# Prisoner's dilemma on a stochastic nongrowth network evolution model

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We investigate the evolution of cooperation on a nongrowth dynamic network model with a death-birth dynamics based on tournament selection. In the limit of large population size, the equilibrium cooperator density is well described by our mean field approximations and inversely related to the average degree in the system. Small populations are also examined and found to deviate considerably from their expected mean field behavior. An expanded replicator equation incorporating Gaussian fluctuations in the strategy densities is then constructed, with its output agreeing well with our simulation data for all sizes. We also briefly comment on the role of strategy mutation in sustaining polymorphic populations in small systems.

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## I. INTRODUCTION

In biology an organism is called an altruist if its behavior enhances the reproductive probability (fitness) of another individual at the expense of its own. An altruist then pays a cost $c$ for its opponent to receive a benefit $b$, while a nonaltruist pays nothing and just receives the benefit. Should such behaviors be genetically encoded and if natural selection is solely interpreted as preserving the traits that contribute to individual fitness, then altruistic behaviors should be at a selective disadvantage with respect to purely selfish ones. Darwin himself was aware of this paradox, which he saw in the proliferation of sterile insect castes.

A mathematical integration of altruism into evolutionary theory did not appear until the 1960s when Hamilton proposed that under certain conditions altruism can be favored by natural selection if the recipient and donor of the altruistic act are genetically related [1], a mechanism termed kin selection. Genetically related individuals have more common alleles than two individuals picked at random, and while the donor of the altruistic act lowers its reproductive chances by doing so it raises the fitness of its relative, who has a good chance of also carrying the allele coding for altruism. Thus Hamilton posited that selection can also act to increase an organism's inclusive fitness, comprised of the reproductive potential of an individual plus its genetic relatives, and the family can be seen as the seed from which altruistic behavior grows. Mathematically, Hamilton's rule takes the form $\frac{b}{c} > \frac{1}{r}$, where $c$ is the cost of altruism to the actor, $b$ is the benefit to the recipient, and $r$ is a coefficient measuring the relatedness of the two. An important conceptual shift included in this viewpoint is that selection acts to preserve not individual organisms but genes in a pool spanning whole populations. Trivers [2] proposed that altruism can evolve if it is reciprocated even if the individuals involved are not related. Group selection [3] holds that altruistic behavior can evolve if selection can act at the level of the group, i.e., a population with more altruists will reproduce faster than a population with fewer altruists. The idea remains controversial to this day, mainly due to the fact that altruistic groups are susceptible to the invasion of cheaters.

Game theory, particularly in its evolutionary form first introduced in [4] and [5], has proved to be a very useful tool in studying the evolution of behavior because it fundamentally describes frequency-dependent selection. The worth of a particular behavior with regard to selection depends on its frequency in the population and thus the behavior of others; an altruistic behavior can be deemed adaptive only if there is a sufficient frequency of altruists. The prisoner's dilemma game [6] has been extensively used to model the evolution of cooperation and altruism between nonrelated individuals. The game describes an interaction between two players each having two strategies available to them, to cooperate $C$ or to defect $D$. A $C$-$C$ outcome yields the payoff $R$ for both players while a $D$-$D$ event will give both players a payoff $P$. Should one player cooperate and the other defect the cooperator will collect $S$ and the defector $T$. The payoffs are arranged such that $T>R>P>S$ and $2R>T+S$. In this setting it is always better to defect, irrespective of the other player's choice. The dilemma lies in that if both players defect they both receive $P$ instead of $R$ should they have both cooperated. In the evolutionary game theory setting, strategies become phenotypes and payoffs become fitness. Games take place between members of the population in a pairwise fashion, and the fittest phenotypes spread over the population. As is customary in the literature, we can make an identification between the language of Hamilton's principle and the prisoner's dilemma payoffs by letting $T=b$, $R=b-c$, $P=0$, and $S=-c$.

In the 1980s Axelrod organized tournaments [7] where contestants were requested to submit strategies to play repeated prisoner's dilemma games against each other for a finite but unknown number of times. The strategies were recipes that specified the player's next move based on stored knowledge of the opponent's past moves. Strategies would then reproduce themselves in proportion to their accumulated payoff after being played with a representative sample of the population. In this setting, it was demonstrated that cooperation is an evolutionarily stable outcome through a process of reciprocity, as evident by the proliferation of the well-known tit-for-tat strategy. In this strategy, the player will cooperate

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until defected against and will then keep defecting until the opponent cooperates, at which point it will switch back to cooperation. Reciprocity requires some sort of opponent recognition mechanism (and thus advanced cognitive faculties), which was deemed sufficient but not necessary for the evolution of cooperation.

The need for cognitive capacity was done away with in [8] where pure $C$ or $D$ strategies occupied the points of a two-dimensional grid. The strategies would play their grid neighbors, tally their total score, and then for the next round copy the strategy of their highest-scoring neighbor (imitation dynamics). Cooperative elements could now survive on the grid by forming clusters that resist invasion by defectors at their borders. The need for memory was thus replaced with spatial structure, much more prevalent in the natural world than advanced cognitive capacity. Variations in the lattice connectivity, topology, and strategy update mechanism have since been extensively studied [9–22].

Doing away with the need for nodes to compare payoffs introduced by imitation dynamics (and thus any semblance of cognitive ability in the players or agents), researchers have recently studied finite systems evolving under stochastic birth-death processes. Besides imitation dynamics, the authors in [23] studied the prisoner's dilemma on static regular graphs of degree $k$ using the frequency-dependent Moran process [24]. In the birth-death Moran process, an individual is chosen for reproduction proportionally to its fitness, and then replaces a randomly chosen neighbor (accordingly, in the death-birth process a node is randomly eliminated and its neighbors fight to colonize the space proportionally to their fitness). The authors report that cooperation is viable only in the death-birth Moran process and only if the benefits, costs, and average degree $k$ are related as $k<\frac{b}{c}$. Similar results are also reported in [25] for nonregular network topologies.

In this work we also employ a two-step death-birth process with the following differences. When an individual is removed, all its associated edges are also deleted from the system. When an individual is born, as a copy of a stochastically chosen fit individual, links are created between the newborn and other individuals through a process controlled by three parameters. Thus the individuals dynamically create the network, which is not a preexisting space to be colonized but an ever-changing relational web. Also, after the death of a node, any fit node and not only its neighbors can parent an offspring, which implies that clustering is not necessarily the mechanism for the evolution of cooperation in our work.

## II. NETWORK DYNAMICS AND SELECTION

Before we introduce our algorithm, consider a population composed of $n$ individuals, $i$ of which adopt the strategy $C$ and $n-i$ adopt the strategy $D$; further let us denote the fraction of cooperators as $x=\frac{i}{n}$ and that of defectors $1-x=\frac{n-i}{n}$. For a well-mixed population where each individual interacts with every other individual (or a representative sample of the population), we can then write

$$W_C = xR + (1-x)S, \tag{1}$$

$$W_D = xT + (1-x)P, \tag{2}$$

$$\bar{W} = xW_C + (1-x)W_D \tag{3}$$

for the payoffs of a cooperator and defector and the mean fitness, respectively.

In the limit $n\to\infty$ the evolutionary game dynamics of this system are well described by the deterministic replicator equation [26], which describes the action of selection on the frequencies of the two types. The replicator equation assumes that strategies always reproduce at a rate proportional to their fitness.

In its discrete time form this equation reads

$$x_{t+1} = \frac{x_t W_C}{\bar{W}} \tag{4}$$

with a similar expression existing for the defector population. Since $T>R>P>S$ we have that $W_D>W_C$, and a population evolving under natural selection with no mutation will eventually reach the monomorphic and absorbing state $i=0$. This is an evolutionary stable state (ESS) in the sense that any mutant cooperators that might arise will have lower fitness than the resident defectors and thus will be unable to spread. The question arises then whether the existence of a polymorphic ESS is possible in the prisoner's dilemma and what are the mechanisms that can bring it forth.

Here we maintain and evolve a population of pure strategists linked by a network whose degree distribution evolves under an algorithm first introduced in [27]. In its original formulation, a time step of the algorithm consists of the following stochastic death-birth process.

(a) Removal. Choose a node at random, with probability $\frac{1}{n}$, and remove it together with all its associated edges.

(b) Duplication. Choose a node at random, with probability $\frac{1}{n-1}$; this is the parent node. Introduce a new offspring node and attach edges between the node and the remaining $n-1$ nodes in the following way. (1) Attach the offspring to the parent with wiring probability $p_p$. (2) Attach the offspring to other nonparent nodes with wiring probability $p_o$ if an edge does not exist between the parent and the other node. (3) Attach the offspring to other nonparent nodes with wiring probability $p_e$ if an edge exists between the parent and the other node.

To the above algorithm we add selection, based on the payoffs a node collects by playing against its neighborhood, and also let offspring inherit the strategy from their parent. In our simulations we let the population evolve under tournament selection [28]. In tournament selection, a subset of the population of size $t$ is selected at random and all those selected play against the nodes in their respective neighborhoods. Their cumulative payoffs are compared and the node with the highest score parents a new offspring. The tournament size $t$ can be thought of as representing the intensity of selection; when $t=n$ the fittest node always reproduces and selection is strong. For $t=1$ we have random drift. In our simulations we use $t=2$; if the tournament nodes happen to have the same total payoff we randomly select one to reproduce. It is also worth noting that, although the tournament winner always reproduces, it is possible that the average fitness of the system will go down after the death-birth process

since removal is random. As noted in [29] this can be a desirable property since in natural populations a fit individual may be replaced by a less fit one.

To initiate our system we cast a random network over the population such that $k=p_o n$ is the mean degree. We also randomly and with equal probability assign a $C$ or $D$ strategy to each individual. Concerning the payoffs we let $T>R>P=S=0$ so that only cooperative links have a positive effect on fitness, a choice that does not alter the essential characteristics of the prisoner's dilemma [8]. In the simulations presented here, since we are primarily concerned with the network effects on strategy frequencies, we use only one set of payoff values and do not explore the payoff dependence.

If we set $p_o=p_e=0$, $p_p=1$ nodes will interact only with their same strategy parent and the population will settle in an $i=n$ state since $R>P$. On the other hand, letting $p_p=p_e=0$ and $0<p_0\leq 1$, the only stable equilibrium is the $i=0$ state. Under our network dynamics it is possible for a node to become isolated even if all the wiring probabilities are greater than zero. This occurs if a node has all of its neighbors progressively removed through its lifetime by death events. An isolated node has no payoff and selection is blind to its strategy since the phenotype expresses itself only through the inclusion of a node to a neighborhood. Such a node can still reproduce by chance (for example, by being compared in the tournament against another node only connected to defectors) and reattach itself to the network through its offspring.

In this set of experiments we examine the parameter set $0<p_o\ll 1$, $p_e=0$, $p_p=1$, which describes a world where elements link up with their parent and a randomly chosen subset of the population, which we vary in size. In this limit a node will on average end up with $p_o n$ randomly formed connections plus a link to its parent, for a total average degree of $k=p_o n+1$. The population structure introduced by the wiring probabilities can then be expressed in the mean fitness calculations as (excluding self-interaction)

$$W_C=(k-1)\frac{i-1}{n-1}R+R \tag{5}$$

for a cooperator, and

$$W_D=(k-1)\frac{i}{n-1}T \tag{6}$$

for a defector. Under natural selection, for a polymorphic population to exist the expected fitnesses of the two types must be equal. Setting $W_C=W_D$, we can calculate the equilibrium cooperator density to be

$$x=\frac{n-k}{n}\frac{R}{(T-R)}(k-1)^{-1}. \tag{7}$$

In the limit $n\to\infty$ we have $(n-k)\to n$ and thus

$$x_\infty=\frac{R}{(T-R)}(k-1)^{-1}. \tag{8}$$

From Eq. (8) we find that for $(k-1)<\frac{R}{T-R}$ $x\to 1$, while for $\infty>(k-1)>\frac{R}{T-R}$ we have coexistence of the two types. We see then that increasing the size of the randomly created average degree "dilutes" the advantage of the cooperative offspring-parent bond with the onset of coexistence defined by the game payoffs. Since $T=b$, $R=b-c$, $P=0$, and $S=-c$, we can conclude that cooperation will prevail if $k\leq b/c$. This result is in line with Hamilton's rule that frequent kin interactions promote cooperation, and its network extension [30,23], which states that networks of high connectedness hamper cooperation as the average degree is an inverse measure of genetic relatedness.

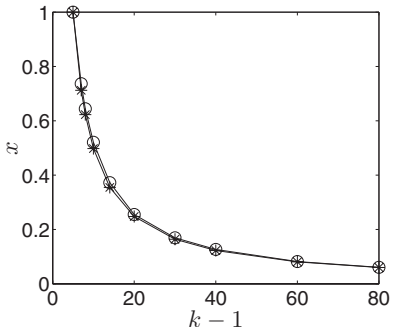


FIG. 1. Equilibrium cooperator density as a function of $k-1=[5,7,8,10,14,20,30,40,60,80]$ in linear scale for systems with $n=2000$. Simulation results (circles) and Eq. (7) prediction (stars).

Multiplying both sides of Eq. (7) by $k-1$, we get

$$x(k-1)=\frac{n-k}{n}\frac{R}{T-R}=k_C=\text{const} \tag{9}$$

with the infinite version being

$$k_{C\infty}=\frac{R}{T-R}=\text{const.} \tag{10}$$

Equations (9) and (10) represent the expected number of cooperating links an element will form at fitness equilibrium due to random sampling of the population. Since defectors can acquire cooperator links only through random sampling, we also have that

$$k_{DC}=k_C=\frac{R}{T-R}, \tag{11}$$

which is the expected number of cooperators adjacent to a defector. Cooperators also link to their parent so

$$k_{CC}=k_{DC}+1=\frac{R}{T-R}+1=\frac{T}{T-R} \tag{12}$$

for the expected number of cooperators adjacent to a cooperator. At equilibrium it should hold that $Rk_{CC}=Tk_{DC}$ so that $k_{CC}=\frac{T}{R}k_{DC}$.

## III. NUMERICAL RESULTS

### A. Coexistence properties and system size dependence

In Fig. 1 we present results for $x$ as a function of $p_o n=k-1$ from agent-based simulations of systems with $n=2000$ and $T=1.2$, $R=1$, $P=S=0$. To compute $x$ we take the en-

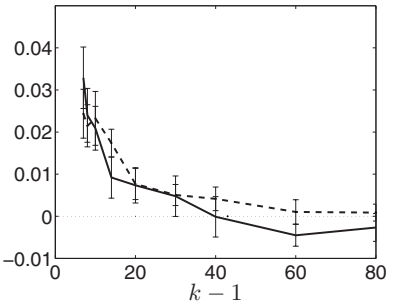


FIG. 2. Difference between simulation results and the predictions of Eq. (7) as a function of $k-1$. $n=2000$ (dashed line) and 1000 (solid line). The units on the $y$ axis are the percentages of cooperators in the population. The error bars represent the standard deviation.

semble average of 60 independent realizations with different initial conditions and then the time average again over the last ten generations. As mentioned in [31], a finite population undergoing stochastic replication with no mutation will eventually enter one of its absorbing states, which in our case is $x=1$ or 0. The time to absorption, however, may be extremely long and all we can do is measure the observables of this preabsorption transient. In what follows we will refer to the preabsorption transient states as equilibrium and focus on issues regarding the time to absorption in future work. From Fig. 1 we can see that the simulation $x$ is roughly in good agreement with the values calculated from the mean field approximation Eq. (7). For $k-1<5$, there is no coexistence and the absorbing state is one with $x=1$; for $k-1>5$ we have coexistence that approximates a power law as $x \propto (k-1)^{\beta}$ with $\beta \approx -1$. In Fig. 2 we show the difference between simulation data and the predictions of Eq. (7) for systems of size $n=2000$ and 1000. By comparing the two lines in Fig. 2, we can see how increasing system size brings the simulation results closer and closer to the mean field predictions.

This invites us then to look at the behavior of systems of even smaller size. In Fig. 3 we show simulation data for systems of size $n=400$. As we can see, these systems approach the behavior of an infinite system for intermediate values of the average degree. For large (i.e., $k-1=40$) or small (i.e., $k-1=7$) average degree, where one of the two types initially has a large fitness advantage over the other, the systems evolve to the absorbing states $x=0$ or 1. For even

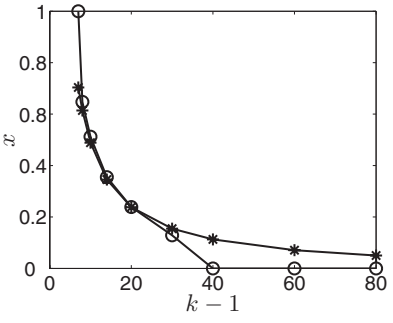


FIG. 3. Equilibrium cooperator density as a function of $k-1=[7,8,10,14,20,30,40,60,80]$ in linear scale for systems with $n=400$. Simulation results (circles) and Eq. (7) prediction (stars).

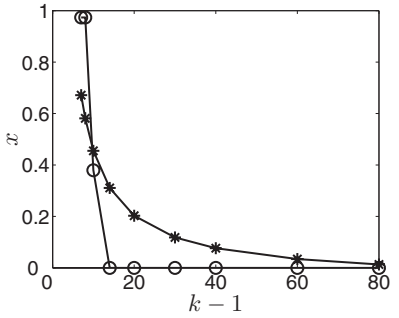


FIG. 4. Equilibrium cooperator density as a function of $k-1=[7,8,10,14,20,30,40,60,80]$ in linear scale for systems with $n=100$. Simulation results (circles) and Eq. (7) prediction (stars). For $k-1=7,8,10$ the $x$ values do not denote the average proportion of cooperators over the realizations but rather the frequency with which the state $x=1$ appears.

smaller $n=100$ systems, Fig. 4, the effect is more pronounced and coexistence is impossible.

Equation (7) predicts that as we increase $n$ we should approach $x_{\infty}$ from below irrespective of $k$. Our data suggest that as we increase $n$ whether we approach $x_{\infty}$ from below or above depends on the average degree. Moreover for systems with $n=100$ we observe only the absorbing boundaries of all $C$ or all $D$.

To summarize, our mean field analysis shows that systems evolve to a stable fixed point consisting of coexisting $C$ and $D$ populations; this is also supported by our simulation data. For small systems our data suggest that the mean field breaks down and the population performs a random walk to the absorbing states. In finite populations the stochastic nature of the death-birth processes leads to chance fluctuations in the population densities. As a consequence the population fluctuates about a population composition that equilibrates fitness. For large enough populations, these fluctuations tend to be suppressed and the population composition approaches that of an infinite system. On the other hand for small populations the fluctuations can severely affect the ESS stability [32–34,31] and chance instead of selection can determine the evolutionary outcome (genetic drift in natural populations [35]). To account for the influence of genetic drift the concept of fixation probability [36] was recently introduced. In a population where $i$ individuals adopt the strategy $A$ and $n-i$ the strategy $B$, the fixation probability $\Phi_i$ denotes the probability that in some future time the population will be made up entirely of $A$ strategists. In this context, for a strategy $B$ to be evolutionary stable against a mutant $A$, it must hold that $W_A < W_B$ and also that $\Phi_{i=1} < \frac{1}{n}$, so that selection opposes the fixation of the mutant through random drift. Of interest is also the time required for the mutant to reach fixation, the fixation time. Although any stochastic process with no mutation will eventually hit an absorbing boundary for any finite $n$, in games with mixed equilibria, and depending on the payoffs used, the time to absorption is an exponential function of the population size [37,38]. As a consequence, the polymorphic equilibria observed for large $n$ drift to absorption at such a slow rate that numerical simulations are not very useful in reproducing them. We will return to this point in our next section.

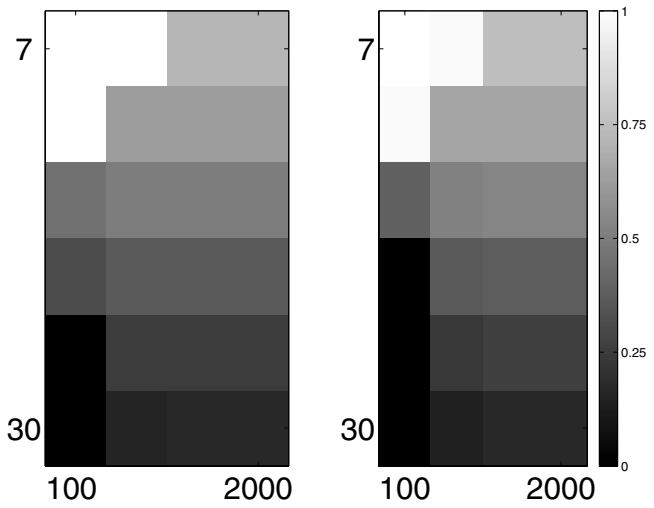


FIG. 5. Iteration of replicator equation with Gaussian fluctuations (left) and simulation data (right) for systems of different sizes and average degrees. The $x$ axis represents the system size $n=[100,400,1000,2000]$ and the $y$ axis the degree $k-1=[7,8,10,14,20,30]$. Both sets of data are averages over 60 experiments. The cooperator density is mapped to a linear color index ranging from black ($x=0$) to white ($x=1$).

As a first attempt to account for the small-population behavior, we hypothesize that in smaller systems density fluctuations bring forth the absorbing states $x=1$ or 0. To this extent we perform a numerical iteration of the discrete replicator, Eq. (4), with the fitnesses of the two types calculated by Eqs. (5) and (6). In each step, after the next generation densities have been calculated, we generate a Gaussian fluctuation with a mean of zero and a standard deviation of $\sigma(n)$, which we then add to the cooperator density and remove from the defector density (we call this a stochastic replicator). To calculate $\sigma(n)$ from our simulation data, we time-average the standard deviation of $x$ over every generation and then ensemble-average over our number of realizations. These data suggest that $\sigma \approx \frac{1}{4\sqrt{n}}$. In Fig. 5 we show a comparison of simulation data and the numerical iteration of our stochastic replicator equation. Comparing the left and right images in the figure, we can see how the stochastic generational replicator and our tournament selection death-birth dynamics are in good agreement. The monomorphic absorbing states are reproduced by the stochastic replicator for small $n$ and the polymorphic states for large $n$. Coexistence starts as the systems get larger and the average degree is at intermediate values. The fit between the output of the stochastic replicator and our simulation data is not perfect; for example, for $n=100$ and $k-1=14$ the simulation data give $x=0$ while iteration of the replicator gives $x=0.308$. Sources of discrepancy between the stochastic replicator and our death-birth dynamics could be the generational versus sequential process and also the selection method, tournament versus fitness proportional (see [39]). This is to be determined in future work where we will construct a difference stochastic replicator explicitly incorporating the microscopic tournament selection and death processes.

This will also require an iterative model for the evolution of the degree distributions since there is a tight coupling between fitness and network structure. This brings us neatly to our next section.

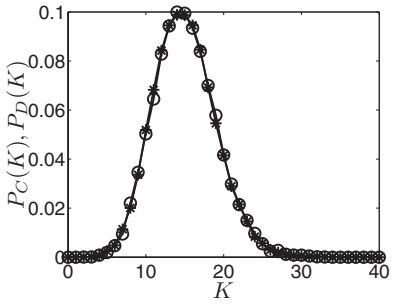


FIG. 6. $P_C(K)$ (stars) and $P_D(K)$ (circles) for systems with $n=2000$, average degree $k=15$, and steady state $x=0.3718$. The data points are ensemble averages over 60 independent experiments.

### B. Degree distributions

The degree distributions in our model are also fitness distributions. Hence an analysis of their equilibrium and dynamical properties captures all the fundamentals of the evolving dynamical system. Here we will briefly examine the distributions at the point where the strategies are in fitness equilibrium. Future work will concentrate on developing iterative coupled degree distribution and strategy models. Let us here introduce the following notation.

$P_C(K)$: The probability to find a cooperator with $K$ neighbors.

$P_D(K)$: The probability to find a cooperator with $K$ neighbors.

$P_C(K_C)$: The probability to find a cooperator with $K_C$ cooperator neighbors.

$P_D(K_C)$: The probability to find a defector with $K_C$ cooperator neighbors.

$P_C(K_D)$: The probability to find a cooperator with $K_D$ defector neighbors.

$P_D(K_D)$: The probability to find a defector with $K_D$ defector neighbors.

In Fig. 6 we show plots from our individual-based simulations for $P_C(K)$ and $P_D(K)$. As we can see there is nothing to distinguish the two types in terms of their neighborhood size. In Fig. 7 we show plots of $P_C(K_C)$ and $P_D(K_C)$. We now

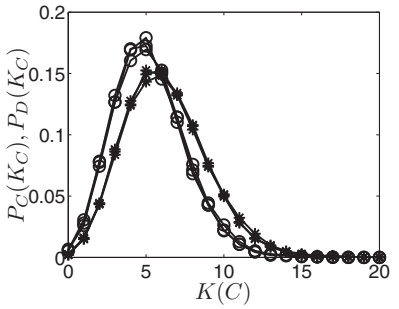


FIG. 7. $P_C(K_C)$ (stars) and $P_D(K_C)$ (points) for three different systems with steady states characterized by $x=0.7355$, 0.5206, and 0.3718. The data points are ensemble averages over 60 independent experiments.

see that $P_C(K_C)$ and $P_D(K_C)$ differ from each other. Furthermore, their shape and position relative to each other remain invariant as $x$ varies. This invariance is a direct consequence of fitness equilibrium and the degree-fitness distribution duality. We can check that the distributions satisfy a dynamically coexisting population scenario by using the distribution data to calculate the following probabilities.

$T^+(i)$: The probability that the number of cooperators will increase from $i$ to $i+1$.

$T^-(i)$: The probability that the number of cooperators will decrease from $i$ to $i-1$.

$T^0(i)$: The probability that the population composition will remain the same.

These probabilities represent the totality of possible events such that

$$T^+(i) + T^-(i) + T^0(i) = 1. \tag{13}$$

In our death-birth dynamics four events can occur. A cooperator can die with probability $d_C$ or be born with $b_C$; a defector can die with $d_D$ or be born with $b_D$. This permits us to write the transition probabilities as

$$T^+(i) = d_D b_C,$$

$$T^-(i) = d_C b_D,$$

$$T^0(i) = d_C b_C + d_C b_D.$$

The death probabilities for the two types are simply proportional to their densities so that $d_C = \frac{i}{n}$ and $d_D = \frac{n-i}{n}$.

When we select two elements to test for reproduction, the one with the highest total payoff reproduces with probability 1. We will distinguish between the cases where the two elements are of the same type and when they are not. When the elements are of the same type, since there is no mutation, an element of that type is added to the population. A cooperator will be born through this event with probability $\frac{i(i-1)}{n(n-1)}$ and a defector with probability $\frac{(n-i)(n-i-1)}{n(n-1)}$.

It is worthy of note that when we compare two individuals of the same type we could have just as well allowed for the less fit to reproduce. This is because, when an individual is born, all of its edges, except the one to the parent, are created at random and what is inherited is only the strategy. The situation becomes different if the elements can inherit a portion of their links from their parent (i.e., $p_e > 0$). Then what is inherited is the type plus the "environment" and it would matter whether we allowed the fitter or the less fit individual to reproduce.

When we select two individuals of different types we further distinguish between the cases where the individuals have the same fitness and when they do not. When they have the same fitness then we select one at random to reproduce regardless of type. As mentioned previously, two elements of different types can have the same fitness only when $\frac{K_{CC}}{K_{DC}} = \frac{R}{T}$; we can then write the probability of an individual being born by chance after being selected for the tournament together with another individual of opposite type but equal fitness as

$$b_{\mathrm{eq}} = \frac{1}{2}\sum_{m=0} P_C\left(\frac{T}{T-R}m\right)\frac{i}{n}P_D\left(\frac{R}{T-R}m\right)\frac{n-i}{n-1} \tag{14}$$

with $m = 0, 1, 2, \ldots, \mathrm{int}\{\frac{n(T-R)}{T}\}$.

When we select a cooperator and a defector with different fitness values the individual with the highest fitness will reproduce. This depends on where on their respective degree distributions they sit in relation to each other. A cooperator with $1 \le K_{CC} \le \frac{R}{T-R}m$ can win over a defector if the defector has a $K_{DC}$ up to and including $K_{CC}-m$, where $m$ is an integer. We can then write the probability that a cooperator was born because it won the tournament against a defector as

$$b_{C_w} = 2\sum_m \sum_{K_{CC}} P_C(K_{CC})\frac{i}{n}\sum_{K_{DC}} P_D(K_{DC})\frac{n-i}{n-1}. \tag{15}$$

The limits are

$$m = 0, 1, 2, \ldots, \mathrm{int}\left\{\frac{n(T-R)}{T}\right\},$$

$$\frac{T}{T-R}(m-1) \le K_{CC} \le \frac{T}{T-R}m - 1,$$

$$0 \le K_{DC} \le K_{CC} - m.$$

For a defector via a similar payoff argument we get

$$b_{D_w} = 2\sum_m \sum_{K_{DC}} P_D(K_{DC})\frac{n-i}{n}\sum_{K_{CC}} P_C(K_{CC})\frac{i}{n-1} \tag{16}$$

with limits

$$m = 0, 1, 2, \ldots, \mathrm{int}\left\{\frac{n(T-R)}{T}\right\},$$

$$\frac{T}{T-R}(m-1) \le K_{DC} \le \frac{T}{T-R}m - 1,$$

$$0 \le K_{CC} \le K_{DC} + m - 1.$$

In Table I we have tabulated the birth and transition probabilities using the ensemble-averaged $P_C(K_C)$ and $P_D(K_C)$ from simulation data for systems with $n=2000$. As is evident, the transition probabilities between the two types are very close; also note how the birth probabilities of the two types are very close to their respective densities such that $\frac{x}{(1-x)} = \frac{b_C}{b_D}$.We thus conclude that for large $n$ our systems are indeed in fitness equilibrium and well described by the mean field as in Eq. (7). The attractive nature of the equilibrium $x$ for large $n$ can also be illustrated from Fig. 8 where we have calculated the ratio $T^+(i)/T^-(i)$ for $i=1,\ldots,n-1$. Since $T^{\pm}(i)$ are functions of the degree distributions, for every $i$ we binomially generate $P_D(K_C)$ with mean $k_{DC}=p_o i$ and then let $P_C(K_C)=P_D(K_C-1)$ (since $p_p=1$ and cooperators on average have one more $C$ link).

As mentioned in our discussion of size-dependent effects, any stochastic process will perform a random walk to an absorbing boundary, in our case $i=n$ or 0, at a rate that depends on $n$. Two quantities that are integral to an understanding of this time dependence are the fixation probability [36], the probability that a single strategy can take over an entire population of the opposite strategy, together with its corresponding time, the fixation time. The fixation probability will

TABLE I. Densities of strategists together with birth and transition probabilities as a function of increasing average degree for systems with $n=2000$.

| $k-1$ | $x/(1-x)$ | $b_C/b_D$ | $T^+(i)$ | $T^-(i)$ | $T^0(i)$ |
|---|---|---|---|---|---|
| 7 | 2.7822 | 2.7872 | 0.1938 | 0.1934 | 0.6128 |
| 8 | 1.8121 | 1.8523 | 0.2232 | 0.2184 | 0.5584 |
| 10 | 1.0846 | 1.0810 | 0.2479 | 0.2488 | 0.5033 |
| 14 | 0.5913 | 0.5978 | 0.2340 | 0.2315 | 0.5345 |
| 20 | 0.3419 | 0.3409 | 0.1888 | 0.1893 | 0.6219 |
| 30 | 0.2024 | 0.2030 | 0.1401 | 0.1396 | 0.7203 |
| 40 | 0.1448 | 0.1472 | 0.1119 | 0.1101 | 0.7780 |
| 60 | 0.0894 | 0.0926 | 0.0777 | 0.0751 | 0.8471 |

in general depend on the ratio of the transition probabilities and thus the degree distributions generated by our wiring probabilities. We are currently working to obtain analytic expressions for the fixation and time probabilities, which will enable us to further gauge the equilibrium properties of our systems as a function of $n$.

Finally, let us mention that, armed with expressions for the transition probabilities and a mean field set of equations that describe how the degree distributions change after a death or birth event, we will be able to iterate an equation for the evolution of $x$ of the form

$$x_{t+1} = T^0(i)x_t + T^+(i)\left(x_t + \frac{1}{n}\right) + T^-(i)\left(x_t - \frac{1}{n}\right). \quad (17)$$

A similar prisoner's dilemma model to ours, consisting of death-birth dynamics and an evolving degree distribution, is also examined in [40] and [41]. In these works the evolution of the network is dictated by parameters that specify the rates at which *C-C*, *C-D*, and *D-D* are formed. If the time scale at which links are created and destroyed ($t_a$) is faster than the time scale of strategy update on each node ($t_s$), then the average fitness of individuals is determined by the steady state fractions of *C-C* and *C-D* links in the system (active links), denoted $\Phi_{CC}$ and $\Phi_{CD}=\Phi_{DC}$. On the other hand, if strategy update is fast compared to the network topology update, when starting from a complete or random network, the only evolutionarily stable outcome is universal defection. If the time scales are comparable, an interplay between these

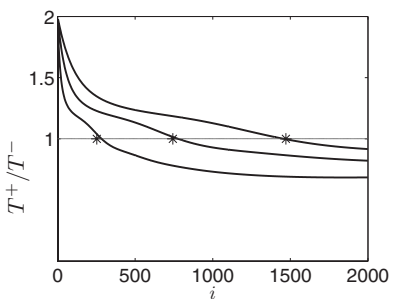


FIG. 8. $T^+(i)/T^-(i)$ as a function of $i$ for different $k-1=7,14,40$. Also shown (stars) are the fixed points $i=xn$ from our simulations.

two processes drives evolution. For $t_a<t_s$ it is then possible to model the evolution of cooperation as taking place on a complete graph but now with each payoff multiplied by the respective fraction, such that the fitness equations become

$$W_C = \Phi_{CC}(i-1)R, \quad (18)$$

$$W_C = \Phi_{CD}iT \quad (19)$$

for $P=S=0$. Essentially, this payoff transformation amounts to absorbing the population structure induced by the wiring probabilities into functions that give the fractions of active links. In our work we have $t_a=t_s$; nonetheless, as we have done up to now, we can assume that the steady state $x$ is to a good approximation a product of the steady state network topology generated by the wiring probabilities. Conversely, $k_{CC}$ and $k_{DC}$ are consequences of selection dynamics. In the limit of large $n$, we can then attempt to compute the steady state $\Phi_{CC}$ and $\Phi_{DC}$ from the wiring probabilities as follows:

$$\Phi_{CC} = \frac{p_p}{(i-1)} + p_o \quad (20)$$

and

$$\Phi_{CD} = p_o \quad (21)$$

such that $\frac{\Phi_{CC}}{\Phi_{CC}} = \frac{p_p+p_o(i-1)}{p_o(i-1)} \approx \frac{k_{CC}}{k_{CC}} = \frac{T}{R}$. In [41] the authors introduce the parameter $r=\frac{\Phi_{CC}-\Phi_{CD}}{\Phi_{CC}}$ which measures the advantage of assortative (*C-C*) over disassortative (*C-D*) links and state that whenever $r>\frac{c}{b}$ the prisoner's dilemma is transformed into a coordination game. In Fig. 9 we show values of $r$ collected from our simulations for different average degrees and hence steady state $x$. On the same plot we show the mean field predictions calculated by Eqs. (20), (21), and (7) and the constant value $\frac{c}{b}=\frac{T-R}{R}$. The mean field curve in the figure shows us that only in the limit of high average degree and low cooperation does $r>\frac{c}{b}$ hold true, whereas otherwise $r=\frac{c}{b}$ and the advantage of assortative *C-C* links counterbalances the cost to benefit ratio. Our simulation results (top curve, Fig. 9) come with a sizable error margin although the simulation $r$ exceeds the predicted $r$ by some margin. What is plain to see is that when $x$ is small the advantage of a *C-C* link is much higher than when $x$ is high. In a sense, the fewer cooperators there are in the system the more valuable they

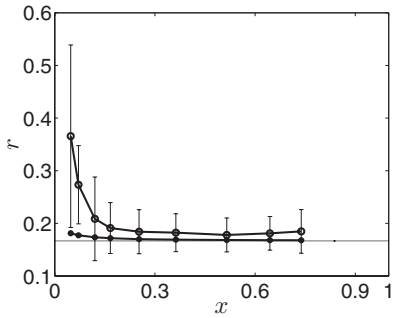


FIG. 9. $r$ as a function of the steady state cooperator density for systems with $n=1000$. Simulation results (with standard deviations) are the top curve, mean field predictions are the bottom curve. The straight line parallel to the $x$ axis indicates the constant $c/b$ value.

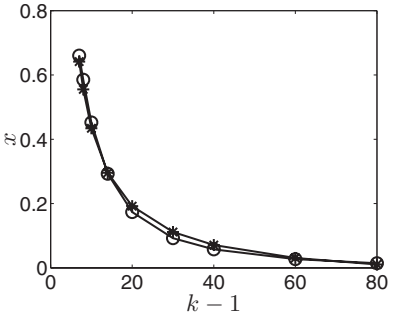


FIG. 10. Equilibrium cooperator density as a function of $k-1=[7,8,10,14,20,30,40,60,80]$ in linear scale for systems with $n=100$. Simulation results (circles) and Eq. (22) prediction (stars). There is a strategy mutation rate at birth of $p_m=0.01$.

become. In terms of the coordination game, at equilibrium our payoff matrix gets transformed to $R\rightarrow\Phi_{CC}R$ and $T\rightarrow\Phi_{CD}T$ with $\Phi_{CC}R=\Phi_{CD}T$ so that fitness equilibrium is attained. This payoff matrix to our knowledge does not correspond to a coordination game. A general model for the coevolution of strategy and network topology in a fixed-connectivity system with death-birth dynamics is also presented in [42] and applied to a variety of evolutionary games. The authors point out that, since the criterion for cooperation to thrive on a graph is $b/c>k$, in systems with high average degree $k$ the benefit obtained by cooperation will have to be much larger than the corresponding cost, which is deemed unrealistic. The authors then demonstrate how giving agents the capacity to probabilistically rewire their links in search of cooperating neighbors at a rate comparable to or higher than the death-birth dynamics can lead to universal cooperation in a prisoner's dilemma setting with $\frac{b}{c}=2$ and $k$ up to 40. In our parameter range presented here, the relation $b/c>k$ is indeed necessary for an all-$C$ state; however, there is essentially no coevolution between the general network properties $k,P(K)$ and the strategy abundances, since there is no mechanism for the feedback of successful links to future generations or link adaptation algorithm [although $P_C(K_C)$ and $P_D(K_C)$ are a consequence and a cause of coexistence]. Our preliminary simulation results (to be presented in the future) for $p_p,p_o$ as in the present paper, $1<p_e\leq 0$, and $\frac{b}{c}=2$ indicate that an all-cooperative state can be reached for $k>40$ through the coevolution of strategy and structure. This would indicate that a link inheritance mechanism could also explain the existence of cooperation in high-$k$ systems.

### C. The effect of strategy mutations

If we introduce mutations, such that the offspring can have the opposite strategy from the parent with probability $p_m$, coexistence can persist indefinitely. The equilibrium-size-dependent $x$ then becomes

$$x=\frac{(n-k)R-p_m(n-1)(T+R)}{n(k-1)(T-R)} \tag{22}$$

and as $n\rightarrow\infty$

$$x=\frac{R-p_m(T+R)}{(T-R)}. \tag{23}$$

In Fig. 10 we show $x$ for systems with $n=100$ together with the mean field predictions of Eq. (22).

As we can see from Fig. 10 the introduction of $p_m$ helps suppress the fluctuations that in small systems can destroy coexistence completely (compare Figs. 10 and 4). Producing individuals of the opposite type has the obvious effect of avoiding the absorbing states. Notice that a mutant offspring can benefit from the link to the parent only when the parent is a cooperator and the offspring a defector. This suggests a mechanism for how the mutations might regulate the fluctuations in density that bring about the absorbing states. When there is a majority of cooperators (in low average degree $k$ environments), a mutant defector offspring will have a high fitness compared to the average in the population, and thus will be more likely to reproduce. As defectors start to spread, and link to their parents, they again start to have lower average fitness than cooperators since in the low-$k$ environment defectors cannot amass the number of cooperator neighbors they need to overcome the absence of payoff from the link to their parent. On the other hand, when there is a defector majority a mutant cooperator offspring will most likely have the same fitness as its parent since $S=P=0$; thus cooperators can spread due to the parent-offspring link. When their numbers start to rise, cooperators are at a disadvantage again as the high average degree environment spells their doom.

## IV. CONCLUSIONS AND FUTURE WORK

To summarize we have shown how coexisting populations can persist in an ever-changing dynamic environment. Our results are in line with Hamilton's rule of kin selection operating on a stochastically created network. Moreover, we have briefly touched on the role of phenotypic mutation and

its ability to regulate coexistence in smaller populations. We plan to continue our research in the role of fluctuations, the influence of selection methods, and the creation of a model for the evolution of the degree distributions. Perhaps more importantly, we plan to examine systems with $p_e > 0$. In this case the offspring inherits a strategy and a set of successful relationships so that selection acts to preserve successful network units and not just individual behaviors.


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