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Network-based criterion for the success of cooperation in an evolutionary prisoner's dilemmaStephen Devlin¹ and Thomas Treloar²¹*Department of Mathematics, University of San Francisco, 2130 Fulton Street, San Francisco, California 94117, USA*²*Department of Mathematics, Hillsdale College, 33 E. College Street, Hillsdale, Michigan 49242, USA*

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We consider an evolutionary prisoner's dilemma on a random network. We introduce a simple quantitative network-based parameter and show that it effectively predicts the success of cooperation in simulations on the network. The criterion is shown to be accurate on a variety of networks with degree distributions ranging from regular to Poisson to scale free. The parameter allows for comparisons of random networks regardless of their underlying topology. Finally, we draw analogies between the criterion for the success of cooperation introduced here and existing criteria in other contexts.

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I. INTRODUCTION

Altruistic behavior among agents in evolving systems, both biological and social, has been widely observed in nature [1–7]. The fact that cooperative behavior can emerge between unrelated individuals in the competitive landscape of natural selection, however, poses a challenge to building realistic models of evolving systems. One tool that has been widely employed to help address this challenge is evolutionary game theory. As a result, game theoretic models that can exhibit realistic phenomena are of great interest to researchers across disciplines including physics, biology, and the social sciences [2–18].

Complex networks have also come to play a central role in the study of evolutionary systems [11–22]. In network-based models, agents occupy the vertices of a network and interact only within their immediate neighborhood consisting of those agents to whom they are connected by network edges. There are various models of agent interaction using mathematical games, the most widely studied being the prisoner's dilemma (PD), which captures, in a precise framework, the temptation to selfishly promote one's own fitness at the expense of a cooperating neighbor [8]. Another critical model component is the updating rule by which agents' strategies in the game evolve over time. A recent paper has shown that a subtle interplay among these various components being used—the structure of the network, the particular form of the game, and the updating rule—govern the long term dynamics [23] of the system and give rise to a wide variety of interesting phenomena.

Nowak and May introduced the network-based approach by showing that cooperation in the PD could become evolutionarily sustainable on a lattice for a wide range of game parameter values [11]. In that paper, agents imitated the most successful strategy among their neighbors. A change in the updating rule to the discrete replicator dynamics, however, significantly reduces the range of parameter values for which cooperation can thrive. On certain *heterogeneous* networks, such as those with heavy-tailed degree distributions that follow an inverse power law, Santos and Pacheco found that, under the replicator dynamics, cooperation could become the dominant population trait for the full range of parameter values [13]. This stands in stark contrast to the well-mixed model of the same dynamics where defection takes over the population

for all game parameter values. Other factors, such as the payoff structure of the game [20] and the particular model for evolution [23], have also been shown to have dramatic effects on the system dynamics. The surveys [12,23] provide a good starting point for exploring the variety of models of evolving systems.

In this paper, we consider a particularly widely studied evolutionary model. We use a payoff matrix that locates the game on the border between the PD and the snowdrift game—the so-called weak PD as in Ref. [13]. Updating is performed synchronously with the discrete replicator dynamics, and our focus is the role the network structure plays in predicting the success of cooperation. We observe that the evolutionary success of cooperation can be accurately predicted from quantitative network parameters. The results build on previous studies of how cooperators survive in an evolutionary PD [15] and the degree to which heterogeneity can be quantified to give insight into the success of altruism [17]. Our primary tools are the generating functions associated with the degree distribution of the network [19]. Comparing predictions to Monte Carlo simulations, we find excellent agreement across networks with varying topologies and varying average degrees. Given the known complexity of these dynamical systems [12,15], the accuracy with which this simple criterion predicts actual dynamics is especially appealing.

Finally, we relate the criterion derived here to existing criteria in other contexts, including kin selection and network reciprocity.

II. PRELIMINARIES

The PD is a widely studied framework in which to model problems of conflict and cooperation [8]. Two players independently choose between cooperation and defection, and players' choices determine (normalized) game payoffs. The payoffs are interpreted as fitness in evolutionary biology as follows: Mutual cooperation gives a payoff R to each player, a defector exploiting a cooperator gets T , an exploited cooperator gets S , and two defectors each give and receive nothing. Payoffs satisfy $T > R > 0 \geq S$, from which it follows that a rational player always defects as the payoffs for defection strictly dominate those for cooperation regardless of the co-player's strategy. Defection is said to weakly dominate when $S = 0$.

The result is a Nash equilibrium in which both players defect and the dilemma arises from an inefficiency of this equilibrium: Both agents could fare better by cooperating [8].

A widely adopted payoff normalization [11,13–17] sets $R = 1$ and $S = 0$ so that the game depends on the single parameter $T = 1 + r$ indicating the temptation toward defection in the game. Taking values of S near zero amounts to an assumption that social interactions are inexpensive. With this normalization, the game lies on the boundary between the PD and the snowdrift game (SG), another commonly studied game of cooperation. In the SG, the bottom two PD game payoffs are reversed so that cooperation is a better unilateral response to defection: $T > R > S > P$ with P as the punishment for mutual defection. In that case, setting $T = 1 + r$, $R = 1$, and $P = 0$, the Nash equilibrium calls for a cooperation probability of $1 - \frac{r}{S+r}$, which is close to zero as long as S is sufficiently close to zero. Qualitatively, the case of $S = 0$ (the so-called weak PD) addresses both games when social interactions are inexpensive and so, is the focus from here on. Although the $S \approx 0$ assumption is both plausible and widely adopted, it is significant, and dropping it has a considerable effect on system dynamics [20]. As mentioned in the Introduction, the interplay among the network, the updating scheme, and the game is subtle, and a change in any of these can have a significant effect on the dynamics of the system. We stress that the criterion derived here is specific to the assumptions of this particular model (see further discussion below).

Evolution is introduced through repeated interactions between agents. Agents engage in a PD with their neighbors and then update their strategy using the replicator dynamics. Replicator dynamics updating models natural selection using agent fitness comparisons that result in stochastic imitation of fitter strategies by less fit strategies. In the repeated PD, payoffs are further required to satisfy $T + S < 2R$ in order to ensure that full cooperation in the population remains Pareto optimal.

When a population of agents is unstructured and agent interactions are random, the replicator dynamics favor defection, and cooperation is driven to extinction. As mentioned in the Introduction, the situation is notably different when the population is structured by a network.

Let \mathcal{N} be a network consisting of vertices and undirected edges where neither loops nor multiple edges are allowed. Agents occupy the network's vertices and are constrained to interact only within their immediate neighborhood defined to be those agents with whom they are connected by an edge. Define a round of play to consist of each agent playing a pure strategy in a PD with all neighbors and accumulating the resulting payoffs. Following a round, agents simultaneously update strategies using the discrete replicator dynamics: If agent x has accumulated payoff P_x and compares her payoff to that of agent y , then x adopts the strategy of y with probability,

$$P_{x \rightarrow y} = \frac{\max\{0, P_y - P_x\}}{(1+r)k_{\max}}.$$

Here, k_{\max} is the larger of the degrees of vertices x and y [13,15–18].

Simulations are performed on various networks (details below) with 10^4 vertices. In each case, we start from a random strategy assignment where the probability of an agent

cooperating is 0.5. A *series* is defined to consist of 10^4 rounds of play with updating. The *series mean* is taken to be the average cooperation level over the last 1000 rounds of the series. For a particular network, 100 series are run, and the equilibrium cooperation level is taken to be the average of these 100 series means. For a network \mathcal{N} and a particular choice of PD parameter r , we let $\rho_{\mathcal{N},r}$ denote this equilibrium cooperation level.

It is well known (and summarized below) that cooperation can become evolutionarily stable in network models of this kind. Moreover, the extent of the evolutionary success of cooperation has been shown to depend greatly on the particular underlying network topology [11–13]. In order to make this relationship more explicit, we recall some basic tools in the study of networks.

Let p_k denote the probability that a random vertex from the network \mathcal{N} has degree k , and let X be the random variable that takes values in the set of all possible vertex degrees in the network. The probability generating function [19] for the distribution of X is given by

$$G(x) = \sum_{k>0} p_k x^k,$$

and gives a first-order approximation of network topology. The degree distribution ignores any other contact information, so $G(x)$ represents a generic network chosen randomly from among all those with the fixed degree distribution. The mean vertex degree V in the network is given by $V = G'(1) = \langle k \rangle$.

Alternatively, a randomly chosen *edge* from the network is k times more likely to lead to a vertex of degree k than a vertex of degree 1. Therefore, if Y is the random variable whose values are the degrees of vertices reached from random edges, then the probability generating function of Y is given by

$$T(x) = \frac{\sum_{k>0} k p_k x^k}{\sum_{k>0} k p_k} = \frac{1}{G'(1)} \sum_{k>0} k p_k x^k = \frac{x G'(x)}{G'(1)}. \quad (1)$$

Define a *random neighbor* to be a vertex reached by first choosing a random vertex in the network, followed by a random edge emanating from that vertex. Assuming that the network is random other than the fixed degree distribution, it follows that $T(x)$ is the probability generating function for the degree distribution of random neighbors. The average degree of a random neighbor N is, therefore, the expected value of Y so that $N = T'(1)$. Note that, if the network is not random, then N need not equal $T'(1)$ [21]. An example of a nonrandom network is one where the probability that an edge leads from a degree j vertex to a degree k vertex is not independent of j , i.e., a network with degree-degree correlations. Since the generating functions G and T contain no information about network size, they represent the limit as the number of vertices grows without bound. The mean-field parameters N and V , consequently, require sufficiently large networks to be meaningful. That said, the results that follow are robust down to networks with 2×10^3 vertices.

A critical factor in the study of cooperation phenomena is network heterogeneity [13–17]. In heterogeneous networks,

a broad diversity of vertex degrees is represented. In the context of the evolutionary PD, network heterogeneity has been shown to be strongly correlated with increased success of cooperation [13,17]. On certain highly heterogeneous networks, such as those with so-called scale-free degree distributions, cooperation can be the dominant population trait for the full range of PD game parameters.

Heterogeneity can be naturally quantified by the variance in the degree distribution. With $\langle k \rangle$ denoting the expected value of the random variable X and $\langle k^2 \rangle$ denoting the expected value of X^2 , one has $\text{Var}[X] = \langle k^2 \rangle - \langle k \rangle^2$. Using the above notation,

$$\text{Var}[X] = G'(1)T'(1) - G'(1)^2 = V(N - V).$$

Fixing the average network degree V , one gets $(N - V)$ or the difference between the degrees of an average neighbor and an average vertex as a measure of network heterogeneity. In what follows, we are interested in this measure of heterogeneity relative to the degree of a random neighbor, namely, the mean-field parameter $\frac{N-V}{N}$. This parameter has the advantage of giving a normalized measure of heterogeneity that lies in the interval $[0, 1)$.

III. RESULTS AND DISCUSSION

We consider the following question: Given a network \mathcal{N} , for what game parameter values r can cooperation flourish? To address this question, we define $r_{0.5}$ to be the value of the game parameter at which point neither a cooperator nor a defector has an advantage (on average) in the network dynamics at equilibrium. The hypothesis is that $r_{0.5}$ marks the point at which each strategy is equally successful, and in the resulting equilibrium, one finds cooperation and defection to be approximately equally prevalent on the network. Thus, $r_{0.5}$ is a threshold at which point the system transitions between dominant cooperation and dominant defection where dominant is defined as representing more than 50% of all vertices. In what follows, we explore the value of $r_{0.5}$ in terms of the network parameters N and V .

To this end, we consider simulated dynamics on networks with varied degree distributions. Networks with K vertices and average degree $2m$ ($m = 2, 3, \text{ or } 4$) are constructed via a two step process introduced in Ref. [22]. First, a network is generated from the algorithm introduced in Ref. [22]. This algorithm uses a single parameter α to interpolate between an Erdős-Rényi random network (ER) [24], and a Barabási-Albert (BA) scale-free network [25]. Starting from a complete graph on n_0 vertices, one of the remaining $K - n_0$ vertices is chosen. This vertex has m edges to attach as follows. With probability $1 - \alpha$, the vertex attaches an edge to an existing vertex with a probability proportional to the existing vertex's degree (i.e., by preferential attachment). With probability α , the edge is connected to any of the existing $K - 1$ network vertices with a fixed probability. This procedure is repeated m times, once for each edge. When $\alpha = 0$, one obtains a BA network with a power law degree distribution, and when $\alpha = 1$, one obtains an ER random graph. Intermediate α 's give hybrid distributions with levels of heterogeneity falling between the heterogeneous BA networks and the essentially homogeneous ER random networks [17]. Networks are generated with $K = 10^4$ vertices and average degree

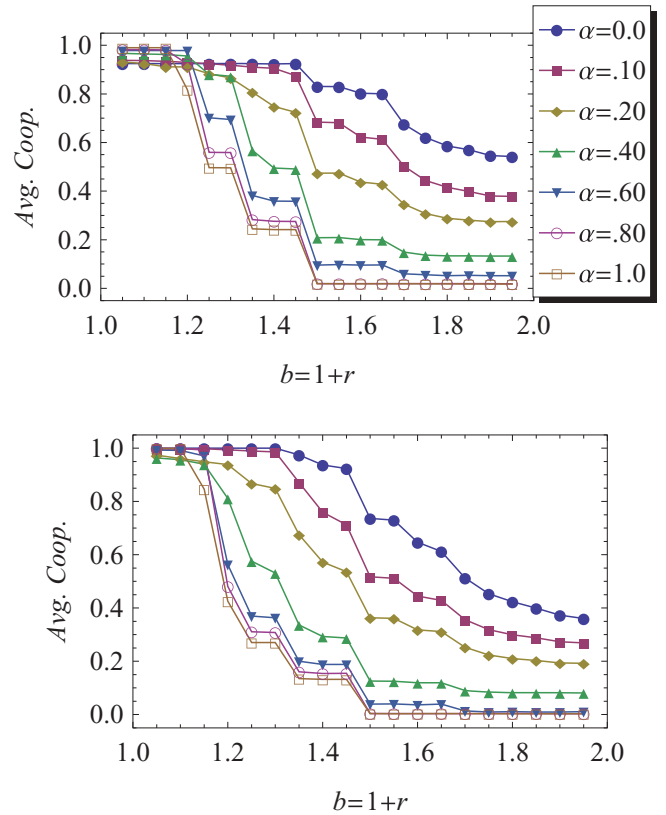


FIG. 1. (Color online) Equilibrium cooperation level as a function of the game parameter $b = 1 + r$ for the $B_{4,\alpha}$ and $B_{6,\alpha}$ families of networks.

$2m \in \{4, 6, 8\}$. For each value of $2m$, networks are generated with $\alpha \in \{0.00, 0.10, 0.20, 0.40, 0.60, 0.80, 1.00\}$. Finally, each network is distilled down to its degree distribution by throwing away all other contact information, and a new network is reconfigured, consistent with that degree distribution, using the configuration model [26]. The result is a maximally random network with the specified degree distribution belonging to a family of graphs, which we denote by $B_{2m,\alpha}$.

Figure 1 shows the average cooperation levels as a function of the parameter of $1 + r$ for average network degrees $V = 4$ and $V = 6$ and with varying levels of heterogeneity determined by α . We see that, for networks with increased levels of heterogeneity, high levels of cooperation are sustained for larger values of r . In Fig. 1, $r_{0.5}$ can be seen as the value of r which gives an average equilibrium cooperation level $\rho_{N,r}$ of approximately 0.5.

The results of the simulations described above are consistent with previous work and are summarized with the temperature plot in Fig. 2. For each simulation, $\rho_{N,r}$ is plotted as a function of the mean-field parameter $\frac{N-V}{N}$ introduced above as well as the game parameter r . Note that the actual transitions from dominant cooperation (darker red) to dominant defection (darker blue) occur in the neutral tan colored regions between red and blue. One can see that, for all networks, the value of $r_{0.5}$ varies linearly with $\frac{N-V}{N}$. Indeed, the black lines in each panel mark the equation,

$$r_{0.5} = \frac{N - V}{N}, \tag{2}$$

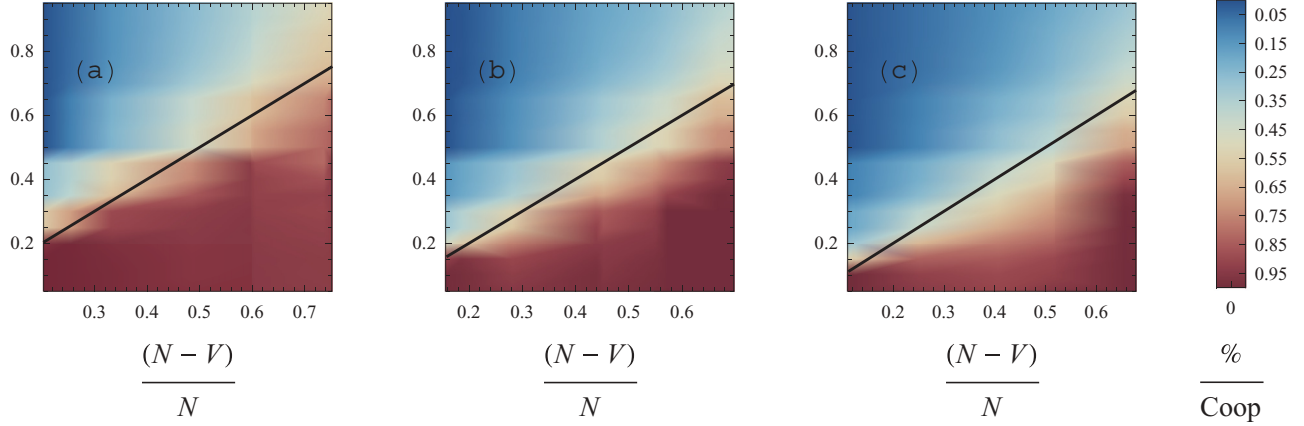


FIG. 2. (Color online) Simulation results for the evolutionary PD on the family of networks $B_{2m,\alpha}$ with varying heterogeneity and average degrees (a) 4, (b) 6, and (c) 8. The equilibrium level of cooperation is given as a temperature plot depending on both the network parameter $\frac{N-V}{N}$ and the cost-to-benefit ratio r . A point (x, y) in the plot, therefore, is colored according to the equilibrium cooperation level in the evolutionary game on a fixed network with heterogeneity given by $x = \frac{N-V}{N}$ and PD cost-to-benefit ratio $y = r$.

where cooperators and defectors should be approximately equally successful and so, are predicted to be equally prevalent. Note that the line given by this simple relationship passes through the neutral or nearly neutral regions of the temperature plot, giving a strong indication of the correlation between the value $r_{0.5}$ arising from simulations and the mean-field network coefficient $\frac{N-V}{N}$. We also note that, on random regular networks where all 10^4 vertices have the same degree, cooperation levels are essentially zero for all values of $r > 0$, which is consistent with Eq. (2) when $N = V$. It must be noted that values of $\frac{N-V}{N}$ beyond 0.70 prove difficult to achieve, at least, in the context of the growth and preferential attachment algorithm. Recall, the reason for using this family of networks was not any particular topology but rather to provide a range of varied topologies and heterogeneity so as to highlight the success of the parameter $\frac{N-V}{N}$ in predicting $r_{0.5}$.

In Fig. 3, we plot simulated $r_{0.5}$ values directly against $\frac{N-V}{N}$ for all networks. The strong linear relationship is again evident.

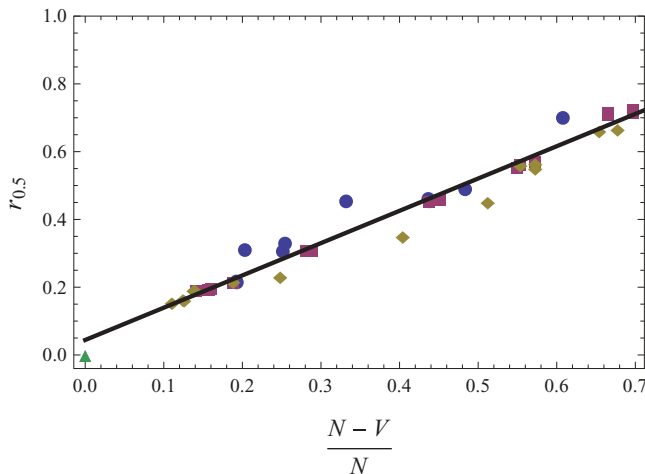


FIG. 3. (Color online) A plot of $\frac{N-V}{N}$ versus $r_{0.5}$. In addition, the figure shows the linear regression line $y = 0.953024x + 0.0442192$ with correlation coefficient $r = 0.986$.

Setting $x = \frac{N-V}{N}$ and $y = r_{0.5}$, we get a linear regression line of

$$y = 0.953024x + 0.0442192, \quad (3)$$

with correlation coefficient $r = 0.986$ ($r^2 = 0.972$). This gives excellent agreement with Eq. (2). We again note the versatility of the mean-field parameter $\frac{N-V}{N}$, giving accurate predictions across networks with very different distributions, different levels of heterogeneity, and different average degrees.

As motivation for the criterion of Eq. (2) and the mean-field parameter $\frac{N-V}{N}$, we consider the results in Refs. [17] and [15]. In Ref. [17], the weighted (by the cost-to-benefit ratio r) average equilibrium cooperation level on the network depended on the network parameter $x = \frac{V}{N}$ in a linear way. More precisely, if we let

$$y = \frac{\sum r \rho_{N,r}}{\sum r},$$

where the sum is taken over all game parameter values r , then a linear regression of y on $x = \frac{V}{N}$ gives $y = -1.0074x + 0.9322$. This can be thought of as a relationship between the *global* average cooperation level on a network, over the full range of the temptation to defect, and the parameter $\frac{V}{N}$. Notice, however, that the regression line is very close to $y = -x + 1$. Indeed, inserting $x = \frac{V}{N}$ in the line gives $y = \frac{N-V}{N}$, the network parameter of Eq. (2). This suggests a kind of mean value relationship whereby the global average cooperation level over all temptation values also gives the local threshold value of the game parameter $r_{0.5}$ where the network transitions from dominant cooperation to dominant defection.

A further understanding of Eq. (2) emerges from a closer look at the dynamics discussed in Ref. [15]. For low temptation to defect, cooperation is the social norm. As the temptation to defect increases, however, the dynamics are governed by three populations: a core (or cores) of cooperating agents, a core (or cores) of defecting agents, and a critical fluctuating population of sometime cooperators and sometime defectors. The resilience of cooperation, as described in Ref. [15], is

determined by interactions between agents on the border of the cooperator core(s). When the temptation to defect becomes great, defectors eventually invade the core by stripping off layer upon layer of exposed cooperators until they are largely eradicated from the population. The resilience of the cooperator core(s) is fundamental to the success of cooperation.

Consider, therefore, an agent interacting within a cluster of cooperators with the cost-to-benefit ratio for the game as given by the normalized payoffs used here. Within the cooperation cluster, the cost c paid by a cooperating agent is $(1+r) - 1 = r$: That is, r is the payoff forgone by cooperating instead of defecting. Likewise, the benefit b received by a cooperating neighbor of a cooperator is 1. This gives us a notion of a localized cost-to-benefit ratio within a cooperator cluster of $\frac{c}{b} = r$. When $r < r_{0.5}$, the game dynamics present an advantage to cooperators within a cluster, and they can resist invasion. In this case, we expect cooperation to thrive. When $r > r_{0.5}$, the advantage shifts to defectors who will infiltrate the cooperator core (on average), and cooperation should fall below 50%. Replacing $r_{0.5}$ with $\frac{N-V}{N}$, we get $\frac{c}{b} = r < \frac{N-V}{N}$ as the condition for cooperation to flourish as in Eq. (2).

Finally, we draw an analogy between the criterion of Eq. (2) and some existing criteria for the evolution of cooperation. A discussion of the notion of network reciprocity in the context of a death-birth process evolving under weak selection is given in Refs. [3,27]. Here, a single network agent is chosen to be replaced each round, and the agent's neighbors compete to pass their strategy along. Weak selection indicates that the game payoffs represent only a small contribution to an agent's baseline fitness. In this context, the fixation probability or the likelihood that cooperation ultimately takes over the

entire network is studied. Although, this is clearly a different evolutionary system than the one studied here, it is interesting to note the connection with their criterion for natural selection to favor cooperation: On a regular network, cooperation is favored when $r < \frac{1}{V}$. This result was extended to nonregular networks in Ref. [28] where the criterion became $r < \frac{1}{N}$. As pointed out in Ref. [27], network reciprocity is reminiscent of Hamilton's rule for kin selection [1].

Hamilton's rule gives a genetic criterion for the emergence of altruistic behavior between individuals when their *genetic relatedness* exceeds the cost-to-benefit ratio of the altruistic act. Genetic relatedness is measured by the probability that two genes, randomly selected from each individual at the same locus, are identical by descent [1]. The parameter $\frac{N-V}{N}$ that arises in Eq. (2) can be thought of as an analogous notion of *relatedness*. Like genetic relatedness, $\frac{N-V}{N}$ lies in the interval $[0,1)$, with larger values indicating increased relatedness. If two networks have the same fixed average degree V , then there is more social cohesion in networks with larger more influential neighbors. As a result, N emerges as the parameter governing social viscosity [29] where larger neighbors increasingly facilitate relatedness and, through this, cooperation. As stressed above, changes to the specific assumptions of the model have far reaching effects on the dynamics of cooperation, and these analogies extend only so far as the particulars of the model used here.

In conclusion, we have shown that a simple criterion, derived using basic ideas from the theory of complex networks, can effectively predict the success of cooperation in a particular evolutionary PD on varied network topologies. Moreover, the analysis suggests a network-based evolutionary rule that nicely parallels existing criteria in other contexts.

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