{A|B}^{(I)} + k_B^{(I)}F_{B|B}^{(I)} + k_A^{(U)}F_{A|B}^{(U)} + k_B^{(U)}F_{B|B}^{(U)}}.$$

The number of bidirected edge $A \leftrightarrow A$ increases by $k_A^{(U)}$. Therefore $p_{AA}^{(U)}$ increases by $2k_A^{(U)}/\left(k^{(U)}N\right)$ with probability

$$\text{Prob}\left(\Delta p_{AA}^{(U)} = \frac{2k_A^{(U)}}{k^{(U)}N}\right) = p_B \mathcal{B}\left(k_A^{(I)},k_A^{(O)},k_A^{(U)}\right) \frac{k_A^{(I)}F_{A|B}^{(I)} + k_A^{(U)}F_{A|B}^{(U)}}{k_A^{(I)}F_{A|B}^{(I)} + k_B^{(I)}F_{B|B}^{(I)} + k_A^{(U)}F_{A|B}^{(U)} + k_B^{(U)}F_{B|B}^{(U)}}.$$

A.2. Updating an A-player. We then investigate the case where an A-player is replaced by a neighboring B-player. Let $k_A^{(Z)}$ and $k_B^{(Z)}$ denote the numbers of A- and B-players among the three types of neighbors, $Z \in \{I,O,U\}$. Such a neighborhood configuration occurs with probability

$$\mathcal{A}\left(k_A^{(I)},k_A^{(O)},k_A^{(U)}\right) = \prod_{Z\in\{I,O,U\}} \binom{k^{(Z)}}{k_A^{(Z)}} \left(q_{A|A}^{(Z)}\right)^{k_A^{(Z)}} \left(q_{B|A}^{(Z)}\right)^{k_B^{(Z)}}. \qquad [12]$$

The average fitness of each A- and B-player is given by

$$F_{A|A}^{(Z)} = 1 + \delta\pi_{A|A}^{(Z)}, \qquad [13a]$$

$$F_{B|A}^{(Z)} = 1 + \delta\pi_{B|A}^{(Z)}, \qquad [13b]$$

where

$$\pi_{A|A}^{(I)} = \pi_A - q_{A|A}^{(O)}a_1 - q_{B|A}^{(O)}b_1 + a_1, \qquad [14a]$$

$$\pi_{B|A}^{(I)} = \pi_B - q_{A|B}^{(O)}c_1 - q_{B|B}^{(O)}d_1 + c_1, \qquad [14b]$$

$$\pi_{A|A}^{(U)} = \pi_A - q_{A|A}^{(U)}(a_1+a_2) - q_{B|A}^{(U)}(b_1+c_2) + a_1 + a_2, \qquad [14c]$$

$$\pi_{B|A}^{(U)} = \pi_B - q_{A|B}^{(U)}(c_1+b_2) - q_{B|B}^{(U)}(d_1+d_2) + c_1 + b_2. \qquad [14d]$$

Under such a neighborhood configuration, the probability that an A-player takes over the empty site is

$$\frac{k_B^{(I)}F_{B|A}^{(I)} + k_B^{(U)}F_{B|A}^{(U)}}{k_A^{(I)}F_{A|A}^{(I)} + k_B^{(I)}F_{B|A}^{(I)} + k_A^{(U)}F_{A|A}^{(U)} + k_B^{(U)}F_{B|A}^{(U)}}. \qquad [15]$$

Therefore, p_A decreases by $1/N$ with probability

$$\text{Prob}\left(\Delta p_A = -\frac{1}{N}\right) = p_A \sum_{k_A^{(I)},k_A^{(O)},k_A^{(U)}} \mathcal{A}\left(k_A^{(I)},k_A^{(O)},k_A^{(U)}\right) \frac{k_B^{(I)}F_{B|A}^{(I)} + k_B^{(U)}F_{B|A}^{(U)}}{k_A^{(I)}F_{A|A}^{(I)} + k_B^{(I)}F_{B|A}^{(I)} + k_A^{(U)}F_{A|A}^{(U)} + k_B^{(U)}F_{B|A}^{(U)}}.$$

The number of incoming edge $A \leftarrow A$ decreases by $k_A^{(I)} + k_A^{(O)}$. Therefore $p_{AA}^{(I)}$ decreases by $\left(k_A^{(I)} + k_A^{(O)}\right)/\left(k^{(I)}N\right)$ with probability

$$\text{Prob}\left(\Delta p_{AA}^{(I)} = -\frac{k_A^{(I)} + k_A^{(O)}}{k^{(I)}N}\right) = p_A \mathcal{A}\left(k_A^{(I)},k_A^{(O)},k_A^{(U)}\right) \frac{k_B^{(I)}F_{B|A}^{(I)} + k_B^{(U)}F_{B|A}^{(U)}}{k_A^{(I)}F_{A|A}^{(I)} + k_B^{(I)}F_{B|A}^{(I)} + k_A^{(U)}F_{A|A}^{(U)} + k_B^{(U)}F_{B|A}^{(U)}}.$$

The number of bidirected edge $A \leftrightarrow A$ decreases by $k_A^{(U)}$. Therefore $p_{AA}^{(U)}$ decreases by $2k_A^{(U)}/\left(k^{(U)}N\right)$ with probability

$$\text{Prob}\left(\Delta p_{AA}^{(U)} = -\frac{2k_A^{(U)}}{k^{(U)}N}\right) = p_A \mathcal{A}\left(k_A^{(I)},k_A^{(O)},k_A^{(U)}\right) \frac{k_B^{(I)}F_{B|A}^{(I)} + k_B^{(U)}F_{B|A}^{(U)}}{k_A^{(I)}F_{A|A}^{(I)} + k_B^{(I)}F_{B|A}^{(I)} + k_A^{(U)}F_{A|A}^{(U)} + k_B^{(U)}F_{B|A}^{(U)}}.$$

A.3. Separation of time scales. Assuming that one replacement event happens in one unit of time, we have the derivatives of p_A, $p_{AA}^{(I)}$, and $p_{AA}^{(U)}$, given by

$$
\begin{aligned}
\dot{p}_A =& \frac{1}{N} \cdot \mathrm{Prob}\left(\Delta p_A = \frac{1}{N}\right) + \left(-\frac{1}{N}\right) \cdot \mathrm{Prob}\left(\Delta p_A = -\frac{1}{N}\right) \\
=& \frac{\delta}{N\left(k^{(I)}+k^{(U)}\right)^2} \left[p_B \begin{pmatrix} k^{(I)}(k^{(I)}-1) q_{A|B}^{(I)} q_{B|B}^{(I)} \left(\pi_{A|B}^{(I)} - \pi_{B|B}^{(I)}\right) \\ + k^{(I)} k^{(U)} q_{A|B}^{(I)} q_{B|B}^{(U)} \left(\pi_{A|B}^{(I)} - \pi_{B|B}^{(U)}\right) \\ + k^{(I)} k^{(U)} q_{A|B}^{(U)} q_{B|B}^{(I)} \left(\pi_{A|B}^{(U)} - \pi_{B|B}^{(I)}\right) \\ k^{(U)}(k^{(U)}-1) q_{A|B}^{(U)} q_{B|B}^{(U)} \left(\pi_{A|B}^{(U)} - \pi_{B|B}^{(U)}\right) \end{pmatrix} - p_A \begin{pmatrix} k^{(I)}(k^{(I)}-1) q_{B|A}^{(I)} q_{A|A}^{(I)} \left(\pi_{B|A}^{(I)} - \pi_{A|A}^{(I)}\right) \\ + k^{(I)} k^{(U)} q_{B|A}^{(I)} q_{A|A}^{(U)} \left(\pi_{B|A}^{(I)} - \pi_{A|A}^{(U)}\right) \\ + k^{(I)} k^{(U)} q_{B|A}^{(U)} q_{A|A}^{(I)} \left(\pi_{B|A}^{(U)} - \pi_{A|A}^{(I)}\right) \\ k^{(U)}(k^{(U)}-1) q_{B|A}^{(U)} q_{A|A}^{(U)} \left(\pi_{B|A}^{(U)} - \pi_{A|A}^{(U)}\right) \end{pmatrix} \right] + O(\delta^2),
\end{aligned}
\qquad [16]
$$

$$
\begin{aligned}
\dot{p}_{AA}^{(I)} =& \sum_{k_A^{(I)}, k_A^{(O)}, k_A^{(U)}} \frac{k_A^{(I)} + k_A^{(O)}}{k^{(I)} N} \mathrm{Prob}\left(\Delta p_{AA}^{(I)} = \frac{k_A^{(I)} + k_A^{(O)}}{k^{(I)} N}\right) \\
&+ \sum_{k_A^{(I)}, k_A^{(O)}, k_A^{(U)}} \left(-\frac{k_A^{(I)} + k_A^{(O)}}{k^{(I)} N}\right) \mathrm{Prob}\left(\Delta p_{AA}^{(I)} = -\frac{k_A^{(I)} + k_A^{(O)}}{k^{(I)} N}\right) \\
=& \frac{1}{N\left(k^{(I)}+k^{(U)}\right)} \left\{ \left[\left(2k^{(I)}-1\right) \left(q_{A|B}^{(I)} - q_{A|A}^{(I)}\right) + 1 \right] p_{AB}^{(I)} + 2k^{(U)} \left(q_{A|B}^{(I)} - q_{A|A}^{(I)}\right) p_{AB}^{(U)} \right\} + O(\delta),
\end{aligned}
\qquad [17]
$$

and

$$
\begin{aligned}
\dot{p}_{AA}^{(U)} =& \sum_{k_A^{(I)}, k_A^{(O)}, k_A^{(U)}} \frac{2k_A^{(U)}}{k^{(U)} N} \mathrm{Prob}\left(\Delta p_{AA}^{(I)} = \frac{k_A^{(I)} + k_A^{(O)}}{k^{(I)} N}\right) \\
&+ \sum_{k_A^{(I)}, k_A^{(O)}, k_A^{(U)}} \left(-\frac{2k_A^{(I)}}{k^{(U)} N}\right) \mathrm{Prob}\left(\Delta p_{AA}^{(I)} = -\frac{k_A^{(I)} + k_A^{(O)}}{k^{(I)} N}\right) \\
=& \frac{2}{N\left(k^{(I)}+k^{(U)}\right)} \left\{ \left[\left(k^{(U)}-1\right) \left(q_{A|B}^{(U)} - q_{A|A}^{(U)}\right) + 1 \right] p_{AB}^{(U)} + k^{(I)} \left(q_{A|B}^{(U)} - q_{A|A}^{(U)}\right) p_{AB}^{(I)} \right\} + O(\delta).
\end{aligned}
\qquad [18]
$$

Analyzing Eqs. (16-18), for sufficiently small selection strength δ, $p_{AA}^{(I)}$ and $p_{AA}^{(U)}$ reaches the equilibrium much faster than p_A. The equilibrium can be obtained by solving

$$
\left[\left(2k^{(I)}-1\right) \left(q_{A|B}^{(I)} - q_{A|A}^{(I)}\right) + 1 \right] p_{AB}^{(I)} + 2k^{(U)} \left(q_{A|B}^{(I)} - q_{A|A}^{(I)}\right) p_{AB}^{(U)} = 0, \qquad [19a]
$$

$$
\left[\left(k^{(U)}-1\right) \left(q_{A|B}^{(U)} - q_{A|A}^{(U)}\right) + 1 \right] p_{AB}^{(U)} + k^{(I)} \left(q_{A|B}^{(U)} - q_{A|A}^{(U)}\right) p_{AB}^{(I)} = 0. \qquad [19b]
$$

Let $x = q_{A|A}^{(I)} - q_{A|B}^{(I)}$ and $y = q_{A|A}^{(U)} - q_{A|B}^{(U)}$, using $q_{A|B}^{(Z)} - q_{A|A}^{(Z)} = \left(p_A - q_{A|A}^{(Z)}\right) / (1 - p_A)$, we have

$$
q_{A|A}^{(I)} = (1-x) p_A + x, \qquad [20a]
$$

$$
q_{A|A}^{(U)} = (1-y) p_A + y. \qquad [20b]
$$

In the case of $k^{(I)} = 0$, from Eq. (19b), we easily get

$$
x = 0, \quad y = \frac{1}{k-1}, \qquad [21]
$$

in agreement with prior work in the strictly bi-directional setting (1). For $k^{(U)} = 0$, we have

$$
x = \frac{1}{k-1}, \quad y = 0. \qquad [22]
$$

In the following, we focus on the case with $k^{(I)} \geq 1, k^{(U)} \geq 1$. Moving the second terms in Eqs. (19a,19b) to the right side and multiplying the two equations, we have

$$
y = \frac{-(2k^{(I)}-1)x + 1}{(2k^{(I)} + k^{(U)} - 1)x + k^{(U)} - 1}. \qquad [23]
$$

Substituting $p_{AB}^{(I)} = p_A \left(1 - q_{A|A}^{(I)}\right)$ and $p_{AB}^{(U)} = p_A \left(1 - q_{A|A}^{(U)}\right)$ into Eqs. (19a,19b), and using Eqs. (20,23), we have

$$
ax^3 + bx^2 + cx + d = 0, \qquad [24]
$$

where

$$
\begin{aligned}
a =& 4\left(k^{(I)}\right)^2 + 2k^{(I)}k^{(U)} - 4k^{(I)} - k^{(U)} + 1, && [25a]\\
b =& -4\left(k^{(I)}\right)^2 - 8k^{(I)}k^{(U)} - 2\left(k^{(U)}\right)^2 + 3k^{(U)} + 1, && [25b]\\
c =& -2k^{(I)}k^{(U)} + 4k^{(I)} - 2\left(k^{(U)}\right)^2 + 5k^{(U)} - 1, && [25c]\\
d =& k^{(U)} - 1. && [25d]
\end{aligned}
$$

According to Eqs. (19a,19b), the solution of Eq. (24), x^*, must satisfy $-1 < x^* < 1$ and $-1 < y(x^*) < 1$, which gives $-\left(k^{(U)} - 2\right) / \left(4k^{(I)} + k^{(U)} - 2\right) < x^* < 1$. Defining $G(x) = ax^3 + bx^2 + cx + d$, with $a > 0$, we have

$$
G(-\infty) < 0, \qquad G\left(-\frac{k^{(U)} - 2}{4k^{(I)} + k^{(U)} - 2}\right) > 0, \qquad G(1) < 0, \qquad G(\infty) > 0. \qquad [26]
$$

Therefore, Eq. (24) has and has only one solution in the interval $(-\left(k^{(U)} - 2\right) / \left(4k^{(I)} + k^{(U)} - 2\right), 1)$. The other two respectively lie in $(-\infty, -\left(k^{(U)} - 2\right) / \left(4k^{(I)} + k^{(U)} - 2\right))$ and $(1, \infty)$.

Defining quantities $m = (3ac - b^2)/(3a^2)$ and $n = (2b^3 - 9abc + 27a^2d)/(27a^3)$, the three roots of Eq. (24) are described by

$$
x_i^* = -\frac{b}{3a} + 2\sqrt{-\frac{m}{3}}\cos\left(\frac{1}{3}\arccos\left(\frac{3n}{2m}\sqrt{-\frac{3}{m}}\right) - i\frac{2\pi}{3}\right), \qquad [27]
$$

for $i = 0, 1, 2$. Since $x_0^* > x_1^* > x_2^*$, the solution for Eqs. (19a,19b) is x_1^*. Eq. (27) tells that x_1^* only depends on the structure properties $k^{(I)}$ and $k^{(U)}$, while is independent of p_A. Then y is obtained by substituting x_1^* into Eq. (23). For simplicity, we still use x to denote x_1^*.

A.4. Diffusion process. After obtaining x and y, besides Eq. (20), we have

$$
\begin{aligned}
&q_{B|A}^{(I)} = (1-x)(1-p_A), \quad q_{A|B}^{(I)} = (1-x)p_A, \quad q_{B|B}^{(I)} = 1-(1-x)p_A,\\
&q_{B|A}^{(U)} = (1-y)(1-p_A), \quad q_{A|B}^{(U)} = (1-y)p_A, \quad q_{B|B}^{(U)} = 1-(1-y)p_A.
\end{aligned} \qquad [28]
$$

Substituting Eqs. (20,28) into Eq. (16) gives

$$
\begin{aligned}
\mathrm{E}(p_A) &= \frac{\delta}{N\left(k^{(I)} + k^{(U)}\right)^2} p_A(1-p_A)\left(\alpha p_A + \beta\right) \quad (\equiv \delta m p_A(1-p_A)\left(\alpha p_A + \beta\right)), && [29a]\\
\mathrm{Var}(p_A) &= \frac{2}{N^2\left(k^{(I)} + k^{(U)}\right)} p_A(1-p_A)\lambda \quad (\equiv n p_A(1-p_A)), && [29b]
\end{aligned}
$$

where

$$
\begin{aligned}
\alpha =& \left[\lambda\gamma - (1-x)\mu - (1-y)\nu\right](a_1 - b_1 - c_1 + d_1)\\
&+ \left[\lambda\gamma - (1-y)\nu\right](a_2 - b_2 - c_2 + d_2), && [30a]\\
\beta =& \left[\left(k^{(I)}x + k^{(U)}y\right)\gamma - \mu x - \nu y\right]a_1 + (\lambda\gamma + \mu x + \nu y)b_1 - (\mu + \nu)c_1\\
&- (k^{(I)} + k^{(U)} - 1)(\gamma + \lambda)d_1 + \left[\left(k^{(I)}x + k^{(U)}y\right)\gamma - \nu y\right]a_2\\
&- \nu b_2 + (\lambda\gamma + \nu y)c_2 - \left[\left(k^{(I)} + k^{(U)}\right)\gamma - \nu\right]d_2, && [30b]\\
\gamma =& k^{(I)}\left(k^{(I)} - 1\right)(1-x^2) + k^{(U)}\left(k^{(U)} - 1\right)(1-y^2) + 2k^{(I)}k^{(U)}(1-xy), && [30c]\\
\lambda =& k^{(I)}(1-x) + k^{(U)}(1-y), && [30d]\\
\mu =& k^{(I)}(1-x)\left(k^{(I)}x + k^{(U)}y - x\right), && [30e]\\
\nu =& k^{(U)}(1-y)\left(k^{(I)}x + k^{(U)}y - y\right). && [30f]
\end{aligned}
$$

Introducing

$$
\psi(v) = \exp\left(-\int^v \frac{2\mathrm{E}(r)}{\mathrm{Var}(r)}dr\right), \qquad [31]
$$

we have the fixation probability $\rho_A(u)$, the probability that a proportion u of A-players take over the whole population, given by

$$
\rho_A(u) = \frac{\int_0^u \psi(y)dy}{\int_0^1 \psi(y)dy} = u + \frac{\delta m}{3n}u(1-u)\left[\alpha u + (\alpha + 3\beta)\right]. \qquad [32]
$$

A.5. Fixation probability. Selection favors A-strategy relative to the neutral drift if $\rho_A(1/N) > 1/N$. For sufficiently large N, the condition is $\alpha + 3\beta > 0$. Selection favors A-strategy over B-strategy if $\rho_A(1/N) > \rho_B(1/N)$, the fixation probability of B-players. Using $\rho_B(1/N) = 1 - \rho_A(1 - 1/N)$, we have

$$\rho_A(1/N) - \rho_B(1/N) = \frac{\delta m(N-1)}{nN^2}(\alpha + 2\beta). \tag{33}$$

For sufficiently large N, the condition for $\rho_A(1/N) > \rho_B(1/N)$ is reduced to $\alpha + 2\beta > 0$, or

$$\begin{aligned} &\left[\bar{\lambda}\gamma - (1+x)\mu - (1+y)\nu\right] a_1 + [\lambda\gamma + (1+x)\mu + (1+y)\nu]\, b_1 \\ &- [\lambda\gamma + (1+x)\mu + (1+y)\nu]\, c_1 - \left[\bar{\lambda}\gamma - (1+x)\mu - (1+y)\nu\right] d_1 \\ &+ \left[\bar{\lambda}\gamma - (1+y)\nu\right] a_2 - [\lambda\gamma + (1+y)\nu]\, b_2 \\ &+ [\lambda\gamma + (1+y)\nu]\, c_2 - \left[\bar{\lambda}\gamma - (1+y)\nu\right] d_2 > 0, \end{aligned} \tag{34}$$

where

$$\bar{\lambda} = k^{(I)}(1+x) + k^{(U)}(1+y). \tag{35}$$

For payoff structure

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a_1, a_2 & b_1, b_2 \\ c_1, c_2 & d_1, d_2 \end{pmatrix} \end{array} \to \begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} -c, b & -c, b \\ 0, 0 & 0, 0 \end{pmatrix} \end{array}, \tag{36}$$

the directions of donating action and strategy dispersal are identical, corresponding to the downstream case. We have

$$\rho_A > \rho_B \leftrightarrow \frac{b}{c} > \frac{\left(k^{(I)} + k^{(U)}\right)\gamma}{\left(k^{(I)}x + k^{(U)}y\right)\gamma - (1+y)\nu}, \tag{37}$$

where x is obtained from Eq. (27), y from Eq. (23), γ and ν from Eqs. (30c, 30f). The term in the right side of Eq. (37) is the critical benefit-to-cost ratio for selection favoring A-strategy over B-strategy, denoted by $(b/c)^*$. In particular, for strictly uni-directional network, with $k^{(U)} = 0$ and $k^{(I)} = k/2$, we have

$$\left(\frac{b}{c}\right)^* = k - 1. \tag{38}$$

Equation (33) can be rewritten to be

$$\rho_A(1/N) - \rho_B(1/N) = \frac{\delta(N-1)\left[\left(k^{(I)}x + k^{(U)}y\right)\gamma - (1+y)\nu\right]}{N\lambda\left(k^{(I)} + k^{(U)}\right)}\left(b - \left(\frac{b}{c}\right)^* c\right). \tag{39}$$

For payoff structure

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a_1, a_2 & b_1, b_2 \\ c_1, c_2 & d_1, d_2 \end{pmatrix} \end{array} \to \begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} b, -c & 0, 0 \\ b, -c & 0, 0 \end{pmatrix} \end{array}, \tag{40}$$

the directions of donating action and strategy dispersal are opposite, corresponding to the upstream case. We have

$$\rho_A > \rho_B \leftrightarrow \frac{b}{c} > \frac{\left(k^{(I)} + k^{(U)}\right)\gamma}{\left(k^{(I)}x + k^{(U)}y\right)\gamma - (1+x)\mu - (1+y)\nu}. \tag{41}$$

For strictly uni-directional network, we have

$$\left(\frac{b}{c}\right)^* > \frac{k(k-1)}{k-2}. \tag{42}$$

A.6. Case of $k \gg 1$. Let p denote the fraction of uni-directional edges and therefore $1-p$ the fraction of bi-directional edges. We have $k^{(I)} = k^{(O)} = kp/2$ and $k^{(U)} = k(1-p)$. Defining $\widetilde{x} = kx$ and substituting these into Eq. (24), we have

$$\widetilde{a}\widetilde{x}^3 + \widetilde{b}\widetilde{x}^2 + \widetilde{c}\widetilde{x} + \widetilde{d} = 0, \tag{43}$$

where

$$\widetilde{a} = pk^2 - (1+p)k + 1, \tag{44a}$$

$$\widetilde{b} = (p^2 - 2)k^3 + 3(1-p)k^2 + k, \tag{44b}$$

$$\widetilde{c} = (-p^2 + 3p - 2)k^4 + (5 - 3p)k^3 - k^2, \tag{44c}$$

$$\widetilde{d} = (1-p)k^4 - k^3. \tag{44d}$$

For $k \gg 1$, a solution for Eq. (43) is

$$\widetilde{x}^* = \frac{1}{2-p}, \tag{45}$$

which further gives the root for Eqs. (19a,19b)

$$x^* = \frac{1}{(2-p)k}. \tag{46}$$

Substituting $x = 1/((2-p)k)$ into Eqs. (23) and (34), and replacing $k^{(I)}$, $k^{(U)}$ with $kp/2$, $k(1-p)$, we can rewrite them to be

$$y = \frac{2}{(2-p)k} \tag{47}$$

and

$$\begin{aligned} &\frac{1}{8}\left[(2-p)^3k^3 - 2(2-p)(3-p)k^2\right](a_1 - d_1 + a_2 - d_2) \\ +&\frac{1}{8}\left[(2-p)^3k^3 - 2(2-p)(7-4p)k^2\right](b_1 - c_1 - b_2 + c_2) + o(k^2) > 0, \end{aligned} \tag{48}$$

which can further simplified to be

$$\left[(2-p)^2k - 6 + 2p\right](a_1 - d_1 + a_2 - d_2) + \left[(2-p)^2k - 14 + 8p\right](b_1 - c_1 - b_2 + c_2) > 0. \tag{49}$$

Accordingly, both critical benefit-to-cost ratios in Eqs. (37) and (41) are

$$\left(\frac{b}{c}\right)^* = \frac{(2-p)^2}{4-3p}k, \tag{50}$$

where $(b/c)^*$ is minimized when $p = 2/3$, and the minimal threshold is $(b/c)^*_{\min} = 8k/9$.

B. Analysis for any population structure. We refer to a prior work (2) to provide the condition for the evolution of cooperation in general directed networks, with independent structures for interaction and strategy dispersal. Let $w_{ij}^{[1]}$ (resp. $w_{ij}^{[2]}$) denote the edge weight in the interaction (resp. dispersal) network. Let $p_{ij} = w_{ji}^{[2]}/\sum_\ell w_{\ell i}^{[2]}$ and π_i denote the probability that a mutant in node i takes over the whole population under neutral drift. We can obtain π_i by solving $\sum_i \pi_i = 1$ and $\pi_i = \sum_j p_{ji}\pi_j$. The solution also involves the coalescence times τ_{ij}, which are obtained by solving the system of equations

$$\tau_{ij} = \begin{cases} 1 + \frac{1}{2}\sum_{k\in\mathcal{N}} p_{ik}\tau_{kj} + \frac{1}{2}\sum_{k\in\mathcal{N}} p_{jk}\tau_{ik} & i \neq j, \\ 0 & i = j. \end{cases} \tag{51}$$

Applying Theorem 2 of Ref. (2), the critical cost-benefit ratio is given by

$$\left(\frac{b}{c}\right)^* = \frac{v_2}{u_2 - u_0} \tag{52}$$

where

$$\begin{aligned} u_0 &= \sum_{i,j,\ell\in\mathcal{N}} \pi_i p_{ij}\tau_{j\ell}w_{\ell j}^{[1]}, \qquad u_2 = \sum_{i,j,k,\ell\in\mathcal{N}} \pi_i p_{ij}p_{ik}\tau_{j\ell}w_{\ell k}^{[1]}, \\ v_2 &= \sum_{i,j,k,\ell\in\mathcal{N}} \pi_i p_{ij}p_{ik}\tau_{jk}w_{k\ell}^{[1]}. \end{aligned} \tag{53}$$

The downstream case corresponds to the structure with $w_{ij}^{[2]} = w_{ij}^{[1]}$ for any $i, j \in \mathcal{N}$. The upstream case corresponds to the structure with $w_{ij}^{[2]} = w_{ji}^{[1]}$.

C. Approximate condition for finite regular networks. In the downstream case, we can use Eq. (52) to derive a more accurate approximation for $(b/c)^*$ in the case of finite regular directed networks. Specifically, we consider a directed graph of size N, for which each vertex has exactly d outgoing edges and d incoming edges; that is, $k_i^{(I)} = k_i^{(O)} = d$ for each vertex i. In this case, we have $p_{ij} = w_{ji}/d$ for each pair i and j, and $\pi_i = 1/N$, for each vertex i.

We introduce the following notation for the expected coalescence time at two ends of a random walk with a specified series of directions:

$$\tau^{\rightarrow} = \frac{1}{N}\sum_{i,j} p_{ij}\tau_{ij}, \qquad [54a]$$

$$\tau^{\rightarrow\rightarrow} = \frac{1}{N}\sum_{i,j,k} p_{ij}p_{jk}\tau_{ik}, \qquad [54b]$$

$$\tau^{\leftarrow\rightarrow} = \frac{1}{N}\sum_{i,j,k} p_{ji}p_{jk}\tau_{ik}, \qquad [54c]$$

$$\tau^{\leftarrow\rightarrow\rightarrow} = \frac{1}{N}\sum_{i,j,k,\ell} p_{ji}p_{jk}p_{k\ell}\tau_{i\ell}, \qquad [54d]$$

and so on. Note that since $\tau_{ij} = \tau_{ji}$, a sequence γ can be reversed without changing the value of τ^{γ}; for example $\tau^{\leftarrow\rightarrow\rightarrow} = \tau^{\leftarrow\leftarrow\rightarrow}$. With this notation, the critical benefit-cost ratio from Eqs. (52)-(53) (in the downstream case, for regular directed networks) becomes

$$\left(\frac{b}{c}\right)^{*} = \frac{\tau^{\leftarrow\rightarrow}}{\tau^{\leftarrow\rightarrow\rightarrow} - \tau^{\rightarrow}}. \qquad [55]$$

We now proceed to develop approximations for the relevant τ^{γ}, where γ represents a sequence of directions (e.g. $\leftarrow\rightarrow$ or $\leftarrow\rightarrow\rightarrow$). Summing Eq. (51) over all i and j yields

$$\sum_{i,j} \tau_{ij} = N^2 + \sum_{i,j} \tau_{ij} - N - \sum_{i,k} p_{ik}\tau_{ik}, \qquad [56]$$

(the last two terms arise from subtracting the $i = j$ case) from which it follows that

$$\tau^{\rightarrow} = N - 1. \qquad [57]$$

For an arbitrary sequence of directions γ, we let p^{γ} denote the average probability that a random walk with these directions terminates at its starting point; for example

$$p^{\leftarrow\rightarrow\rightarrow\rightarrow} = \frac{1}{N}\sum_{i,j,k,\ell} p_{ji}p_{jk}p_{k\ell}p_{\ell i}.$$

Then Eq. (51) gives the relation

$$\tau^{\gamma} = 1 + \frac{1}{2}\left(\tau^{\leftarrow\gamma} + \tau^{\gamma\rightarrow}\right) - p^{\gamma}(1 + \tau^{\rightarrow}),$$

where $\leftarrow\gamma$ and $\gamma\rightarrow$ denote sequence concatenation on the left and right, respectively, with the specified arrows. Using Eq. (57), this relation simplifies to

$$\tau^{\gamma} = 1 + \frac{1}{2}\left(\tau^{\leftarrow\gamma} + \tau^{\gamma\rightarrow}\right) - Np^{\gamma}. \qquad [58]$$

In particular, we have

$$\tau^{\rightarrow} = 1 + \frac{1}{2}\left(\tau^{\leftarrow\rightarrow} + \tau^{\rightarrow\rightarrow}\right), \qquad [59a]$$

$$\tau^{\rightarrow\rightarrow} = 1 + \frac{1}{2}\left(\tau^{\leftarrow\rightarrow\rightarrow} + \tau^{\rightarrow\rightarrow\rightarrow}\right), \qquad [59b]$$

$$\tau^{\leftarrow\rightarrow} = 1 + \tau^{\leftarrow\rightarrow\rightarrow} - N/d, \qquad [59c]$$

$$\tau^{\rightarrow\rightarrow\rightarrow} = 1 + \frac{1}{2}\left(\tau^{\leftarrow\rightarrow\rightarrow\rightarrow} + \tau^{\rightarrow\rightarrow\rightarrow\rightarrow}\right) - Np^{\rightarrow\rightarrow\rightarrow}, \qquad [59d]$$

$$\tau^{\leftarrow\rightarrow\rightarrow} = 1 + \frac{1}{2}\left(\tau^{\leftarrow\leftarrow\rightarrow\rightarrow} + \tau^{\leftarrow\rightarrow\rightarrow\rightarrow}\right) - Np^{\leftarrow\rightarrow\rightarrow}. \qquad [59e]$$

Above we have used the fact that a path of the form $\rightarrow\rightarrow$ cannot return to its initial vertex ($p^{\rightarrow\rightarrow} = 0$), while a path of the form $\leftarrow\rightarrow$ returns with probability $p^{\leftarrow\rightarrow} = 1/d$. Using Eq. (57) and Eq. (59c), we can rewrite Eq. (55) as

$$\left(\frac{b}{c}\right)^{*} = \frac{\tau^{\leftarrow\rightarrow\rightarrow} - N/d + 1}{\tau^{\leftarrow\rightarrow\rightarrow} - N + 1}. \qquad [60]$$

Combining Eq. (57), Eq. (59a), Eq. (59b), and Eq. (59c) gives

$$\begin{aligned} N - 2 &= \frac{1}{2}\left(\tau^{\leftarrow\rightarrow} + \tau^{\rightarrow\rightarrow}\right) \\ &= 1 + \frac{3}{4}\tau^{\leftarrow\rightarrow\rightarrow} + \frac{1}{4}\tau^{\rightarrow\rightarrow\rightarrow} - \frac{N}{2d}, \end{aligned} \qquad [61]$$

which can rewritten as

$$\frac{3}{4}\tau^{\leftarrow\rightarrow\rightarrow} + \frac{1}{4}\tau^{\rightarrow\rightarrow\rightarrow} = N + \frac{N}{2d} - 3. \tag{62}$$

We now introduce a "cutoff" approximation that τ^{γ} is the same for all paths γ of length four. Then comparing Eq. (59d) and Eq. (59e) gives

$$\tau^{\rightarrow\rightarrow\rightarrow} = \tau^{\leftarrow\rightarrow\rightarrow} - N\left(p^{\rightarrow\rightarrow\rightarrow} - p^{\leftarrow\rightarrow\rightarrow}\right). \tag{63}$$

Let us introduce the quantity $\Delta = \frac{1}{4}\left(p^{\rightarrow\rightarrow\rightarrow} - p^{\leftarrow\rightarrow\rightarrow}\right)$, which describes the tendency of the graph to have cyclic rather than acyclic triangles. Then substituting Eq. (63) into Eq. (62) gives

$$\tau^{\leftarrow\rightarrow\rightarrow} = N\left(1 + \frac{1}{2d} + \Delta\right) - 3. \tag{64}$$

Substituting in Eq. (60) yields

$$\left(\frac{b}{c}\right)^{*} = \frac{N\left(1 - \frac{1}{2d} + \Delta\right) - 2}{N\left(\frac{1}{2d} + \Delta\right) - 2}.$$

Recalling that $k = 2d$, we have our final result:

$$\left(\frac{b}{c}\right)^{*} = \frac{k(1+\Delta) - 1 - 2\frac{k}{N}}{1 + k\Delta - 2\frac{k}{N}}. \tag{65}$$

In particular, for $k \ll N$, this becomes approximately

$$\left(\frac{b}{c}\right)^{*} = \frac{k(1+\Delta) - 1}{1 + k\Delta}. \tag{66}$$

As Δ increases, the critical benefit-cost ratio in Eq. (65) becomes increasingly favorable for cooperation. This provides mathematical justification for the finding that cooperation is facilitated by cyclic triangles, but hindered by acyclic triangles.

3. Network motifs

Let k_i denote node i's degree, including $k_i^{(I)}$ incoming edges, $k_i^{(O)}$ outgoing edges, and $k_i^{(U)}$ bi-directed edges, i.e. $k_i = k_i^{(I)} + k_i^{(O)} + k_i^{(U)}$. In the following, we treat each bi-directional as two uni-directional edges, namely an 'incoming' and an 'outgoing' edges.

A. Triangular cycle motif. In the downstream dispersal, we consider the motif of triangular cycles, such as $i \to j \to \ell \to i$ ($j \neq \ell$). For node i, the number of such triangular cycles is $\sum_{j,\ell} w_{ij} w_{j\ell} w_{\ell i}$. For node i, the number of in-out pairs (i.e. an incoming edge and an outgoing edge, like $y \to i$ and $i \to j$ but $y \neq j$) is $k_i^{(I)} k_i^{(O)} + k_i^{(U)}(k_i - 1)$. For each in-out pair, if there exists an edge from the target node of i's outgoing edge to the source node of i's incoming edge, a triangular cycle appears. Therefore, the number of in-out pairs is the possibly largest number of triangular cycles for node i. We introduce a quantity

$$\mathcal{C}_1 = \frac{\sum_{i,j,\ell \in \mathcal{N}} w_{ij} w_{j\ell} w_{\ell i}}{\sum_{i \in \mathcal{N}} \left(k_i^{(I)} k_i^{(O)} + k_i^{(U)}(k_i - 1)\right)} \tag{67}$$

to measure the global frequency of triangular cycles in a directed network. A larger $\mathcal{C}_1$ means more triangular cycles.

B. In-in pair motif. In the case of upstream dispersal, we consider the motif of in-in pairs, such as $j \to i \leftarrow \ell$ ($j \neq \ell$). For node i, the number of in-in pairs is $\left(k_i^{(I)} + k_i^{(U)}\right)\left(k_i^{(I)} + k_i^{(U)} - 1\right)$, and the number of all edge pairs is $\left(k_i + k_i^{(U)}\right)\left(k_i + k_i^{(U)} - 1\right)$. We introduce the quantity

$$\mathcal{C}_2 = \frac{\sum_{i \in \mathcal{N}} \left(k_i^{(I)} + k_i^{(U)}\right)\left(k_i^{(I)} + k_i^{(U)} - 1\right)}{\sum_{i \in \mathcal{N}} \left(k_i + k_i^{(U)}\right)\left(k_i + k_i^{(U)} - 1\right)}. \tag{68}$$

This quantity measures the normalized fraction of in-in pairs in the directed network, and a larger value of $\mathcal{C}_2$ means a greater frequency of in-in pairs.

C. Acyclic triangle motif. For a strictly uni-directional network we measure the frequency of acyclic triangles using the following quantity:

$$\begin{aligned}\mathcal{C}_3 =& \frac{\sum_{i,j,\ell}\left(w_{ij}w_{j\ell}w_{i\ell}+w_{ij}w_{\ell j}w_{\ell i}+w_{ji}w_{j\ell}w_{\ell i}\right)}{\sum_i k_i^{(I)}k_i^{(O)}+\frac{1}{2}\sum_i k_i^{(I)}(k_i^{(I)}-1)+\frac{1}{2}\sum_i k_i^{(O)}(k_i^{(O)}-1)}\\ =&\frac{6\sum_{i,j,\ell}w_{ij}w_{j\ell}w_{i\ell}}{\sum_i k_i(k_i-1)},\end{aligned} \qquad [69]$$

where the numerator denotes the actual number of acyclic triangles, and the denominator represents the possible largest number of acyclic triangles given the network topology.

We used the algorithm specified below to generate strictly uni-directional regular graphs with N nodes, degree k (incoming degree $k/2$ and outgoing degree $k/2$), and different values of $\mathcal{C}_3$:
(1) Arrange N nodes in a circle and label them $\{1,2,\cdots,N\}$ clockwise;
(2) Let d_{ij} denote the distance between nodes i and j in the clockwise direction (i.e. $d_{12}=1$, $d_{21}=N-1$, $d_{1N}=N-1$, $d_{N1}=1$); Let $\mathcal{D}=\{1,2,\cdots,N-1\}$ denote the set of all possible distances;
(3) Select $k/2$ random and different values from $\mathcal{D}$, denoted by the set $\mathcal{K}$;
(4) Connect each node (as source node of a directed edge) to those nodes with distances in $\mathcal{K}$.
For $k=4$ and $\mathcal{K}=\{1,2\}$, the resulting graph has only acyclic triangles. For $k=4$ and $\mathcal{K}=\{1,N-1\}$, the resulting graph has only cyclic triangles. For fixed k, this algorithm always generates graphs with the same value of $\mathcal{C}_2$ (due to the same incoming and outgoing degree for each node), while different sets of $\mathcal{K}$ can lead to different values of $\mathcal{C}_1$ and $\mathcal{C}_3$.

In a strictly uni-directional regular network, the quantities $\mathcal{C}_1$ and $\mathcal{C}_3$ can be related to the quantities introduced in Section C by

$$p^{\rightarrow\rightarrow\rightarrow}=\frac{2\mathcal{C}_1}{k}, \qquad p^{\leftarrow\rightarrow\rightarrow}=\frac{4\mathcal{C}_3(k-1)}{3k^2}, \qquad [70]$$

and so

$$\Delta=\frac{p^{\rightarrow\rightarrow\rightarrow}-p^{\leftarrow\rightarrow\rightarrow}}{4}=\frac{\mathcal{C}_1}{2k}-\frac{\mathcal{C}_3(k-1)}{3k^2}. \qquad [71]$$

Eqs. (66) and (71) provide analytical insight into our empirical observations that triangular cycles favor and acyclic triangles inhibit cooperation.

4. Empirical networks

In the friendship nomination network of high school students (obtained from Adolescent health questionnaire in 1994, ADD health), a directed edge means that the source node nominates the target node as his or her best friend (3). We study friendship nominations of students from ten communities. The network dataset is available after requesting access, at
https://networks.skewed.de/net/add_health#comm1_draw

In the family visitation network of San Juan Sur, Costa Rica, a directed edge means that one family (source node) visits another family (target node) (4). The network dataset is freely and publicly available at
http://vlado.fmf.uni-lj.si/pub/networks/data/esna/visits.htm

In the friendship rating network of residents on the Australian National University campus, a directed edge means that the source node rates the target node as a friend (5). The network dataset is freely and publicly available at
http://konect.cc/networks/moreno_oz/

In the physician trust network in Illinois, a directed edge means that the physician at the source node trusts or asks for professional advice from the target node (6). The network dataset is freely and publicly available at
https://downloads.skewed.de/mirror/konect.cc/files/download.tsv.moreno_innovation.tar.bz2

In the Twitter follower network (based on a snowball sample crawl across "quality" users in 2009), a directed edge means that the source node is followed by the target node (7). We extract the largest strongly connected component of each network and treat all edges with weight one. The network dataset is freely and publicly available at
https://networks.skewed.de/net/twitter

Downstream / Upstream

RR — A (Downstream)

Proportion, p \ Average degree $\bar{k}$	20	40	48	50	52	54	56
1.0	33.3	198.1	1185.9	+/−	-129.3	-66.8	-46.2
0.9	29.5	144.1	414.6	665.5	1512.3	+/−	-1213.1
0.67	27.3	121.5	288.0	396.8	609.4	1209.9	14903.7
0.5	27.8	126.8	314.6	447.0	731.5	1782.1	-5541.0
0.1	31.4	174.6	729.1	2001.3	-3331.7	-955.6	-575.3
0.0	32.7	196.0	1176.0	∞	-1274.0	-661.5	-457.3

RR — E (Upstream)

Proportion, p \ Average degree $\bar{k}$	20	40	48	50	52	54	56
1.0	31.8	193.9	1184.4	+/−	-1259.1	-653.4	-452.9
0.9	28.3	140.9	405.4	650.2	1464.4	+/−	-1218.9
0.67	26.7	120.0	284.3	391.4	599.7	1181.2	+/−
0.5	27.4	125.9	312.2	443.2	724.1	1752.0	-5786.4
0.1	31.4	174.5	728.6	1999.3	-3332.7	-955.2	-575.1
0.0	32.7	196.0	1176.0	∞	-1274.0	-661.5	-457.3

ER — B (Downstream)

Proportion, p \ Average degree $\bar{k}$	20	40	48	50	52	54	56
1.0	36.2	224.0	2245.4	-3196.6	-927.4	-564.6	-414.2
0.9	31.6	156.5	487.1	851.8	+/−	-2895.5	-941.8
0.67	28.8	129.2	317.8	449.7	728.6	1722.6	+/−
0.5	29.2	134.8	348.5	511.1	899.2	3083.6	-2598.1
0.1	33.0	188.3	915.3	4186.6	-1897.2	-797.9	-518.9
0.0	34.4	212.9	1735.1	-4132.3	-992.0	-583.1	-421.6

ER — F (Upstream)

Proportion, p \ Average degree $\bar{k}$	20	40	48	50	52	54	56
1.0	32.5	203.1	1477.9	+/−	-1067.1	-602.2	-429.1
0.9	29.1	147.0	442.1	739.4	1978.9	+/−	-1038.3
0.67	27.7	125.5	305.7	429.2	683.6	1521.6	+/−
0.5	28.5	132.3	340.0	495.7	859.1	2702.4	-2848.5
0.1	32.9	187.8	909.5	4075.2	-1913.7	-800.2	-519.7
0.0	34.4	212.9	1735.1	-4132.3	-992.0	-583.1	-421.6

SW — C (Downstream)

Proportion, p \ Average degree $\bar{k}$	20	40	48	50	52	54	56
1.0	33.0	198.5	1233.0	+/−	-1242.3	-654.2	-454.5
0.9	29.3	144.5	420.4	681.8	1603.4	+/−	-1162.3
0.67	27.3	122.1	291.6	403.3	624.6	1271.5	+/−
0.5	27.8	127.6	319.0	455.8	754.4	1920.3	-4581.1
0.1	31.6	176.4	755.1	2199.5	-2923.9	-920.0	-562.8
0.0	32.8	198.3	1245.4	-22887.5	-1209.0	-644.4	-449.4

SW — G (Upstream)

Proportion, p \ Average degree $\bar{k}$	20	40	48	50	52	54	56
1.0	32.4	198.7	1307.4	+/−	-1187.3	-635.1	-444.0
0.9	28.8	143.2	416.9	675.9	1597.4	+/−	-1161.4
0.67	26.9	121.2	289.1	399.5	617.5	1250.7	+/−
0.5	27.6	127.1	317.4	453.4	749.3	1896.9	-4708.7
0.1	31.5	176.4	755.1	2200.9	-2918.8	-919.4	-562.6
0.0	32.8	198.3	1245.4	-22887.5	-1209.0	-644.4	-449.4

SF — D (Downstream)

Proportion, p \ Average degree $\bar{k}$	20	40	48	50	52	54	56
1.0	+/−	+/−	-441.4	-334.0	-274.4	-236.8	-207.6
0.9	500.7	+/−	+/−	+/−	-701.7	-463.4	-347.1
0.67	223.9	310.5	474.7	1009.6	+/−	+/−	-867.1
0.5	210.0	303.1	460.4	883.1	+/−	+/−	-789.0
0.1	330.0	603.0	1836.7	+/−	-844.2	-510.8	-364.7
0.0	410.7	903.2	+/−	-1195.3	-594.0	-410.5	-312.0

SF — H (Upstream)

Proportion, p \ Average degree $\bar{k}$	20	40	48	50	52	54	56
1.0	182.8	265.5	405.9	771.4	+/−	-1548.3	-634.9
0.9	146.7	197.9	269.1	397.0	691.9	+/−	+/−
0.67	146.5	186.8	247.3	347.3	546.3	1142.6	+/−
0.5	161.4	219.3	301.7	454.6	842.8	+/−	+/−
0.1	311.7	550.3	1397.7	+/−	-932.0	-538.4	-377.3
0.0	410.7	903.2	+/−	-1195.3	-594.0	-410.5	-312.0

Fig. S1. Intermediate frequency of uni-directional edges is optimal for cooperation on random networks. We consider four classes of networks: random regular networks (RR), Erdös-Rényi networks (ER) (8), Watts-Strogatz small-world networks (SW) with rewiring probability 0.1 (9), and Barabási-Albert scale-free networks (BA-SF) (10). For each class, we generated $10,000$ strictly bi-directional networks each with $N = 100$ nodes, for several values of the average node degree $\bar{k}$. For each such network we randomly select a proportion p of edges and convert them to be uni-directional, with randomly chosen orientation. For each resulting network we compute the critical benefit-to-cost ratio $(b/c)^*$ required to favor cooperation, and we plot the mean value, given p and $\bar{k}$, in the tables. In the regions displayed in blue, all ratios are positive and cooperation can evolve for some choice of benefits and costs. In red regions, all ratios are negative and spite is favored instead of cooperation. The symbol '$+/-$' means that a fraction of critical ratios are positive and a fraction negative; and the symbol '∞' means that cooperation is never favored, regardless of how large the benefit.

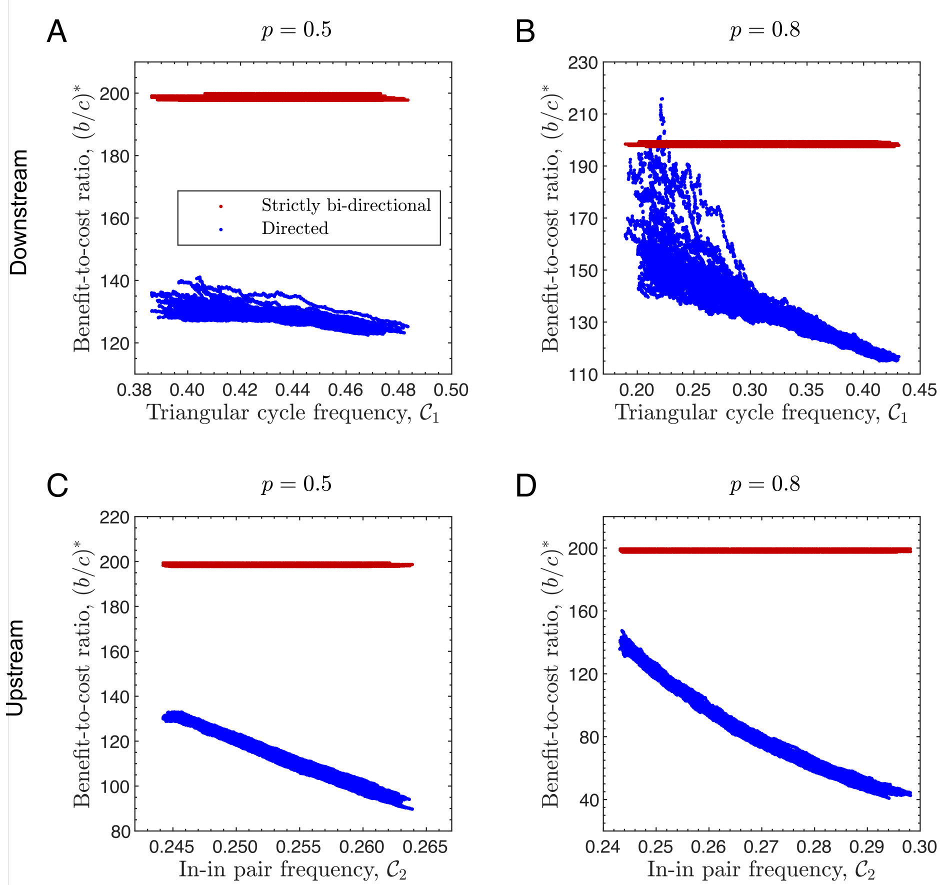

Fig. S2. Adjusting edge orientation effects evolutionary outcomes in directed networks. Here we investigate small-world networks with $N = 100$ and $\bar{k} = 40$, and with fraction of uni-directional edges $p = 0.5$ (AC) or $p = 0.8$ (BD) (see Fig. 5 in the main text for all other parameters and detailed caption).

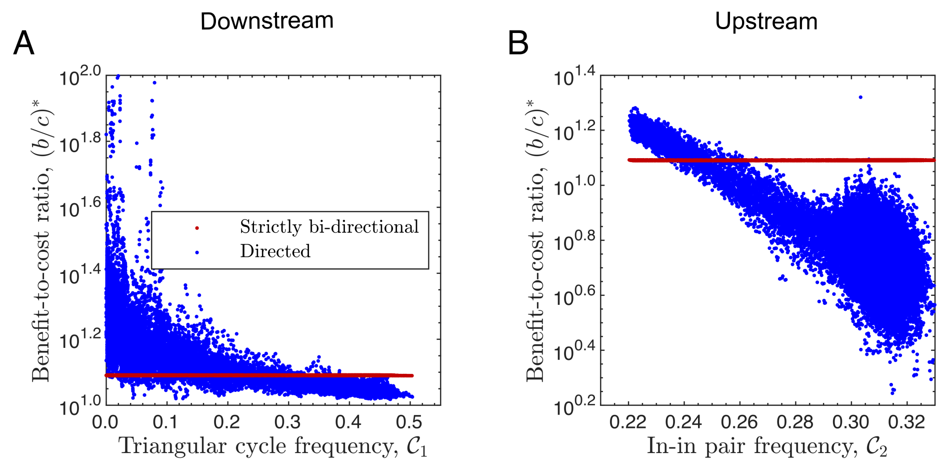

Fig. S3. Adjusting edge orientation affects evolutionary outcomes in sparse directed networks. Here we investigate small-world networks with $N = 100$ and $\bar{k} = 10$, $p = 1.0$ (see Fig. 5 in the main text for all other parameters and detailed caption).

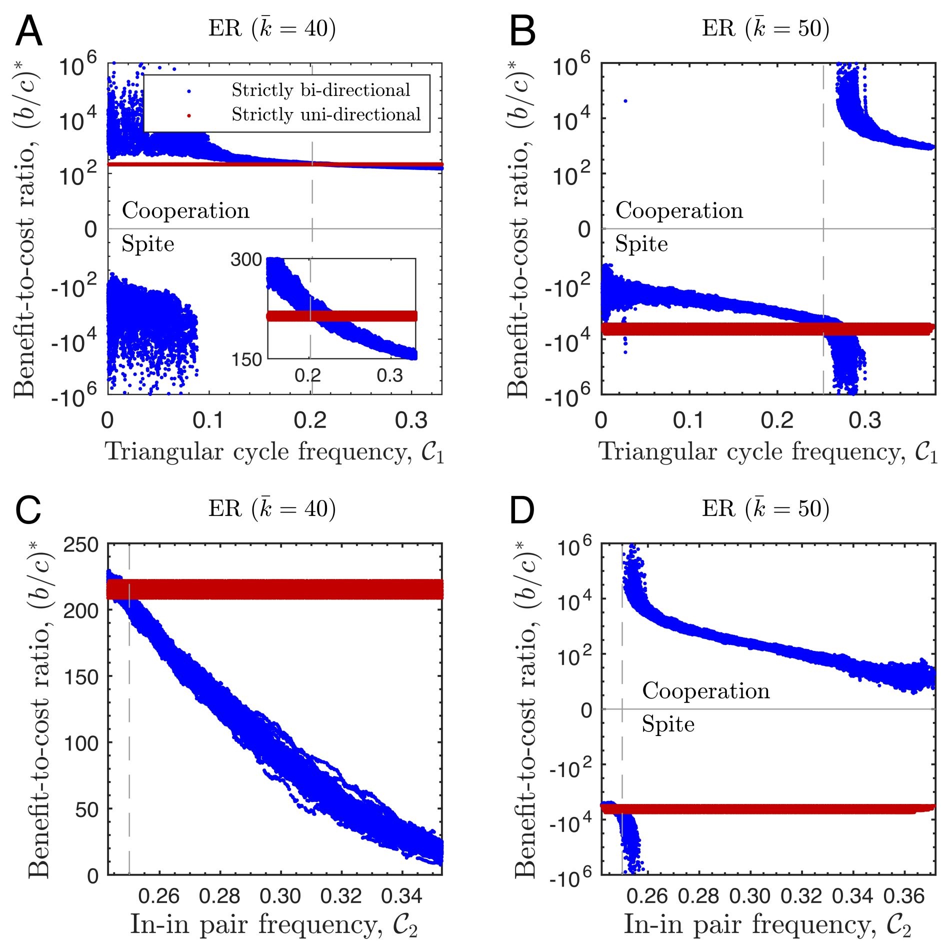

Fig. S4. Adjusting edge orientation affects evolutionary outcomes in random networks. Here we investigate Erdös-Rényi random networks (see Fig. 5 in the main text for all other parameters and detailed caption).

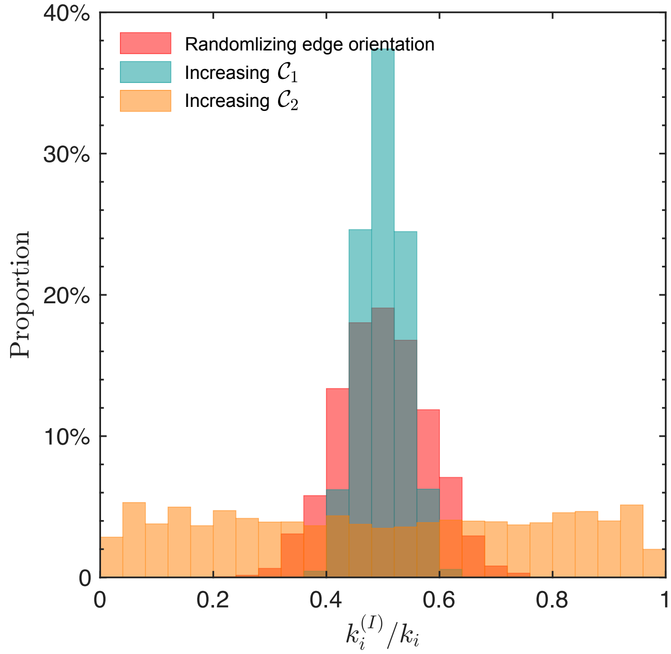

Fig. S5. The distribution of node in-degrees for different motif frequencies. Random edge orientation leads to an intermediate heterogeneity of the node in-degree distribution. Increasing the frequency of triangular cycles ($\mathcal{C}_1$) leads to the homogeneity in node in-degree distribution, meaning each node has roughly the same number of incoming neighbors as outgoing neighbors. Increasing the frequency of in-in pairs ($\mathcal{C}_2$) causes large heterogeneity in node in-degree distribution, meaning some nodes have more incoming neighbors than outgoing neighbors while other nodes have more outgoing neighbors than incoming neighbors.

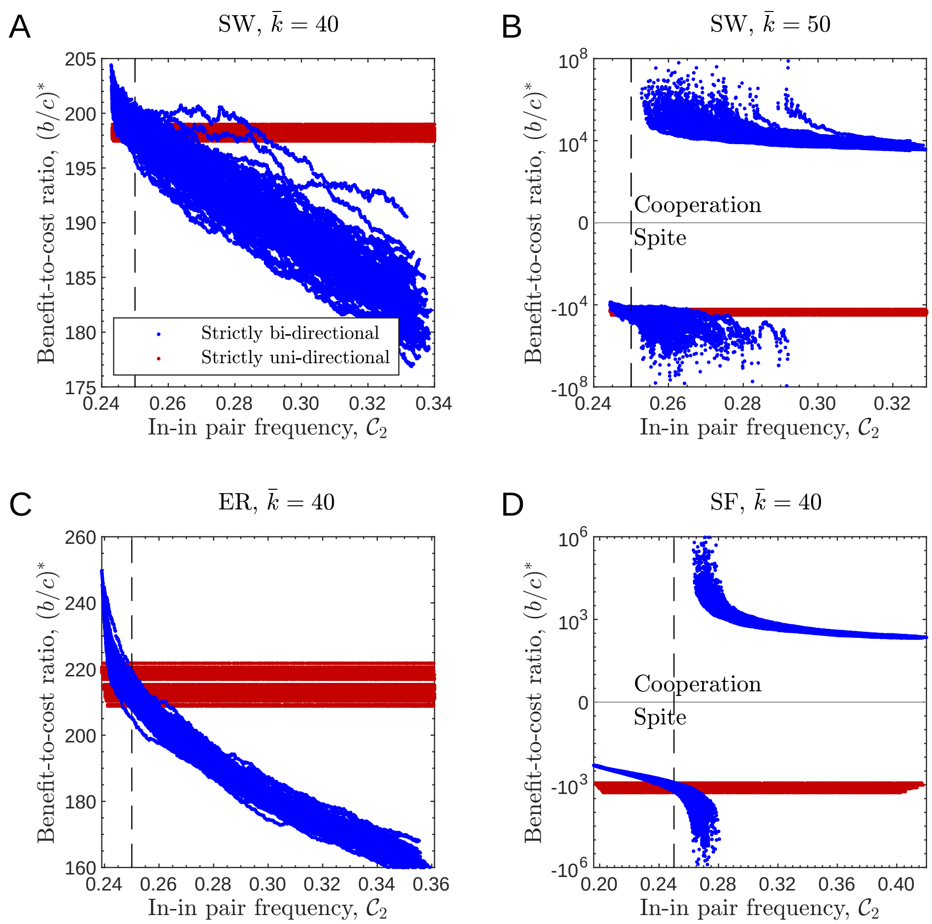

Fig. S6. Evolution of cooperation in networks with directional interactions and bi-directional strategy dispersal. We consider small-world (SW), random (ER), and scale-free networks (SF) of size $N = 100$ and average node degree $\bar{k} = 40$ and $\bar{k} = 50$. By modifying the edge orientation to increase the motif level (in-in pair frequency, $\mathcal{C}_2$), the critical benefit-to-cost ratio for cooperation decreases (AC) monotonously, and is often lower than the critical ratio for strictly bi-directed networks. Even when a bi-directional network allows for spite, modifying the edge orientation for game play can rescue cooperation. (see Fig. 5 in the main text for all other parameters and detailed caption.)

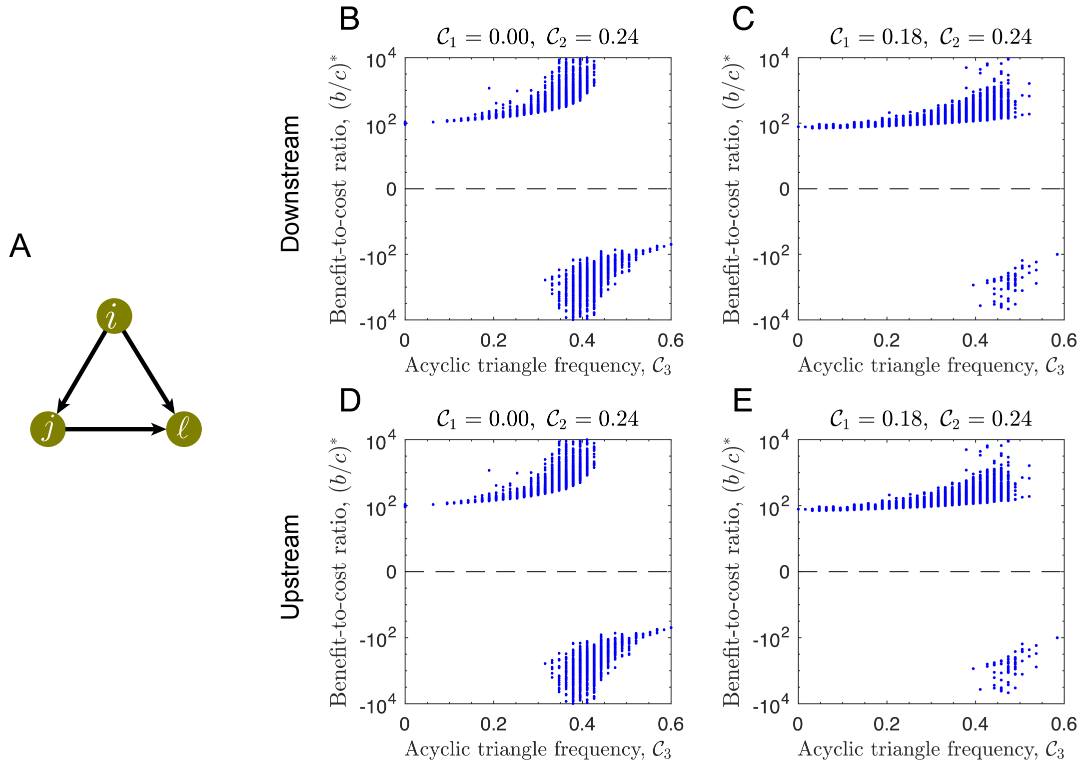

Fig. S7. Acyclic triangles inhibit the evolution of cooperation. (A) Diagram of the acyclic triangle motif, $i \to j \to \ell \leftarrow i$. We generated 2×10^6 graphs of size $N = 50$ and node degree $k = 20$ by the algorithm described in SI Appendix, section 3C. Among of them, $4,881$ have $\mathcal{C}_1 = 0.00$ and $\mathcal{C}_2 = 0.24$, and $299,360$ have $\mathcal{C}_1 = 0.18$ and $\mathcal{C}_2 = 0.24$. (BC) The critical benefit-to-ratio as a function of $\mathcal{C}_3$ in the downstream case. (DE) The critical benefit-to-ratio as a function of $\mathcal{C}_3$ in the upstream case. The larger the value of $\mathcal{C}_3$ (the more acyclic triangles), the more detrimental the directed network is for cooperation, under both downstream and upstream dispersal.

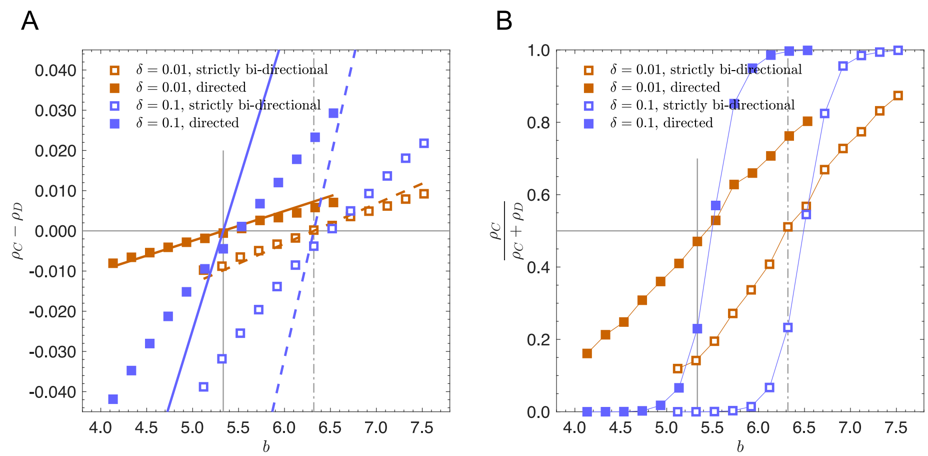

Fig. S8. Asymmetric interactions facilitate cooperation, under moderate selection. We consider random regular networks of size $N = 200$ and degree $k = 6$, with strictly bi-directional interactions (open squares), or with a mixture of bi-directional and uni-directional interactions (solid squares; each node has 2 incoming edges, 2 outgoing edges, and 2 bi-directed edges). We consider two values of selection strength: $\delta = 0.01$ and $\delta = 0.1$. (A) The presence of uni-directed edges decreases the critical benefit-to-cost ratio $(b/c)^*$ required for cooperation to be favored ($\rho_C > \rho_D$). Dots show results averaged over 10^6 replicate Monte Carlo simulations; vertical lines show analytical results for $(b/c)^*$ in the limit of weak selection. The solid lines are analytical predictions for $\rho_C - \rho_D$ in the limit of weak selection (Eq. (39)), which are accurate for $\delta = 0.01$. (B) We also plot the ratio $\rho_C > /(\rho_C + \rho_D)$, which quantifies how often the population will be found in the fully-cooperative state under rare reversible mutation. The impact of selection is substantial even for $\delta = 0.01$, in the sense that the population is typically dominated by cooperation even when b/c slightly exceeds $(b/c)^*$. Parameters: $c = 1$.

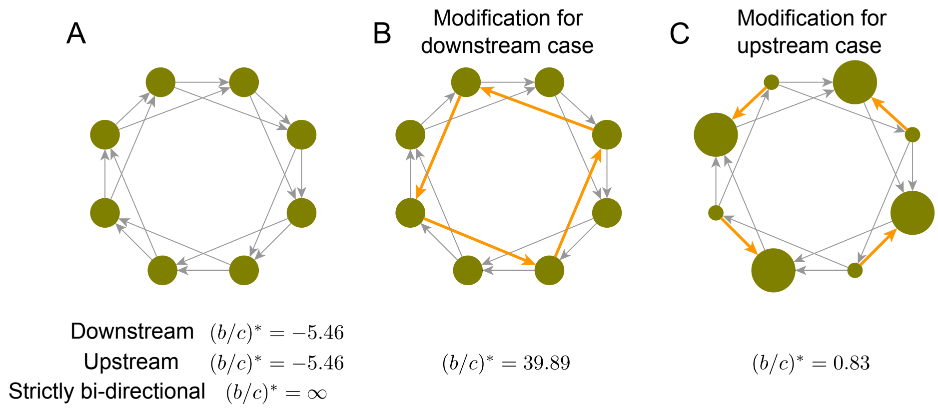

Fig. S9. An example of adjusting edge orientations to promote cooperation. (A) A directed cycle that makes cooperation impossible to evolve in both downstream and upstream cases. (B) Cooperation is rescued in downstream case by adjusting edge orientations (marked in orange) to increase triangular cycles. (C) Cooperation is rescued in upstream case by adjusting edge orientations (marked in orange) to increase in-in pairs or increase the heterogeneity in nodes' in-degrees, so that a few nodes have more incoming edges (large node size) while the other nodes have more outgoing edges (small node size).

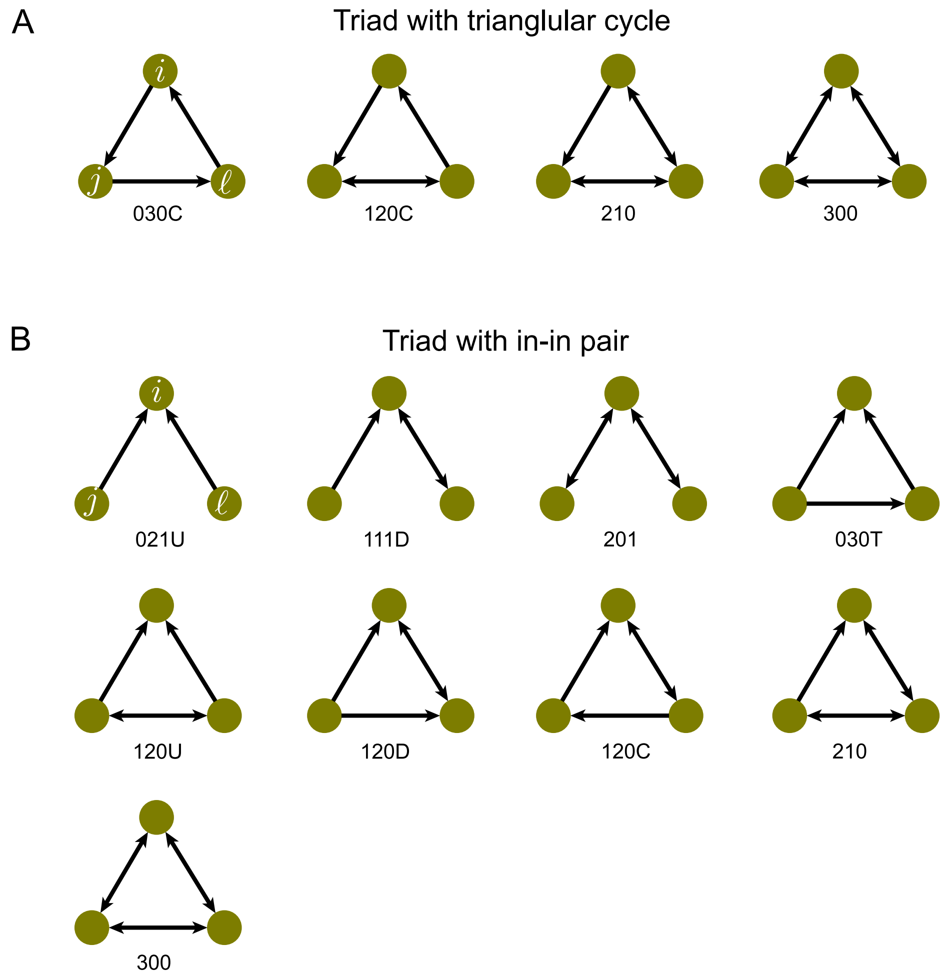

Fig. S10. Distinct triads in the MAN typology of Holland et al. (11–15) that contain the motifs we study: triangular cycles and in-in pairs. (A) Triads that contain a triangular cycle. (B) Triads that contain an in-in pair.

Table S1. Evolution of cooperation in empirical directed networks. The table summarizes the proportion of directed edges (p) and the critical benefit-to-cost ratio required to favor cooperation for the empirical networks assuming downstream strategy dispersal ($(b/c)^*_{\text{emp,d}}$) or upstream dispersal ($(b/c)^*_{\text{emp,u}}$). For comparison, the table also presents the critical ratio after removing all directionality information and treating all edges as bi-directional ($(b/c)^*_{\text{un}}$), or after randomizing the orientation of directional edges ($(b/c)^*_{\text{rand,d}}$ and $(b/c)^*_{\text{rand,u}}$, averaged over 100 random assignments of orientations)

Name	Nodes	Social ties	p	$(b/c)^*_{\text{un}}$	$(b/c)^*_{\text{rand,d}}$	$(b/c)^*_{\text{rand,u}}$	$(b/c)^*_{\text{emp,d}}$	$(b/c)^*_{\text{emp,u}}$
ADD Comm33	1148	5958	0.68	6.16	5.74	5.12	5.44	4.01
ADD Comm36	1671	12934	0.71	8.84	8.22	7.41	8.49	6.04
ADD Comm40	1679	14684	0.73	10.27	9.49	8.61	7.91	6.03
ADD Comm41	1640	13774	0.73	9.59	8.88	8.05	7.87	5.62
ADD Comm49	1149	9076	0.68	9.32	8.64	7.81	7.19	6.51
ADD Comm50	2155	17940	0.72	9.55	8.91	7.99	7.54	5.43
ADD Comm52	1263	7992	0.67	7.19	6.70	5.97	6.68	4.73
ADD Comm58	953	6370	0.66	7.82	7.26	6.54	6.51	5.22
ADD Comm61	846	4558	0.65	6.28	5.85	5.23	5.75	4.91
ADD Comm84	524	3228	0.71	7.19	6.72	5.97	6.53	4.64
Families in Costa Rica (4)	40	67	0.45	3.95	3.84	3.53	3.88	3.20
Australian National University campus (5)	213	1716	0.54	21.49	19.23	18.31	19.82	15.86
Physicians in Illinois (6)	95	381	0.80	10.41	9.75	8.38	8.32	5.07
Twitter users (7)	1726	5690	0.79	8.83	9.50	6.75	6.47	3.06

Table S2. Triangular cycles and in-in pairs in empirical networks. The table summarizes the frequencies of triangular cycles ($\mathcal{C}_1$) and in-in pairs ($\mathcal{C}_2$) in empirical (emp) networks and associated random versions of these networks (rand). We generated the random networks by randomly distributing directed edges, while keeping the number of directed edges the same as in the corresponding empirical network. Results are shown for the average over 100 independently generated random networks.

Name	$\frac{(\mathcal{C}_1)_{\mathbf{emp}}-(\mathcal{C}_1)_{\mathbf{rand}}}{(\mathcal{C}_1)_{\mathbf{rand}}}$	$\frac{(\mathcal{C}_2)_{\mathbf{emp}}-(\mathcal{C}_2)_{\mathbf{rand}}}{(\mathcal{C}_2)_{\mathbf{rand}}}$
ADD Comm33	22.68%	12.94%
ADD Comm36	21.07%	16.04%
ADD Comm40	8.70%	21.43%
ADD Comm41	11.30%	20.83%
ADD Comm49	24.78%	17.01%
ADD Comm50	16.69%	21.17%
ADD Comm52	26.76%	10.33%
ADD Comm58	22.31%	12.65%
ADD Comm61	27.77%	9.84%
ADD Comm84	21.16%	16.48%
Families in Costa Rica	21.83%	11.43%
Australian National University campus	15.54%	6.33%
Physicians in Illinois	-2.32%	34.91%
Twitter users	-17.27%	84.82%

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