

Cooperators and connectivity: cooperation is more prevalent in network hubs

Sam P. Brown^{1*} & Li Kang^{2*}

(1) Section of Integrative Biology, University of Texas at Austin, 1 University Station C0930, Austin TX 78712, USA (2) Institute of Theoretical Physics, Chinese Academy of Science, Beijing, 100080 P. R. China.

**These authors contributed equally to this work*

The evolution of cooperation is a fundamental problem in biology, underlying questions from the molecular to the societal scale. The prisoner's dilemma (PD), a two-person game in which players can either cooperate or defect, is a common metaphor for the study of the evolution of cooperation. In a well-mixed (mean-field) population, cooperators are certain to go extinct in the PD as they are efficiently exploited by defectors. However, when the PD is played in a regular square lattice, cooperators can coexist with defectors. Recent work has begun to explore the behaviour of the PD played on different network structures. Here we study the behaviour of the simple (non-iterated) PD on scale-free networks, and contrast these results with behaviour on regular networks. Our results illustrate that scale-free networks enhance the persistence of cooperators (compared to regular square lattices), with cooperators concentrated in high-degree nodes.

INTRODUCTION

The evolution of cooperation is a fundamental problem in biology. Why should an individual sacrifice its own success in order to increase the success of another? Surely selfish individuals must always outcompete altruistic individuals, as they receive the benefits of cooperation without paying any costs? Yet from genes to nations, we find examples of persistent cooperation (Maynard Smith & Szathmary 1995; Dugatkin 1997; Crespi 2001; Sachs *et al.* 2004).

The Prisoner's dilemma

Perhaps the most famous metaphor for the evolution of cooperation is the Prisoner's dilemma. The prisoner's dilemma presents two interacting players with a simple choice, to cooperate or to defect (Axelrod 1984; Doebeli & Hauert 2005). An act of cooperation entails a benefit b to a recipient and a cost c to the actor ($b > c > 0$). If they both cooperate, they each receive a 'reward', $R = b - c$, which is larger than the 'punishment', $P = 0$, obtained if they both defect. If one defects while the other cooperates, the defector receives the 'temptation' payoff, $T = b$, which is greater than R , and the cooperator receives the sucker's payoff $S = -c$, which is less than P . Hence $T > R > P > S$ (Table 1). Given the relative magnitude of the payoff values, a rational player should always defect in 'one-off' encounters, regardless of whether the other player cooperates or not (defection is an evolutionary stable strategy, Maynard Smith 1982; likewise pure defection is the only stable equilibrium in a replicator dynamics treatment, Hofbauer & Sigmund 1998). Thus the paradoxical outcome is total defection, despite a higher pay-off occurring when everyone cooperates.

The fact that the simple PD game results in complete defector dominance makes the PD an excellent baseline for testing additional mechanisms that might enhance the survival

of cooperation. The essential feature of any mechanism promoting altruism is that cooperators are more likely to interact with other cooperators than expected by chance (Frank 1998; Doebeli & Hauert 2005). Key non-exclusive mechanisms favouring cooperator assortment (together with seminal references) include kin-selection (Hamilton 1964a,b), reciprocity / reputation (Trivers 1971; Axelrod & Hamilton 1981; Nowak & Sigmund 1998) and spatial extension (Nowak & May 1992). In this paper we will focus on the effects of spatially structured populations on the fate of cooperators. Unlike a number of arguments based on kin selection, reciprocity or reputation, spatially explicit models do not require any form of recognition, memory or conditional behaviour in order to allow the persistence of cooperators.

Spatial cooperative games

Nowak & May (1992) explored the consequences of placing cooperators and defectors in a two dimensional spatial array, limiting their interactions to immediate neighbours (see methods). In contrast to random mixing, this spatial restriction on partnerships enabled the persistence of cooperators. A subsequent flood of related papers has illustrated that the maintenance of cooperation in spatially structured PD is a robust phenomenon (recently reviewed by Doebeli & Hauert 2005). The key mechanism of persistence in spatial models is believed to be the clustering of cooperators, ensuring that cooperators more often interact with other cooperators and thus receive higher payoffs than defectors (who more often encounter defectors). This argument has some analytical support from the use of pair-approximation techniques (Van Baalen & Rand 1998), and more generally is consistent with a kin-selection interpretation (Doebeli & Hauert 2005).

Simulations supporting the general conclusion that spatial structure favours the persistence of cooperators have largely focussed on regular square lattices, where

interactions (including reproduction) are limited to the nearest four or eight neighbours. Intriguingly, a number of recent studies have begun to point to an enhancement of cooperation in more randomly-structured networks, countering the expectation that regular lattices will promote cooperation through their facilitation of clustering (Abramson & Kuperman 2001; Masuda & Aihara 2003; Doebeli & Hauert 2005; Hauert & Szabó 2005, but see Ifti *et al.* 2004). For example, Hauert & Szabó (2005) showed that random regular graphs (all individuals have the same number of neighbours, but neighbours are drawn randomly from the population) support cooperation over a wider parameter range than for an equivalent (same degree number) lattice, while regular small-world networks (a regular lattice with some proportion of nodes randomly rewired, Watts & Strogatz 1998) showed an intermediate level of support for cooperation. Other recent studies have explored variations in the number of neighbours. Vainstein & Arenzon (2001) found that ‘diluted’ lattices (where some nodes are left vacant) support higher frequencies of cooperators over a wide parameter range.

In this paper we focus on the effects of variation in the numbers of neighbours (the contact or degree number). Rather than use diluted lattices where only small variations in degree number can be made, we focus on scale-free networks. Scale-free or power-law networks obey power-law degree distributions, ensuring that while most individuals have few neighbours, some individuals have many. Many biological networks including human social networks can be empirically described by scale-free networks (Albert & Barabási 2002). Vukov and Szabó (2005) recently studied the PD game on a scale-free hierarchical network, but they found that cooperation could not be maintained in this system. In a modified system with extended horizontal links (forming a hierarchical lattice; no longer scale-free). They found that cooperators could persist, and that they tended to be concentrated in the higher levels of the lattice hierarchy. Santos & Pacheco (2005) have found very recently that in a preferential-attachment scale-free network, cooperators can persist. Here we explore the PD game played on random scale-free

networks, and investigate both conditions for persistence and biases in the location of cooperators within the network.

METHODS

To model the PD in a spatially structured population, individuals are arranged on a network (typically a regular lattice) and interact only within a limited local neighbourhood. Each individual (with fixed strategy C or D) plays the PD with each of its neighbours, receiving a payoff for every interaction as described in Table 1. The mean of its payoffs represents its performance or fitness P . To describe natural selection, we need to track the fate of cooperators and defectors over many generations. To do this, we periodically ‘update’ the identity of each node (individual) in the network. In a biological context, the application of the update rule can be considered as representing the death of focal individual x , and its replacement by either its own progeny (same strategy) or that of a neighbour (potentially a different strategy). First, a randomly-selected individual x is selected for update, then its fitness is compared to a randomly-selected neighbour y . The node of individual x will take on the strategy of individual y with a probability proportional to the difference in performance $P_y - P_x$. Otherwise, the focal node will continue with the strategy of individual x . Following Hauert & Szabo 2005, we use a transition probability given by $[1 + \exp(-(P_y - P_x)/k)]^{-1}$, where k denotes the amount of noise. Under this update formulation, while the strategy of a higher-fitness neighbour is likely to be adopted, it is also possible (if unlikely) that the strategy of a lower-fitness neighbour is adapted in its place.

Constructing a scale-free network

To build a scale-free network, we first assigned each vertex i with a randomly selected degree (contact number) k_i drawn from the probability distribution $P(k) = k^{-\gamma}$. We then attached k_i stubs (half-edges) to each vertex i , under the constraint that the total number

of stubs must be even. Finally, we randomly chose pairs of half-edges and connected them into full edges until no stubs remain, under the sole constraint that multiple edges are disallowed. The power-law degree distribution for a sample network is illustrated in figure 1. We note that the avoidance of multiple edges introduces a slight element of disassortativity to our network.

RESULTS and DISCUSSION

What happens when the PD is played over non-homogeneous environments? We focus on the effect of contact number heterogeneity. Individuals may vary in their number of contacts for a number of reasons – e.g. personality differences, division of labour, geographic heterogeneity (physical integration / isolation), demographic heterogeneity (high resource / low resource); etc. Any/all of these factors can contribute to contact distributions, often described by scale-free distributions. We then ask, can cooperators persist in these networks? And if so, where in these networks will cooperators prevail?

Our principal results are twofold. First, we show that cooperators can persist in random scale-free networks (figures 2, 3), and for a wider parameter range than for an equivalent (same mean degree number) regular lattice (figure 4). In keeping with previous studies of the spatial PD with stochastic update rules (reviewed by Doebeli & Hauert 2005), we find that the initial frequency of cooperators and defectors has effectively no influence on the equilibrium prevalence of cooperators (figures 2, 3). The new result that random scale-free networks are more supportive of cooperation than regular lattices (figure 4) adds weight to the growing conclusion that cooperation is more favoured in more randomly structured networks (Abramson & Kuperman 2001; Masuda & Aihara 2003; Doebeli & Hauert 2005; Hauert & Szabó 2005, Santos &

Pacheco 2005; but see Ifti et al 2004). The behaviour of the PD in scale-free networks has scarcely been considered, however it is noteworthy that one published study of the PD in a completely non-random hierarchical scale-free network illustrated that cooperators could not persist in this structure (see the appendix to Vukov and Szabó 2005). Thus we see that for both regular and scale-free networks, network clustering appears to inhibit the maintenance of cooperation. The reasons for this effect remain an open question.

Our second principal result illustrated that for parameters permitting the persistence of cooperators, cooperators are more commonly found in highly connected nodes, and are relatively scarce in the network periphery (figure 5). This is in many respects a surprising result. Increasing the neighbourhood size (and hence degree number) in a regular lattice has been reported to reduce cooperation, ultimately converging to the mean-field result of complete defector domination for sufficiently large neighbourhoods (Ifti *et al.* 2004), thus we might expect by extension to a scale-free network that cooperation would thrive in the low-degree periphery, an expectation given further strength by the common prejudice that rural (low degree) folk are more cooperative.

So why might we find in contrast that cooperation is favoured in highly connected nodes? Here we outline a working hypothesis that underlines our ongoing work in this area. If we accept that for the PD, spatial clustering of cooperators helps cooperators to spread, then we can make a simple conjecture: As an approximation, Cs spread when their proportion of cooperator neighbours C_n is greater than a threshold x/k , where k is their neighbourhood size. So isolated cooperators ($C_n < x/k$) are likely to die out – consistent with the initial drop in the frequency of cooperators for all starting conditions (figure 2), as the starting conditions are likely by chance to create a number of isolated cooperators. If the population proportion of cooperators is less than x/k , ie cooperators are globally rare, we can expect a greater initial mortality of cooperators (figure 2).

However, by chance, some cooperators will have locally higher frequencies, ie for some cooperators, $C_n > x/k$. Given an initial random seeding of cooperators and defectors, this local result is more likely to happen in low degree nodes, due to sampling error (higher variance in C_n for lower values of k). However, as the global proportion of cooperators rises and exceeds the threshold x/k , we would then find the opposite effect of sampling error: low degree nodes would be more likely by chance to have $C_n < x/k$, and so cooperators would then become more scarce in low-degree nodes., as observed at equilibrium (Figure 5).

The main prediction of this argument is that if the global frequency of cooperators is initially low, then during the growth phase of cooperators we expect cooperators to be more prevalent in low degree nodes (ie cooperators would spread from low degree nodes). However, when cooperators become sufficiently common (towards equilibrium) they would then become less common in low degree nodes (figure 5). In our ongoing work, we will look at the transient frequency of cooperators at low and high degree nodes to test this idea. Furthermore, we will extract data on the clustering of cooperators through time, to estimate the mean and variance of C_n through time, and for different degree numbers.

Looking further ahead, a number of related projects can be envisaged. Repeating our analyses for alternative network structures would be informative. By extending our study of scale-free networks to consider assortative versus disassortative networks (our current network is close to being assortatively neutral) we could make further progress on understanding the role of both cooperator and network clustering in underpinning the maintenance of cooperation. Another natural extension would be to use alternative cooperative games. Even within two-player two-strategy cooperative games, there are alternatives to the prisoner's dilemma (snowdrift and stag-hunt games. Doebeli & Hauert 2005). Extending the scope to continuous and multiplayer games allows many

more potential outcomes. Finally, we would like to draw attention to the intriguing possibilities of allowing network evolution in cooperative games. By allowing cooperators to alter or even expand the network (e.g. by making peripheral habitat liveable – Harms 2001), we introduce a feedback between network structure and agent strategy. This feedback could be implemented by allowing payoffs and/or neighbour identity to influence locally-adaptive changes in the structure of the network, and could ultimately shed light on the dynamic tensions between the shape of social networks and the strategies of their agents.

ACKNOWLEDGEMENTS

We are very grateful to the SFI and the ITP for putting together a wonderful summerschool, and for financing our attendance. We would also like to thank all the other summerschool attendees for a very stimulating time in Beijing. SPB is supported by the Human Frontier Science Program.

REFERENCES

- Abramson G & Kuperman M 2001 Social games in a social network. *Phys Rev E* 63, 030901-1-4
- Albert R & Barabási AL 2002 Statistical mechanics of complex networks. *Rev. Mod. Phys.* 74, No. 1,
- Axelrod R 1984 *The evolution of cooperation*. Basic Books, New York.
- Axelrod R & Hamilton WD 1981 The evolution of cooperation. *Science* 211, 1390-1396.
- van Baalen M & Rand DA 1998 The unit of selection in viscous populations and the evolution of altruism. *J Theor Biol* 193, 631-648.

Crespi BJ 2001. The evolution of social behaviour in microorganisms. *Trends. Ecol. Evol.* 16, 178-183.

Dugatkin LA 1997 *Cooperation Among Animals: An Evolutionary Perspective*. Oxford University Press, Oxford.

Doebeli M & Hauert C 2005 Models of cooperation based on the prisoner's dilemma and the snowdrift game. *Ecology Letters* 8, 748-766.

Frank SA 1998 *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ.

Hamilton WD 1964a The genetical evolution of social behaviour I. *J Theor Biol* 7, 1-16.

Hamilton WD 1964b The genetical evolution of social behaviour II. *J. Theor Biol* 7, 17-52.

Hauert C & Szabó G 2005 Game theory and physics. *Am J Phys* 73, 405-414.

Hofbauer J & Sigmund K 1998 *Evolutionary Games and Population Dynamics*. Cambridge University Press, Cambridge.

Ifti M, Killingback T & Doebeli M 2004 Effects of neighbourhood size and connectivity on the spatial continuous prisoner's dilemma. *J Theor Biol* 231, 97-106.

Masuda N & Aihara K 2003 Spatial prisoner's dilemma optimally played in small-world networks. *Phys Lett A* 313, 55-61.

Maynard Smith J & Szathmáry E 1995 *The Major Transitions in Evolution*. WH Freeman & Co., Oxford.

Nowak MA & Sigmund K 1998 Evolution of indirect reciprocity by image scoring. *Nature* 393, 573-577.

Nowak MA & May RM 1992 Evolutionary games and spatial chaos. *Nature* 359, 826-829.

Sachs JL, Mueller UG, Wilcox TP, & Bull JJ 2004. The Evolution of Cooperation, *Quarterly Review of Biology* 79, 135-160.

Santos FC & Pacheco JM 2005. Scale-free networks provide a unifying framework for the emergence of cooperation. *Phys. Rev. Letts.* 95, 098104.

Trivers RL 1971 The evolution of reciprocal altruism. *Q Rev Biol* 46, 35-57

Vainstein MH & Arenzon JJ (2001) Disordered environments in spatial games. *Phys. Rev. E.* 64, 051905-1-6.

Vukov J and Szabó G (2005) Evolutionary prisoner's dilemma game on hierarchical lattices. *Phys Rev E* 71, 036133-1-6.

Watts DJ & Strogatz SH 1998 Collective dynamics of 'small world' networks. *Nature* 393, 440-442.

FIGURE LEGENDS

Figure 1. Degree distribution for a scale-free network. The probability that a node has k neighbours (degree k), given a power-law distribution of k with an exponent $\gamma = 2.1$.

Figure 2. Percentage cooperators as a function of time (Monte-Carlo steps or generations) for three initial conditions. In each run, by 200 generations the share of cooperators has equilibrated to approximately 45%. $\gamma = 2.1$. $b = 1.02$, $c = 0.02$.

Figure 3. Equilibrium frequency as a function of initial frequency. As hinted by figure 2, we find the equilibrium share of cooperators to be robust against variations in the initial frequency of cooperators. $\gamma = 2.1$. $b = 1.02$, $c = 0.02$.

Figure 4. Equilibrium cooperator frequency as a function of the cost/net-benefit ratio $r = c/(b-c)$. Black squares, regular lattice; red squares, scale-free network. To aid comparisons between these network structures, we standardized the number of nodes and then tuned the exponent γ to ensure the difference in edge numbers was less than 0.15%. The resulting γ was 2.91. We find that the scale-free network enhances the share of cooperators over a range of values of r , and increases the critical value of r above which cooperators cannot persist (akin to behaviour on a random regular graph, see Hauert & Szabo 2005).

Figure 5. Ratio of cooperators to defectors (C:D), as a function of degree number, k . Following the random seeding of cooperators and defectors, the initial C:D ratio is almost constant across different values of k . However at equilibrium, the fraction of cooperators increases with the degree in the final state.

Table 1. Payoff matrix for the Prisoner's dilemma. The top row presents the rewards for cooperation (C) in terms of benefit b and cost c , dependent on playing against a cooperator (C) or a defector (D). The second row presents the rewards for defection (D). This matrix conforms to the prisoner's dilemma whenever $b > c > 0$.

	C	D
C	$b-c$	$-c$
D	b	0

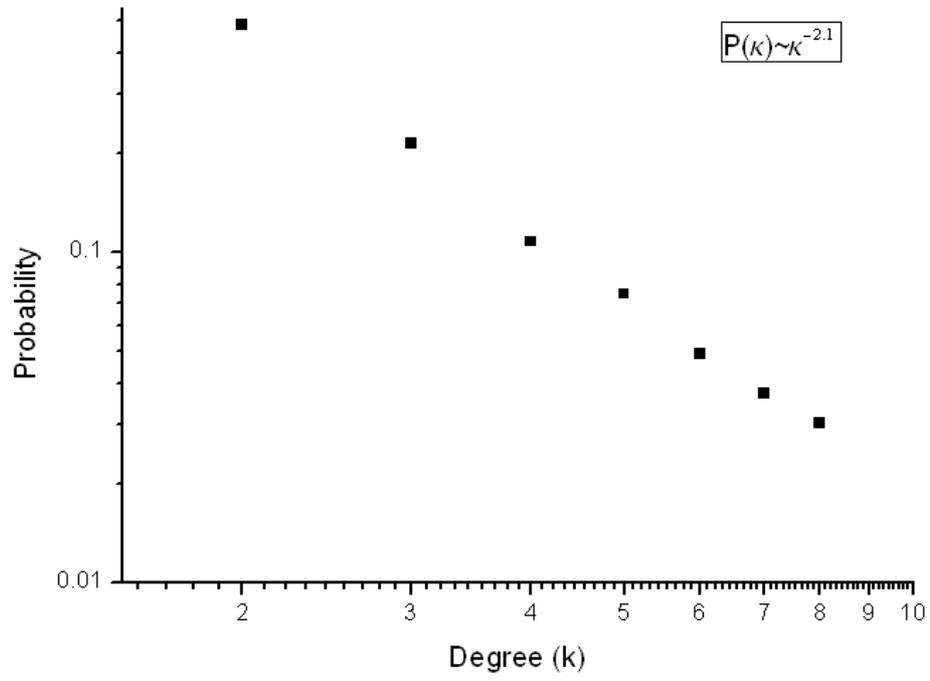


Figure 1.

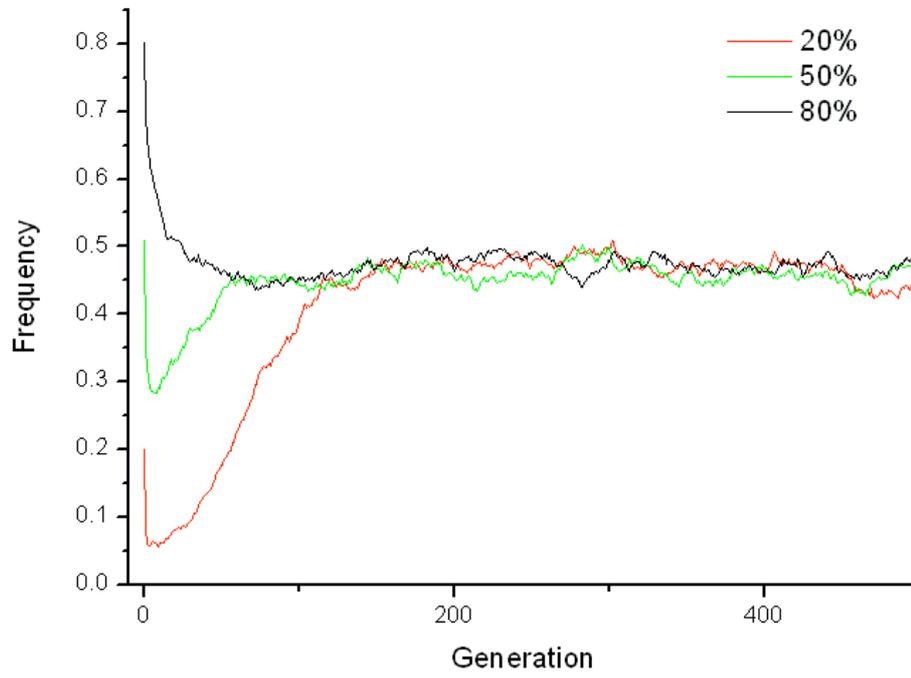


Figure 2.

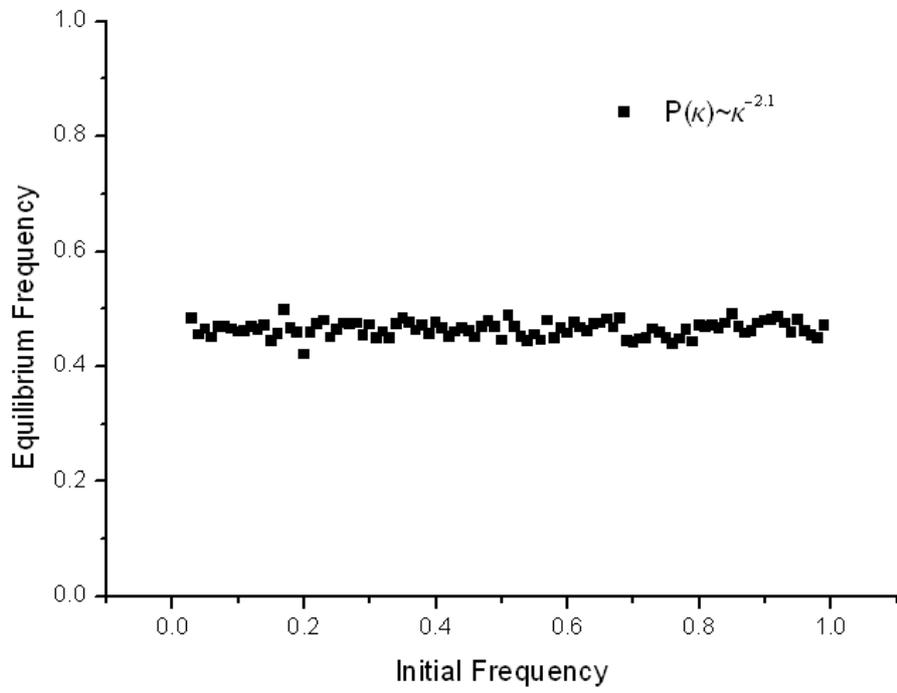


Figure 3.

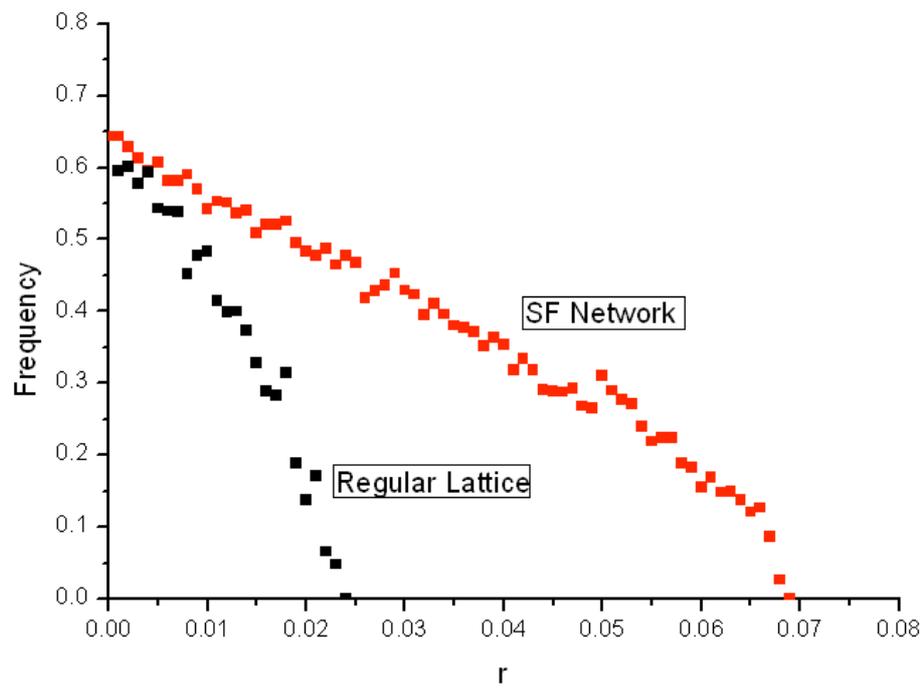


Figure 4.

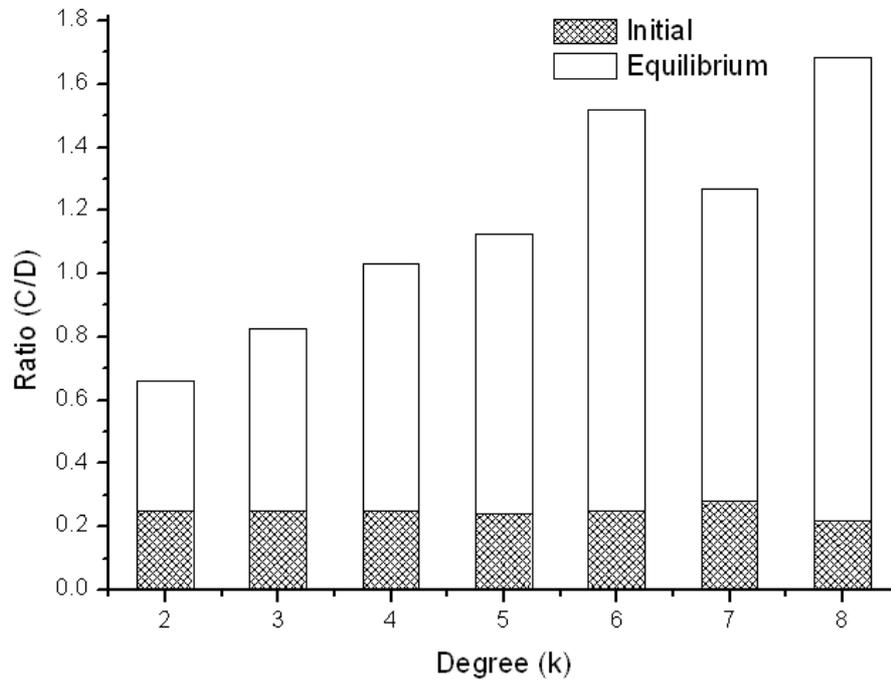


Figure 5.