

The interface of unidirectional rewards: Enhanced cooperation within interdependent networks



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ABSTRACT

As a way to induce cooperation more effectively, positive incentives have emerged in social species forefront to negative incentives. To assess their effects in cooperation networks, we simulated a social scenario in which reward behaviors are dispensed unilaterally. To do so, we let evolve asymmetric rewards within two specular, interdependent networks, whose individuals in an upper layer have the right to reward corresponding players displaying, likewise, cooperative or defective behavior in the lower layer. With this setup, rewarded players in the lower layer can obtain a payoff equivalent to the amount of the cost of granting reward from the upper layer. Peculiarly, we find that cooperators survive for larger reward values regardless of how high the temptation to defect is. Notably, cooperators in the upper network thrive even if the temptation to defect is pretty high. By further analyzing the nature of social interactions, we find that defection is the winning strategy when rewards originated pro-socially, and that cooperation instead wins by invading the whole system when rewards originated anti-socially. These results are consistent when crosschecked to a theoretical analysis here purposely drawn up. Our work highlights the need of including complex network structures when analyzing asymmetric incentives in the evolution of cooperation, both in human and non-human species.

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1. Introduction

Darwin emphasized the significance of competition in the theory of natural selection [1]. Likewise, in the opposite spectrum, cooperation is vital in evolution, allowing individuals to better cope and adapt to everchanging environments [2–4]. From refined practices such as group hunting in some carnivore species, to most complex mechanisms of taxpaying and voting in human societies, cooperation behavior especially among unrelated individuals has inspired a wealth of research. To date, it keeps being pointed out as one of the top twenty most significant questions to address on how social species have evolved [5]. Although cooperation allows for the maximization of collective and long-term benefits in group-living species [6,7], selfish individuals are not excluded from evolution, and the temptation to free-ride for pursuing personal and short-term benefits keeps thriving in many populations [8].

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After kin selection theory and the concept of inclusive fitness was proposed [9], cooperation amongst unrelated individuals was expanded by the reciprocal altruism hypothesis [10]. Being able to choose to cooperate or defect in repeated interactions is a key element in the maintenance and stabilization of cooperation [3], a custom model used for studying reciprocity in repeated interactions in nature [11,12].

In order to foster cooperation, some positive and negative incentive systems emerged in social species [13–15]. When interactions are direct and not mediated by third parties, individuals are willing to pay the cost for rewarding or punishing the opponents to level out their reciprocal payoffs [16]. Even without a direct reciprocity mechanism, subjects can also reward or punish each other because in repeated exchanges they acquire some knowledge, forming memory and experience that will also lead to third party reputation [17,18]. When rats are able to donate food to a partner in an experimental task, they increase the partners propensity to help [19,20]. Vampire bats can build up grooming relationships so to donate food at a reciprocated cost [21].

According to the difference of execution styles, such positive (or negative) incentives can be divided into peer rewarding (or punishment) and pool rewarding (or punishment) [22]. Moreover, compared with the most common pro-social incentive behaviors, anti-social reward and punishment have become the focus of more recent attention [16,23–25]. And a number of theoretical and empirical results verified that these incentive systems can have indeed a favorable impact on cooperation [18,26–28].

In a large meta-analysis of reward and punishment, Daniel Balliet et al. proposed that incentives do promote cooperation in social dilemmas. However, experimental data have failed to confirm that positive and negative reciprocity are correlated [29]. Specifically, Attila Szolnoki and colleagues studied a spatial public goods game with defection, reward, punishment and a fourth strategy that combines the latter two together. They found that three pure strategies are significantly more effective at suppressing defection than the fourth combined strategy [13]. As mechanisms of stimulating cooperation, such positive and negative interactions can lead to different consequences [30]. This was more in detailed looked at by David Rand et al. who studied public goods games followed by punishment only, by reward only and by both of them. They concluded that reward outperforms punishment in repeated public goods games when contributions and payoff are relatively high [14]. Different from punishment, rewarded subjects give proof of not wanting to retaliate, but, on the contrary, they strengthen their positive interactions with the emergence of reciprocation [31]. People, thus, are inclined to choose reward when given the choice to do so [18]. In most papers we mentioned above, authors have always considered symmetric setups. However, a more realistic situation to be considered is the one of asymmetric interactions, such as the asymmetric ability to dispense reward, possibly leading to asymmetric payoffs [32–38].

Except for direct and indirect reciprocity, network reciprocity is also one of five main elements shaping the evolution of cooperation [39]. Inspired by the pioneering work in two-dimensional regular lattice [40], heterogeneous topological structures, such as random network [41], small-world network [42] and scale-free network [43,44], attracted extensive attention. However, in nature, social networks have more than one structure that can coexist and evolve from one to the other, such as seen with social, communication and transportation networks. For example, the household of one person can be regarded as a network unit, being in turn connected to network units of colleagues and friends, etc. Obviously, assuming that all the nodes are located in the same, isolated network is an oversimplification. Interdependent networks, defined as a combination of networks that are connected in a nontrivial way, have been proposed to study various evolutionary games in recent years [45]. These networks allow us to consider interactions not only within a single network, but also among multilayered networks [46,47]. In order to establish connections between two or more interdependent networks, coupling through utilities is regarded as a simple and direct way [46]. Although payoffs play an important role in the success of strategies in the realm of evolutionary games, there are alternative ways to couple interdependent networks. The decision of whether adopting the strategy from one randomly selected neighbors is based not only on the payoff of his neighbor in a given network, but on the popularity of the related player in the other network [48]. Besides symmetric interdependent networks, two networks are given different functions, wherein one layer is used for payoffs calculating and the other is used for strategy updating [49].

Organisms connected in special network configurations can be found in nature such as those holding symbiotic relationships [50,51]. An example is provided by the honeyguide and the honey badger [52,53]. Honeyguides are beeswax-eating birds hunting for honeycombs to feed on. These birds are unable at opening hives due to their small bodies. The honey badgers from *Mellivora capensis* spp., being themselves also beeswax-eaters, have evolved the ability to deal with the hazardous hives. The symbiotic relationship allows the two to get together first so that the honeyguide finds the hives; the badger can then break open the honeycombs and give a share of the honey to the honeyguides as reward. The social networks of these two different species become therefore connected when feeding on honey. Firstly, the birds guide the badgers to the food resource, providing a service from the birds network to the badgers network. Simply focusing on the food sharing act, instead, it is up to the badger to unilaterally dispense honey to the honeyguide, making this reward an asymmetric one, dispensed from the badger network to the honeyguide network.

Here, we limit as well our focus to asymmetric positive incentives of reward in these types of interdependent networks, in which only individuals in an upper layer reward individuals in a lower layer. Distinctively, such positive incentives occur only if corresponding individuals in the lower layer use the same strategy of the executor of the reward. That is, cooperators pro-socially reward cooperators and defectors anti-socially reward defectors. In the honeyguide-badger situation, this situation would apply when each species in its own network layer either have the possibility to thrive and cooperate among their own species members, because of favorable feeding conditions, or they overall defect within each others layers,

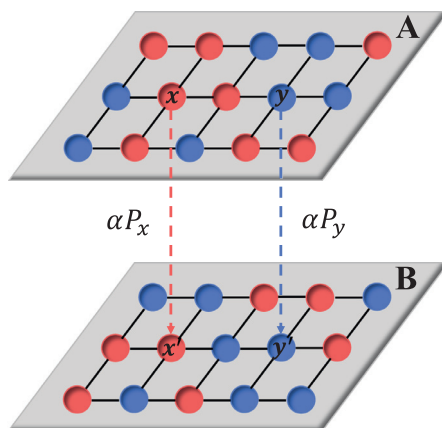


Fig. 1. Schematic representation of the model of interdependent networks. The red nodes denote cooperative players whereas the blue nodes denote defective players. In addition to having pairwise interactions with the 4 neighboring nodes in the same layer, players in layer A can reward the corresponding players in layer B, as long as they display the same cooperative or defective strategies. These reward acts linking the two layers are costly. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

because of a lack of external resources. If individuals reward other non-affiliated members according to their perceived benefit of previously received help, both layers would get conditioned by each others, becoming highly interdependent the longer the interactions succeed. We find that this structure allows cooperation to persist and even dominate when the temptation to defect holds fairly high values and the behavior of cooperators in the two layers are not synchronous.

2. Mathematical model

A prisoners dilemma (PD) game with reward was here implemented in interdependent networks, where players are arranged in each node of $L \times L$ square lattices with periodic boundary conditions (Fig. 1). Initially, each player in layer A and layer B is assigned as a cooperator (C) or a defector (D) with equal probability. Dyads of players can profit by playing the PD games with their direct four neighbors in the same layer. In detail, a cooperator can obtain a reward R when his opponent is also a cooperator, or he can only get the suckers payoff, S . A defector can receive nothing if his opponent behaves like him, P . When encountering a cooperative opponent, there exists a temptation to defect, T . In general, Donor & Recipient (D & R) game, where $T = b$, $R = b - c$, $P = 0$, and $S = -c$, is a representative for PD. In this way, dilemma strength $Dg' = (T - R)/(R - P) = Dr' = (P - S)/(R - P) = c/(b - c)$. Without loss of generality, we adopt the weak PD game, where $R = 1$, $T = b$ ($1 < b \leq 2$) and $P = S = 0$, by referring to a specific form of D & R game [54–58]. Although the weak PD game falls in between the PD game and snowdrift game, it is found that the universal results of PD game can also be obtained under the weak PD game [40,43].

As shown in Fig. 1, the cooperative (defective) player x (y) in the upper layer A can reward the corresponding player x' (y') in the lower layer B only if they display the same strategies with a cost of αP_x (αP_y). Here, P_x (P_y) is the total payoff of player x (y) in layer A. α , instead, is a factor dependent on the cost of rewarding. Accordingly, the corresponding player x' (y') in layer B receives the reward αP_x (αP_y) directly. That is, the fitness of player x and x' that meet the above conditions are (the same as player y and y'):

$$\begin{cases} F_x = P_x - \alpha P_x, \\ F_{x'} = P_{x'} + \alpha P_x, \end{cases} \quad (1)$$

The above process assumes the characteristic of a pro-social act when C rewards C, and anti-social when D rewards D. It is worth noting that the reward is unidirectional, since only players in layer A have the right to reward the corresponding players in layer B. Moreover, the fitness increase of the rewarded agents is only equal to their payoffs.

Each player in both layers A and B has an opportunity to learn from the strategies of his neighbors. If player x decides to adopt the strategy of his neighbor z , we satisfy the Fermi function:

$$W(s_x \leftarrow s_z) = \frac{1}{1 + \exp[(F_x - F_z)/K]}, \quad (2)$$

where the fitness F_z of player z becomes identical to the one of player x . K quantifies the uncertainty over the strategy adoption process. For simplicity sake, we set $K = 0.1$ in this paper.

This model complies with an asynchronous updating rule, where every player in both layers have a chance to evolve their strategies once on average during a Monte Carlo step (MCS). The initial distribution of C and D in both networks is random throughout the analysis, except for a specific initial configuration in Fig. 3 and Fig. 4. The system can achieve stabilization

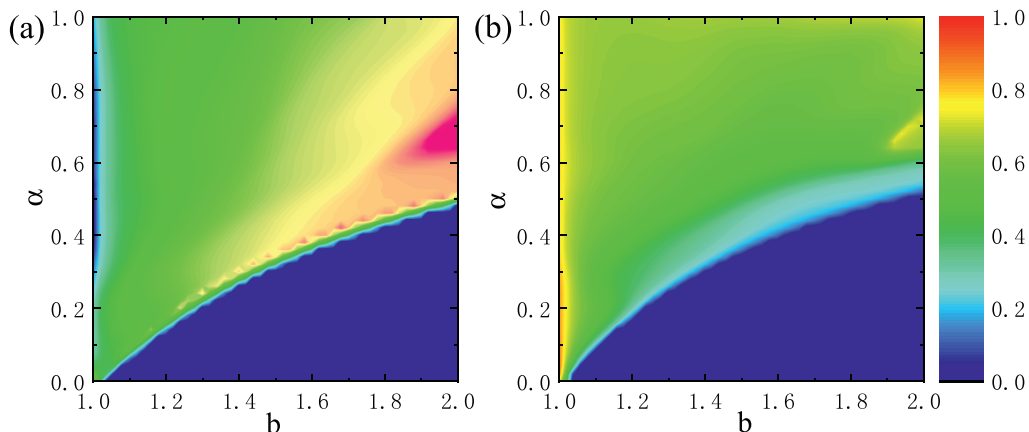


Fig. 2. Phase diagram of average frequencies of cooperation ρ_C depending on the temptation to defect b and the reward factor α in (a) layer A and (b) layer B.

by iterating the above process over 10^4 MCS. In order to avoid a bias of finite size effect, the layer size varies from $L = 300$ to $L = 10^3$. The final results are averaged over 10 runs for each parameter.

3. Results

In order to have an overview of the average cooperation rates in our interdependent networks, we examine the fraction of cooperation ρ_C as a function of the temptation to defect b and the reward factor α . As shown in Fig. 2, the strategy distribution is similar, but not the same between layer A and B. In general, cooperators can always survive when b is small regardless of the value of α . The region for cooperators and defectors coexisting in the system shrinks with growing value of b , where defectors dominate the population when α is relatively small. However, for extremely small b (e.g. $b = 1$), cooperators nearly go extinct in layer A, while ρ_C approximates to 65% in layer B. As the value of b increases, ρ_C goes up to optimal, and then goes down with decreasing α in layer A. Especially when b falls in the interval of $[1.92, 2]$, cooperators dominate the system for larger α . At the same time, the regions belonging to cooperators and defectors are close in space when defectors do not dominate layer B anymore. There is also a little difference on the boundary of all D and coexisting area between two layers, where cooperators can survive in layer A. This effect reverses in layer B. In order to get a better understanding of this asymmetric phenomenon, we investigate the evolution of strategies in both layers.

In Fig. 3, we show the evolutionary snapshots of the strategies distribution, which initially is fixed. Cooperators are located inside the circle, while defectors are located outside of the circle. Here, the wine (or red) color denotes cooperators with (or without) reward mechanism, likewise, the gray (or white) color denotes defectors with (or without) reward mechanism. For the sake of convenience, we indicate individuals colored by wine, red, gray and white respectively as pro-social cooperators (in layer A and rewarded cooperators in layer B), non-rewarded cooperators, anti-social defectors (in layer A and rewarded cooperators in layer B) and non-rewarded defectors.

In the initial iterations of the game, regardless of their strategies, agents on the boundary can invade each other's regions, so that the strategies in the upper and lower layers do not correspond any longer one to one fully. In layer A, agents who reward need to pay some costs, while agents in layer B receive the corresponding rewards. It follows that agents in layer A decrease their fitness. Conversely, corresponding agents in layer B increase their payoffs due to the additional rewards. For $b = 1$, defectors do not hold any advantage over cooperators. In this case, the region of non-rewarded defectors expands gradually in the upper layer because of exploiting the pro-social cooperators located in the inner and outer ring. Similarly, in the outer ring, non-rewarded cooperators move outward by invading the regions with anti-social defectors. At the same time, cooperators show an increase in number, and move inward in the lower layer. As time goes on, non-rewarded defectors and non-rewarded cooperators become the majority in both upper and lower layers. Due to the survival difficulty of pro-social cooperators in the upper layer, rewarded cooperators in the lower layer fade away even if they can obtain additional rewards. The upper layer stabilizes to full defection until the vanishing of pro-social and rewarded cooperators, whereas the lower layer holds a mixture of both cooperators and defectors. Likewise, the evolution of strategy pairs for each layer in Fig. 4 takes place the same phenomena with what happened in Fig. 3. As shown in Fig. 4(a) and (b), the fraction of DD links increases rapidly until dominance after a brief period of constant in layer A, whereas CC links reduce to extinction. Meanwhile, CD links only exist for a moment and a little bit. In layer B, the fraction of CC links reaches a peak and then decreases when CC links in layer A on the way out. For small temptation to defect, the prosperity of cooperators in the lower layer results in cooperators who pay the reward cost are outmatched by defectors who do not need to reward others in the upper layer.

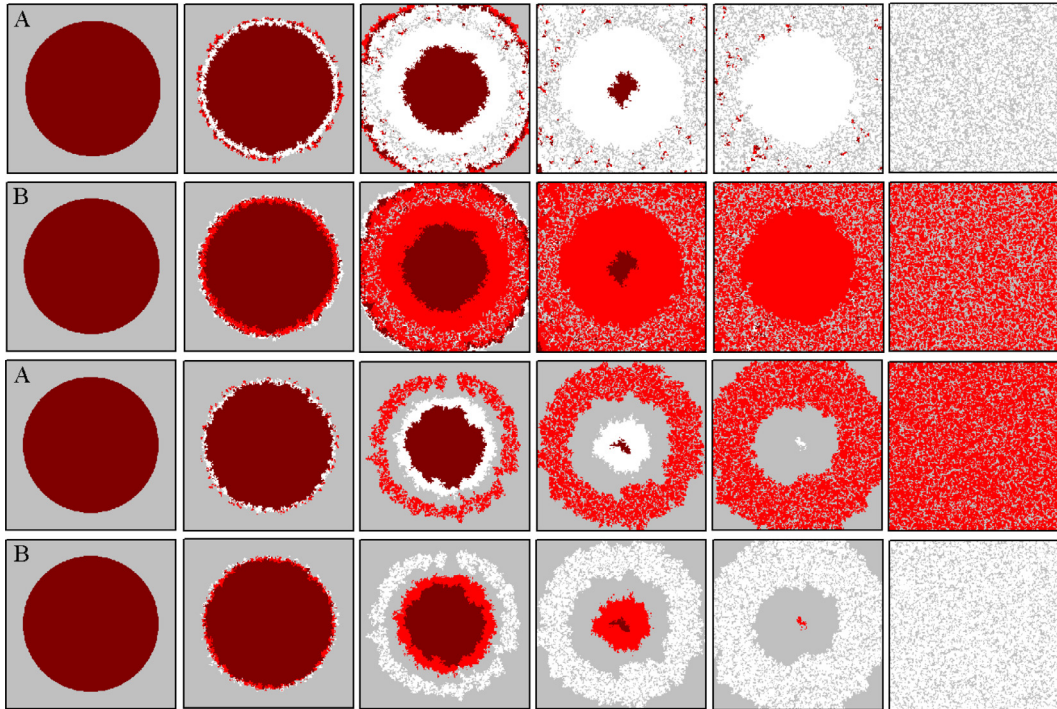


Fig. 3. Evolutionary snapshots of strategy distribution in the upper layer A and in the lower layer B for $b = 1$, $\alpha = 0.4$ (the first two rows) and $b = 1.5$, $\alpha = 0.34$ (the last two rows). The wine and gray colors denote cooperators and defectors who are connected by rewards from layer A to B; red and white, instead, denote cooperators and defectors without such connections. From left to right, the Monte Carlo steps are 0, 20, 100, 200, 300 and 10000. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

For larger value of b ($b = 1.5$), anti-social defectors increase rapidly in both of the two layers. Due to the not small value of α ($\alpha = 0.34$), anti-social defectors in the upper layer lose their advantage, even though they can earn more when they interact with non-rewarded cooperators. However, rewarded defectors in the lower layer have a clear advantage for high values of temptation to defect and of rewards. Consequently, non-rewarded cooperators located on the outer ring spread in layer A, and in layer B rewarded defectors go occupying the region of non-rewarded cooperators. We therefore obtain antipodal results in the first two rows of Fig. 3. As shown in Fig. 4(c) and (d), DD links are enhanced simultaneously in both layers for larger b . Defectors in layer A thus lose their advantage gradually since they need to pay the reward cost, while (rewarded) defectors in layer B can dominate the population.

The time evolution of cooperation rates ρ_C and strategy pairs for corresponding individuals in two layers are shown in Fig. 5. Intuitively, ρ_C goes down slightly in both layer A and B when $b = 1$ and $\alpha = 0.4$ (Fig. 5 (a)). This directly leads to a decrease of C-C as well as an increase of D-D pairs. Due to the reduced temptation to defect, defectors are unable to invade the areas occupied by cooperators, whereas those cooperators who successfully survive from the exploiting of the defectors can increase in number by forming prevailing clusters. Along with the continuous decline of ρ_C in layer B, cooperators start to recover space in layer A, and the areas of C-D and D-C pairs also start to differ. However, cooperators in layer A do not persist for long, reducing rapidly in number until dying out. At the same time, ρ_C reaches a peak and then keeps stable at a higher level in layer B. Hence, only the D-C and D-D pairs persist in the system. When b is pretty large ($b = 1.5$), cooperators rapidly go extinct in layer B, while in layer A, cooperation declines first and then it increases until achieving stability, following negative feedback. In this case, the D-C and C-C pairs disappear, and the fraction of D-D pairs achieves the highest value when ρ_C reduces to the minimum in both layers. Eventually, the fraction of C-D and D-D stabilize and coexist in the system.

In order to validate the above results from the numerical simulations, we theoretically consider the transition probability of cooperators transforming into defectors $w(C \rightarrow D)$ and the probability of defectors transforming into cooperators $w(D \rightarrow C)$ [59]. Since these two transition rates cannot be calculated by theoretical analysis, $w(C \rightarrow D)$ and $w(D \rightarrow C)$ are obtained by simulations:

$$w(C \rightarrow D) = \frac{\sum_{s_x=C} W(s_x \leftarrow s_z)}{N_C}, \quad w(D \rightarrow C) = \frac{\sum_{s_x=D} W(s_x \leftarrow s_z)}{N_D}, \quad (3)$$

where N_C (or N_D) is the amount of cooperators (or defectors) in the population. $W(s_x \leftarrow s_z)$ is the Fermi function in Eq. (2). Considering the effect of neighbors over strategy updating, we only calculate $W(s_x \leftarrow s_z)$ of player x under the condition of

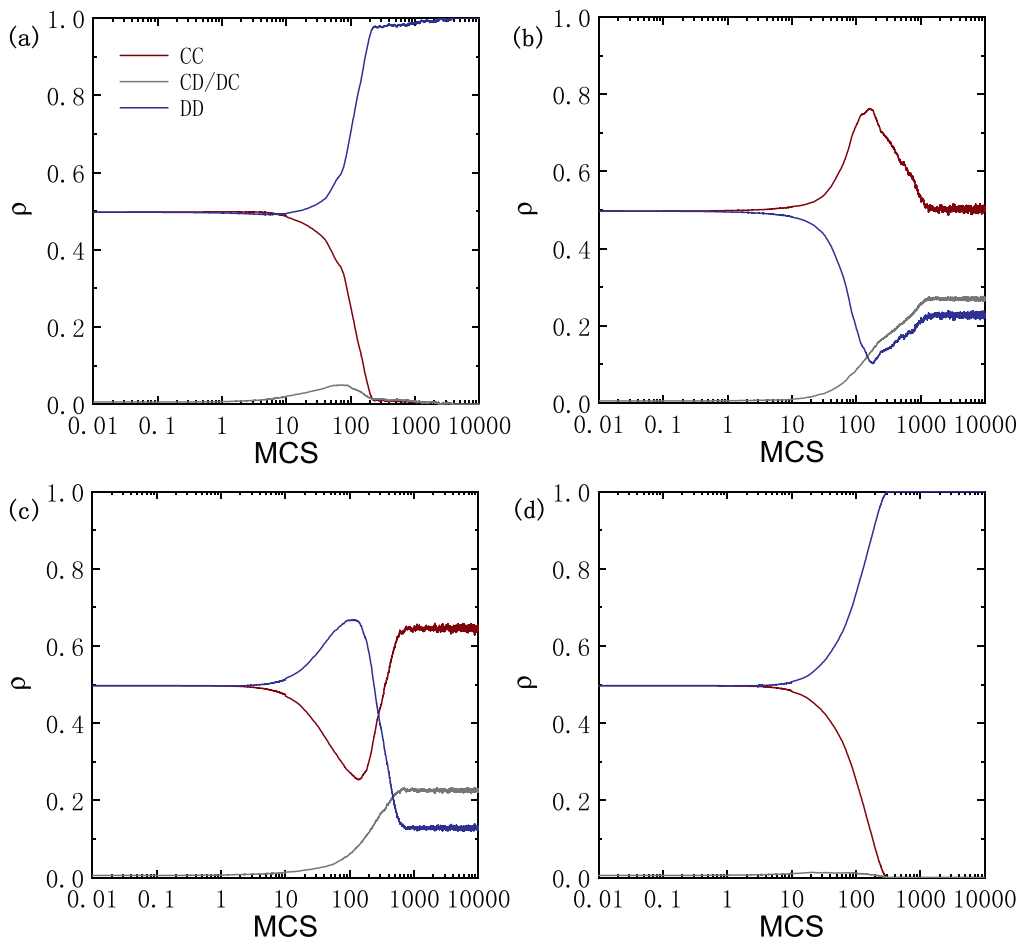


Fig. 4. Time-series of fractions of strategy pairs C-C, C-D and D-D for $b = 1$, $\alpha = 0.4$ ((a) and (b)) and $b = 1.5$, $\alpha = 0.34$ ((c) and (d)) in layer A and B, respectively. Panels in the left (or right) column show the evolution in layer A (or B). The initial distribution of strategies in accordance with that in Fig. 3.

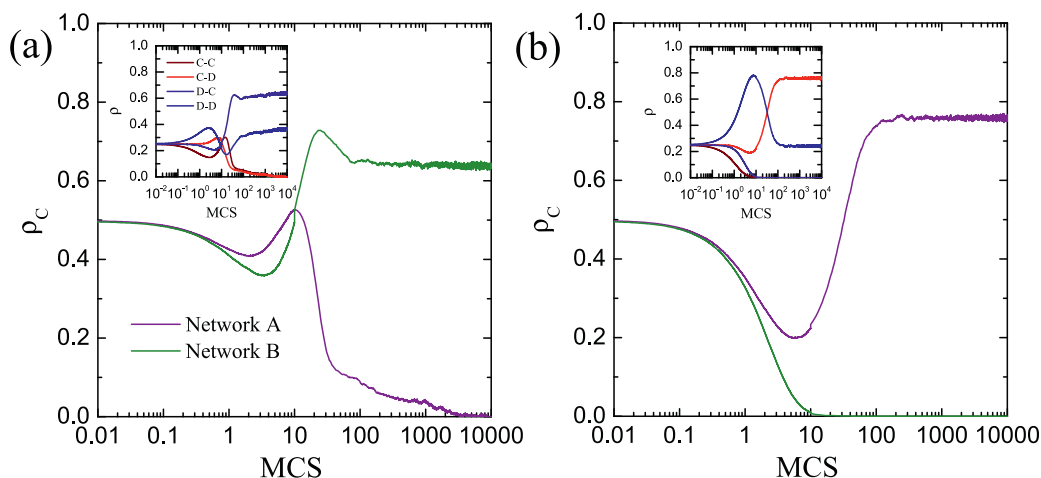


Fig. 5. Cooperation rates ρ_C throughout evolutionary time courses of Monte Carlo steps (MCS) for (a) $b = 1$, $\alpha = 0.4$ and (b) $b = 1.5$, $\alpha = 0.34$ in layer A (purple) and layer B (green). The inner graphs depict the fraction of strategy pairs for corresponding individuals in two layers throughout time. Here, the letter before the hyphen indicates the strategy in layer A, and the letter after hyphen indicates the strategy in layer B (C-C, C-D, D-C, D-D). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

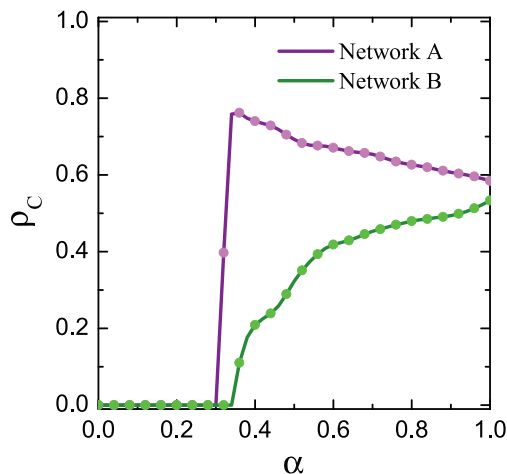


Fig. 6. The fraction of cooperators ρ_C as a function of the reward factor α for $b = 1.5$ in our interdependent networks. The lines and dots represent the results from both numerical simulations and theoretical analysis.

choosing a different strategy with one randomly selected neighbor. Here, we separate the cases of cooperators and defectors for obtaining $w(C \rightarrow D)$ and $w(D \rightarrow C)$, respectively. Therefore, the motion of ρ_C can be expressed as

$$\tilde{\rho}_C = (1 - \rho_C)w(D \rightarrow C) - \rho_C w(C \rightarrow D), \tag{4}$$

In theory, the cooperation level can be calculated when the system reaches the steady state, that is, $\tilde{\rho}_C = 0$ [60]. Substituting that into Eq. (4), we obtain

$$\rho_C = \frac{w(D \rightarrow C)}{w(C \rightarrow D) + w(D \rightarrow C)}, \tag{5}$$

In Fig. 6, we show the cooperation level ρ_C in dependence on the reward factor α in layer A and B. In line with the results for $b = 1.5$ in Fig. 2, defectors dominate the interdependent networks for small values of α . When $\alpha > 0.3$, ρ_C goes up to about 0.75 rapidly and then drops gradually in layer A, while in layer B, ρ_C increases monotonously with a short delay. We conclude this theoretical analysis confirms and validates the results of the numerical simulations.

In the main model, pro-social and anti-social reward can coexist. We further explore two extreme conditions that only one of them can take place among agents in different layers. The phase diagrams of cooperation level for pro-social reward only and anti-social reward only are shown in Fig. 7. The phenomena are the same in layer B for the above two cases: cooperators can survive only if b is pretty small regardless of the value of α . However, in layer A, defectors dominate in most regions only when allowing pro-social reward. In this case, cooperators can only survive for pretty small values of α and b . Conversely, cooperators can easily occupy the whole system when only anti-social rewards are dispensed. In detail, $\rho_C = 1$ for larger α as well as lower α when b is small. Comparing the above two conditions, anti-social reward provides a facilitated environment for cooperators to thrive in layer A. When encountering cooperators, defectors in layer A need to pay the cost for rewarding corresponding defectors in layer B, they therefore lose their original advantage. Thus, cooperators can dominate the system ultimately.

4. Discussion

With this work, we have studied how asymmetric positive incentives can be dispensed between interdependent networks, in the specific case in which individuals in an upper layer reward corresponding players in a lower layer displaying their same strategy. In this simulation instance, the reward action cannot be reciprocated from the lower layer to the upper layer, as it is often the case in mutualisms in which one party produces most resources the host served by several symbionts, making the relationship asymmetric. According to this setup, agents in the upper network layer who dispense these rewards pay a cost which is equivalent to the amount of the reward. By means of large numerical simulations, we found a different evolution of cooperation in the two layers. When the temptation to defect b is pretty small, cooperators almost disappear in layer A and make up nearly half of the population in layer B. When the temptation to defect increases, instead, the situation is reversed. That is, the cooperation rate raises even up to 1, in the upper layer, while it is held down to about 50% in the lower layer. Aided by the visual representation of evolutionary snapshots, we found the potential cause of this phenomenon. Agents who dispense reward and non-rewarded agents lose their initial payoff advantage of dispensing asymmetric rewards. The theoretical analysis confirmed the numerical simulations. Finally, we investigated this evolution of sociality more in

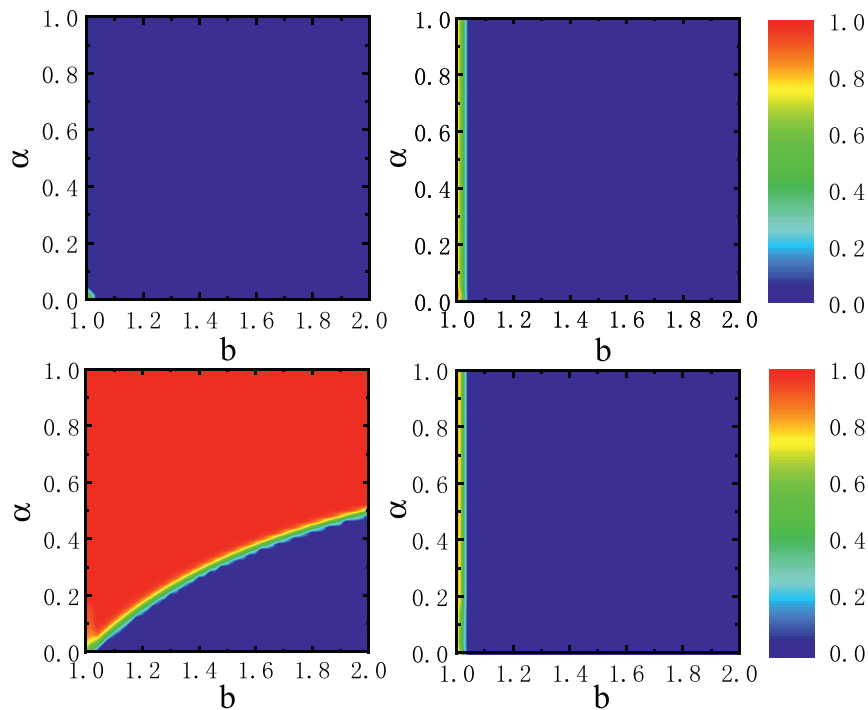


Fig. 7. Phase diagram of average frequencies of cooperation ρ_C depending on the temptation to defect b and the reward factor α in layer A (left) and layer B (right) when only pro-social (the upper row) and anti-social (the lower row) reward can occur.

detail by analyzing separately the two types of reward, namely, pro-social reward only and anti-social reward only. The entirely different phenomena can be found, where defectors dominate the population when rewards originated pro-socially, and cooperators instead win when rewards originated anti-socially.

In this paper, we propose a novel study of asymmetric reward in interdependent networks. Different from the previous studies [45], the asymmetric reward is performed among interdependent layers. That is to say, players in two layers establish relationship through asymmetric reward, which can be regarded as a new way to couple multi-layers. The unilateral dispensation of reward breaks the equilibrium of exchanged behaviours shown in the previous studies in which there were symmetric exchanges [46]. Here, the layer that performs the reward has a higher cooperation level than the layer that receives the reward. In real life, rewards can be dispensed not only between dyads, but also among multiple players. This is a limitation of this simple study. Multiple partner interactions allow generalising evolution of cooperation further. Examples of animal societies implementing multi-partner cooperation are several, but scant has been the specific analysis of these strategies under a game theoretical approach. The few, non-experimental models developed comprise lions defending their territories [61] and male dolphin alliances [62]. An exception digging into the empirical motifs of cooperation was implemented in vervet monkeys [63]. In humans, one person can reward a group of people simultaneously. Moreover, in some cases, the cost of reward may not be evenly paid by the sender(s) and the receiver(s). As future directions, these more realistic situations shall be considered.

We have studied here the effect of positive incentives in a specific network representation of the evolution of cooperation often occurring in mutualistic interactions. It shall be noticed that negative incentives (namely, punishment) are also found to a certain extent in nature, in particular displayed by hosts such as plants, mammals [64], but also microorganisms with symbiotic relationships and humans segregating within different hierarchies [65].

Interdependent networks can help disentangling the type of relationships that can at times be lopsided and asymmetric between parties, holding diverse interests out of the cooperative acts. We have here shown how the network setup of the interacting individuals plays a role in influencing the outcome of the cooperation. We therefore advocate the use of complex network analysis for better understanding cooperation phenomena occurring in behavioral economics, sociology, ecology, ethology, not to forget the cognitive sciences, and other related disciplines [26,66–68].

CRediT authorship contribution statement

Yifan Liu: Conceptualization, Data curation. **Yini Geng:** Formal analysis, Writing - original draft. **Chunpeng Du:** Validation, Investigation, Visualization. **Kaipeng Hu:** Software. **Chen Shen:** Conceptualization, Methodology. **Riccardo Pansini:** Resources, Writing - review & editing. **Lei Shi:** Writing - review & editing, Supervision, Funding acquisition.

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