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Collapse and rescue of cooperation in evolving dynamic networks

Erol Akçay
Department of Biology, University of Pennsylvania

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Address: 433 S University Avenue, Philadelphia, PA, 19104
Phone: (215)-573-6601
Email: eakcay@sas.upenn.edu
ORCID ID: 0000-0001-8149-7124

Abstract

The evolutionary dynamics of social traits depend crucially on the social structure of a population, i.e., who interacts with whom. A large body of work studies the effect of social structure on behaviors such as cooperation, but relatively little is known about how social structure itself coevolves with social traits. Here, I use a simple yet realistic model of within-group social structure to study such coevolution. In this model, social connections are either inherited from a parent or made with random individuals. My model shows cooperation can evolve when individuals make few random connections, but the presence of cooperation selects for increased rates of random connections, which leads to the collapse of cooperation. Inherent costs of social connections can prevent this negative feedback, but the more beneficial cooperation is, the higher linking costs have to be maintain it, and linking costs can negate some or all of the aggregate benefits of cooperation. Exogenously maintained social inheritance can mitigate the latter problem and allow cooperation to persist and increase the average fitness of a population. These results illustrate how coevolutionary dynamics can constrain the long-term persistence of cooperation.

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Introduction

Cooperation is easy to evolve. In the last half century, we have discovered that there are myriad ways natural selection can favor organisms providing benefits to each other. These pathways include population structure [1], phenotypic feedbacks [2, 3], payoff synergies [4], partner choice [5], among others [e.g., see reviews in 6–8]. When operating together, these pathways to cooperation can reinforce [6, 9–11] or counteract each other [12]. This extensive literature overwhelmingly tries to explain how cooperation can persist in the face of conflicts of interests. But with so many ways cooperation might be selected for, it is worth asking why cooperation is not even more prevalent.

The answer to this question lies in how the conditions leading to cooperation themselves evolve, i.e., how selection acts on the setting in which the interaction takes place [i.e., the payoff structure, interaction network, etc. 13, 14], and how the setting coevolves with cooperation. This question has recently been garnering attention. An emerging common thread is that these coevolutionary processes might impose inherent limits to the maintenance of cooperation in the long term. For example, in a model of evolution of incentives for cooperation, Akçay and Roughgarden [14] showed that incentives that favor cooperation may invade but not fix, leading to stable polymorphisms where cooperation and defection are both maintained in the population. In another model of payoff evolution, Stewart and Plotkin [15] showed a different kind of dynamic self-limitation: when cooperation is established in the population, it tends to drive the evolution of payoffs for cooperation so high that the temptation for defecting becomes overwhelming, leading to the collapse of cooperation. In a model incorporating environmental feedbacks that affect the payoffs, Weitz et al. [16] showed that negative feedbacks between social strategies and environmental variables that favor them can create oscillations between cooperative and non-cooperative outcomes. More recently, Mullon et al. [17] showed that in settings where dispersal and cooperation coevolves, selection might result in stable polymorphisms where non-cooperators persist by evolving higher dispersal rates.

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One major factor in the evolution of cooperation is the social structure of groups (i.e., who interacts with whom), represented by social networks [18, 19]. Social networks and variation in individuals' positions in them are shown to affect important life history traits such as reproductive success [20], survival [21, 22], infant survival [23], as well as selection on particular behaviors [24], and resilience of social groups [25]. Yet despite the emerging evidence about the importance of dynamic fine-scale social structure, it has not yet been integrated fully into social evolutionary theory, where most models deal with special kinds of networks [e.g., lattice structured, 26], fixed networks [27–29], dynamic networks with random connections [30, 31], or shifting connections amongst a fixed set of individuals [32–34]. A recent study by Cavaliere et al. [35] comes closest to the current work: they model the evolution of cooperation on a dynamic heterogenous network structured by pure social inheritance (as defined below), though without a feedbacks between the evolutionary dynamics of social structure and cooperation (see Discussion for more). Although each of these modeling approaches capture important aspects of how population structure affects cooperation, we know relatively little about how social traits might evolve in more realistic dynamic social networks, and how these traits might feed back on the structure of networks.

This gap is in part caused by the lack of a generally applicable model for network dynamics that can capture important features of social networks and variation therein. Recently, Ilany and Akçay [36] proposed such a model, where social ties are formed by a mixture of individuals "inheriting" connections from their parents, i.e., connecting to their parents' connections, and randomly connecting to others. They showed that this simple process of social inheritance can capture important features of animal networks such as their degree and clustering distributions as well as modularity. Importantly, the animal networks investigated by Ilany and Akçay tended to have relatively high probabilities of social inheritance, while having low (but non-zero) probability of random linking. These findings suggest that the social inheritance process is a good candidate for modeling the fine-scale dynamics of animal social networks and the evolution of social behaviors on them. Importantly, they raise the question of how social inheritance af-

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fects the evolutionary dynamics of social behaviors, and how social inheritance coevolves with these behaviors.

In this paper, I present a computational model of the evolution of a cooperative behavior on a dynamic network that is assembled through social inheritance. I find that cooperation evolves when the probability of random linking is low, mostly independently of the probability of social inheritance. However, when these two linking probabilities themselves coevolve with cooperation, I show that in cooperative populations, probabilities of random linking are selected to increase, which in turn leads to the collapse of cooperation. This result highlights a new way in which some forms of cooperation can inherently be self-limiting. I then show that costs of making and maintaining social links can counteract the self-limiting feedback through the evolution of social structure. At the same time, costly links lead to unexpected non-monotonic patterns in long-term frequency of cooperation. Overall, my results shed light on new kinds of evolutionary feedbacks between traits that structure social networks and the social behaviors that evolve on them.

Model

My model builds on Ilany and Akçay's [36] by adding selection caused by social interactions on a dynamic, binary, and undirected network. I assume a death-birth process, where at each time step, a random individual is selected to die, and another individual is selected to reproduce to replace them. The newborn individual makes social connections as follows: (i) it connects to its parent with certainty, (ii) it connects to other individuals that are connected to its parent (at the time of birth) with probability p_n and (iii) it connects to other individuals that are not connected to its parent (at the time of birth) with probability p_r. Ilany and Akçay [36] showed that this basic model (with no selection) can capture important aspects of social structure in the wild. In my first model, p_n and p_r are fixed and are the same for every individual. Then, I let the linking probabilities p_n and p_r be heritable and vary between individuals, so that they evolve according to their fitness

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consequences.

Social interaction and fitness

To add selection caused by social interactions, I assume that each individual can be of one of two types: cooperators and defectors. Cooperators provide a benefit B to their partners (those that are connected to them on the network), distributed equally amongst all partners. In other words, if a given cooperator individual has d connections, each of its partners acquire a benefit B/d from it. Cooperators also pay a fixed cost C, regardless of the number of type of their connections. This game is a special case of the "coauthor game" of Jackson and Wolinsky [37]. Intuitively, it represents an interaction where cooperators have a fixed time or energy budget to help others [e.g., by spending time grooming –or writing papers with– others 38], and that this benefit is divided equally amongst an individual's connections. Defectors pay no cost of helping, provide no benefits, but benefit from the cooperators they are connected to. Finally, I allow the possibility that there is negative or positive synergism between cooperators, such that when two cooperators interact, their payoff is incremented by $D/(d_i d_j)$, where D is the synergistic benefit. Thus, the payoff of an individual i at time-step t, $u_i(t)$, is given by:

$$u_i(t) = \sum_{j \neq i} p_j a_{ij} \left(\frac{B}{d_j(t)} + p_i \frac{D}{d_i(t) d_j(t)} \right) - p_i C \ , \tag{1}$$

where $p_j \in \{0, 1\}$ is the frequency of the cooperator allele in individual j, $a_{ij} = 1$ if i and j are connected, and 0 otherwise, and $d_j(t)$ is the degree (number of connections) of player j at time t. An individual with payoff u_i has fitness w_i, given by:

$$w_i = (1 + \delta)^{u_i} \ , \tag{2}$$

where $\delta > 0$ is the strength of selection.

An alternative to this payoff structure can be imagined where cooperators sup-

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ply a constant benefit per link. The realism of constant total or constant per link benefits depend on the absolute magnitude of benefit and the variation in degree one observes in the networks. If variation in degree is high [as happens, for example, when social inheritance is high 36], then it is less realistic to assume individuals can ramp up production of benefits indefinitely with partner numbers such that each partner continues to enjoy the same benefit. Thus, I focus on the fixed total benefit model in the main text, and present in the Supplementary Material SI–2, results for the case where cooperators provide a fixed benefit to each partner and pay a fixed cost per partner.

I assume deaths occur randomly, independent of payoff or social network position. The probability of a given individual being selected to reproduce at a given time step, $\pi_i(t)$, is proportional to their fitness in the preceding time step, $w_i(t-1)$:

$$\pi_i(t) = \frac{w_i(t-1)}{\sum_j w_j(t-1)} \tag{3}$$

At each reproduction event, the offspring copies its parent's cooperation type with probability $1-\mu$; with probability μ, the offspring switches to the other type. The cooperation type of an individual remains unchanged during their lifetime.

Evolution of linking probabilities

To model the coevolution of the linking probabilities p_n and p_r with cooperation, I let them vary between individuals, and be genetically inherited from parents. With probability μ_l, each of the p'_n and p'_r of the offspring (independently) undergo mutation, whereupon they become $p'_n = p_n + \epsilon_n$, and $p'_r = p_r + \epsilon_r$, where p_n and p_r denote the parent's linking probabilities, and ϵ_n and ϵ_r are distributed normally with mean zero and standard deviation σ_n and σ_r, respectively. To restrict p_n and p_r to the unit interval $[0, 1]$, I set the numerical values to be at the relevant boundary if mutations fall outside this range.

To investigate how costs of making and maintaining social connections can

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alter the coevolutionary dynamics, I use the following extended payoff function:

$$u_i(t) = \sum_{j \neq i} p_j a_{ij} \left(\frac{B}{d_j(t)} + p_i \frac{D}{d_i(t) d_j(t)} \right) - p_i C - d_i(t) C_{\text{link}} \,, \tag{4}$$

where C_{link} is the per-link cost of maintaining a social connection.

Simulations

I analyze the above model using simulations written in the Julia programming language [39]. The simulation code is available at `https://github.com/erolakcay/CooperationDynamicNetworks`. Briefly, networks are initialized as random networks, and run without selection for an inital burn-in period of 20 generations (i.e., $20 \times N$ time steps). This burn-in period is sufficient to produce networks that have the stationary properties of the social inheritance process [36]. Then, I allocate the cooperation trait randomly to all individuals (i.e., with expected frequency of cooperation 0.5), and turn on selection. For simulations with evolving linking probabilities, I initialize the individual p_n and p_r values from a normal distribution with standard deviation given by the mutational variances σ_n and σ_r, and mean by initial values $p_n = 0.5$ (except for the fixed p_n scenario) and $p_r = 0.0001$. These initial values do not have any effect on the long-run dynamics of the system as the system quickly evolves away from them.

Results

Fixed linking probabilities

I first consider the fate of a cooperation allele in groups that have fixed probabilities of random linking p_r and social inheritance p_n, and no costs to linking. I find that cooperation is maintained only under relatively low p_r (Figure 1). Interestingly, for most of its range p_n makes relatively little difference in the long-term frequency of cooperation. This indifference breaks down at very high levels of p_n,

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which disfavors cooperation. These results represent relatively straightforward cases of kin selection: low random linking and not too high social inheritance produces high assortment between connected individuals, so that cooperators benefit more from interactions with other cooperators (see Supplementary Figure SI 1). Higher probability random linking reduces the assortment, as might be expected. Intuitively, we might expect higher social inheritance to increase assortment and therefore favor cooperation, but in fact, the effect of social inheritance on assortment is neutral or negative (at high p_n). This is because in the current model offspring have the same probability of inheriting all connections their parents make, regardless of whether those connections where inherited or made randomly. At high social inheritance, however, networks evolve to be very densely connected which reduces the potential for assortment [36, Figure SI 1]. In more densely connected networks, the average benefit per link obtained from a cooperative partner also decreases due to the dilution effect (see eq. (1)). This also works against cooperation (compare with results for the prisoner's dilemma game with constant benefit per link in SI section SI–2).

With positive synergism between cooperators the picture changes slightly. As expected, stronger synergistic interactions (higher D) make cooperation possible for a larger range of p_n and p_r value (Figure 2), as synergism generates benefits that are only available to other cooperators [4, 40]. However, this added benefit is mainly realized at low levels of social inheritance, when the average degree of individuals is low and therefore the synergistic benefits are less diluted. As a result, with positive synergism, increasing both social inheritance and random linking probabilities (both of which increase the average degree of individuals) favors defection.

Coevolution of linking probabilities leads to collapse of cooperation

Next, I let the linking probabilities p_n and p_r coevolve with cooperation. Figure 3 shows a collection of sample trajectories that start with a low probability of random

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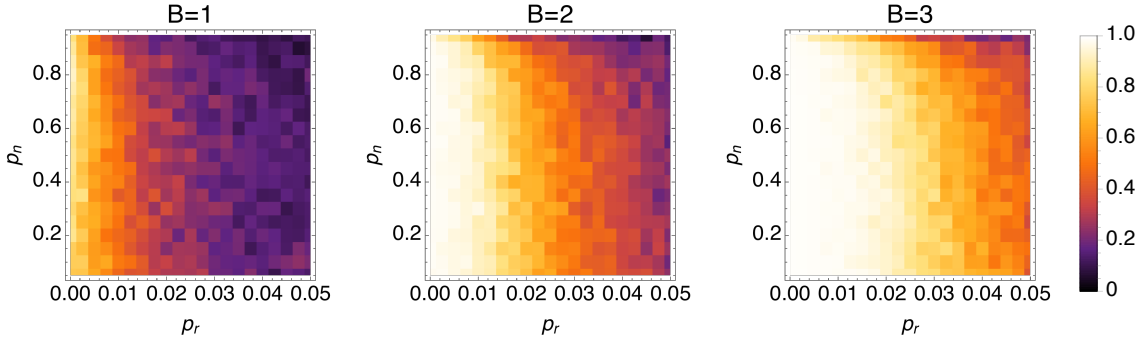

Figure 1: The frequency of cooperation as a function of p_n and p_r when these linking probabilities are kept fixed in the population for different values of the benefit B. For each combination of linking probabilities, the simulation was run for 500 generations (each generation equals N death-birth events). I recorded the frequency of cooperation at intervals corresponding to N. The color in each cell depicts the average frequency of cooperation over the last 400 generations for 100 replicate simulations. Parameters are $N = 100$, $C = 0.5$, $D = 0$, $\mu = 0.001$, $\delta = 0.1$, $C_{\text{link}} = 0$.

linking. Cooperation is quickly established in the population, but once it is established, it creates selection for the probability of random linking, p_r, to increase. Increased p_r in turn reverses selection on cooperation, and defection is established again in the population. These dynamics reveal that cooperation is self-limiting when the social structure co-evolves with it: once cooperation establishes in a population, it creates selection against the social structure that allowed it to evolve in the first place. The intuition behind this result is quite simple and general: in a cooperative population, it pays to make connections with any individual, since there is likely to be a benefit to be had from that connection. Therefore, individuals with higher probability of random linking (and thus, more connections) fare better in a cooperative population. This leads to a population with high probability of random linking, where we know cooperation cannot persist.

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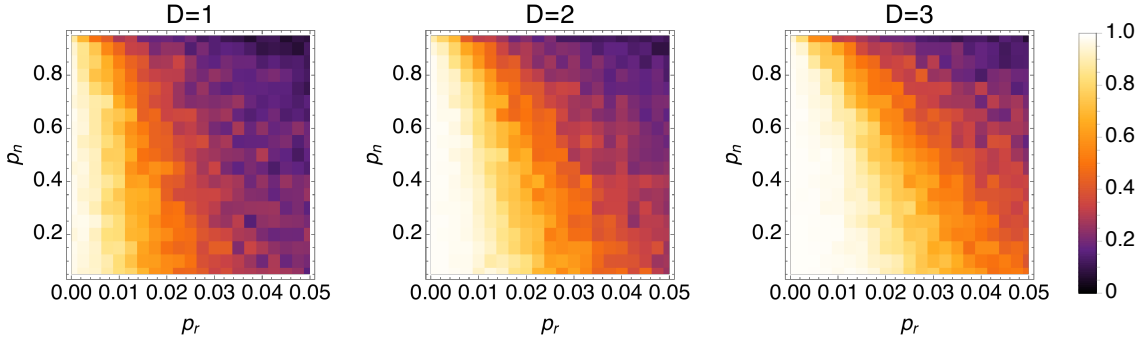

Figure 2: The effect of synergism on the frequency of cooperation as a function of p_n and p_r. The simulations are run as in Figure 1. Parameters are $N = 100$, $B = 1$, $C = 0.5$, $\mu = 0.001$, $\delta = 0.1$, $C_{\text{link}} = 0$.

Costs of linking can rescue cooperation

One possible mechanism that can counteract these dynamics is when making and maintaining social links is inherently costly, regardless of one's phenotype or that of partners. Such costs can counteract the incentive to seek out more connections, and prevent the linking probabilities (specifically, p_r) from crossing the threshold beyond which cooperation cannot be sustained. Figure 4 confirms that costs of social connections can prevent cooperation from limiting itself: for a given value of benefit B, as the cost of linking, C_{link} increases, the long-term average frequency of cooperation tends to increase. Interestingly however, this long-term average displays a non-monotonic pattern in B for moderate to high C_{link}: as B increases from low values, cooperation at first becomes more prevalent, as one might intuitively expect. In contrast, at higher values of B, making cooperation more beneficial reduces its long-term frequency. This "paradox of enrichment"[1] is another manifestation of the self-limiting nature of cooperation in dynamic networks: as the benefit from cooperation increases, so does the incentive to make random links in a cooperative population. Therefore, p_r evolves to higher values, which eventually undermines cooperation. Equivalently, a higher cost of linking is required to

[1]No relation to the paradox of enrichment observed in prey-predator dynamics [41].

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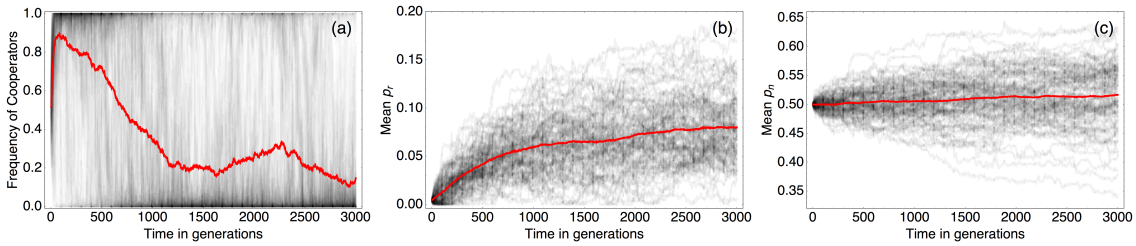

Figure 3: Density of trajectories of frequency of cooperation (a), mean p_r (b) and mean p_n (c) from 200 replicate simulations, depicting coevolution of the linking probabilities with cooperation. In each panel, darker regions correspond to a higher proportion of replicate trajectories passing through that point. The red curve in each panel depicts the mean of 100 trajectories. Each trajectory starts with $p_r = 0.001$ and $p_n = 0.5$, which for these parameter values favors cooperation. Accordingly, cooperation is established quickly after starting at frequency 0.5, as indicated by the bright spot at the upper left corner of panel (a), which indicates most trajectories initially converge to high frequency of cooperation. However, this is followed by an increase in the mean p_r value of the population (panel (b)), and cooperation soon collapses, with trajectories increasingly spending time near zero frequency of cooperation. After cooperation has collapsed, p_r continues its upward trajectory but under somewhat relaxed selection. In contrast to p_r, there is no strong directional selection on p_n, and trajectories spread out in both directions from the initial value in panel (c). Parameter values are $N = 100$, $B = 2$, $C = 0.5$, $D = 0$, $\mu = 0.001$, $\mu_l = 0.01$, $\delta = 0.1$, $\sigma_n 0.01$, $\sigma_r = 0.01$.

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keep p_r low and maintain cooperation. This effect can be seen by looking at the average p_r (Figure 4(b)), which increases with B for a given cost of linking. We observe this non-monotonicity of cooperation and increase of p_r with the benefit B in both strong and weak selection (compare with Supplementary Figure SI 6).

A final paradoxical result in Figure 4(c) is that even when cooperation is sustained, the costs incurred may be too high, such that the average fitness of the population (calculated using equation (4)) can actually be lower in a more cooperative population than a less cooperative one (e.g., compare $B = 2$ and $C_{\text{link}} = 0$ and C_{link}=0.4 in Figure 4(c)). More generally, for a given level of benefit B, the mean fitness of a population follows a non-monotonic pattern with the costs of linking: the mean fitness first decreases and then increases with C_{link}. In other words, even though cooperation can be rescued by costs of social connections, the victory may prove phyrric.

When the main benefits from cooperation come from synergistic payoffs, cooperation tends to be stable when links are also costly, as shown in Figure 5 for weak selection (strong selection yields similar results). Here, synergism and costs of linking interact positively: for a given (non-zero) cost of linking, increasing synergy increases the frequency of cooperation, and vice versa. As a result, the more synergistic the payoffs, the lower the cost of linking required to maintain cooperation. Like the no-synergism case, cooperation tends to be accompanied by low p_r and p_n. Furthermore, p_n and p_r display monotonically decreasing patterns in both synergism and cost of linking 5(b,d), resulting in very sparsely connected networks (see Supplementary Figure SI 5). This is because synergistic benefits are inversely proportional to the product of degrees, and therefore selection on reducing the mean degree of cooperators is strong. In general, synergistic payoffs, together with some costs of linking promote cooperation and increase mean fitness 5(c), but result in very

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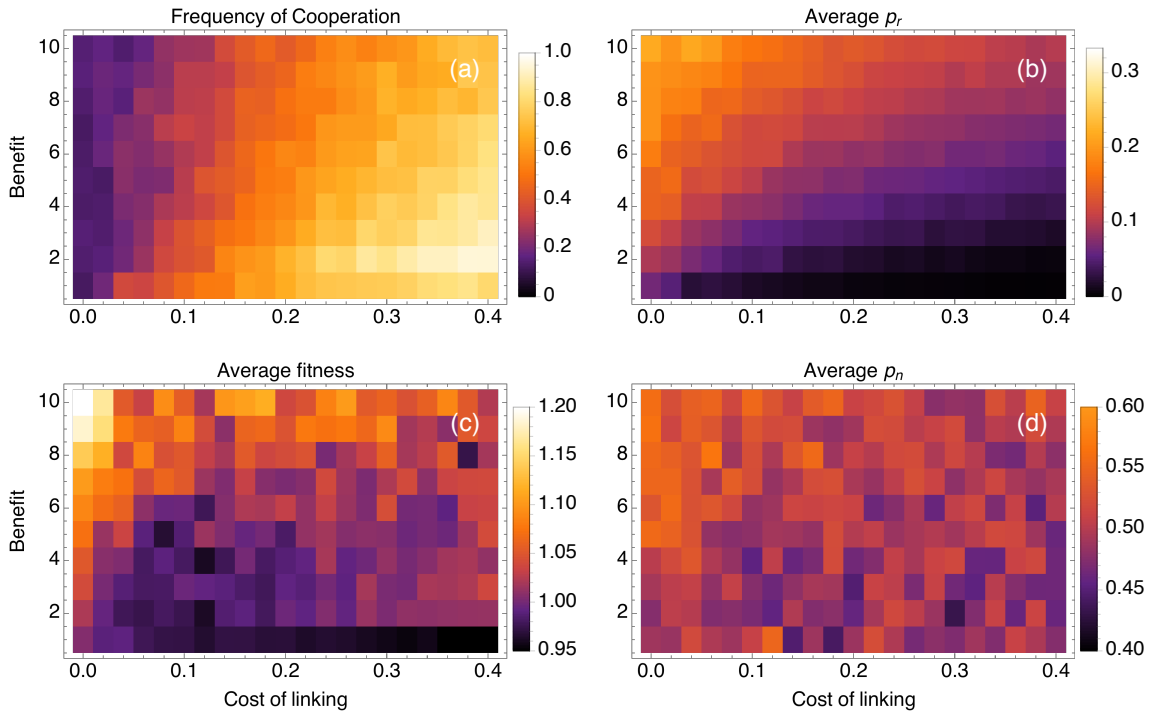

Figure 4: Mean frequency of cooperation (a), p_r (b), p_n (d), and average fitness (c) over 10 replicate simulations, averaged across time, as a function of the benefit from cooperation and the cost of linking. Each simulation was initiated with $p_r = 0.0001$, $p_n = 0.5$, frequency of cooperation at 0.5, and run for 10^5 generations (10^7 time steps). Averages over the final 8×10^4 generations (sampled once each generation) are shown. Note that these simulations are run over longer time-periods than the ones in Figure 1 to give the system time to explore the larger (and continuous) state space that includes the evolving linking traits. Parameter values are $N = 100$, $C = 0.5$, $D = 0$, $\mu = \mu_l = 0.001$, $\sigma_n = \sigma_r = 0.01$, $\delta = 0.1$.

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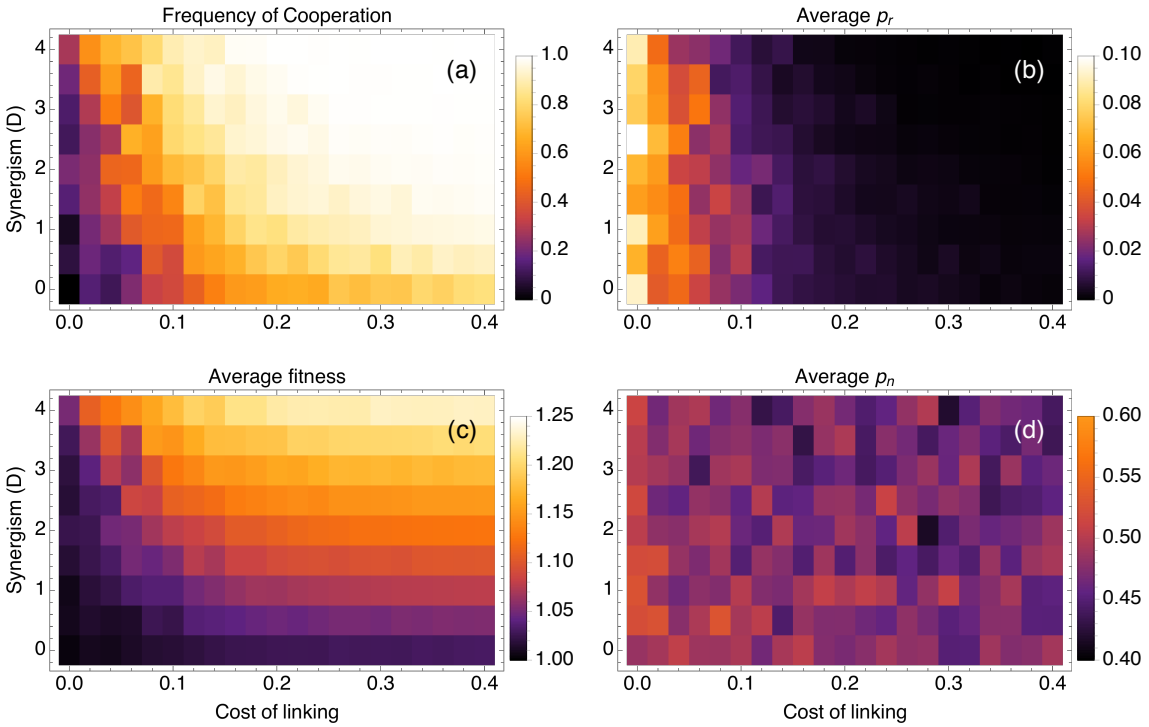

Figure 5: Effect of synergistic payoffs on cooperation (a) and the linking probabilities p_r (b), p_n (d), and the mean fitness (c). Simulations and averages were performed as in Figure 4. Here, $B = 1$; the other parameters as in Figure 4.

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Exogenously high social inheritance can rescue cooperation

One surprising aspect of the preceding results is that there is relatively little selection on the probability of social inheritance p_n due to feedbacks from the social trait, in contrast to the probability of random linking, p_r. This suggest that social inheritance might predominantly evolve due to other selection pressures or as a pleiotropic consequence of group living (e.g., due to offspring passively being in proximity of their parent's connections). This raises the question of how cooperation and p_r fare when social inheritance is fixed by an exogenous factor. Figure 6 shows that when p_n is fixed exogenously but p_r is left free to co-evolve with cooperation, high social inheritance can maintain high frequency of cooperation in conjunction with costly linking. This result may appear to be in contradiction with my first results above when both linking traits are fixed, where higher p_n, holding p_r fixed, reduces cooperation. The contradiction is resolved by observing that when p_n is high, and links are costly, p_r will evolve to be lower, because the higher p_n the higher marginal cost of higher p_r due to the steeper increase in the expected mean degree of an individual [Figure 2 of 36]. This means that for a given benefit from cooperation, the marginal cost of increased random connections equal to the marginal benefits at a lower level of p_r, which favors cooperation. Biologically, this means that high social inheritance, if evolved (and maintained) for reasons other than cooperative benefits, can also function to sustain cooperative populations (see Discussion for more).

Discussion

I use a simple dynamical network model that is able to reproduce important characteristics of animal social structure based on social inheritance [36], and investigate how a social behavior such as cooperative investments can evolve under such dynamics. My results show that cooperation tends to evolve under low rates of random linking. Interestingly, the probability of social inheritance makes little difference for most of its range, except at high levels, where it disfavors cooper-

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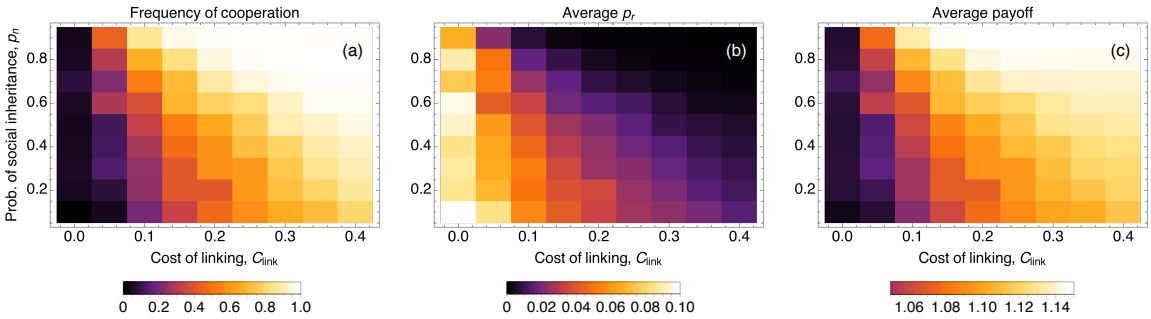

Figure 6: Effects of exogenously fixed level of social inheritance p_n when the probability of random linking is evolving. Here, $B = 2$, $C = 0.5$, $D = 0$, $\mu = \mu_{link} = 0.001$, $\sigma_r = 0.01$.

ation, which is contrary to the intuition that inheriting more links should make networks more assortative. This intuition, however, comes from an implicit assumption that the overall connectivity of a network stays the same, so inheriting more links means making fewer random connections. This is not the case in the current model. More interesting patterns arise when linking probabilities coevolve with cooperation. Cooperation readily evolves when networks start with low levels of random linking, but once it does, selection increases the rate of random linking, undermining cooperation. Costs of linking can counteract this self-limitation of cooperation, however, they also have to contend with a second kind of self-limitation, where as cooperation becomes more beneficial, the level of linking costs required to maintain cooperation at high frequency increases and may negate some or all of the benefit from cooperation. Exogenously maintained high levels of social inheritance or synergistic payoffs from cooperation can help overcome this self-limitation problem, allowing cooperation to establish with relatively low costs of linking. But in the case of synergistic payoffs, the resulting networks are sparsely connected with low p_n and p_r.

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Collapse and rescue of cooperation

These results add to a growing theoretical literature that is uncovering cases where evolutionary dynamics lead to the establishing of cooperation, only to undermine it through altering the conditions that select for it in the first place. Previous results uncovered such negative feedbacks operating through the payoff structure of a game, whether by direct evolution of payoffs [14, 15] or through environmental feedbacks that alter the returns from different strategies [16]. Here, I identify a different kind of dynamical feedback between cooperation and the setting in which it evolves. By focusing on the interplay between a simple yet realistic model of network dynamics and social behaviors, I show that the structure of the society that favors cooperation can itself fall victim to cooperation. This logic behind this phenomenon applies generally beyond the current model: cooperation tends to be favored when population assortment is high. But regardless of the details of the process of acquiring connections, in cooperative populations, connections with most individuals are beneficial, and therefore individuals in such populations would be selected for making more connections indiscriminately. All else being equal, this would lead to more mixing in the population, which in turn disfavors cooperation. Thus, coevolution of the network structure with social traits such as cooperation sets up a fundamental negative feedback that has not previously been recognized. Furthermore, the negative feedback is stronger with higher benefits of cooperation, which increases the temptation to link randomly at high rates.

Costs to making and maintaining connections might counteract this negative feedback by reducing selection for increased probability of making random connections. Accordingly, I find that with high enough costs, cooperation can be maintained. Maintenance of social bonds in many animal and human societies involves costly investments [42, 43], which in many cases are not beneficial to either party. Previous theory hypothesized that such costs might serve signal partner quality [44] or building trust [45]. My results show that regardless of their function at the level of the pair of individuals, costs of maintaining bonds shape the social structure of a group in a way that facilitates cooperation. Therefore, it is possible

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that such costs can evolve through cultural or genetic selection at the group level as a group-level adaptation that sustains selection for cooperation within groups. However, this expectation is tempered by the fact that even when cooperation is rescued, the costs of linking may be too high for cooperation to be a net benefit to the population on average (Figure 4c).

A potential way for populations to avoid such a pyrrhic victory for cooperation is when social inheritance is kept high by factors exogenous to the current model. Then, costs of linking can promote cooperation and high payoffs (Figure 6). This happens because high social inheritance effectively increases the costs of random linking, as these links are more likely to get inherited, and therefore increase the average degree of a lineage [36]. Thus, for a given cost of linking, higher p_n means higher marginal costs of increasing p_r, which in turn means that p_r evolves to a lower level, which maintains more cooperation. I furthermore show that at least under weak selection, coevolving cooperation will not strongly oppose selection on p_n due to other factors. Taken together, these results suggest a potential pathway to cooperation where high social inheritance can evolve for reasons other than cooperation, including possibly group-level selection on behavioral (or institutional) traits that favor both social inheritance and some costs of linking, thereby favorign within group cooperation. Exploring the multi-level evolutionary dynamics of linking traits and their costs is likely to yield further interesting insights.

Finally, it is worth noting that the connection costs do not rescue cooperation in the Prisoner's Dilemma game (see SI section SI–2.2), where the benefits and costs from cooperation increase linearly with degree. This happens because connection links in such a scenario only serve to effectively increase the costs of cooperation. If cooperation evolves for a given level of linking costs, it implies that the benefit of being connected to a cooperator exceeds the joint costs of cooperation and linking. Therefore, random linking will necessarily increase and cooperation will collapse. This represents another way in which cooperation can be too beneficial for its maintenance.

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Alternative pathways to cooperation in dynamic networks

A potential way to avoid these fundamentally self-limiting dynamics of cooperation is partner choice [5], i.e., preferentially interacting with cooperators or avoiding defectors. Papers by Pacheco et al. [30] and Santos et al. [31] provide models of evolution of cooperation through partner choice in dynamic networks. In these models, players make and break connections with each other at rates that depend on the type of the partners. These models show that cooperation can evolve and be stable in dynamically changing networks. However, these models consider type-dependent linking rates as exogenously fixed, and do not consider how they might co-evolve with cooperation. When the coevolutionary dynamics are considered, it is likely that we would recover the self-limiting nature of cooperation in these models as well. This is because at highly cooperative populations, there would be little need to maintain differential connection rates, which means that they would erode, setting up the stage for the collapse of cooperation. Previous models have shown that in pairwise interactions adequate mutation rate [46] or immigration from a source population with high variation [47] is required to maintain choosiness and thus cooperation. How the dynamics of partner choice operate in a network context remains to be explored.

Another mechanism that can maintain cooperation is direct reciprocity between interacting individuals [2, 3]. While I do not model reciprocity explicitly, we know that in pairwise interactions, the effects of reciprocity can be accounted for by a synergistic payoff function, where reciprocators achieve an extra benefit not available to non-reciprocators [10, 40]. I find that synergistic payoffs such as those that might be expected from reciprocal cooperation tend to (unsurprisingly) favor cooperation, but they are still subject to the self-limitation problem. However, with reciprocity, the self-limitation problem is resolved more easily and costs of linking that prevent high random linking act in concert with synergistic benefits, rather than antagonistically like they do with additive benefits. This pattern is consistent with previous results that show behavioral responses and population structure tend to act in synergy with each other [9–11]. One caveat here is that strong syn-

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ergism tends to select for sparsely connected networks with low p_n and p_r, due to the dilution effect on synergistic benefits.

Parallels between network and spatially structured populations

It is interesting to relate the results in network-structured populations presented here to the rich literature on spatially structured models of social evolution, where dispersal determines a newborn's social partners. For example, Koella [48] modeled a scenario where investment into cooperation can coevolve with dispersal and interaction distances on a lattice. When dispersal and interaction were fixed and local, cooperation readily evolved, but when dispersal distance coevolves with cooperation, defectors evolve long-distance dispersal which leads to reduced investment by cooperators, analogous to what happens on my model with increased random linking and subsequent collapse of cooperation. When interaction neighborhood also evolves, cooperators and defectors can coexist in spatially alternating bands, with cooperators interacting hyper-locally. Another paper, by Smaldino and Schank [49], explores how movement traits coevolve with cooperation in a spatially structured population where individuals move around a lattice looking for partners. They find that cooperation is more successful with less movement, which in terms of the interaction networks would correspond to most individuals staying near their parents and therefore making fewer random links and socially inheriting more. In contrast, when defectors moved a lot, they did better as they were able to find and exploit cooperator clusters. When cooperators and defectors used their respective best movement strategies, Smaldino and Shank observed persistently polymorphic populations. Likewise, Mullon et al. [17] found that in patch-structured populations, cooperators and defectors can coexist with the former evolving low dispersal rates and the latter high. These results are analogous to those I find in larger networks (see SI section SI–1.4), where cooperators and defectors can coexists for periods of time with cooperators evolving low linking probabilities and defectors high. Another interesting result from a lattice-structured model to compare to the current paper is that of Smaldino et al. [50],

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who found that increasing the costs of cooperation can favor cooperation in the long-run. This result is some ways analogous to my finding that higher benefits can reduce the long-term frequency of cooperation, but happens due to a different mechanism: in Smaldino et al., high costs first cause most cooperators to die out, followed by defectors. Cooperators can then re-invade an empty landscape in clusters, which are subsequently surrounded by defectors but can get big enough to avoid the costs of being taken advantage of.

Cooperation and network structure in the short and long-term

The closest existing model to the present one is one by Cavaliere et al. [35], who consider the evolution of cooperation in a population with fixed (and moderately high) social inheritance, but no random linking. Consistent with my results with fixed linking probabilities, their populations evolve to be mostly cooperative. However, Cavaliere et al. find in their simulations that cooperative populations were densely connected while defector networks are sparse. This pattern arises because in cooperative societies more connected individuals are selected for, especially since Cavaliere et al. assume that the benefit per link from a cooperator is constant rather than being diluted as 1/degree as in this model. Although Cavaliere et al. assume no variation in individuals' linking traits, individuals can still pass down their higher degree to their offspring through social inheritance, which happens in my model as well. However, since this effect is purely due to social inheritance, and not the evolution of linking traits themselves, it does not limit cooperation in the long-term. In contrast, once the average linking probabilities (especially p_r) evolve to high values in my model, the population spends more time in low-cooperation states. It is also worth noting that the change in network structure found by Cavaliere et al. requires relatively strong selection (e.g., very high absolute values of B and C); under weak selection, the presence or absence of cooperation by itself has a relatively small effect.

It is interesting to ask how the linking probabilities that favor cooperation compare to observed social networks in the wild. Ilany and Akçay [36] find that animal

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social networks tend to be characterized by moderate to high social inheritance, p_n (0.5-0.8), and low p_r (0-0.1). These linking probabilities are generally consistent with the presence of cooperation for a range of payoff parameters in my model. Therefore, my results suggest that conditions for cooperation might be met in the wild. When the linking probabilities themselves evolve, I find that the random linking probability, p_r, responds to different selective forces in an intuitive way: evolved p_r decreases with increasing costs of linking, and increases with increasing benefits from cooperation. On the other hand, the social inheritance probability, p_n seems to be somewhat less intuitive: at least under weak selection, p_n behaves largely neutrally, exhibiting little sensitivity to benefits of cooperation or costs of linking (see SI for a discussion of patterns under strong selection). Therefore, my results suggest that other factors that are not modeled here, such as obtaining support in social conflicts or between-group selection (as discussed above), might select for higher social inheritance. Alternatively, p_n might be high simply as a by-product of the parent-offspring associations (offspring spending a lot of time with their parents and therefore the parents' connections).

In conclusion, my results show that the evolution of social traits such as cooperation can have unexpected consequences for the social structure that determines the direction of social selection. I identify a fundamental negative feedback that causes cooperation to be self-limiting through its effects on the social network structure. These results highlight the need to understand dynamic feedbacks between selection acting social traits and the environment in which they evolve. These feedbacks might help explain why not every cooperation problem in nature will be solved despite the myriad theoretical mechanisms available in principle, or why the solution might not always prove to be beneficial on the net. Focusing on these feedbacks will allow us to move beyond explaining how selection can favor cooperation in principle to predicting when the conditions that favor it are likely to exist.

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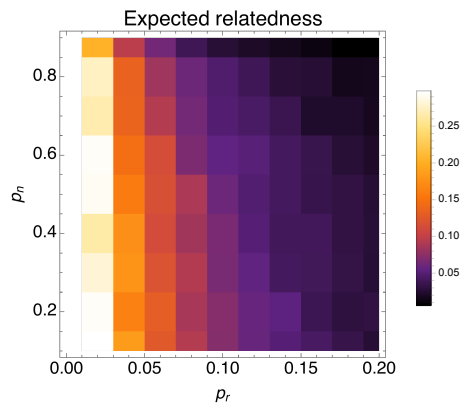
Supplementary Information

SI–1 Supplementary Figures for the coauthor game

SI–1.1 Assortment and mean degree in networks with fixed p_n and p_r

Supplementary Figure SI 1 shows the expected relatedness under neutrality as a function of the (fixed) linking probabilities p_n and p_r. Supplementary Figure SI 2 shows the relationship between mean degree of networks for fixed linking probabilities, for the same simulations as in Figure 1.



Supplementary Figure SI 1: Expected relatedness (calculated as the regression coefficient between the cooperation types of connected individuals) in neutrally evolving networks as a function of p_n and p_r. As can be seen in the figure, relatedness decreases with increasing p_r, and at high values of p_n, explaining the patterns we observe for cooperation. For each value of linking probabilities, networks are run for 2000 time steps and the regression on the resulting network is averaged over 100 replicates. $N = 100$, $\mu = 0.001$.

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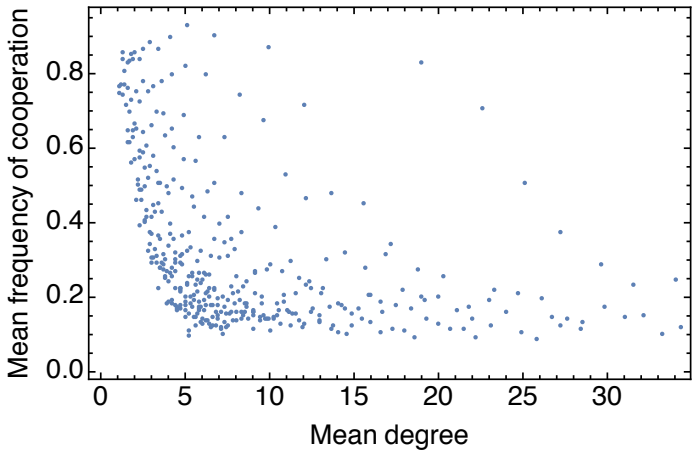

Supplementary Figure SI 2: Mean frequency of cooperation vs mean degree in networks with fixed linking traits, for the same simulations as in Figure 1. As the figure shows, there is a general negative relationship between degree and the frequency of cooperation, but the mean degree of a network does not uniquely fix the frequency of cooperation.

SI–1.2 Results with larger network sizes

Supplementary Figures SI 3 and SI 4 depict results with evolving networks for network sizes $N = 200$ and $N = 500$, respectively. They show that long-term average evolutionary patterns remain unchanged with network size. Supplementary Figure SI 5 plots the mean degree in evolved networks with synergistic benefits (same setting as Figure 5 in the main text). In section SI–1.4 below, I discuss results that look at polymorphisms within populations in larger networks.

SI–1.3 Results under strong selection

In the main text, I present results under relatively weak selection ($\delta = 0.1$), where the social trait does not directly affect the social structure (but does affect it through the evolutionary feedback on structuring traits). Here, I present results with stronger selection $\delta = 0.5$), where the network structure is directly affected by the presence or absence of cooperation on the network.

The main patterns for the co-evolution of cooperation and linking traits under

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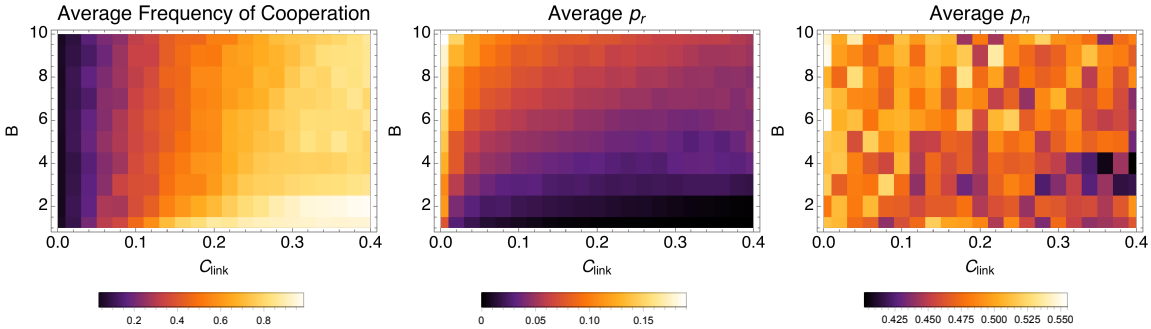
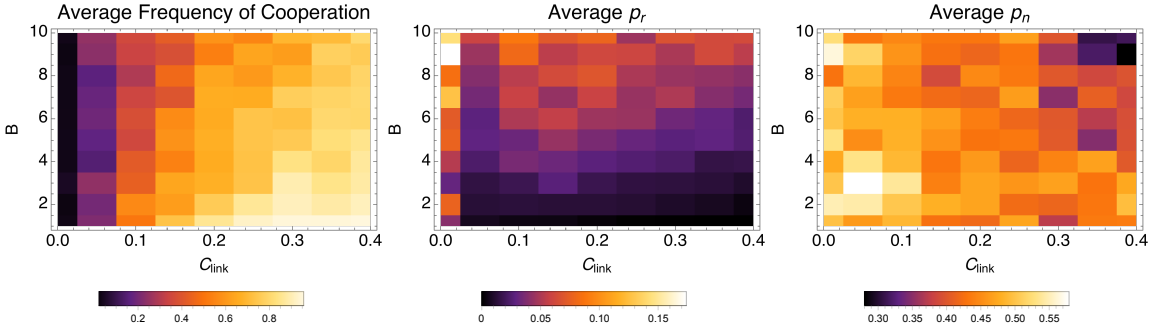


(a) (b) (c)

Supplementary Figure SI 3: Mean frequency of cooperation (a), p_r (b) and p_n (c) for larger networks $N = 200$. As in figure 4, each simulation was initiated with $p_r = 0.0001$, $p_n = 0.5$, frequency of cooperation at 0.5, and run for 10^5 generations. Values shown are means across the last 80,000 generations (in this case, 1.6×10^7 time steps). Other parameters values are $C = 0.5$, $D = 0$, $\mu = \mu_l = 0.01$, $\delta = 0.5$, $\sigma_n = \sigma_r = 0.01$.



(a) (b) (c)

Supplementary Figure SI 4: Mean frequency of cooperation (a), p_r (b) and p_n (c) for larger networks with $N = 500$. Simulations are run as in Supplementary Figure SI 3, except for 2×10^4 generations. Values shown are means across the last 10^4 generations (5×10^6 time steps). Other parameters values are $C = 0.5$, $D = 0$, $\mu = \mu_l = 0.01$, $\delta = 0.5$, $\sigma_n = \sigma_r = 0.01$.

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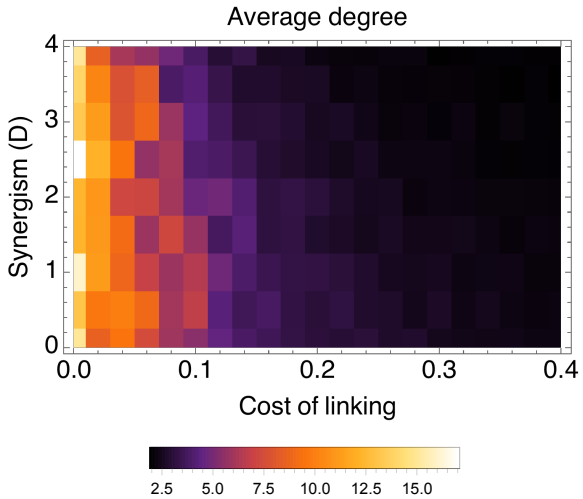

Supplementary Figure SI 5: Mean degree of evolved networks with synergistic benefits, for the same simulations as in Figure 5 in the main text, showing that when cooperation is maintained with synergistic benefits and linking costs, population evolve to be very sparsely connected.

strong selection are similar to under weak selection. However, under strong selection, social inheritance experiences more directional selection, and a somewhat unexpected pattern emerges. In particular, p_n initially decreases as B increases from low values (Supplementary Figure SI 6(c); see also Supplementary Figure SI 7 for a finer resolution look at this region). This is caused by a subtle parent-offspring conflict over social inheritance. In a cooperative population, offspring inheriting links is costly for the parent, as the benefit the parent receives from its connections will get diluted, in addition to receiving less benefit from the offspring. As B increases, the resolution of this conflict tends to favor the parents, since in a cooperative population and strong selection, only the highest-degree individuals tend to produce, and over time accumulate even more degrees. Thus, parents on average have much higher reproductive value than newborns, and therefore the conflict is resolved in their favor, with lower p_n. With further increasing benefit, p_r increases, and the dilution effect gets less important (since it scales as $1/d$), which shifts the resolution back towards the offspring's favor.

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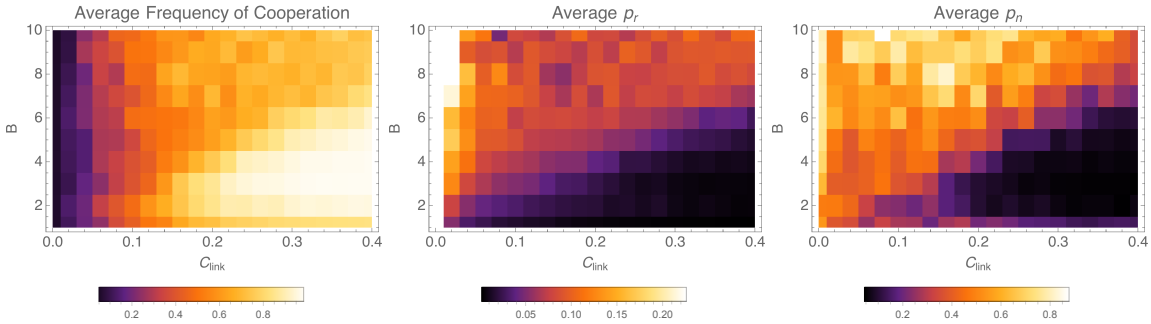
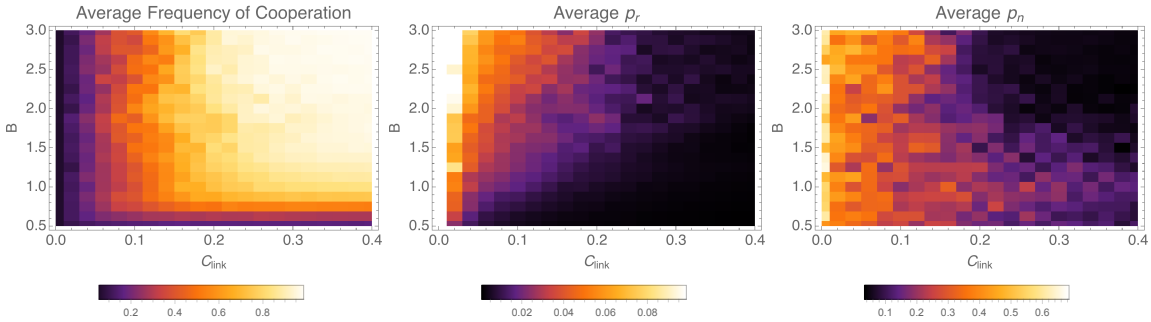


(a) (b) (c)

Supplementary Figure SI 6: Coevolution of cooperation and linkint traits under strong selection. Mean frequency of cooperation (a), p_r (b) and p_n (c) over 10 replicate simulations, averaged across time, as a function of the benefit from cooperation and the cost of linking. Each simulation was initiated with $p_r = 0.0001$, $p_n = 0.5$, frequency of cooperation at 0.5, and run for 10^5 generations. The first 2×10^4 were discarded to capture the steady-state of the stochastic dynamics, so that the shown averages are means across the 80,000 generations. Parameter values are $N = 100$, $C = 0.5$, $D = 0$, $\mu = \mu_l = 0.01$, $\delta = 0.5$, $\sigma_n = \sigma_r = 0.01$.



(a) (b) (c)

Supplementary Figure SI 7: A finer-scale look at the mean frequency of cooperation (a), p_r (b) and p_n (c) at low values of the benefit B under strong selection. As in Supplementary Figure SI 6, each simulation was initiated with $p_r = 0.0001$, $p_n = 0.5$, frequency of cooperation at 0.5, and run for 10^5 generations. Values shown are means across the 80,000 generations. Parameter values are $N = 100$, $C = 0.5$, $D = 0$, $\mu = \mu_l = 0.01$, $\delta = 0.5$, $\sigma_n = \sigma_r = 0.01$.

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SI–1.3.1 Apperance of high social inheritance under strong selection

As Supplementary Figure 4c above shows, under strong selection p_n evolves to be low when cooperation is selected for. This would appear to be inconsistent with observed values of high p_n. It is possible that the strong selection case, where there is high skew with one or a few highly connected individuals doing most of the reproduction, does not accurately reflect natural populations. An alternative explanation lies in the fact that Ilany and Akçay [36] assume a neutrally evolving population, whereas strong selection changes the network structure. As shown in Supplementary Figure SI 8, a given "true" value of p_n with strong selection generally results in networks where a neutral model would infer higher values of p_n.

SI–1.4 Evolution in large networks: polymorphisms and cycling

In the above, I focused on the long-term average frequency for cooperation and linking probabilities across different costs and benefit levels. These averages are informative for small population sizes, where due to drift the population will spend most of its time fixed (or almost fixed) for one type or the other, thus quantities averaged over longer time-periods are more informative. In larger populations, the population composition is less affected by drift, and therefore becomes more informative. Simulations in larger networks show that cooperators and defectors can co-occur persistently (though not necessarily stably), or cycle through phases of high cooperation with low p_r and low cooperation with high p_r, as shown in Supplementary Figure SI 9. The two regimes can happen in the same population evolving under the same parameters at different times.

When cooperators and defectors co-occur, they experience diverging selection pressures on the linking traits (Supplementary Figure SI 10). Cooperators are selected to minimize both inherited and random connections, while defectors are selected to increase their connection rates, especially the random linking probabilities. This divergence requires cooperators to be relatively common in the population, which happens when linking is costly, so that random connections are

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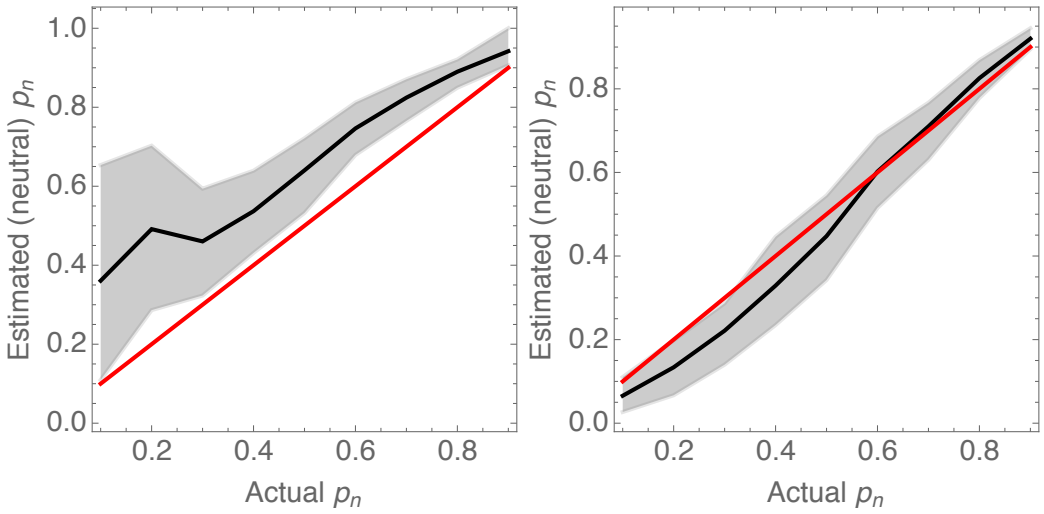

(a) $\delta = 0.5$ (b) $\delta = 0.1$

Supplementary Figure SI 8: Strong selection due to cooperation and high benefits creates the appearance of higher social inheritance than would be inferred under neutrality. In both panels, the black line depicts mean values of estimated p_n from 100 replicate networks, while the gray region shows the 90% confidence intervals and the red line estimated p_n = actual p_n. I simulated 100 replicate networks using $B = 4$, $C = 0.5$, $N = 100$, $p_r = 0.01$, $\mu = 0.01$, and p_n varying between 0.1 and 0.9. At the end of 20 generations, I sampled the network, calculating its mean degree and local clustering coefficients. I used the analytical expressions for the mean degree and clustering coefficients from Ilany and Akçay [36] to estimate the p_n and p_r coefficients that would produce these mean values under neutral dynamics. Panel (a) shows that networks under strong selection appear to have significantly higher neutral p_n estimates than their actual p_n. This effect disappears with relatively weak selection (Panel b).

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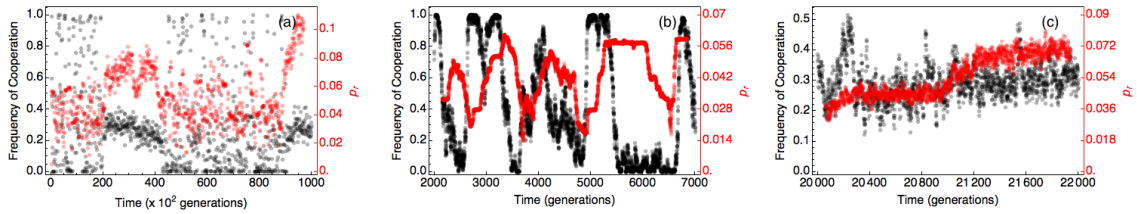

Supplementary Figure SI 9: Sample simulation illustrating the possibility of both cycling and persistent polymorphisms in larger networks. In all panels, the frequency of cooperation is in black, whereas the mean probability of random linking is in red. Panel (a) shows the time trajectory for 10^5 generations (i.e., 5×10^7 time steps), sampled at 100 generation intervals. Panel (b) and (c) show detailed trajectories for periods in the same simulation where the population is cycling vs. maintained as a polymorphism, respectively, recorded every generation. When the population is cycling, it maintains low variance in p_r, the mean value of which increases when cooperation is high, and decreases. Conversely, when the population is polymorphic, p_r has higher variance, due to defectors and cooperators having different values of p_r (see also Supplementary Figure SI 10). For this simulation run $N = 500$, $B = 10$, $C = 0.5$, $D = 0$, $C_{\text{link}} = 0.1$, $\delta = 0.1$, $\mu = \mu_l = 0.001$, $\sigma_n = \sigma_r = 0.01$.

likely to provide a benefit. However, as defectors increasingly make more random connections, the benefit each can get from a given cooperative connection decreases due to the dilution of benefits in the coauthor game. This continues until the average degree of cooperators becomes too high, and the benefit from them too diluted, to compensate for the cost of linking, at which point the highly connected defector lineage goes extinct (Supplementary Figure SI 10). This pattern is especially apparent with moderate benefits and intermediate linking costs (as in Supplementary Figure SI 10), where cooperators can be maintained at high frequency. Under such conditions, the cycle of a minority fraction of defectors with increasing linking probabilities until they go extinct can repeat itself.

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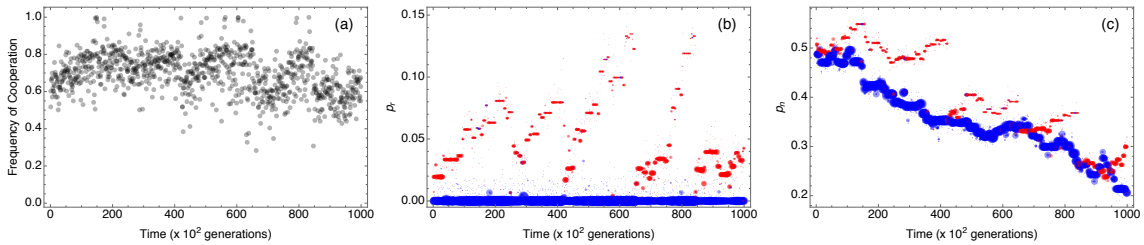

Supplementary Figure SI 10: Trajectories of frequency of cooperation (a), p_r (b), and p_n (c) in a larger population ($N = 500$) where a polymorphism can be maintained between cooperation and defection. In panels (b) and (c), blue color denotes cooperators, red defectors, and the size of the points is proportional to the frequency of that particular cooperation-linking probability genotype. Here, $B = 2$ and $C_{\text{link}} = 0.2$, which is a condition that supports a high average frequency of cooperation. The simulation was run for 10^5 generations (i.e., 5×10^7 time steps), with the population distribution recorded every 100 generations. It shows that in polymorphic populations, cooperators and defectors evolve divergent linking traits: while cooperators stably evolve low p_r and p_n values, defectors evolve higher p_r and to some extent, p_n values. However, increasing p_r is associated with the extinction of defectors, followed by their reemergence by mutation from the standing cooperator population with low p_r and p_n values, at which point the cycle repeats itself.

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SI–2 Results with the Prisoner's Dilemma game

In this section, I describe the same dynamical network model with a different payoff structure. In particular, instead of cooperators providing a fixed benefit that gets divided between all their connections and paying a fixed cost regardless of their degree, I assume that each cooperator provides a fixed per connection benefit, and pay a fixed cost per connection. In other words, the payoff to an individual is now:

$$u_i(t) = 1 + \sum_{j \neq i} p_j a_{ij} \left(B + p_i D\right) - p_i d_i(t) C - d_i(t) C_{\text{link}} \,, \tag{SI–1}$$

Otherwise, the model works as described in the main text. One feature of the payoff function (SI–1) is that the cost of cooperation and costs of linking work in exactly the same way. As shown below, that means that costs of linking cannot rescue cooperation of this kind.

SI–2.1 Fixed linking probabilities

First, I keep p_n and p_r fixed and look at the long-term frequency of cooperation. Supplementary Figure SI 11 shows the results for strong selection (results are similar for weak selection). As in the coauthor game, cooperation evolves when p_r is low. On the other hand, somewhat differently from the coauthor game in the main text, p_n has a non-monotonic effect on cooperation: both low and high values of p_n select against cooperation compared to intermediate values. This is because unlike the coauthor game, the benefits from a cooperative partner do not get diluted over all the connections of the partner, and low p_n reduces the opportunity for cooperators to form mutually cooperating clusters. Therefore, forming more connected clusters favors cooperation, until the network becomes too connected. Incidentally, these results are directly comparable with those of Cavaliere et al. [35], who consider a model with $p_r = 0$ and vary p_n and the probability to connecting to the parent. Thus, their model with probability of connecting to the parent corresponds

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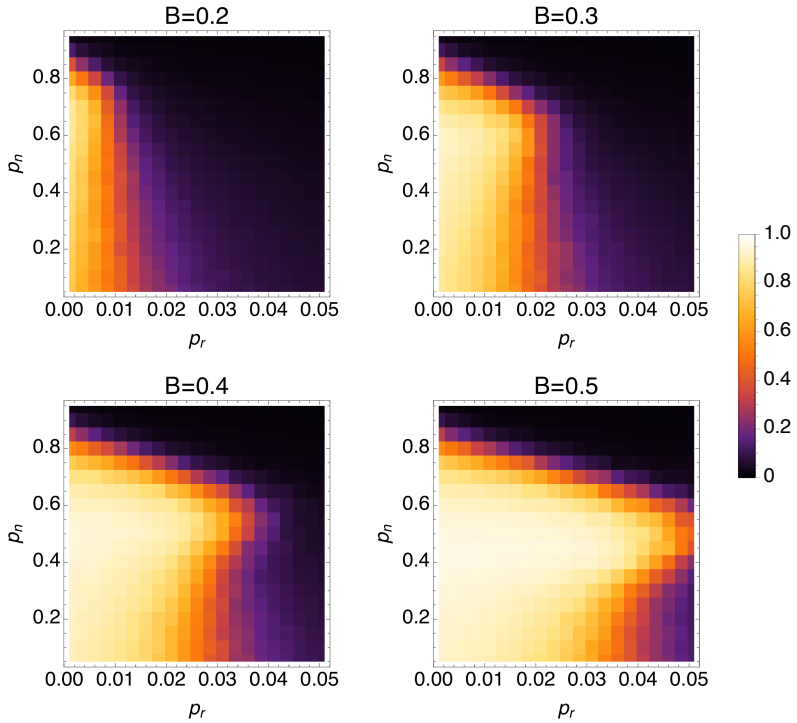

Supplementary Figure SI 11: Long-term frequency of cooperation for fixed values of p_n and p_r with strong selection ($\delta = 0.5$), $C = 0.1$, and B as given at the top of each panel. Simulations are run as in Figure 1: 100 replicate populations of 100 individuals were simulated for 500 generations (50,000 time steps) and the average frequency of cooperation in the last 400 generations are calculated. Mutation rate $\mu = 0.01$.

to the left-hand boundaries in Supplementary Figure SI 11. Thus, my results are consistent with the observation of Cavaliere et al. that cooperation persist in the population most of the time as long as p_n is not too high.

SI–2.2 Evolving linking probabilities

Next, I let the linking probabilities co-evolve, as with the coauthor game in the main text, with the possibility of costly linking $C_{\text{link}} > 0$. As Supplementary Figure SI 12 shows, the self-limitation of cooperation is present again here. Moreover, we observe that costs of linking do not rescue cooperation. The reason can be seen

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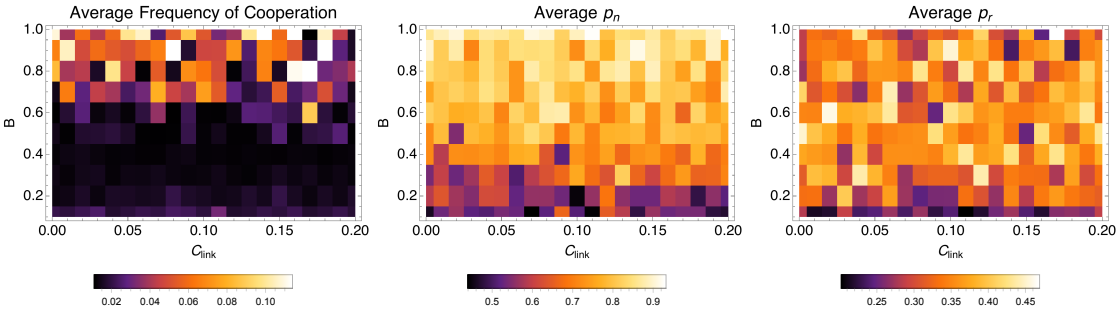

(a) (b) (c)

Supplementary Figure SI 12: Long-term average frequency of cooperation, p_n, and p_r with evolving linking probabilities.

in the payoff function (SI–1): the linking costs just add an additional cost that is constant per link, exactly as the costs of cooperation for the prisoner's dilemma game (with the difference that they are paid by all individuals). That means if cooperation is favored by an initial configuration (say, with low p_r and intermediate p_n), it means that the costs of linking is low enough to be overcome by the benefits. In that case, selection will always favor higher linking probabilities (specifically, higher p_r), which will bring about a population structure where cooperation cannot persist anymore. Overcoming this feedback in the Prisoner's Dilemma therefore requires mechanisms other than costly linking (e.g., partner choice, or synergistic payoffs due to reciprocity).