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Collapse and rescue of cooperation in evolving dynamic networks

Erol Akçay
Department of Biology, University of Pennsylvania
eakcay@sas.upenn.edu

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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 how the social structure co-evolves with social traits. Here, I present a model of such coevolution, using a simple yet realistic model of within-group social structure. In this model, social connections are either inherited from a parent or made by meeting random individuals. My model shows that while certain conditions on the social structure (low probability of making random connections) can select for cooperation, the presence of cooperation selects against these conditions, leading to the collapse of cooperation. Inherent costs of making social connections unrelated to cooperation can prevent this negative feedback. However, the more beneficial cooperation is, the higher linking costs have to be to counteract the self-limitation. These results illustrate how coevolutionary dynamics can constrain the long-term persistence of cooperation or the aggregate benefits from it.

Introduction

Cooperation is easy to evolve. In the last half century, we discovered that there are myriad ways natural selection can favor organisms providing benefits to each other. These pathways include population structure (Hamilton, 1964), phenotypic

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feedbacks (Trivers, 1971; Axelrod and Hamilton, 1981), payoff synergies (Queller, 1985), partner choice (Bull and Rice, 1991), among others (e.g., see reviews in Lehmann and Keller, 2006*a*; West et al., 2007; Nowak, 2006). When operating together, these pathways to cooperation can reinforce (Lehmann and Keller, 2006*b*; Akçay and Van Cleve, 2012; Van Cleve and Akçay, 2014; Van Cleve, 2017) or counteract each other (Akçay, 2017). 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. Akçay et al., 2010; Akçay and Roughgarden, 2011), and how the setting coevolves with cooperation. This question has recently been garnering attention. An emerging common thread from this recent literature is that such coevolutionary processes might impose inherent limits to the maintenance of cooperation in the long term. In a model of evolution of incentives for cooperation, Akçay and Roughgarden (2011) 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 (2014) 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 cheating becomes overwhelming, leading to the collapse of cooperation. In a model incorporating environmental feedbacks that affect the payoffs, Weitz et al. (2016) 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. (2017) showed that in settings where dispersal and cooperation coevolves, selection might result in stable polymorphisms where non-cooperators persist by evolving higher dispersal rates.

One major factor in the evolution of cooperation is the social structure of groups (i.e., who interacts with whom), represented by social networks (Wey et al., 2008; Pinter-Wollman et al., 2013). Social networks and variation in individuals' positions in them are shown to affect important life history traits such as reproductive success (Schülke et al., 2010), survival (Silk et al., 2010; Lehmann et al., 2015), infant survival (Silk et al., 2003), as well as selection on particular behaviors (Farine and Sheldon, 2015), and resilience of social groups (Goldenberg et al., 2016). Yet despite the emerging evidence about the importance of dynamic fine-scale social

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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, Rousset and Billiard, 2000), fixed networks (Ohtsuki et al., 2006; Taylor et al., 2007; Allen et al., 2017), or dynamic networks with random connections (Pacheco et al., 2006; Santos et al., 2006). Cavaliere et al. (2012) 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 they do not consider the feedbacks between the evolutionary dynamics of social structure and the social trait (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 (2016) 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 (2016) 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 affects 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 independent 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 is 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 can lead to non-trivial and non-monotonic patterns in both cooperation and linking prob-

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abilities. Overall, my model highlights how the feedbacks between the evolving traits that structure social networks and the social behaviors that evolve on them can limit or enable cooperation.

Model

My model builds on Ilany and Akçay (2016) by adding selection caused by social interactions on a dynamic 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 (2016) 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 vary between individuals and evolve as a result of their fitness 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 (1996). Intuitively, it represents an interaction where cooperators have a fixed time or energy budget to help others (e.g., spending time grooming –or writing papers with– others), and that connections have to share this benefit equally (as we are considering binary networks for this model). Defectors pay no cost of helping, provide no benefits, but benefit from the cooperators they are connected to. In the Supplementary Material SI–2, I present results with a different payoff structure where cooperators provide a fixed benefit to each partner and pay a fixed cost per partner. 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

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$D/(d_i d_j)$, where D is the synergistic benefit. Thus, the payoff of an individual i at time-step t, $u_i(t)$, is given by:

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

where $p_j \in \{0, 1\}$ is the frequency of the cooperaor 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.

I assume deaths occur randomly, independent of payoff or social network position. On the other hand, 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 alter the coevolutionary dynamics, I use the following extended payoff function:

$$u_i(t) = 1 + \sum_{j \neq i} p_j a_{ij} \left(\frac{B}{d_j(t)} + \mathbb{1}_i \frac{D}{d_i(t) d_j(t)} \right) - p_i C - d_i(t) C_{link} \,, \tag{4}$$

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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 (Bezanson et al., 2017). The simulation code is available at `https://github.com/erolakcay/CooperationDynamicNetworks`.

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. 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, which disfavors cooperation.

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). 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, in the coauthor game with positive synergism, increasing both social inheritance and random linking probabilities favors defection.

Coevolution of linking probabilities leads to collapse of cooperation

Next, I let the linking probabilities p_n and p_r coevolve with the cooperative trait. Figure 3 shows a collection of sample trajectories that start with a low probability of random linking. Cooperation is quickly established in the population, but once it is established, it creates selection pressure for the probability of random linking, p_r, to increase. That in turn reverses selection on cooperation, and defection is established again in the population. These dynamics reveal that cooperation is self-limiting in a setting where the social structure co-evolves with it: once cooperation establishes in a population, it creates selection against the social structure

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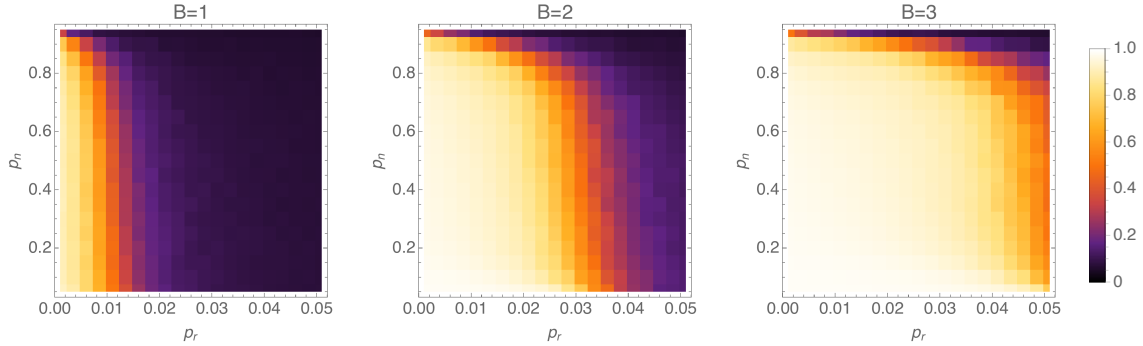

Figure 1: The frequency of cooperation as a function of p_n and p_r when these linking probabilities are kept fixed in the population for different values of the benefit B under strong selection. For each combination of linking probabilities, the simulation was run for 500 generations (each generation equals N death-birth events). We 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 $N = 100$, $C = 0.5$, $\mu = 0.01$, $\delta = 0.5$. Patterns with weaker selection are qualitatively similar.

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.

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 connections with random individuals, and prevent the linking probabilities (specifically, p_r) from crossing the threshold beyond which cooperation cannot be sustained. Figure 4 shows what happens when maintaining social connections is costly. It confirms the conjecture 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-

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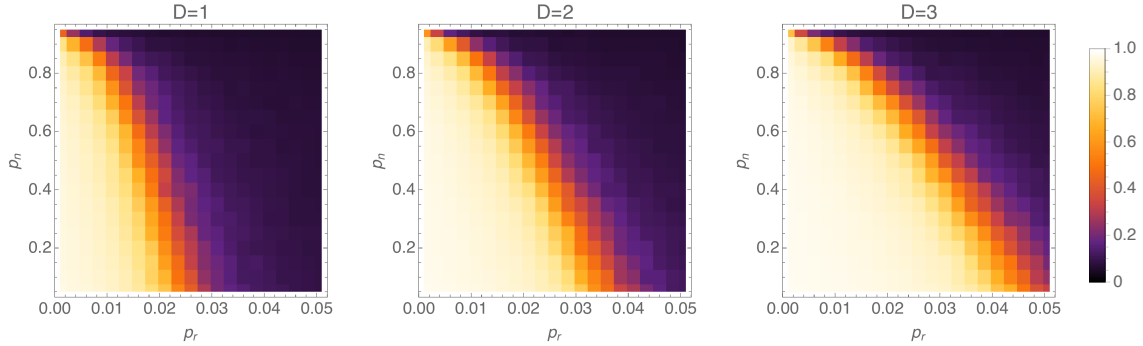

Figure 2: The effect of synergism on the frequency of cooperation as a function of p_n and p_r. The simulations are run as in Figure 1. Parameters are $N = 100$, $B = 1$, $C = 0.5$, $\mu = 0.01$, $\delta = 0.5$.

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 (see also Figure SI 1(a)), as one might intuitively expect. However, at higher values of B, we observe the opposite effect: making cooperation more beneficial reduces its long-term frequency. This "paradox of enrichment" 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 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 observer the non-monotonicity of cooperation and increase of p_r with the benefit B in both strong and weak selection (panels (a,d,b,e) of Figure 4).

Finally, under strong selection a somewhat unexpected pattern emerges. The probability of social inheritance, p_n (Figure 4(c)), initially decreases as B increases from low values (see Figure SI 1 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

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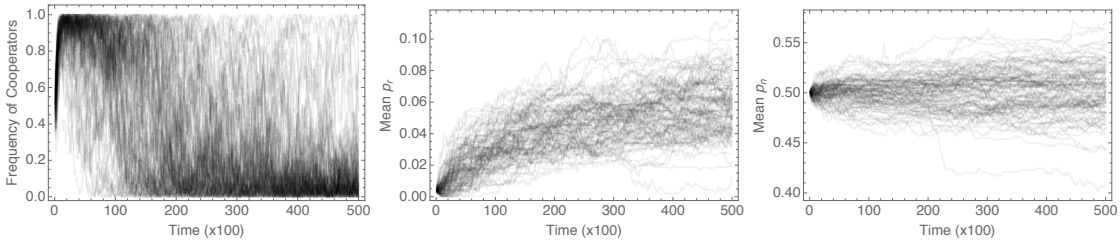

(a) (b) (c)

Figure 3: Trajectories of frequency of cooperation (a), mean p_r (b) and mean p_n (c) from 100 replicate simulations, depicting coevolution of the linking probabilities with cooperation. Each trajectory starts with a low $p_r = 0.001$ and $p_n = 0.5$, which for these parameter values favors cooperation (compare with Figure 1). Accordingly, cooperation is established quickly after starting at frequency 0.5. However, this is followed by an increase in the mean p_r value of the population, and cooperation soon collapses: starting around generation 100, trajectories increasingly spend time at zero frequency of cooperation. After cooperation has collapsed, p_r continues its upward trajectory but under relaxed selection. In contrast to p_r, there is no strong selection on p_n. Parameter values are $N = 100$, $B = 2$, $C = 0.5$, $D = 0$, $\mu = 0.001$, $\mu_l = 0.01$, $\delta = 0.5$, $\sigma_n = \sigma_r = 0.01$.

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. Under weak selection, we do not observe this pattern. Instead, p_n is under much weaker selection, but in the same general direction as p_r (Figure 4(f)).

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 strong selection (weak 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. This is because in our model synergistic benefits are inversely proportional to the product of degrees, and therefore selection on reducing the mean degree of cooperators is strong.

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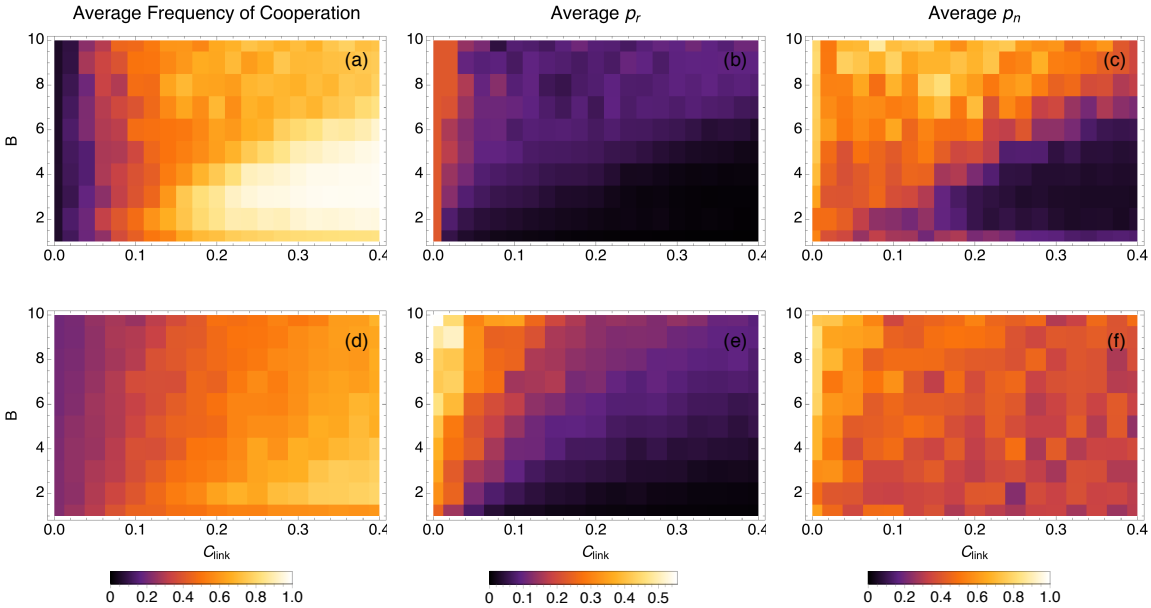

Figure 4: Mean frequency of cooperation (a,d), p_r (b,e) and p_n (c,f) over 10 replicate simulations, averaged across time, as a function of the benefit from cooperation and the cost of linking. Upper row: strong selection, $\delta = 0.5$; lower row: weak selection, $\delta = 0.1$. Each simulation was 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. Parameter values are $N = 100$, $C = 0.5$, $D = 0$, $\mu = \mu_l = 0.01$, $\sigma_n = \sigma_r = 0.01$.

Discussion

Here, I use a simple dynamical network model that is able to reproduce important characteristics of animal social structure based on social inheritance (Ilany and Akçay, 2016), 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, but once cooperation evolves, selection tends to increase 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. I also show that synergistic payoffs from cooperation can help overcome both of the self-limitation problems, allowing cooperation to

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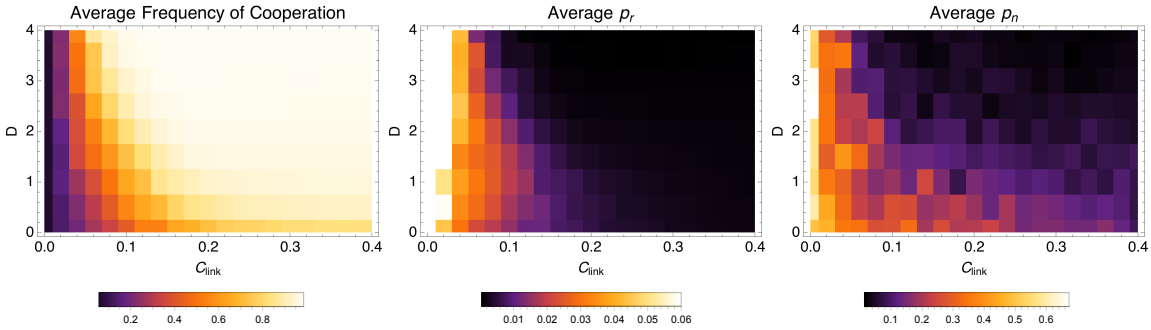

(a) (b) (c)

Figure 5: Effect of synergistic payoffs on cooperation (a) and the linking probabilities (b and c). Simulations and averages were performed as in Figure 4. Here, $B = 1$; the other parameters as in Figure 4, with $\delta = 0.5$, corresponding to strong selection.

establish with relatively low costs of linking.

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 (Akçay and Roughgarden, 2011; Stewart and Plotkin, 2014) or through environmental feedbacks that alter the returns from different strategies (Weitz et al., 2016). 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: 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 connections less discriminately. 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.

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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 (Mauss, 1950; Henkel et al., 2010), which in many cases are not beneficial to either party. Previous theory hypothesized that such costs might serve signal partner quality (Sozou and Seymour, 2005) or building trust (Bergstrom et al., 2008). 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 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. 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 benefits from cooperation increase linearly with degree. This represents another way in which cooperation can be too beneficial for its maintenance.

One way to get out of this dynamic is partner choice (Bull and Rice, 1991), i.e., preferentially interacting with cooperators or avoiding defectors. Papers by Pacheco et al. (2006) and Santos et al. (2006) 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 given, 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 rate, which would erode, setting up the stage for the collapse of cooperation. Previous models have shown that in pairwise interactions adequate mutation rate (McNamara et al., 2008) or immigration from a source population with high variation (Foster and Kokko, 2006) 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 (Trivers, 1971; Axelrod and Hamilton, 1981). 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 (Fletcher and

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Zwick, 2006; Van Cleve and Akçay, 2014). 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 (Akçay and Van Cleve, 2012; Van Cleve and Akçay, 2014; Van Cleve, 2017).

Cooperation and network structure in the short and long-term

The closest existing model to the present one is one by Cavaliere et al. (2012), who consider the evolution of cooperation in a population with social inheritance, but no random linking. Consistent with my finding that cooperation requires low rate of random linking, they found that their populations spent a lot of time at high frequency of cooperation. They found an interesting consequence of cooperation or defection being established in a population: cooperative populations in their simulations were densely connected while defector populations are sparse. This effect happens 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 interesting to ask how the linking probabilities that favor cooperation compare to observed social networks in the wild. Ilany and Akçay (2016) find that animal 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 in-

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creasing 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. But under strong selection, p_n evolves to be low when cooperation is selected for (Figure 4c), which 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 (2016) assume a neutrally evolving population, whereas strong selection changes the network structure. As shown in Figure SI 2, 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.

In conclusion, my results show that the evolution of social traits such as cooperation can have unexpected consequences for the environmental and social conditions that affect 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. Such an understanding 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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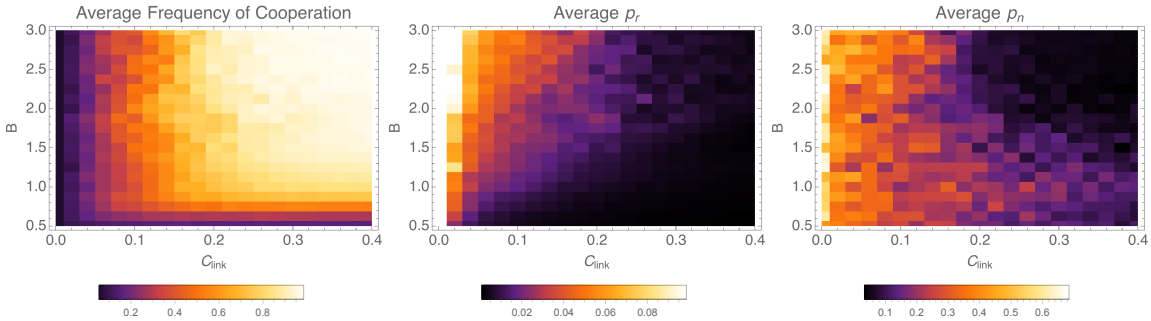

(a) (b) (c)

Supplementary Figure SI 1: 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. 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 80,000 generations. Parameter values are $N = 100$, $C = 0.5$, $D = 0$, $\mu = \mu_l = 0.01$, $\delta = 0.5$, $\sigma_n = \sigma_r = 0.01$.

Supplementary Information

SI–1 Supplementary Figures for the coauthor game

Figure SI 1 presents a finer-scale look at the same case as in Figure 4, panels a-c. Figure SI 2 shows how selection can alter the estimated p_n and p_r parameters.

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:

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

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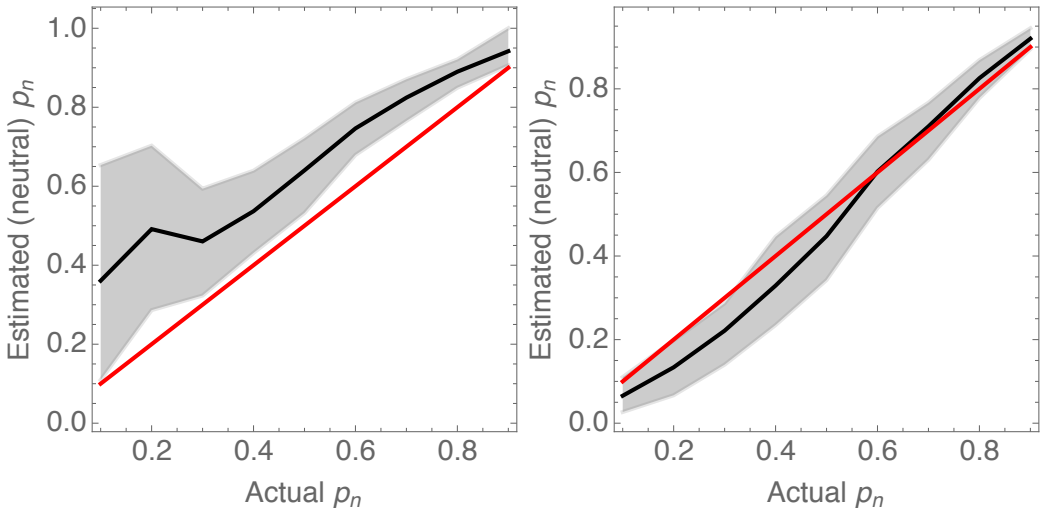

(a) $\delta = 0.5$ (b) $\delta = 0.1$

Supplementary Figure SI 2: 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 (2016) 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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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. Figure SI 3 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. (2012), 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 to the left-hand boundaries in Figure SI 3. 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 $C_{link} > 0$. As Figure SI 4 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 in the payoff function (SI–1): the sole effect of linking costs is to make cooperation costlier: 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).

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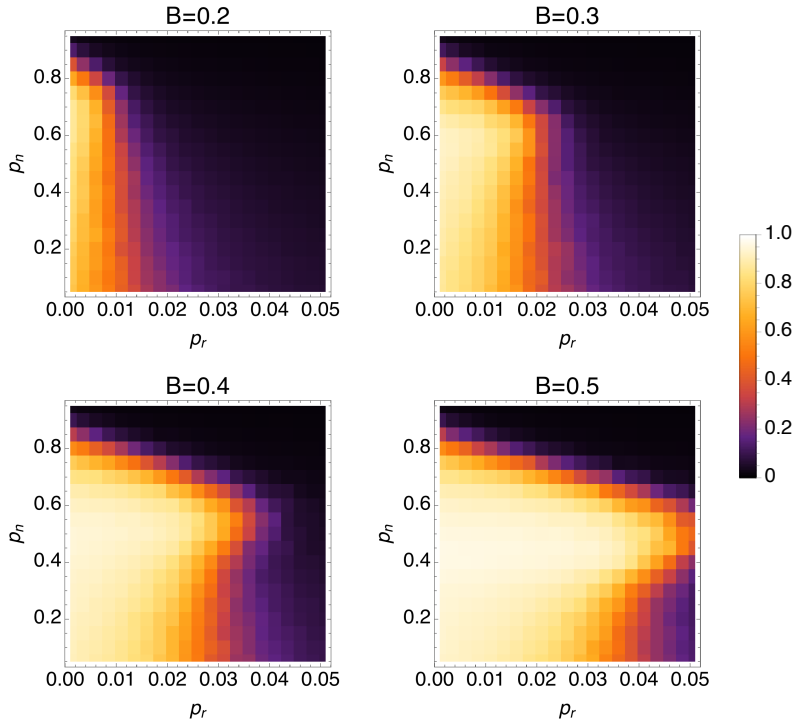
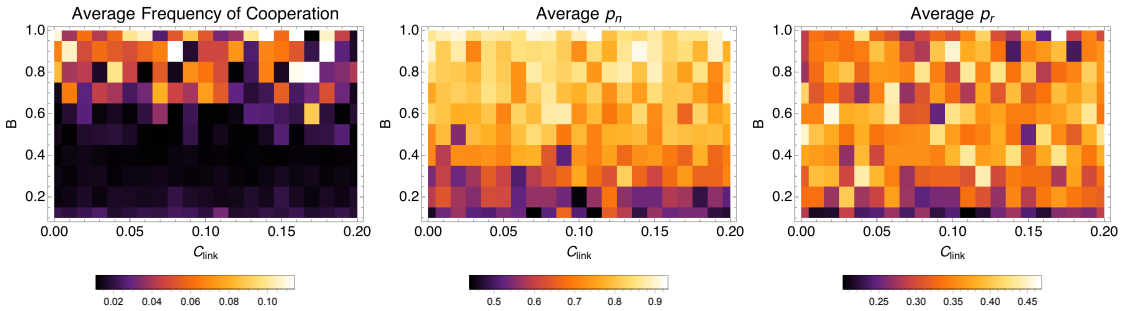


Supplementary Figure SI 3: Long-term frequency of cooperation for fix values of p_n and p_r with strong selection ($\delta = 0.5$), $C = 0.1$, and B as given at the top of each panel. Simulations are run as in Figure 1: 100 replicate populations of 100 individuals were simulated for 500 generations (50,000 time steps) and the average frequency of cooperation in the last 400 generations are calculated. Mutation rate $\mu = 0.01$.



(a) (b) (c)

Supplementary Figure SI 4: Long-term average frequency of cooperation, p_n, and p_r with evolving linking probabilities.