Evolution of cooperation with asymmetric social interactions

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How cooperation emerges in human societies is both an evolutionary enigma and a practical problem with tangible implications for societal health. Population structure has long been recognized as a catalyst for cooperation because local interactions facilitate reciprocity. Analysis of population structure typically assumes bidirectional social interactions. But human social interactions are often unidirectional—where one individual has the opportunity to contribute altruistically to another, but not conversely—as the result of organizational hierarchies, social stratification, popularity effects, and endogenous mechanisms of network growth. Here we expand the theory of cooperation in structured populations to account for both uni- and bidirectional social interactions. Even though unidirectional interactions remove the opportunity for reciprocity, we find that cooperation can nonetheless be favored in directed social networks and that cooperation is provably maximized for networks with an intermediate proportion of unidirectional interactions, as observed in many empirical settings. We also identify two simple structural motifs that allow efficient modification of interaction directions to promote cooperation by orders of magnitude. We discuss how our results relate to the concepts of generalized and indirect reciprocity.

cooperation | evolutionary game theory | asymmetric relationships | directed graphs

The past year has crystallized the real-life importance of a long-standing enigma: When will individuals incur personal costs for the benefit of others? Confronted with a global pandemic, some individuals and societies have responded with prosocial behavior, such as volunteering as frontline workers, donating protective materials and supplies, and adhering to strict quarantine policies (1, 2). Whereas in other groups or at other times defection has dominated, as individuals chose to forgo face masks, to refuse readily available vaccination, or to flaunt travel restrictions and other measures for public health. Understanding the spread and maintenance of cooperation is now widely recognized as an important practical problem with tangible benefits, especially as we tackle global problems of collective action in public health, resource management, and climate change (3).

The last few decades have seen a proliferation of theoretical research into the evolutionary origins of cooperation and the dynamics of its spread. The literature has revealed several key insights into this enigma (4). Population structure is perhaps the most widely discussed mechanism that can promote cooperation (5, 6), and it has been studied by computer simulation (7–9), mathematical analysis (10–21), and experiments with human subjects (22). In structured populations individuals interact only with their neighbors—through either physical or social ties—and behaviors also spread locally. Population structure has the potential to favor the evolution of cooperative behaviors that would otherwise be disfavored in well-mixed populations (5–7, 11, 16, 17). In network-structured populations, for example, nodes represent individuals and edges typically represent social interactions between connected individuals (9–12, 14–19); in set-structured populations, each individual is located in one or more social circles (23); and in multilayer-structured populations,

social interactions occur in multiple different domains, such as online and offline interactions, and payoffs to an individual are summed across domains (20, 24).

Despite different approaches to describing population structure, nearly all research on this topic has assumed that social interactions and behavioral spread are bidirectional (7–20, 22). That is, if Alice provides a benefit to Bob when behaving altruistically, Bob is presumed to provide a benefit to Alice when behaving altruistically; moreover, if Alice has a chance to imitate Bob's behavior, then so too can Bob imitate Alice's behavior. The assumption of bidirectionality simplifies analysis and enables simple intuitions for how population structure permits the spread of cooperation (11).

But bidirectional models neglect the prevalence of asymmetric relationships in human social interactions (25). An asymmetric relationship arises when one individual has the opportunity to act altruistically toward another, but there is no opportunity for any reciprocal action. Asymmetric relationships also constrain the spread of behavior: One individual has the opportunity to copy the strategic behavior of another, but not conversely. Such asymmetries are commonly found across diverse domains of human social interactions, arising from social stratification, organizational hierarchies, popularity effects, and endogenous

Significance

Humans have a remarkable, but not ubiquitous, tendency toward altruism. This behavior reflects a classic enigma in evolutionary theory: When and why would individuals forgo selfish interests to help strangers? Population structure is known to catalyze cooperation because it enables local reciprocity—I help you, and you help me. But this explanation assumes bidirectional social interactions, whereas human interactions are often unidirectional: One individual has the opportunity to contribute altruistically to another, but not conversely. Here we uncover a surprising result, that directionality can actually facilitate cooperation. We study this effect theoretically and also in empirical social networks. We suggest several practical implications, including how to modify the directions of social interactions to promote cooperation.

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mechanisms of network growth (26–40). For example, in the empirical friendship network of an Australian National University campus, more than half of the relationships are unidirectional: One student regards another as a friend, but not conversely (41). In the network of Twitter followers (based on a snowball sample crawl across "quality" users in 2009), more than 99% of follower relationships are unidirectional (42). Other examples include email networks (34) and trust and advice networks (35, 43)—which all exhibit a high proportion of unidirectional social interactions. Asymmetric interactions are also widespread outside of the human social domain, in systems such as international trade (trade volumes and tariffs between countries) (25) and river and stream flow (movement of microorganisms, nutrients, and organic matter) (44–46).

Recent advances in network science have established that edge directionality can qualitatively alter dynamics across a range of systems, including in disease spread (47) and synchronization (48). The empirical prevalence of directed social interactions, and its remarkable impact on dynamics in other settings, leaves an open question: How does directionality affect the evolution of cooperation?

Asymmetric relationships are likely to fundamentally alter the evolution of cooperation, compared to the classic case of bidirectional relationships. A bidirectional relationship allows for (but does not guarantee) reciprocal cooperation between a pair of individuals, which occurs when both individuals choose an altruistic behavior. Moreover, a bidirectional relationship enables the spread of cooperative behavior: If one individual imitates a neighbor's altruistic behavior, then the neighbor will subsequently experience reciprocity—so that two altruistic neighbors help each other, and two defecting neighbors harm each other. This phenomenon of "network reciprocity" (4) along bidirectional edges is known to facilitate the local spread of cooperation and retard the spread of defection. But prosocial spread and reciprocity cannot occur along a unidirectional edge, because only one individual has the opportunity to contribute toward another, and not conversely. Since reciprocity is disrupted, unidirectional interactions may make it difficult, or even impossible, for cooperation to emerge in structured populations.

Here we study the evolution of cooperation in structured populations with directed interactions. We uncover a surprising and general result: Directionality can actually facilitate cooperation, even though it disrupts reciprocity. We prove analytically that cooperation can evolve in populations with directional interactions and that an intermediate level of directionality is most beneficial for cooperation. In fact, converting a portion of links to be unidirectional can even promote cooperation on a bidirectional network whose topology otherwise disfavors the emergence of cooperation. Furthermore, we identify two simple network motifs that are critical to determining the evolution of cooperation and that provide insights into how best to optimize edge directions to stimulate cooperation, by orders of magnitude. Our analysis reveals a profound effect of asymmetric social interactions for the evolution of behavior in structured populations.

Model

We model a population of N individuals engaged in pairwise social interactions with their neighbors. Each player engages with each of the player's neighbors in a simple social dilemma called the donation game (49), choosing either to cooperate (C) or defect (D). A cooperative act means paying a cost c to provide the player's opponent with a benefit b. In general, selection can favor cooperation in structured populations provided the benefit-to-cost ratio b/c is sufficiently large (11, 16). Here, we analyze how the critical benefit-to-cost ratio required to support cooperation depends upon directionality in the structure of social interactions. Although we focus on the donation game as a well-established model for a social dilemma (49), our method of analysis provides general conditions for the evo-

lution of cooperation for arbitrary asymmetric pairwise games (*SI Appendix*, section 2A).

We describe population structure by a directed network with N nodes, labeled $\mathcal{N} = \{1, 2, \cdots, N\}$, and edges $\{w_{ij}\}_{i,j \in \mathcal{N}} \in \{0, 1\}$. Here $w_{ij} = 1$ means there is a directed edge originating from source node i and pointing to target node j, whereas $w_{ij} = 0$ means no such edge. An edge between i and j is unidirectional if $w_{ij} = 1$ and $w_{ji} = 0$ or if $w_{ij} = 0$ and $w_{ji} = 1$. The edge is bidirectional if $w_{ij} = w_{ji} = 1$, which is equivalent to having two unidirectional edges in opposite directions. We call a network "directed" if it contains any mixture of uni- and bidirectional edges. And if all edges are unidirectional (bidirectional), we say the network is strictly unidirectional (bidirectional).

Each node represents an individual whose strategy, at any time, is either cooperate or defect. Let s_i denote player i's strategy ($s_i = 1$ means C and $s_i = 0$ means D). In each generation, a donation game is played along each directed edge. If the player at a source node cooperates, the player pays cost c to provide a benefit b to the player at the target node; while a defector at the source node pays no cost and provides no benefit. If a bidirectional edge connects nodes i and j, then the donation game is played twice along the edge, with each node assuming the role of potential donor and potential recipient. After games have been played along all directed edges, each player accumulates payoffs summed across all interactions, so that the total payoff to i is given by

$$\pi_i = -c \sum_{j \in \mathcal{N}} w_{ij} s_i + b \sum_{j \in \mathcal{N}} w_{ji} s_j. \quad [1]$$

The payoff is then transformed to a "reproductive" rate $F_i = 1 + \delta \pi_i$, where δ denotes the selection intensity (50). Our analysis assumes weak selection, $0 < \delta \ll 1$, meaning that payoff differences have small effects on the evolutionary dynamics (50, 51). This assumption has a long history in population genetics (52) and evolutionary biology (53), and it has also been used to formulate predictions for behavioral experiments with human subjects (54). In addition to our mathematical analysis under weak selection, we also simulate stronger selection strengths, and we find that our predictions are qualitatively unchanged and even quantitatively accurate when the selection strength is moderate.

After receiving payoffs based on their current strategies, individuals have the opportunity to update their strategies by payoff-biased imitation of other players. In general, the network along which strategies spread (or disperse) may not be the same as the network of pairwise game interactions. In particular, at the end of each generation, a random player i is selected uniformly at random to "die" (or, equivalently, selected to update the player's strategy), and the player imitates the strategy of one of the player's neighbors in the directed dispersal network, selected proportional to the neighbor's reproductive rate.

Although our analysis applies to an arbitrary strategy dispersal network (*SI Appendix*, section 2B), we focus on two specific cases of dispersal networks, termed "downstream" and "upstream" dispersal. The dispersal edges in both the upstream and downstream cases are the same, and they agree with the edges in the pairwise game interaction network. However, in the downstream case, the edge directions in the dispersal network are identical to those of the interaction network; and in the upstream case the edge directions for strategy dispersal are reversed relative to the directions of the interaction network (Fig. 1). And so, in the downstream case, player j successfully disperses player j's strategy to i with probability

$$e_{j \to i} = \frac{1}{N} \frac{w_{ji} F_j}{\sum_{\ell \in \mathcal{N}} w_{\ell i} F_\ell}. \quad [2]$$

Whereas in the upstream case, player j successfully disperses player j's strategy to i with probability

$$e_{j \to i} = \frac{1}{N} \frac{w_{ij} F_j}{\sum_{\ell \in \mathcal{N}} w_{i\ell} F_\ell}. \quad [3]$$
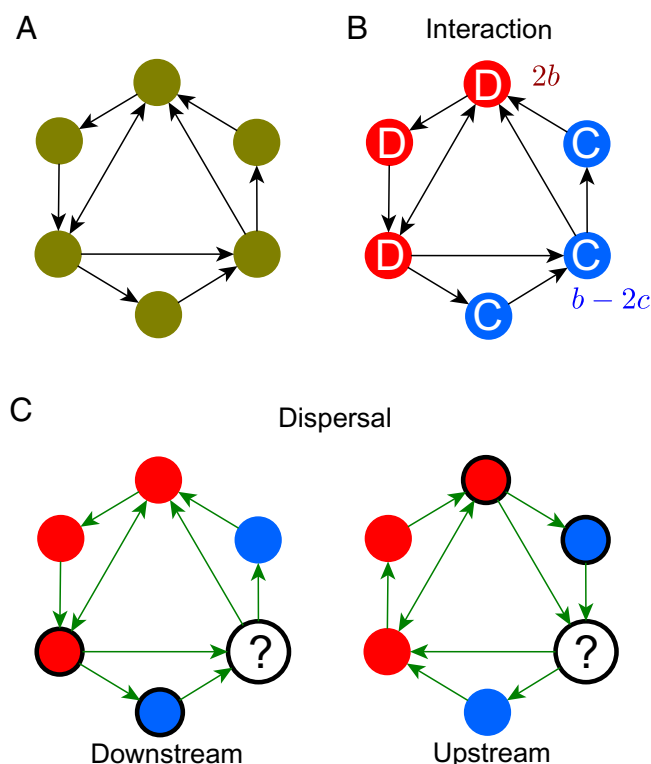
Fig. 1. Evolutionary games with asymmetric interactions. (*A*) A population structure is described by a directed network. (*B*) Individuals (nodes) engage in pairwise social interactions along directive edges. A cooperative individual at a source node pays a cost *c* to generate a benefit *b* to a recipient at a target node; whereas a defector pays no cost and generates no benefit. Each player *i* accumulates a total payoff, summed over all pairwise directed interactions (two examples are indicated). (*C*) After accumulating payoffs, a random individual *i* (denoted by a question mark) is chosen to update the individual's strategy according to payoff-biased imitation. All neighbors pointing to *i* in the dispersal network compete to spread their strategies to *i*, with a probability proportional to their reproductive rate. We consider two cases of strategy dispersal: In the downstream case strategies disperse in the same direction as social interactions occur; in the upstream case strategies disperse in the opposite direction.

The two types of dispersal we study originate from classical notions of generalized reciprocity and indirect reciprocity in evolutionary game theory (55, 56). For example, when considering a sequence of interactions $i \to j \to \ell$, generalized reciprocity describes the situation when individual *j* receives a donation from the cooperative individual *i*, and subsequently *j* imitates *i*'s behavior (strategy *C*) and applies it to benefit a third party, individual ℓ. In this process, the donation in the game $i \to j$ and the dispersal of strategy $i \to j$ occur along the same direction, corresponding to downstream dispersal. By contrast, indirect reciprocity describes the situation when individual *i* observes individual *j* making a donation to a third party, ℓ, and then individual *i* imitates the cooperative behavior of *j* (strategy *C*) and makes a donation to *j*. In this case, the donation in the game ($i \to j$) and the dispersal of strategy (j to i) occur in the opposite directions, corresponding to upstream dispersal. And so the downstream and upstream cases correspond to two different modes of social imitation: where individuals choose to copy prosocial behavior when it benefits a third party (upstream) or where they choose to copy prosocial behavior when it benefits them directly (downstream). When all edges are bidirectional, game play and strategic spread are the same in both upstream and downstream cases, and they coincide with classical models of structured populations (11, 16, 21).

Results

We study the evolution of cooperation by quantifying the chance that a single mutant type, introduced at a random node, will eventually spread and overtake the entire population. We assume that the population structure for strategy dispersal is connected, meaning that for any pair of individuals $i, j \in \mathcal{N}$ there is a series of directed edges connecting *i* to *j* in the network of strategy dispersal. We let ρ_C (respectively ρ_D) denote the probability that a single mutant cooperator in an otherwise defector population (respectively, a mutant defector in an otherwise cooperator population) eventually spreads to the entire population and reaches an absorbing state of all cooperators (respectively defectors). We say that selection favors cooperation over defection provided $\rho_C > \rho_D$ (50), meaning that novel cooperative behavior is more likely to overtake defection than conversely.

Cooperation Can Evolve in Strictly Unidirectional Networks. We start by studying whether cooperation can be favored on strictly unidirectional networks, which contain no bidirectional edges. To consider this problem we first recall the key intuition used in prior studies to explain why bidirectional population structures can favor cooperation. In that setting, once a cooperator disperses a strategy to a neighbor, the cooperator will benefit from reciprocity in the next generation, receiving donations from the neighbor. By contrast, if a defector disperses a strategy to a neighbor, the defector will suffer in the next generation and receive nothing from the neighbor. Thus, the formation of "cooperator clusters" and "defector clusters" favors the evolution of cooperation in bidirectional networks (7), which is an example of the more general phenomena of inclusive fitness (5, 6, 57) and reciprocal altruism (58).

This intuition for the effect of population structure on cooperation relies on reciprocity; and so it does not apply in the setting of directed edges, and especially not in the strictly unidirectional setting. For example, in the downstream case, if a cooperative player *i* disperses a strategy along edge w_{ij} to player *j*, then player *j* is unable to reciprocate by donating to *i*, because there is no edge from *j* to *i*. Likewise, a defector who spreads a strategy will not be retaliated against by defection. And so, lacking the mechanism of network reciprocity, we might expect that directed graphs cannot favor the evolution of cooperation.

Despite the simple intuition above, it turns out that strictly unidirectional graphs can indeed favor cooperation. To see this, we start by studying random regular networks as a special case, which facilitates intuition and enables simple analytic equations for the likelihood of alternative evolutionary outcomes. [Our method of analysis can also be applied to arbitrary directed networks, as described in *SI Appendix*, section 2B, although solutions for fixation probabilities in general require solving a system of $O(N^2)$ linear equations.] We prove that in a strictly unidirectional random regular network, where each node has $k/2$ incoming edges and $k/2$ outgoing edges, selection favors the evolution of cooperation if (*SI Appendix*, section 2A)

$$\frac{b}{c} > k - 1 \qquad [4]$$

in the downstream case and

$$\frac{b}{c} > \frac{k(k-1)}{k-2} \qquad [5]$$

in the upstream case, provided the number of nodes *N* is sufficiently large. For finite regular networks we also provide a finite-population correction for the benefit-to-cost ratio that promotes cooperation (*SI Appendix*, section 2C).

Fig. 2 illustrates a simple intuition for this surprising result, by considering how a single mutant cooperator can spread in a population of defectors. Initially, the cooperator has a lower
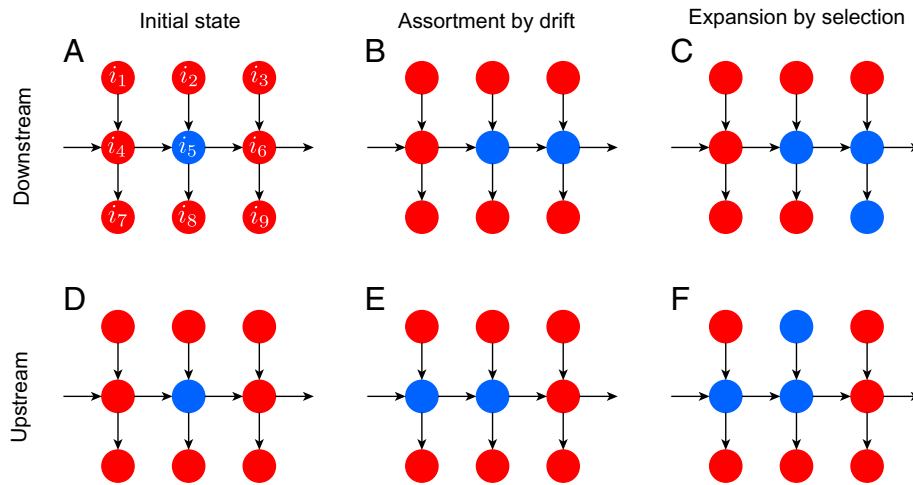
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Fig. 2. The spread of cooperation on unidirectional networks. Shown is how evolution can favor cooperation on a strictly unidirectional graph, initially by positive assortment of cooperative types followed by selective spread of cooperation. In the case of downstream dispersal (*A–C*), a single mutant cooperator (blue circle) occurs in a population of defectors (red circles). Initially, cooperation spreads locally due to stochastic drift, from node i_5 to its downstream neighbor node i_6 (*A* and *B*). After drift establishes a set of assorted cooperative nodes, selection then favors subsequent spread of cooperation. In particular, the donation from node i_5 increases the fitness of i_6 relative to i_6's competitors vying to spread to downstream neighbor i_9, so that selection favors the spread of cooperation from i_6 (*C*). Under upstream dispersal, assortment is established by drift when i_5 spreads i_5's strategy to the upstream neighbor i_4 (*D* and *E*). The donation from node i_4 increases the fitness of cooperator i_5 relative to i_5's competitors, so that selection favors the spread of cooperation from i_5 (*F*). This example illustrates a strictly unidirectional random regular graph of incoming degree 2 and outgoing degree 2, with some nodes not depicted.

reproductive rate than the cooperator's competitors, and cooperation can spread only by stochastic drift. In the case of downstream dispersal, stochastic drift of cooperation to a downstream neighbor serves to increase the neighbor's fitness, which then promotes further downstream spread favored by selection. Whereas for upstream dispersal, cooperation drifts from the initial mutant to an upstream neighbor, which serves to increase the mutant's own fitness so that selection then favors spread to a different upstream neighbor. In both cases, cooperation initially spreads by stochastic drift, causing positive assortment of cooperative nodes, which then favors further spread of cooperation by selection. But the pattern of spread, and the identity of which nodes benefit from early stochastic events, differs in the case of upstream versus downstream dispersal.

We can add quantitative detail to this intuition by considering an individual's expected payoff over the long-term evolutionary process. When an individual dies (or, equivalently, is chosen to update the individual's strategy), all the individual's incoming neighbors in the dispersal network compete to reproduce and spread their strategy to the vacancy (Fig. 3*A*). Cooperation is favored to spread by selection if an incoming cooperative neighbor, such as node i, has a higher expected payoff than an incoming defecting neighbor, j. Our analysis shows that such a cooperative node i has $k/(2(k-1))$ more incoming cooperative neighbors, in a random regular graph, than a defecting competitor j does (*SI Appendix*, Eq. **22**); and so i receives $bk/(2(k-1))$ greater benefit than does j. At the same time, though, the cooperator i pays a cost $ck/2$ along $k/2$ interactions, whereas the defector j avoids these costs. And so the cooperator i's payoff exceeds j's if the net benefit exceeds the cost; i.e., $bk/(2(k-1)) > ck/2$, leading to the condition $b/c > k - 1$. We can analyze the upstream case in an analogous way. The slight difference is that in the upstream case, the cooperator i has $(k-2)/(2(k-1))$ more incoming cooperative neighbors than a defector competitor j has, and so the evolution of cooperation requires a slightly higher benefit-to-cost ratio, $b/c > k(k-1)/(k-2)$.

Cooperation Thrives When Directionality Is Intermediate. Many empirical networks of social interaction exhibit an intermediate proportion of unidirectional edges (32, 34, 35, 37–39). Prior studies on such empirical networks retained only the topology of nodes

and edges and assumed that all interactions are bidirectional (59). A natural question is how a mixture of uni- and bidirectional interactions influences behavioral evolution.

Let p denote the proportion of edges that are unidirectional. In a random regular network with degree k, each node then has $kp/2$ unidirectional incoming edges, $kp/2$ unidirectional outgoing edges, and $k(1-p)$ bidirectional edges. For the sufficiently large network size N and large node degree k, for both downstream and upstream dispersal, we prove that selection favors cooperation over defection provided (*SI Appendix*, section 2A)

$$\frac{b}{c} > \frac{(2-p)^2}{4-3p}k. \qquad [6]$$

When $p = 0$ (a strictly bidirectional network), we recover the well-known condition $b/c > k$ (11). When $p = 1$ (a strictly unidirectional network), we have $b/c > k$, which approximates Eqs. **4** and **5** for large k. In general, though, an intermediate proportion of unidirectional edges, namely $p = 2/3$, minimizes the benefit-to-cost ratio required for selection to favor cooperation (Fig. 4). And so not only is the evolution of cooperation possible on k-regular networks whose edges are all unidirectional, but also in fact cooperation is made easier when an intermediate portion of edges is unidirectional. This finding suggests that prior studies, which assume all interactions are bidirectional, underestimate the capacity for realistic population structures to catalyze cooperation.

Fig. 3*B* provides the key intuition to explain why an intermediate proportion of unidirectional edges is optimal for cooperation. We focus on the downstream case, as the upstream case can be analyzed analogously. Players receive benefits not only from the incoming neighbors connected by unidirectional edges (marked by I), but also from neighbors connected by bidirectional edges (marked by U). Our analysis (*SI Appendix*, Eqs. **46** and **47**) shows 1) the difference $p_{C|C}^{(I)} - p_{C|D}^{(I)}$ exceeds zero and is monotonically increasing with the proportion of directed edges, p, and 2) this probability difference is twice as large for bidirectional edges than it is for unidirectional incoming edges; i.e., $p_{C|C}^{(U)} - p_{C|D}^{(U)} = 2(p_{C|C}^{(I)} - p_{C|D}^{(I)})$. Starting from a strictly bidirectional
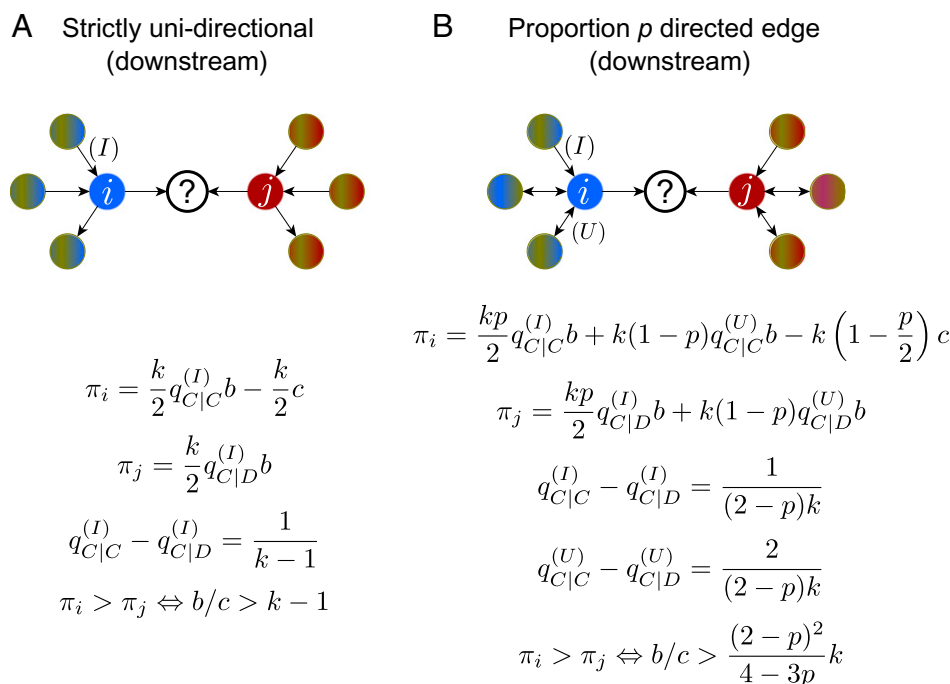
A Strictly uni-directional
(downstream)

B Proportion p directed edge
(downstream)

$$\pi_i = \frac{k}{2}q_{C|C}^{(I)}b - \frac{k}{2}c$$

$$\pi_j = \frac{k}{2}q_{C|D}^{(I)}b$$

$$q_{C|C}^{(I)} - q_{C|D}^{(I)} = \frac{1}{k-1}$$

$$\pi_i > \pi_j \Leftrightarrow b/c > k-1$$

$$\pi_i = \frac{kp}{2}q_{C|C}^{(I)}b + k(1-p)q_{C|C}^{(U)}b - k\left(1-\frac{p}{2}\right)c$$

$$\pi_j = \frac{kp}{2}q_{C|D}^{(I)}b + k(1-p)q_{C|D}^{(U)}b$$

$$q_{C|C}^{(I)} - q_{C|D}^{(I)} = \frac{1}{(2-p)k}$$

$$q_{C|C}^{(U)} - q_{C|D}^{(U)} = \frac{2}{(2-p)k}$$

$$\pi_i > \pi_j \Leftrightarrow b/c > \frac{(2-p)^2}{4-3p}k$$

Fig. 3. Conditions that favor cooperation on directed networks. When an individual updates a strategy, the individual's neighbors such as cooperator i and defector j compete to disperse their strategy into the vacant space (denoted ?). Cooperation is favored to spread only if the payoff to i exceeds the payoff to j, $\pi_i > \pi_j$. Our analysis shows that a cooperator i has a greater chance of having an incoming cooperative neighbor than a defector does: $q_{C|C}^{(I)} > q_{C|D}^{(I)}$ (*SI Appendix*, Eqs. **22 and 46**). (*A*) In a strictly unidirectional network, cooperator i receives benefits from $k/2$ incoming neighbors and pays costs to each of $k/2$ outgoing neighbors; whereas defector j receives benefits from $k/2$ incoming neighbors, but pays no costs—which yields expressions for π_i and π_j. Selection then favors cooperation provided $b/c > k-1$. (*B*) In networks with a proportion p of directed edges, i and j each receive potential benefits from $kp/2$ incoming neighbors connected by unidirectional edges (*I*) and from $k(1-p)$ neighbors connected by bidirectional edges (*U*); and cooperator i pays costs to $k(1-p/2)$ neighbors. Selection favors cooperation provided $b/c > (2-p)^2k/(4-3p)$. Shown are payoff expectations in the downstream case, for large k.

graph ($p = 0$), converting some edges to unidirectional ($p > 0$) increases $p_{C|C}^{(U)} - p_{C|D}^{(U)}$, thereby increasing the benefit that a cooperator obtains from bidirectional neighbors. But as the proportion of unidirectional edges increases yet further, the total number of bidirectional edges decreases and this reduces the net benefit that the cooperator receives from cooperative neighbors. As a result of these two opposing effects, an intermediate pro-

portion of unidirectional edges is optimal: $p > 0$ increases the chance that a cooperator's neighbors are cooperators, whereas $p < 1$ maintains a sufficient number of bidirectional neighbors.

Our analysis of k-regular graphs shows that directed interactions can stimulate cooperation, but these results do not account for population heterogeneity, which is common in human social networks. To address this, we proceed to investigate four classes
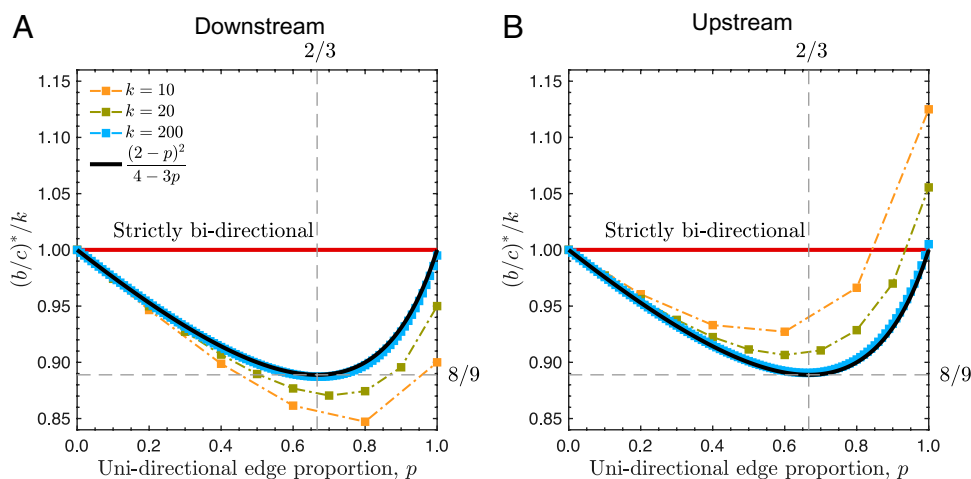

Fig. 4. An intermediate proportion of unidirectional edges is optimal for cooperation. We consider random regular networks with a proportion p of unidirectional edges. Each node has $kp/2$ incoming edges, $kp/2$ outgoing edges, and $k(1-p)$ bidirectional edges. *A* and *B* display the critical benefit-to-cost ratio $(b/c)^*$ required to favor cooperation, as a function of the unidirected edge proportion p and scaled by node degree k. Colored squares represent numerical results for arbitrary k (see *SI Appendix*, Eq. **37** for the downstream case and *SI Appendix*, Eq. **41** for the upstream case). The black line plots a simple analytic expression (Eq. **6**) that holds in the limit of large k, where cooperation is easiest to evolve for $p = 2/3$. The red line indicates the critical ratio for a strictly bidirectional network (11), $(b/c)^* = k$.

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of heterogeneous networks: random regular networks in which nodes can have different numbers of incoming, outgoing, and bidirectional edges; random networks; small-world networks; and scale-free networks (*SI Appendix*, Fig. S1). For each class, we generate bidirectional networks of various average node degree $\bar{k}$, and then we randomly convert a proportion p of edges to be unidirectional. For all four classes of heterogeneous networks, we find that an intermediate proportion of directed edges is most beneficial to cooperation, for both downstream and upstream strategy dispersal (see *SI Appendix*, section 2B for the calculation of benefit-to-cost ratios on any directed network). For example, on a strictly bidirectional network ($p = 0$), if cooperation is favored for some benefit-to-cost ratio, increasing p will decrease the ratio required for the evolution of cooperation. Some strictly bidirectional networks disfavor cooperation altogether, regardless of the benefit-to-cost ratio, or they may even favor the evolution of spite, a kind of antisocial behavior in which an individual pays a cost to hurt others. Even on strictly bidirectional networks that disfavor cooperation altogether, we find that converting some bidirectional edges to unidirectional can rescue cooperation. Overall, for all four classes of heterogeneous networks we study, the optimal proportion of directed edges to facilitate cooperation is close to 2/3, as in the case of random regular networks.

Edge Orientation Matters. Our analyses of random regular networks have assumed a homogeneous distribution of directional edges pointing toward or away from each node. Under this assumption, as Eq. **6** indicates, the benefit-to-cost ratio required to promote cooperation depends only on the node degree ($\bar{k}$) and the proportion of edges that are unidirectional (p). In general, though, some nodes may have a larger proportion of incoming edges than other nodes, and the local structure of edge orientations may determine the evolutionary outcome. In this section we explore the strategic assignment of edge orientations, to understand how this feature of network topology influences the evolution of cooperation. In particular, we identify two key network motifs—one relevant in the upstream case and one in the downstream case—that depend on edge orientation and strongly influence the fate of cooperation on directed networks.

We focus our analysis on strictly unidirectional networks, paying attention now to the orientation of each edge. Let k_i denote node i's degree, including $k_i^{(I)}$ incoming edges and $k_i^{(O)}$ outgoing edges; i.e., $k_i = k_i^{(I)} + k_i^{(O)}$. In the downstream case, where strategies spread in the same direction as game interactions, we consider the motif of "triangular cycles," such as $i \to j \to \ell \to i$ (Fig. 5A). For node i, the number of such triangular cycles is $\sum_{j,\ell} w_{ij} w_{j\ell} w_{\ell i}$. We normalize the number of such triangles through node i by its maximal value, given the node's in-degree and out-degree, and define the quantity

$$\mathcal{C}_1 = \frac{\sum_{i,j,\ell} w_{ij} w_{j\ell} w_{\ell i}}{\sum_i k_i^{(I)} k_i^{(O)}} \qquad [7]$$

to measure the (normalized) frequency of triangular cycles in the directed network. A large value of $\mathcal{C}_1$ means there is a large frequency of triangular cycles, given the incoming and outgoing node degrees.

In the upstream case, where strategies spread in the opposite direction to game interactions, we consider the motif of "in-in pairs," such as $j \to i$ and $\ell \to i$ for node i in Fig. 5D. For node i, the number of in-in pairs is $k_i^{(I)} \left(k_i^{(I)} - 1 \right)$. We normalize the number of such in-in pairs by the total number of edge pairs for node i and define the quantity

$$\mathcal{C}_2 = \frac{\sum_i k_i^{(I)} \left(k_i^{(I)} - 1 \right)}{\sum_i k_i (k_i - 1)} \qquad [8]$$

to measure the global frequency of in-in pairs in the directed network. A large value of $\mathcal{C}_2$ means there is a large frequency of in-in pairs, given the incoming and outgoing node degrees.

For downstream dispersal, edge orientations that produce a large proportion of triangular cycles are beneficial to the evolution of cooperation (Fig. 5 B and C). Whereas a directed network with random orientations may require a very high benefit-to-cost ratio for cooperation, adjusting only edge directions (reversing orientations of existing directed edges) to increase the frequency of triangular cycles ($\mathcal{C}_1$) can markedly decrease the benefits required for cooperation (Fig. 5B). Furthermore, even when a directed network with random orientations disfavors cooperation altogether, for any benefit-to-cost ratio, adjusting edge orientations to increase triangular cycles can rescue cooperation (Fig. 5C).

In-in pairs have analogous, beneficial effects on cooperation in the case of upstream strategy dispersal (Fig. 5 E and F). Moreover, the effects of triangular cycles and in-in pairs, in the downstream and upstream contexts, respectively, persist across a large sample of regular, random, and directed networks with a mixture of uni- and bidirectional edges and even when connections are sparse (*SI Appendix*, section 3 and Figs. S2–S4). The only counterexample occurs when heterogeneity in node degree is extremely large (such as a heavy-tailed degree distribution), which mitigates the cooperation-promoting effects of triangular cycles in the downstream setting.

There is a simple intuition for why triangular cycles promote cooperation in the downstream setting and in-in pairs promote cooperation in the upstream setting. Although immediate reciprocity is impossible on a strictly unidirectional network, in the downstream case the triangular cycle $i \to j \to \ell \to i$ allows cooperator i to receive reciprocity via two-step strategy dispersal: Cooperation spreads from i to downstream neighbor j, and then i's donation to j supports further spread of cooperation to j's downstream neighbor ℓ, who in turn reciprocates i's cooperative behavior. This effect is second best to pairwise reciprocity, and orienting edges to produce triangular cycles proves to be efficient for promoting cooperation. In the upstream case, by contrast, the triangular cycle does not favor cooperation: After cooperation spreads from i to an upstream neighbor ℓ, ℓ gains no fitness advantage to facilitate further spread. Instead, node i benefits from the newly cooperative neighbor ℓ, which serves to attract other incoming neighbors of i to imitate i's cooperative trait. Therefore, a larger number of incoming neighbors to a cooperative node, corresponding to more in-in pairs, facilitates the spread of cooperation under upstream dispersal.

The two motifs, triangular cycles and in-in pairs, are often mutually exclusive. Reorienting edge directions to increase the frequency of triangular cycles, $\mathcal{C}_1$, tends to decrease the frequency of in-in pairs, $\mathcal{C}_2$, and vice versa (Fig. 6A and *SI Appendix*, Fig. S5). Fig. 6 B–D illustrates three directed networks with various frequencies of these motifs, while also showing each node's in-degree relative to its total degree $k_i^{(I)}/k_i$ (*SI Appendix*, Fig. S5). As these examples illustrate, when edge orientations are optimized to increase the frequency of triangular cycles (Fig. 6C), this has the effect of homogenizing the in-degree and out-degree across the network. Whereas optimizing the frequency of in-in pairs (Fig. 6D) leads to extreme heterogeneity in the in-degree/total-degree ratios across nodes—so that a few nodes serve primarily as sources, and a few nodes serve primarily as sinks. These qualitative observations provide some intuition into what features of degree heterogeneity across a directed network are likely to stimulate cooperation, for the downstream case of strategy imitation (homogeneous in-degrees) or the upstream case (heterogeneous in-degrees).

Aside from the two extreme cases of strictly upstream or strictly downstream strategy dispersal, we have also investigated their combination: bidirectional dispersal. Directed social
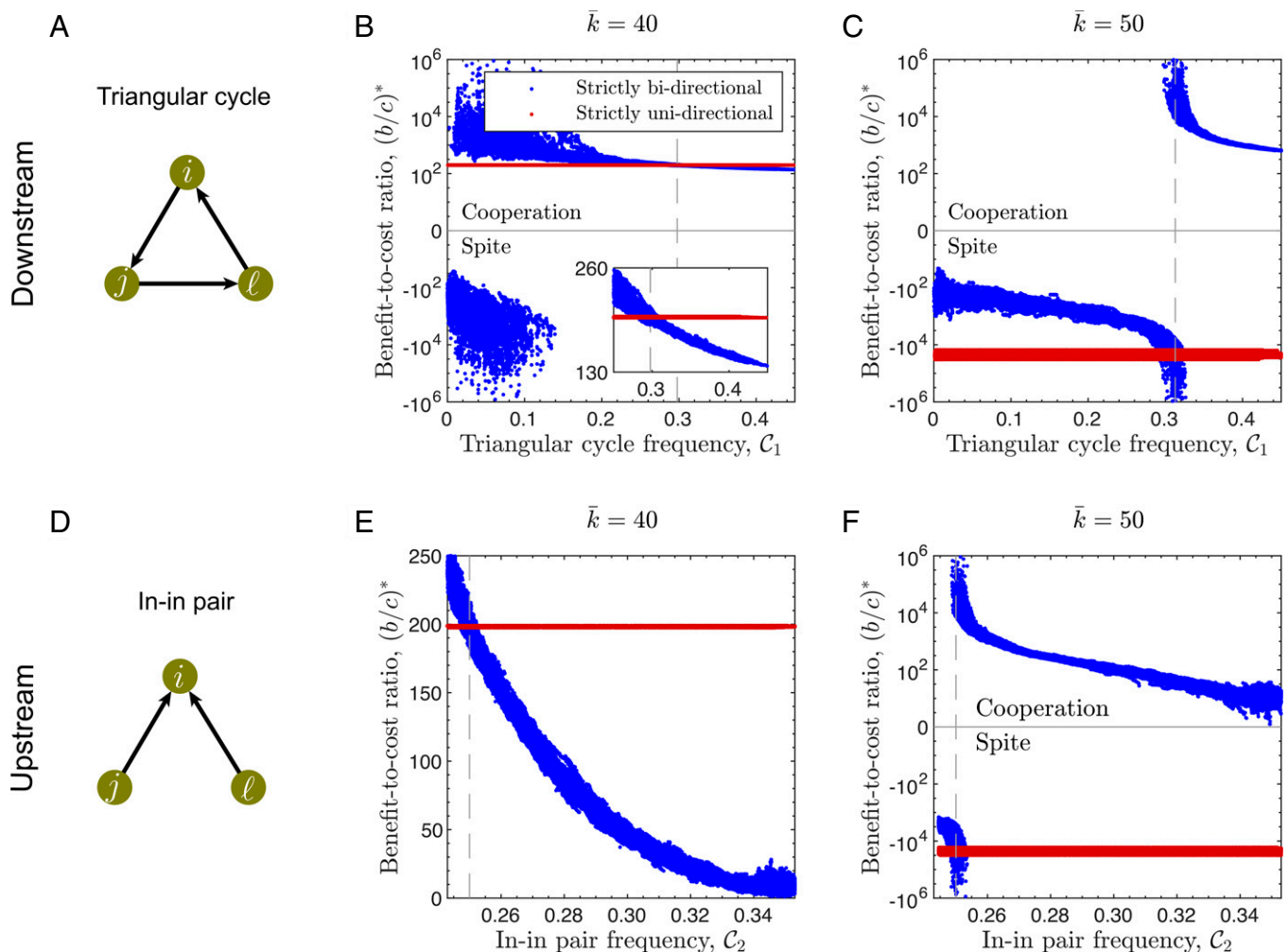
Fig. 5. Network motifs that facilitate cooperation. We study two network motifs: the triangular cycle in the case of downstream behavioral dispersal (*A*) and the in-in pair in the case of upstream dispersal (*D*). We plot the critical benefit-to-cost ratio required to favor the evolution of cooperation as a function of the frequency of these motifs, C_1 (*B* and *C*) and C_2 (*E* and *F*). In each case, we start with a strictly bidirectional Watts–Strogatz small-world network (60) generated with rewiring probability 0.1, and we plot the critical ratio in red. We convert all edges to unidirectional, assigning random orientations, and plot the resulting frequency of motifs (vertical dashed lines). By systematically adjusting edge orientations we can either increase or decrease the motif frequencies, C_1 and C_2. A high frequency of triangular cycles facilitates cooperation in the downstream case; and a high frequency of in-in pairs facilitates cooperation in the upstream case. In some cases the network favors the evolution of spite, as indicated by a negative value of $(b/c)^*$; adjusting edge directions to increase motif frequency can often rescue cooperation in such cases. Shown are results for 100 sampled Watts–Strogatz networks, each with $N = 100$ nodes. For each network, we explore 10,000 motif frequencies by adjusting edge orientations.

interactions (that is, directed game play) still promote cooperation in this setting (*SI Appendix,* Fig. S6), and we find that, here, the in-in pair motif is more important than the triangular cycle: Increasing the number of in-in pairs reduces the benefit-to-cost ratio for cooperative spread and it can even rescue cooperation from spite.

In addition to triangular cycles and in-in pairs, we find another simple motif called an "acyclic triangle" that can strongly influence the evolution of cooperation. An acyclic triangle refers to the structure $i \rightarrow j \rightarrow \ell \leftarrow i$ (*SI Appendix,* Fig. S7A). Unlike triangular cycles or in-in pairs, a high frequency of acyclic triangles inhibits cooperation, for both downstream and upstream strategy dispersal (*SI Appendix,* Fig. S7 *B* and *C*)—a phenomenon that is predicted by our approximate condition on finite regular networks (*SI Appendix,* section 2C). This result is also intuitive, because, if a cooperator i and defector j compete for a vacant node ℓ, i's donation to j weakens i's advantage over i's competitor j.

Finally, we investigated directionality and strategic evolution on 14 empirical social networks (*SI Appendix,* section 4). These networks were assembled from social surveys on friendship nominations among high school students in the National Longitudinal Study of Adolescent Health (32), data on physical visitations among families in a Costa Rican town (61), surveys of friendship ratings on a university campus (41), the referral network among a sample of physicians in Illinois (35), and the follower network among a sample of Twitter users (42). The proportion of unidirectional edges is substantial in these empirical networks of social interactions—ranging from $p = 45\%$ to $p = 80\%$. Moreover, as a result of the topology of these empirical networks, cooperation in the donation game would evolve more readily on such networks, for either upstream or downstream strategic spread, compared to a process that ignores directionality and treats all edges as bidirectional.

Discussion

Population structure has long been recognized as a catalyst for cooperation that cannot otherwise spread in a well-mixed society. And yet most theoretical analysis of this effect has assumed bidirectional social interactions, even though actual human interactions are often unidirectional. Directionality arises
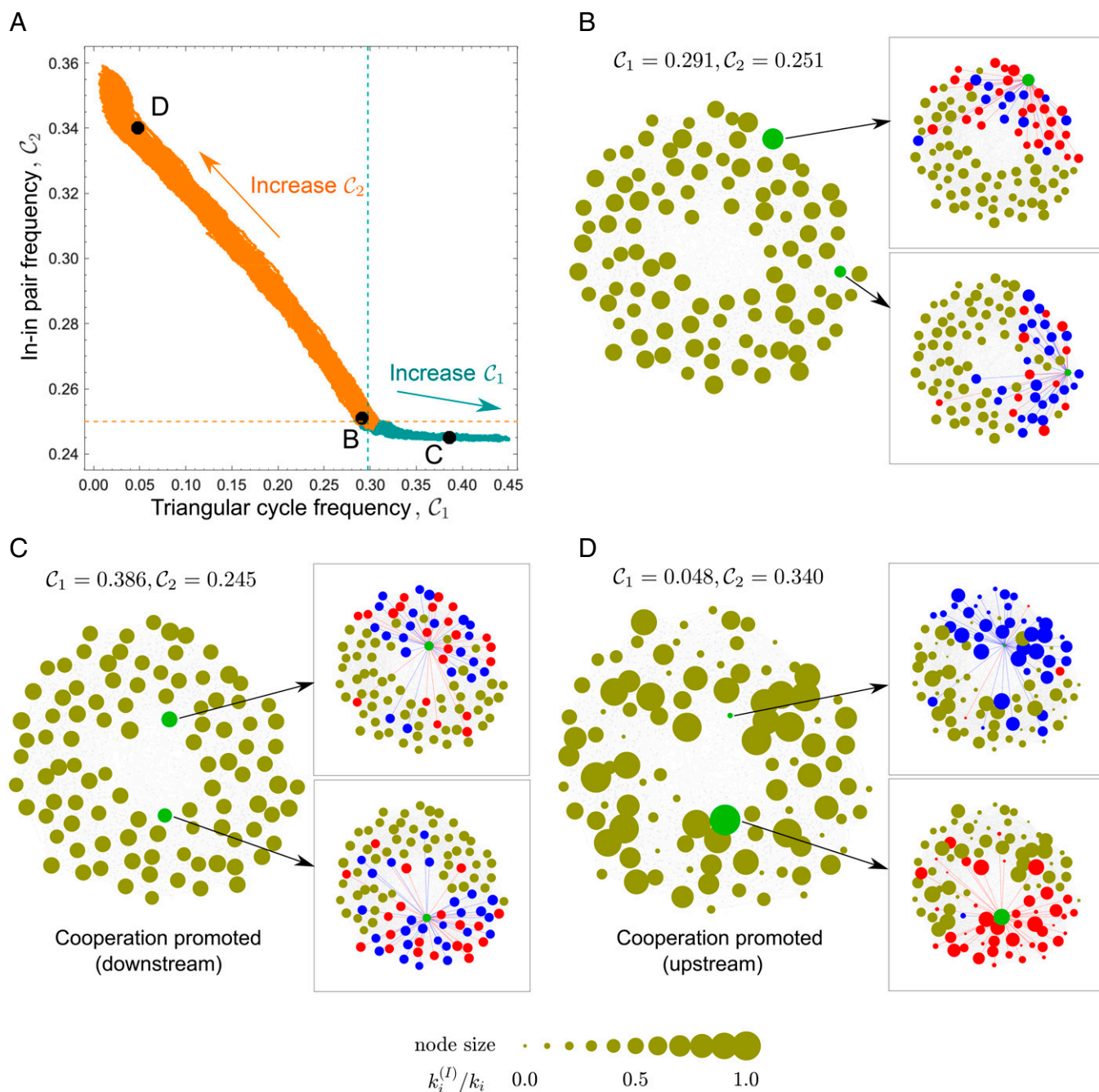
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Fig. 6. Motif frequency and node degrees. We generated 100 Watts–Strogatz small-world networks (60) with size $N = 100$, average degree $\bar{k} = 40$, and rewiring probability 0.1. (*A*) After making all edges unidirectional and assigning random orientations, we measured the frequency of triangular cycles and in-in pairs (vertical and horizontal dashed lines). We then modified edge directions either to increase $\mathcal{C}_1$ (teal) or to increase $\mathcal{C}_2$ (orange), recording both $\mathcal{C}_1$ and $\mathcal{C}_2$, which are anticorrelated. *B*–*D* illustrate three example networks with intermediate, high, and low frequency of triangular cycles, as indicated on the network of *A*. For each example network, the displayed size of each node i is proportional to its in-degree relative to its total degree, $k_i^{(I)}/k_i$. In each network, the connections of two representative nodes (green circle) are highlighted, with red circles denoting incoming neighbors and blue circles outgoing neighbors. A large frequency of triangular cycles is associated with homogeneity of in-degree/out-degree (*C*), and this tends to promote cooperation under downstream behavioral dispersal (Fig. 5 *A*–*C*). Whereas a large frequency of in-in pairs is associated with heterogeneity of in-degree/out-degree (*D*), and this tends to promote cooperation in the case of upstream dispersal (Fig. 5 *D*–*F*).

in real-life settings as the result of organizational hierarchy, social stratification, and popularity effects, as well as endogenous mechanisms of network growth in, e.g., online social networks. But the impact of directed interactions for cooperation has not been thoroughly studied, by either theoretical analysis or empirical experimentation. One reason why directionality may have been neglected is that, a priori, unidirectional interactions

would seem to only impede cooperation, because they remove the possibility of pairwise reciprocity (5–7).

Our results contravene the simple intuition that directionality should impede cooperation. Even though it disrupts reciprocity, we have proved analytically that cooperation can be favored to evolve in populations with strictly unidirectional social interactions and directional spread of behavior. This analysis is based

on the same theoretical framework and assumptions that have been widely applied to study the emergence of cooperation in bidirectional social structures (11, 62). The intuitive explanation for our results rests on the initial spread of an altruistic mutant by stochastic drift, which produces assortative pairs of cooperators who then facilitate further spread by selection. The pattern of spread, however, and whether early stochastic events benefit the initial mutant or the mutant's one-step neighbor depend on whether strategy dispersal is upstream or downstream. The same basic intuition explains why prosocial spread is optimized for an intermediate proportion of unidirectional edges. And so our analysis reflects, in a directed setting, how the algebra of assortativity drives the evolution of cooperation (63).

Our analysis is based on the assumption of weak selection, where payoffs derived from game interactions have only a small effect on imitation dynamics and strategic spread. Weak selection increases the relative strength of stochastic drift, which is beneficial during the initial stage of cooperative spread. A sole cooperator has a lower payoff than nearby defectors, and therefore spread relies on drift at the initial stage (Fig. 3 *A* and *B*). However, once positive assortment among cooperators is established by drift, further cooperative expansion is favored by selection (Fig. 3 *B* and *C*), and stronger selection would favor it more readily. And so, in total, the long-term prospects for cooperation depend on the balance of these two opposing effects. Our simulations under moderate selection show that analytic predictions derived under weak selection are accurate, including both the critical benefit-to-cost ratio and the fixation probability of cooperators (*SI Appendix*, Fig. S8). And the qualitative prediction that asymmetric interactions favor cooperation holds even under yet stronger selection (*SI Appendix*, Fig. S8). Our analysis offers a fairly complete understanding of how directed network structures influence the chance of absorption in either all cooperation or all defection. The time required to reach this absorbing state, however, remains a difficult mathematical problem, even in the limit of weak selection. Although we conjecture that downstream dispersal will lead to more rapid absorption, this topic remains an open question for future research. Likewise, the dynamics under alternative imitation processes, such as birth–death or pairwise comparison, remain open areas for future study.

Recent, systematic study of bidirectional networks has found that cooperation will be disfavored, regardless of the benefit-to-cost ratio, for roughly 60% of networks of size $N = 6$ nodes (16) and likewise for large portions of large networks as well (64). Many of these networks even favor the evolution of spite (16). Yet we have found that, even for such networks, conversion of some bidirectional edges to unidirectional can rescue cooperation. An important implication is that asymmetric interactions provide an alternative method of modifying population structure to promote cooperation—besides severing old ties and building new ones, as has been explored in the bidirected setting (16, 20, 59) (*SI Appendix*, Fig. S9). In particular, we have identified two specific structural motifs, triangular cycles for downstream behavior dispersal and in-in pairs for upstream dispersal, that efficiently guide structural modifications to favor the spread of cooperative behavior.

Our results on structural motifs are reminiscent of seminal work on social hierarchies by Chase (29, 31). Using experiments on hens, Chase showed how double-dominance and double-subordinance relationships serve as microfoundations for social stratification (29, 31). Davis (26), Holland and Leinhardt (27, 30), Davis and Leinhardt (28), and Faust (33) introduced a typology of 16 different triads, based on three kinds of pairwise relationships—mutual reciprocal action, asymmetric action, and nonreciprocal action. Although their classification scheme does not precisely map onto game-theoretic models in networked populations (which lack the "no-action" relationship), we can

compare our definitions of triangular cycle and in-in pair to the typology of Holland and Leinhardt (27, 30). Our definitions are broader than those of Holland and Leinhardt (27, 30) because a triangular cycle in our sense refers to all triads of nodes containing the motif $i \to j \to \ell \to i$, including possibly other directed edges. This definition comprises four different triads in Holland and Leinhardt's (27, 30) classification (*SI Appendix*, Fig. S10*A*); likewise, our in-in pair occurs in nine different triads under Holland and Leinhardt's (27, 30) typology (*SI Appendix*, Fig. S10*B*).

Several prior studies have considered the role of directionality in population structure on the spread of mutant types (65–68). But in those studies the fitness advantage of the mutant is fixed, independent of type frequency. By contrast, our study considers frequency-dependent fitness effects that therefore describe game-theoretic interactions: An individual's payoff depends on both the individual's type and the neighbors' types. The question of directionality in models of social behavior has been analyzed in at least one prior paper (10), but only in the case of two specific networks: a directed circle network, where each node has one incoming neighbor and one outgoing neighbor, and a superstar network (10). In those two cases the effect of directionality is to repress cooperation. But our analysis applies to arbitrary directed network structures and we find that, in general, directionality tends to favor cooperation.

Our results reveal the importance of directed interactions for the long-term prospects of cooperative behavior in a population. Our analysis also highlights an interesting relation between the direction of social interactions and the direction of behavioral spread (or dispersal). We have focused on two opposite extremes: downstream dispersal, in which behavior spreads in the same direction as directed social interactions, and upstream dispersal, in which behavior spreads in the opposite direction. The former is roughly analogous to generalized reciprocity—a player who received help from another player feels motivated to help the third player in turn (55). This mode of dispersal is also reminiscent of the asymmetric interactions between parents and their offspring (69). Whereas upstream dispersal is roughly analogous to indirect reciprocity—the player who helped another player receives a benefit from a third party (56). Despite these similarities, the form of reciprocity arising from directed dispersal of behavior differs from generalized reciprocity and from indirect reciprocity: The dispersal mechanism is payoff dependent while the latter mechanisms are action dependent. A synthetic understanding of reciprocity based on conditional behavior versus reciprocity achieved by payoff-biased imitation remains an important topic for future research.

Materials and Methods

Complete derivations of our mathematical results are detailed in *SI Appendix*, section 2. We briefly outline these derivations below.

Analysis of Asymmetric Games on Random Regular Networks. The population structure is described by a directed, unweighted random regular network with degree k, with a proportion p of unidirectional edges. Each node has $kp/2$ incoming edges, $kp/2$ outgoing edges, and $k(1 - p)$ bidirectional edges. The payoff structure for a general asymmetric game along a directed edge w_{ij} is

$$\begin{array}{cc} & \begin{array}{cc} A & \quad B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a_1, a_2 & b_1, b_2 \\ c_1, c_2 & d_1, d_2 \end{pmatrix}. \end{array} \qquad [9]$$

The entry (X, Y) in the payoff matrix means that when the source node (i) uses the strategy in the row and the target node (j) uses the strategy in the column, the former obtains payoff X and the later obtains payoff Y. Using a pair approximation and associated diffusion process (*SI Appendix*, section 2A), for sufficiently large node degree k and population size N, we prove that selection favors the A strategy over the B strategy if

$$\left[(2 - p)^2 k - 6 + 2p \right] (a_1 - d_1 + a_2 - d_2)$$
$$+ \left[(2 - p)^2 k - 14 + 8p \right] (b_1 - c_1 - b_2 + c_2) > 0, \qquad [10]$$

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for both downstream and upstream dispersal. For the donation game, the payoff structure is

$$
\begin{array}{cc}
 & \begin{array}{cc} C & D \end{array} \\
\begin{array}{c} C \\ D \end{array} & \begin{pmatrix} -c,b & -c,b \\ 0,0 & 0,0 \end{pmatrix},
\end{array}
\tag{11}
$$

and selection favors cooperation over defection if

$$
\frac{b}{c} > \frac{(2-p)^2}{4-3p}k.
\tag{12}
$$

Analysis of Donation Games on Arbitrary Networks. We apply the method of ref. 21 to derive conditions for the evolution of cooperation on arbitrary directed networks, with independent structures for interactions and strategy dispersal. Let $w_{ij}^{[1]}$ (respectively $w_{ij}^{[2]}$) denote the edge weights for the interaction (respectively dispersal) network. The downstream case corresponds to a structure with $w_{ij}^{[2]} = w_{ij}^{[1]}$ for all $i,j \in \mathcal{N}$; and the upstream case corresponds to a structure with $w_{ij}^{[2]} = w_{ji}^{[1]}$.

Let $p_{ij} = w_{ji}^{[2]} / \sum_\ell w_{\ell i}^{[2]}$ and π_i denote the probability that a mutant at node i will eventually fix in the population under neutral drift. As described in *SI Appendix*, section 2B, we can obtain π_i by solving $\sum_i \pi_i = 1$ and $\pi_i = \sum_j p_{ji}\pi_j$. The condition for cooperation also involves the coalescence times τ_{ij}, obtained by solving the linear system of equations

$$
\tau_{ij} = \begin{cases} 1 + \frac{1}{2}\sum_{k\in\mathcal{N}} p_{ik}\tau_{kj} + \frac{1}{2}\sum_{k\in\mathcal{N}} p_{jk}\tau_{ik} & i \neq j, \\ 0 & i = j. \end{cases}
\tag{13}
$$

The critical cost–benefit ratio is given by

$$
\left(\frac{b}{c}\right)^* = \frac{v_2}{u_2 - u_0},
\tag{14}
$$

where

$$
\begin{aligned}
u_0 &= \sum_{i,j,\ell \in \mathcal{N}} \pi_i p_{ij} \tau_{j\ell} w_{\ell j}^{[1]}, \\
u_2 &= \sum_{i,j,k,\ell \in \mathcal{N}} \pi_i p_{ij} p_{ik} \tau_{j\ell} w_{\ell k}^{[1]}, \\
v_2 &= \sum_{i,j,k,\ell \in \mathcal{N}} \pi_i p_{ij} p_{ik} \tau_{jk} w_{k\ell}^{[1]}.
\end{aligned}
\tag{15}
$$

Data Availability. All study data are included in this article and/or *SI Appendix*.

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