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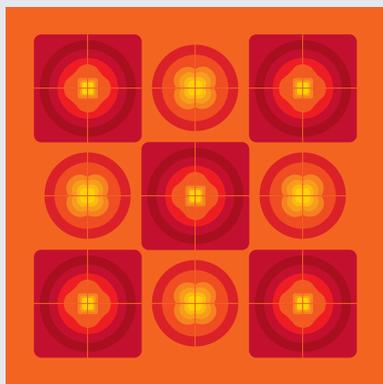
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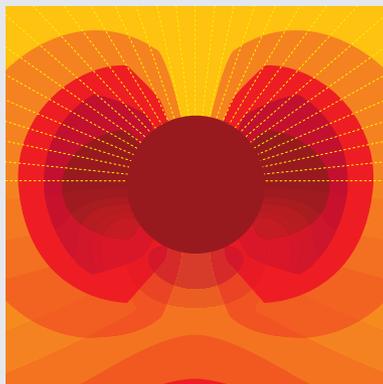
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Influence of network structure on cooperative dynamics in coupled socio-ecological systems

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Abstract – Interactions in real-world social and biological organizations are complex. Spatial structures or social networks enable clusters of cooperators to outcompete defectors when the altruistic act of a cooperator benefits only its neighbors. In this context, it had been shown that cooperation is favored if the benefit-to-cost ratio of the altruistic act exceeds the average number of interactions. This implies that cooperation survives better in societies with less social ties. For coupled socio-ecological systems in which an unselfish act is assumed to benefit all users who have open access to the resource, we show that when social sanction is present, the opposite can happen: cooperation can be easily promoted in populations where virtually everyone knows everyone else but not in populations that possess fewer connections.

Evolution works through intense competition between individuals who strive to maximize their benefits. Yet, cooperative collaborations are witnessed in many levels of social and biological organizations. For examples, genes cooperate in genomes [1] and hunters gather to hunt food. To understand the observed persistence of cooperation, various mechanisms have been proposed to elucidate how natural selection can lead to cooperative behavior. An important case is to abandon the well-mixed population hypothesis (*i.e.* everyone interacts with everyone else) with the more realistic one of assuming that each individual only interacts with agents in its neighborhood. In particular, since interactions in almost all of the social and biological organizations are complex, complex network tools are relevant to the study of the survival of cooperative behavior in social systems. Indeed, the asymptotic survival of cooperative behavior was reported for various types of social networks [2–7]. Several intriguing results had also been obtained for this. Notably, cooperation is shown to be favorable if the benefit-to-cost ratio of the altruistic act exceeds the average number of interactions [8]. When social ties follow a scale-free distribution, the resultant social diversity was shown to be able to promote cooperation in

social networks [9–12]. Besides, adaptive selection of network ties by individuals on evolving graphs were shown to have considerable influence on the evolution of cooperation [13–17].

While various models of cooperative dynamics in social systems are being established, the study of cooperative behavior has recently been extended to coupled socio-ecological system. This is especially notable because most of Earth's ecosystems have been seriously degraded by human activities such as large-scale fishing and freshwater use. Cooperation in the sense of restraining the use of natural resources to a sustainable level is necessary to limit harmful consequences of ecosystem degradation. In particular, intensive empirical studies have been carried out over the last two decades to investigate the depletion and sustainable development of common pool resources [18–25]. Agent-based numerical simulation and game theoretical approaches have also been employed to study the dynamics of cooperative behaviors in coupled socio-ecological systems [26–31]. Recently, Tavoni *et al.* [32] have introduced an analytical model to study the establishment of cooperative behavior in coupled socio-ecological systems through social ostracism against defectors who overuse

the common pool resources. Through this simple model, three regimes of stationary state of the evolutionary dynamics, namely the defector equilibrium, the cooperator equilibrium and the mixed equilibrium have been identified. Note that the population is assumed to be well mixed in this model. Here, we have extended the study to populations with complex interaction patterns. In particular, we have modeled the interaction of individuals with their neighbors based on the approach of a complex network of social interactions. With this, we aim to understand how the survival of cooperative behavior is impacted by the average number of social ties.

In this paper, the model in ref. [32] is used to study the influence of network structure on the effectiveness of social sanction in promoting cooperative behavior in the extraction of common pool resources. We shall first briefly discuss the original model before introducing the networked interaction into the model. In the model, agents who harvest a renewable resource are of two categories, those that co-operate and those that do not co-operate. The effort put in by agents of the first category is e_c and they harvest the resource at a socially agreed-upon acceptable level. On the other hand, agents of the second category choose to extract more resource by putting in a greater level of effort, $e_d = \mu e_c$, where $\mu > 1$. If f_c is the proportion of cooperators and N is the total number of agents, the mean effort exerted by the agents is given by

$$E = N[f_c e_c + [1 - f_c]e_d].$$ (1)

Let R be the resource level, we can represent the harvest F from the application of the resource based on the Cobb-Douglas production function with decreasing returns to scale

$$F = \gamma E^{\alpha} R^{\beta},$$ (2)

with $E \geq 0$, $F > 0$ and $\alpha + \beta < 1$. Note that this guarantees the existence of an optimal value for e_c. Then, the production gain for the agents who co-operate takes the form

$$\pi_c = \frac{e_c}{E} F - w e_c,$$ (3)

while that for the agents who defect is

$$\pi_d = \frac{e_d}{E} F - w e_d.$$ (4)

Note that w is the opportunity cost of labour.

For agents who defect and violate the social norm, there is an extra cost to pay, which is captured by the following ostracism function:

$$O(n_c) = h e^{t e^{g n_c}}.$$ (5)

Here, h, t, g are parameters governing, respectively, the maximum sanctioning, the sanctioning effectiveness threshold and the growth rate of the function. By considering such nonlinear function, the ostracism process operates only when the cooperator community is sufficiently

large. It increases rapidly when the size of the cooperator community is sufficiently large, and it then saturates as the proportion of cooperator further increases. Such a consideration is in accordance with the community ostracism pattern discussed by Lindbeck in ref. [33]. Since each individual only interacts with agents in its neighborhood, we assume that the effect of the sanctions imposed on the norm violator is dependent only on the fraction of cooperator in its neighborhood (n_c). This is similar to the threshold model used in ref. [34] in which the decision of an agent will be altered only when the overall opinion of its neighbors exceeds a threshold value. Analogously, a defector will be affected by the pressure of social sanction only when the fraction of cooperator in its neighborhood exceeds a threshold value. In our simulation, by choosing $t = -150$, social sanction operates only when $f_c > 0.3$. This leads to the following payoff for defectors with n_c fraction of cooperative neighbors:

$$U_d(n_c) = \pi_d - O(n_c)\frac{\pi_d - \pi_c}{\pi_d}.$$ (6)

Note that such a social cost is not included in the payoff for agents who co-operate:

$$U_c = \pi_c.$$ (7)

Beside the social dynamics, dynamics of the common pool resource and its interaction with the social dynamics are also taken into account. It is given by the following differential equation:

$$\dot{R} = c - d\left[\frac{R}{R_{max}}\right]^{\kappa} - qER.$$ (8)

Note that the first term on the right relates to the refurbishment of the resource, the second term models its natural depreciation, while the last term depict the degradation due to extractive effort with q being a technological factor. By coupling dynamics of the ecosystem to the evolution of the social system, individual benefit is affected not only by the social factor but also by condition of the ecosystem. The presence of an ecological feedback is vital for the stable coexistence of both types of agents at equilibrium. Without the feedback, the difference between production gain of the two types of agents depends only on the difference between the extractive effort and is constant for different population composition. Thus, mixed equilibrium will not be observed.

Evolution of the population composition is studied by means of the replicator dynamics. Specifically, an individual is allowed to compare their payoffs with a neighbor which is randomly matched and decide whether to switch its strategies depending on whether the utility of the latter is above the individual. The probability that an agent switches its strategy is proportional to the difference between its payoff and the payoff of the matched neighbor.
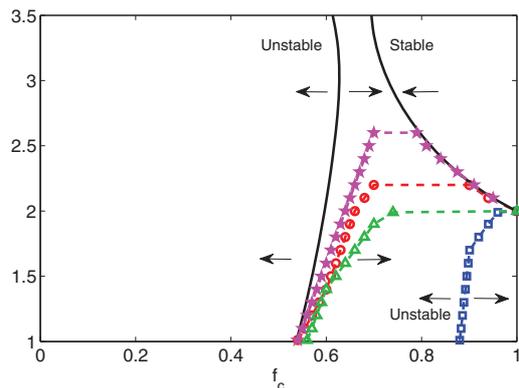
Fig. 1: (Colour on-line) Numerical estimation of the loci $\sum_i \rho_i^* O(n_{c_i}) = \pi_d(e_d, R^*)$ based on results from 500 simulations performed for random networks with $N = 50$. The average number of social ties considered are $k = 40$ (stars), $k = 20$ (circles), $k = 10$ (triangles) and $k = 2$ (squares). Note that the theoretical results for the loci of the well-mixed population is shown as a solid curve for comparison. The arrows shown in the figure indicate the direction in which the composition of the population evolves.

This leads to the following differential equation for the population composition:

$$
\begin{aligned}
\dot{f}_c &= f_c[U_c - \bar{U}] \\
&= f_c[1 - f_c][U_c - \bar{U}_d] \\
&= f_c[1 - f_c]\frac{\pi_d - \pi_c}{\pi_d}\left[\sum_i \rho_i O(n_{c_i}) - \pi_d\right]. \quad (9)
\end{aligned}
$$

Here, $\bar{U}$ denotes the average payoff of the population, $\bar{U}_d$ denotes the average payoff of the defectors and ρ_i gives the probability of occurrence of the fraction of n_{c_i} cooperators in the defectors' neighborhoods. Note that the subscript i of n_{c_i} indicates that n_c takes discrete instead of continuous range of values since n_{c_i} is a member of the sets of fractions with fixed denominators.

Numerically, we simulate the replicator dynamics for social networks with network size $N = 50$ and average degree $k = 2, 10, 20$ and 40 for various values of μ and initial fraction of population that co-operate (f_{c_0}). Here, the networks used are Erdos-Renyi graphs and the parameters used are: $R_{max} = 200$, $c = d = 50$, $\kappa = 2$, $q = 1$, $w = 15$, $\gamma = 10$, $\alpha = 0.6$, $\beta = 0.2$, $e_c(R^* = 84.91) = 0.483/N$, $h = 0.34$, $g = -10$ and $t = -150$.

The stable and unstable loci, *i.e.* when

$$
\sum_i \rho_i^* O(n_{c_i}) = \pi_d(e_d, R^*), \quad (10)
$$

are estimated and shown in fig. 1. In eq. (10), ρ_i^* and R^* denote distribution of n_{c_i} and resource level at equilibrium. For a well-mixed population [32], there are two loci, one on the left which is unstable and the other on the right which is stable. Note that the system will evolve towards either the defector equilibrium ($f_c^* = 0$), the cooperator
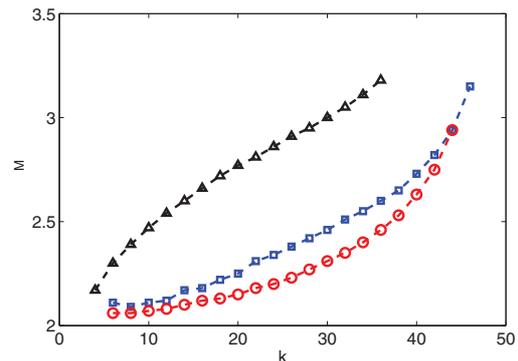

Fig. 2: (Colour on-line) Dependence of the minimum values of μ with which defector equilibrium is always observed for any $f_{c_0} < 1$ on the average degree of the social network. The results are obtained separately by solving eq. (11) (triangles), eqs. (12), (13) (circles), and the simulation of the replicator dynamics (squares).

equilibrium ($f_c^* = 1$) or the mixed equilibrium (the stable loci) depending on the initial composition of the population f_{c_0} as indicated by the arrows shown in the figure. Here, f_c^* denotes the fraction of cooperators at equilibrium. If the initial fraction of cooperative agents is lower than the value of f_c of the unstable locus, the system will evolve towards the defector equilibrium. For initial f_c higher than the values shown in the unstable locus, the system will evolve towards either cooperator equilibrium or mixed equilibrium depending on whether the effort difference between the cooperators and the defectors is greater than 2. The stable locus gives the f_c^* of the corresponding mixed equilibrium. Lastly, for initial f_c larger than the values shown in the stable locus, the system will evolve towards the mixed equilibrium provided that $f_{c_0} \neq 1$. Similar loci are plotted for population with networked social interaction. Interestingly, cooperation is found to survive better in the well-mixed population and not as good in population with smaller average number of social ties. As the average number of social ties decreases, cooperative behavior becomes more vulnerable against the increase of μ. For networks with various degree, we simulate the replicator dynamics 500 times and find the minimum values of μ with which defector equilibrium is always observed for any $f_{c_0} < 1$. The result is shown in fig. 2. As shown, μ_M increases as k increases. Furthermore, the resource level at equilibrium is found to be dependent on the network degree as well (see fig. 3). With the same initial fraction of cooperative agents, populations with large numbers of social interactions are able to cooperate better and evolve towards the mixed equilibrium with higher level of available resource. In contrast, populations with small numbers of social interactions evolve towards the defector equilibrium and their resource level are lower.

It is noteworthy that our result is opposite to the findings of ref. [8]. This is a consequence of cooperation being promoted based on different mechanisms in these two models. In ref. [8], the altruistic act of a cooperator
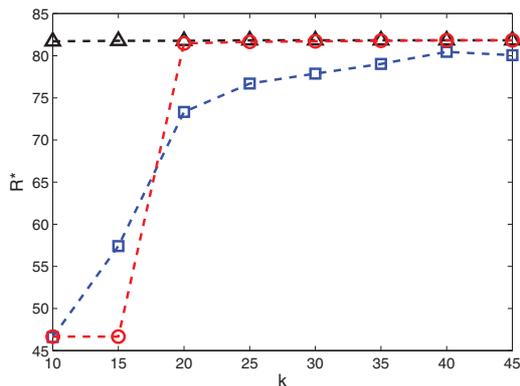
Fig. 3: (Colour on-line) Dependence of the equilibrium level of resource (R^*) on the social network degree for populations started with $f_{c_0} = 0.7$. Here, $N = 50$ and $\mu = 2.1$. The results are obtained separately by solving eq. (11) (triangles), eqs. (12), (13) (circles), and averaging over 500 simulations of the replicator dynamics (squares).
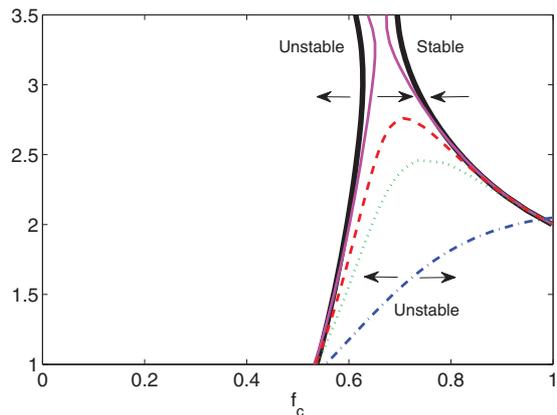

Fig. 4: (Colour on-line) The loci $\sum_i \rho_i^* O(n_{c_i}) = \pi_d(e_d, R^*)$ solved for regular networks with $N = 50$ and $k = 40$ (solid line), $k = 20$ (dashed line), $k = 10$ (dotted line), $k = 2$ (dash-dotted line) by assuming a random connection between the defectors and the cooperators. Theoretical results for the loci of the well-mixed population are shown as a thick solid curve for comparison.

which benefits its neighbour is made effective mainly from the spatial structure of cooperator and defector. This allows some cooperators to be rewarded more than the defectors by connecting only to other agents of the same type. Otherwise, a defector is always rewarded more than a cooperator when there is a direct connection between them. Hence, by clustering together, cooperators are able to outcompete defectors. However, as the number of social tie increases, it is harder for cooperators to connect only to other cooperators. In the well-mixed population, this is possible only when all agents in the population are cooperators. On the other hand, cooperation is promoted through social sanction in the model discussed in this paper. Since all the users share the common pool resource, a defective extractive pattern inevitably affects all other users. In this case, social sanction can be an important mechanism to promote cooperation. Nonetheless, as indicated by our simulation result, this mechanism works well only when the number of interactions is large. For population with less number of social ties, it is more likely for the defectors to cluster together to minimize the effect of social sanction from the cooperator community.

To understand the observed influence of network structure on the survival of cooperative behavior, we next examine the microscopic connection pattern of the two types of agents. Specifically, we solve eq. (10) by considering a regular network with fixed degree k for the sake of simplicity, in which case the fraction of cooperators can only take the following discrete range of values: $n_{c_i} = i/k$ for $i = 0, 1, \ldots, k$. Then, we make the assumption that the connections between cooperators and defectors are random, which gives rise to the following cooperative probability distribution of the defectors' neighborhoods:

$$\rho_i = \binom{k}{i} C^i D^{k-i} \qquad (11)$$

with $C = \frac{N f_c}{N-1}$ and $D = \frac{N[1-f_c]-1}{N-1}$.

With this assumption, we plot the unstable and stable loci for various values of k in fig. 4 based on our solution. In addition, μ_M is shown in fig. 2 for social networks with different degrees. The dependence of the equilibrium resource level on the network degree is shown in fig. 3. Interestingly, a similar conclusion can be drawn: the effectiveness of ostracism in promoting social cooperation decreases as the number of social ties decreases. For a well-mixed population, all defectors are subjected to the same neighborhood and hence the same amount of ostracism. The networked social interaction introduces different neighborhoods for each agent. The magnitude of the ostracism varies among defectors with diverse compositions of neighborhood. This leads to the diversity in the fitness of the defectors. Defectors with less cooperative neighbors are subjected to less sanction and their fitness is higher. In contrast, defectors with more cooperative neighbors have lower fitness and are thus easily eliminated through the process of selection.

While the outcome in fig. 4 gives the same trend as the networked results in fig. 1, we observe that the analysis given by fig. 4 has overestimated the effectiveness of social sanction in the promotion of cooperation. This results from not accounting for the evolution of the underlying replicator dynamics which has the effect of causing both cooperators and defectors to cluster with agents of the same type. This clustering phenomenon had in fact been numerically demonstrated in ref. [9]. In order to model this phenomenon, we shall assume that each agent has a higher probability of connecting to other agents of the same type in our simplified regular network of fixed degree k. We expect that such an assumption would lead to the formation of defector clusters, which minimizes the effect of social ostracism in promoting cooperation. For

simplicity, we shall assume that there is only one defector cluster and one cooperator cluster. We next determine the cooperative probability distribution of the defectors' neighborhoods for this. For each defector, the fractions of its neighbors that cooperate can only take the discrete range of values n_{c_i} as before. $\rho(n_{c_i})$ gives the probability that a randomly chosen defector has i cooperative neighbors. To study the maximum clustering effect among the defectors, we assume each defector to connect to all other defectors when their degree is larger than or equal to the number of defectors. After connecting to the $N[1-f_c]-1$ defectors, there are still $k - N[1-f_c] + 1$ number of links left. These links will then connect the defector to $k - N[1-f_c] + 1$ number of cooperators. All defectors are assumed to connect in the same way. Hence, the cooperative probability distribution of defectors' neighborhood is given by

$$\rho = \begin{cases} 1, & \text{for } n_c = \frac{k+1-N[1-f_c]}{k}, \\ 0, & \text{for other } n_c. \end{cases} \quad (12)$$

On the other hand, if the number of defectors is larger than the network degree, i.e. $N[1-f_c] > k$, we have that most of the defectors connect only to defectors for maximum clustering effect. For these defectors, $n_c = 0$. Nevertheless, we assume a nonzero probability for defectors to connect to cooperators, otherwise, the network will be separated into two isolated clusters of cooperators and defectors. For simplicity, we assume a connection to at most one cooperator per defector, with the probability of a defector linking to a cooperator being $k_{dc}/[N[1-f_c]]$. Here, k_{dc} denotes the number of connections between the defector and the cooperator clusters. If there are k_{dd} connections within the defector cluster, then $k_{dd} + k_{dc} = Nk[1-f_c]$. In this case, we have

$$\rho = \begin{cases} 1 - \frac{rk}{r+1}, & \text{for } n_c = 0, \\ \frac{rk}{r+1}, & \text{for } n_c = \frac{1}{k}, \\ 0, & \text{for other } n_c. \end{cases} \quad (13)$$

where $r = k_{dc}/k_{dd}$. Here, we have chosen

$$r = \frac{1}{N[1-f_c]-1}. \quad (14)$$

For a cycle with $k = 2$, this separates the network into a cluster of defector and a cluster of cooperator with two connections between the clusters. Note that eqs. (12) and (13) do not model the actual clustering process in the evolution of the population's composition. Instead, it is formulated to study the effect of clustering on cooperative dynamics. With this, we plot the unstable and stable loci in fig. 5 by solving eq. (10) using ρ of eqs. (12) and (13) for various values of k. The corresponding estimation of μ_M is shown in fig. 2 and the dependence of equilibrium resource level on the network degree when clustering effect
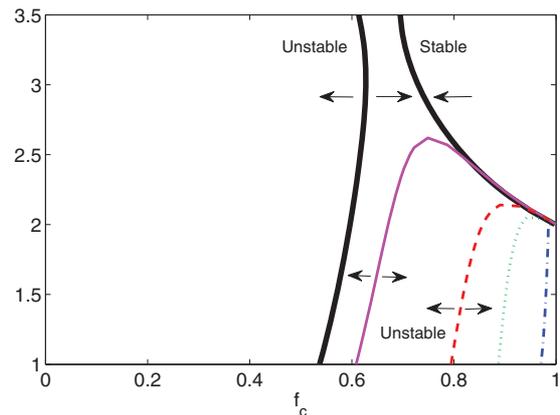

Fig. 5: (Colour on-line) The loci $\sum_i \rho_i^* O(n_{c_i}) = \pi_d(e_d, R^*)$ solved for regular networks with $N = 50$ and $k = 40$ (solid line), $k = 20$ (dashed line), $k = 10$ (dotted line), $k = 2$ (dash-dotted line) using the clustering assumption. Theoretical results for loci of the well-mixed population are shown as a thick solid curve for comparison.

is present is shown in fig. 3. Indeed, the clustering has lowered the effectiveness of social sanction in the promotion of cooperative behavior. Furthermore, it is interesting to note that the result given by eqs. (12) and (13) is closer to that given by numerical simulation of the replicator dynamics. This implies that agents of the same type indeed tend to cluster together during the process of replicator dynamics.

While our results show that a restriction on social ties has important consequences on the level of cooperation in coupled socio-ecological system, one may also wonder on the influence of network topology on the survival of cooperative behaviour. For this, we have considered the representation of social interactions by means of networks with different topologies. In particular, we compare the results given by Erdos-Renyi networks, scale-free networks generated by the Chung-Lu model [35] and more realistic networks with communities of different sizes generated through a benchmark approach [36]. In addition, we have generalized our study by considering a larger network size of $N = 500$. The simulation was carried out for $\mu = 2.1$ and $f_{c_0} = 0.7$. We observed that the results (see fig. 6) are similar to those of a smaller population sharing a common pool resource. Specifically, as the average number of social ties decreases, social ostracism is found to be less effective in promoting cooperative behavior in all networks. Nonetheless, the survival of cooperative behavior in populations connected by different networks of interaction is observed to be slightly different. The fraction of cooperative agents at equilibrium depends more sensitively on the initial connection pattern between cooperators and defectors for the scale-free network and the benchmark network due to the heterogeneity in the network degree distribution. For agents connected with scale-free network interactions, the probability for the population to evolve towards the mixed equilibrium is higher. On the other hand, when
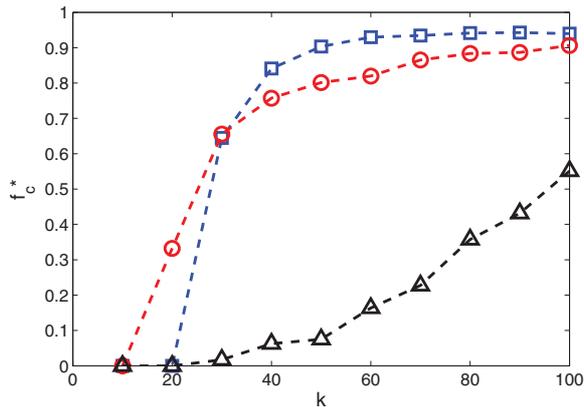
Fig. 6: (Colour on-line) Dependence of f_c^* on the network degree for random (squares), scale-free (circles) and benchmark networks (triangles) with $N = 500$. Here, $\mu = 2.1$ and $f_{c_0} = 0.7$. For the benchmark network, the number of community is 6 and the average mixing parameter is 0.5. Each data point is obtained by averaging over 500 simulation results.

the community structure is introduced in the social network, defectors cluster together easily and the population has a higher probability to evolve towards the defector equilibrium.

In summary, the above analysis indicates that the diversification of the cooperator composition in the defectors' neighborhood in a network environment with the presence of defector clustering due to replicator dynamics has the effect of enlarging the basin of attraction of the defector equilibrium state as observed in fig. 1. This results from social ostracism being less effective in curtailing the tendency to defect within a more restricted network environment. In this environment, our results demonstrate the important role of social interaction between agents who adopt distinct resource appropriation strategies in sustainable management of socio-ecological systems. In particular, if agents who do not cooperate are cut off from the society, it would make them more likely to keep their selfish way which can bring serious degradation to the ecosystem. In this respect, our results have provided deeper insights into the manner in which governance structures can have important influence on the sustainable management of socio-ecological systems. Subsequently, a practical approach to adaptively increase or rewire the network ties can be further explored to encourage cooperative behavior.

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