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Article

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Evolution of prosocial behavior in multilayer populations

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Abstract

Human societies include many types of social relationships. Friends, family, business colleagues, online contacts, and religious groups, for example, can all contribute to an individual's social life. Individuals may behave differently in different domains, but their success in one domain may nonetheless engender success in another. The complexity caused by distinct, but coupled, arenas of social interaction may be a key driver of prosocial or selfish behavior in societies. Here, we study this problem using multilayer networks to model a population with multiple domains of social interactions. An individual can appear in multiple different layers, each with separate behaviors and environments. We provide mathematical results on the resulting behavioral dynamics, for any multilayer structure. Across a diverse space of structures, we find that coupling between layers tends to promote prosocial behavior. In fact, even if prosociality is disfavored in each layer alone, multilayer coupling can promote its proliferation in all layers simultaneously. We apply these techniques to six real-world multilayer social networks, ranging from the networks of socio-emotional and professional relationships in a Zambian community, to the networks of online and offline relationships within an academic University. Our results suggest that coupling between distinct domains of social interaction is critical for the spread of prosociality in human societies.

The scale and sophistication of global human societies are due in no small part to cooperation. Altruistic behavior that benefits the collective, and entails personal costs to the individual, has long been recognized as an important aspect of both human and non-human societies[1]. Just as prosocial behaviors have unquestionably shaped the past, they will also play a major role in shaping the present and future. From the collective action necessary to prevent the spread of COVID-19 in the short term[2,3], to efforts to combat climate change for future generations[4,5], cooperation is a critical precursor to social prosperity.

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At the same time, the emergence and stability of prosocial behaviors is perplexing in light of Darwin's notion of "survival of the fittest"[6,7]. Several mechanisms have been proposed to explain their widespread abundance[8], most notably spatial structure, which constrains interaction and dispersal patterns within a population[9–17]. The effects of population structure on cooperation have been studied theoretically, using computer simulations[18], by approximation techniques[19], and by direct analysis of special cases[20,21]; and they have been observed empirically in laboratory experiments[22]. The latest mathematical results allow for exhaustive analysis of large families of heterogeneous population structures[23–25] and arbitrary initial configurations of individuals[26]. A large portion of population structures favor antisocial traits, such as spite[27], which is simultaneously intriguing and concerning.

Nonetheless, a single network cannot capture the complexity of social structures in human societies. Individuals typically form many different types of social relationships. They enjoy leisure time with friends and encounter colleagues in the workplace. They have physical contact with those who are nearby and participate in online social networks to keep in touch with friends who are more distant[28–32]. Each type of relationship forms a domain in which interactions take place, and individuals may behave differently in different domains. Success in one domain, such as wealth accumulated in business settings, may nonetheless have an impact on success in other domains, such as influence and trustworthiness of opinions expressed on social media. The tendency of an individual's behavior to spread is therefore often dependent on their aggregate success across the domains in which they interact – which introduces a form of coupling between different social domains.

Prior studies of prosocial behavior using evolutionary game theory have either focused on a single domain or assumed that all domains are undifferentiated—all domains are governed by the same game and individuals use the same strategy against all opponents[9–21,23–27]. In practice, however, altruistic acts involve different costs and benefits in different domains, such as donating a dollar to someone in person versus sharing a useful tip on social media. As a result, an individual is likely to exhibit different behaviors in distinct domains. Compared with a growing literature on the dynamics and structural analysis of multiple-domain coupling[33,34], the evolution of prosocial behavior has received much less attention[35,36]. Mathematical results on this topic also remain absent, even for the simplest cases.

In this study, we use a multilayer network to describe a population with multiple domains of strategic interactions. Each layer describes the network of interactions that occur in given domain, and the players can adopt different behavioral strategies in different domains. An individual's behavior in a given domain is preferentially copied by others in that domain, based on the individual's aggregate success across domains. We provide mathematical results applicable to any multilayer structure (i.e. the number of layers and connections within each layer), any initial strategy configuration, and any strategy update rule in each layer. A thorough analysis of all two-layer networks with small size, a sample of large two-layer random networks, and six empirical multilayer social networks, demonstrates that coupling layers tends to strongly promote cooperation. If cooperation is disfavored in each layer alone, or even if layers individually favor spite, coupling layers can often promote cooperation in all layers. The multiple domains that structure human societies thus serve as a natural breeding ground for cooperation to flourish.

Model

We model a population of individuals engaged in pairwise social interactions in multiple domains, or layers. Each individual uses separate strategies and plays distinct games in each layer. An individual's accumulated payoff over all layers governs how much influence she has on her peers' strategy updates in each layer.

In our model, nodes represent individuals and edges describe their social interactions. The population structure is described by a two-layer network, so that each individual corresponds to a node in layer one and an associated node in layer two (see Supporting Information for analysis of more than two layers). Interactions within layer one occur along weighted edges $w_{ij}^{[1]}$; and interactions in layer two occur along weighted edges $w_{ij}^{[2]}$. The degree of node i in layer one is $w_i^{[1]} = \sum_{j=1}^{N} w_{ij}^{[1]}$, whereas it is $w_i^{[2]} = \sum_{j=1}^{N} w_{ij}^{[2]}$ in layer two.

Players engage in a donation game in every domain. In each layer, a player must choose either to cooperate (C) or defect (D) with her neighbors in that layer. A cooperative act means paying a cost of c to provide the opponent with a benefit. The size of the benefit may differ across layers: b_1 in layer one and b_2 in layer two. Defection incurs no cost and provides no benefit to the opponent. A player's strategy may differ across layers, and so we let $s_i^{[1]} \in \{0, 1\}$ denote player i's strategy in layer one and $s_i^{[2]} \in \{0, 1\}$ in layer two, where 1 denotes cooperation and 0 defection. This multilayer donation game is depicted in Fig. 1.

In each successive time step, each individual plays game one with all her neighbors in layer one, and she plays game two with all her neighbors in layer two. Each player i obtains

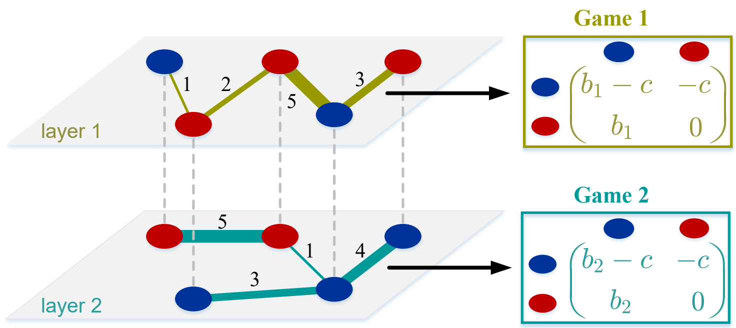

Figure 1: Evolutionary games in multilayer populations. A population with two domains of social interaction is described by a two-layer network, with edge weights $w_{ij}^{[1]}$ in layer one and $w_{ij}^{[2]}$ in layer two (see numbers next to edges for this example). Each player occupies a node in layer one and an associated node in layer two, as indicated by dashed lines. Each player adopts a (possibly different) strategy in each layer, such as cooperation (blue) or defection (red). In each successive time step, each player i plays game one with all her neighbors in layer one and derives an average payoff $u_i^{[1]}$ in layer one; the player also plays game two with all her neighbors in layer two and obtains average payoff $u_i^{[2]}$. Player i's total payoff is the sum across layers, $u_i = u_i^{[1]} + u_i^{[2]}$, which determines her reproductive rate, $f_i = \exp(\delta u_i)$. After all social interactions occur, a random player i is selected to update her strategy in layer one by copying that of a random neighbor j with probability proportional to j's total fitness $w_{ij}^{[1]} f_j$ (i.e. preferential copying of successful individuals). At the same time, a (possibly different) player k updates his strategy in layer two, by copying that of a random neighbor h proportional to $w_{kh}^{[2]} f_h$. We focus our analysis on donation games, in which each player chooses whether to pay a cost (c) to provide a benefit to her neighbor. The benefit may be different in layer one (b_1) than in layer two (b_2).

edge-weighted average payoff $u_i^{[1]}$ in layer one and $u_i^{[2]}$ in layer two, given by

$$
\begin{aligned}
u_i^{[1]} &= -c s_i^{[1]} + b_1 \sum_{j=1}^{N} p_{ij}^{[1]} s_j^{[1]}, \\
u_i^{[2]} &= -c s_i^{[2]} + b_2 \sum_{j=1}^{N} p_{ij}^{[2]} s_j^{[2]},
\end{aligned}
\tag{1}
$$

where $p_{ij}^{[1]} = w_{ij}^{[1]}/w_i^{[1]}$ and $p_{ij}^{[2]} = w_{ij}^{[2]}/w_i^{[2]}$. Player i's total payoff is the sum of those obtained in each layer, namely $u_i = u_i^{[1]} + u_i^{[2]}$. The total payoff across layers determines the rate at which a player's strategy spreads (i.e. its "reproductive rate"), $f_i = \exp(\delta u_i)$, where $0 < \delta < 1$ is the intensity of selection[37]. The regimes $\delta \ll 1$ corresponds to weak selection[38,39] and $\delta = 0$ corresponds to neutral drift.

At the end of one time step, a random player i is selected to update her strategy in layer one. With probability proportional to $w_{ij}^{[1]} f_j$, player i's strategy in layer one is replaced by player j's strategy in layer one. This update rule ensures that a player preferentially copies the strategy of successful individuals. At the same time, a random player k is selected to update his strategy in layer two. With probability proportional to $w_{kh}^{[2]} f_h$, player k's strategy in layer two is replaced by h's strategy in layer two. We focus on this form of "death-birth" updating[19], and we also analyze other mechanisms such as pairwise-comparison updating, birth-death updating, and a mixture of the two (i.e. different update rules for different layers; see Supporting Information).

Results

In the absence of innovation (mutation), the population eventually settles into an absorbing state in which all players either cooperate or defect, in each layer. The absorbing state in the two layers may be different, e.g. cooperation in layer one and defection in layer two. In general, selection can favor cooperation provided the benefit-to-cost ratio b/c is sufficiently large[19]. Here, we analyze how the critical benefit-to-cost ratio to support cooperation in layer one, $(b_1/c)^*$, depends on coupling with a second layer.

Let $\rho_C^{[1]}$ denote the probability that all players eventually cooperate in layer one, starting from some fixed configuration of cooperators and defectors. We use $\left(\rho_C^{[1]}\right)^\circ$ to denote this probability under neutral drift, i.e. when $\delta = 0$. Selection is said to favor the emergence and fixation of cooperation (or cooperation replacing defection) in layer one when the inequality $\rho_C^{[1]} > \left(\rho_C^{[1]}\right)^\circ$ holds[10,19,37]. We focus primarily on the probability that cooperation will fix under weak selection, compared to neutral drift. In Supporting Information, we also compare the fixation probability of cooperation to the fixation probability of defection, and we find qualitatively similar results using this relative measure.

General rule for the evolution of cooperation in multilayer populations To analyze the evolution of cooperation in multilayer networks, we adapt techniques from the study of strategy assortment in single-layer networks[23,25,26], based on random walks within the network. It is necessary to first understand what a random walk in a multilayer network looks like. In a two-layer network, we define a random walk as follows: a step from node i to j in layer one (respectively layer two) occurs with probability $p_{ij}^{[1]}$ ($p_{ij}^{[2]}$). An (n, m)-step random walk in the network means an n-step random walk in layer one followed by an m-step random walk in layer two, where the beginning of the second random walk corresponds to the end of the first (e.g. Fig. 2B).

We let θ_n denote the probability that the starting and ending nodes of an n-step random walk in layer one both employ the same strategy. For example, θ_1 quantifies the correlation, or assortment, of strategies between neighboring nodes in layer one. Similarly, we let $\phi_{n,m}$ denote the probability that the starting and ending nodes of an (n, m)-step random employ the same strategy. For example, $\phi_{0,1}$ quantifies the strategy assortment between a node in layer one and a random neighbor in layer two. We can obtain θ_n and $\phi_{n,m}$ by solving systems of $O\left(N^2\right)$ linear equations (see Methods).

For any two-layer population structure and any initial strategy configuration, we have derived a general condition for when cooperation in layer one is favored by selection:

$$\theta_1 b_1 + \phi_{0,1} b_2 - \theta_0 c - \phi_{0,0} c > \theta_3 b_1 + \phi_{2,1} b_2 - \theta_2 c - \phi_{2,0} c. \tag{2}$$

Informally, this condition states that a cooperative neighbor of a node in layer one must have a higher payoff than a random neighbor. The four terms on the left side quantify the benefits and costs to a cooperative neighbor, where $\theta_1 b_1$ and $\theta_0 c$ denote the benefits and costs from layer one, and $\phi_{0,1} b_2$ and $\phi_{0,0} c$ denote the benefits and costs from layer two. The four terms on the right quantify the benefits and costs to a random neighbor, where $\theta_3 b_1$ and $\theta_2 c$ (respectively $\phi_{2,1} b_2$ and $\phi_{2,0} c$) denote the benefits and costs from layer one (layer two). These eight quantities collectively govern the fate of cooperation in multilayer networks, as depicted in Fig. 2. A special case of equation (2) is when layer one evolves independently from layer two, so that there are no benefits and costs arising from layer two, in which case selection favors cooperation whenever $\theta_1 b_1 - \theta_0 c > \theta_3 b_1 - \theta_2 c$.

Coupled ring networks The general rule derived above allows one to study how multiple domains of social interactions influence the prospects for cooperation, in arbitrary interaction networks. We start with an illustrative example based on a two-layer ring network. We consider $N = 10$ individuals are arranged in a ring, each with two neighbors in each layer. Initially, a single individual in each layer is cooperative, and the cooperator in layer one is connected to the cooperator in layer two (see Fig. 3A). When the two layers evolve independently, or in the absence of layer two, cooperation is favored by selection in layer one only if the benefit-to-cost ratio, b_1/c, exceeds a critical value, $(b_1/c)^* = 8/3$ (dashed vertical line in Fig. 3B). But when the two layers are coupled and $b_2/c = 10$, then critical value $(b_1/c)^*$ is reduced to 1.74 (solid vertical line in Fig. 3B). In other words, coupling games between layers promotes cooperation in layer one, making it far easier to evolve than in the absence of layer two. The reason is that, when layers are coupled, a player's success in one layer depends not only on her payoffs obtained in that layer, but also on her interactions in the other layer. In this case, the cooperator in layer one is being exploited by two neighboring defectors, as seen in Fig. 3A, but nonetheless she receives an extra benefit from a cooperative neighbor in layer two, who increases her fitness and promotes the spread of her (cooperative) strategy in layer one (see also SFig. 3 for further details).

Figure 4 illustrates more generally how multilayer coupling affects evolutionary dynamics in ring networks. When the two layers evolve separately, cooperation is favored in layer one only if b_1/c exceeds the olive dashed line; and cooperation is favored in layer two only if b_2/c exceeds the blue dashed line. Selection thus favors cooperation in both layers only when b_1/c

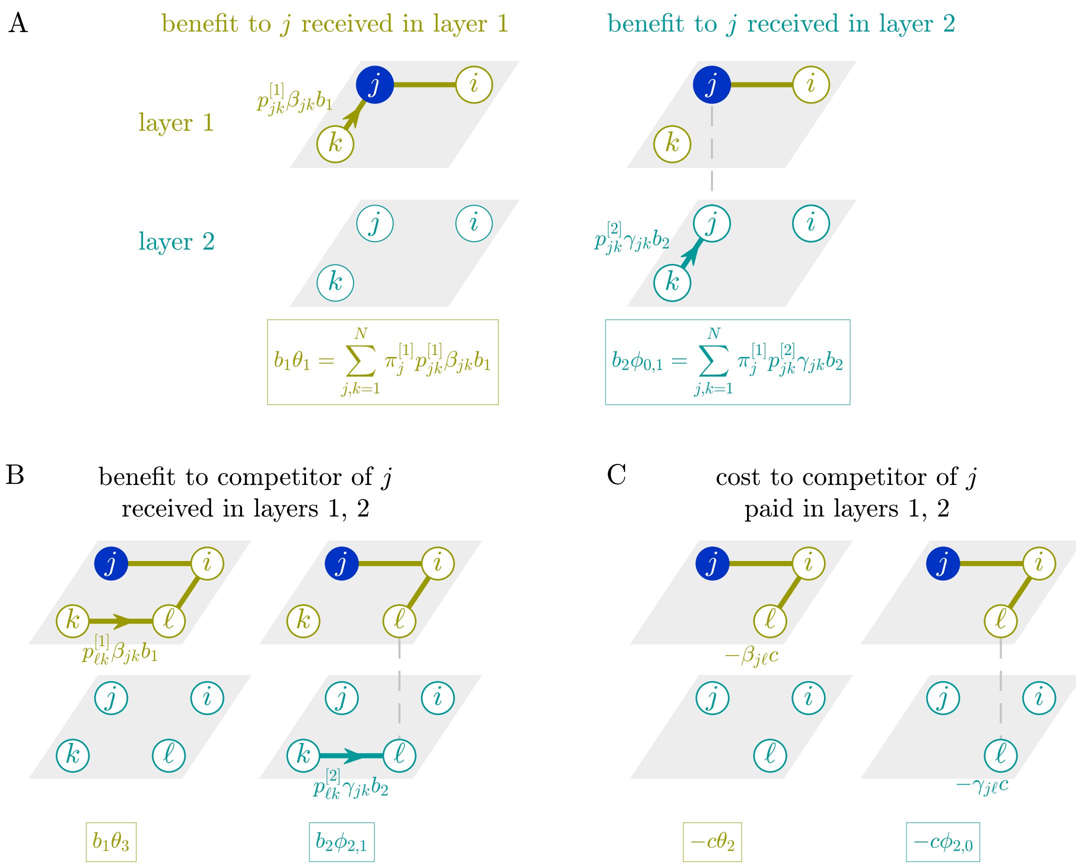

Figure 2: General rule for the evolution of cooperation in multilayer populations. We consider what happens when individual i is chosen to update her strategy in layer one, and her neighbors compete to have their strategy copied. Cooperation will be selectively favored in layer one if a cooperative neighbor, node j, has greater expected payoff than a random neighbor, node ℓ. Node j receives an average benefit $b_1\theta_1$ from its own one-step neighbors in layer one (panel A, left). Node j also receives an average benefit $b_2\phi_{0,1}$ from its own one-step neighbors in layer two (panel A, right). The expression for θ_1 (respectively $\phi_{0,1}$) accounts for the probability $p^{[1]}_{jk}$ ($p^{[2]}_{jk}$) that a random walk moves from node j to k in layer one (layer two); and for the probability β_{jk} (γ_{jk}) that node k has the same strategy in layer one (layer two) as node j has in layer one (see also Supporting Information). Node j pays the cost $c\theta_0$ as a cooperator in layer one and $c\phi_{0,0}$ in layer two. Node j's net payoff is therefore $\theta_1 b_1 + \phi_{0,1}b_2 - (\theta_0 c + \phi_{0,0}c)$. Any competitor of j, such as node ℓ, is also vying to have its strategy copied. Note that in layer one, node ℓ is two steps away from node j. Node ℓ receives an average benefit $b_1\theta_3$ (respectively $b_2\phi_{2,1}$) from its one-step neighbors in layer one (layer two), who are three steps away in layer one (two steps away in layer one and one step away in layer two) from node j, as shown in panel B. Whenever ℓ is a cooperator she pays cost c, leading to an average cost $\theta_2 c$ in layer one and $\phi_{2,0}c$ in layer two (panel C). Node ℓ's net payoff is therefore $\theta_3 b_1 + \phi_{2,1}b_2 - (\theta_2 + \phi_{2,0})c$. Selection will favor cooperation only if $\theta_1 b_1 + \phi_{0,1}b_2 - \theta_0 c - \phi_{0,0}c > \theta_3 b_1 + \phi_{2,1}b_2 - (\theta_2 + \phi_{2,0})c$.

and b_2/c lie in region κ. Coupling layers moves the benefit-to-cost ratio required for cooperation in layer one to olive solid line, and it moves the benefit-to-cost ratio required in layer two to blue solid line – in both cases expanding the parameter range of costs and benefits that favor cooperation. In particular, the region λ reveals the remarkable fact that even if cooperation is

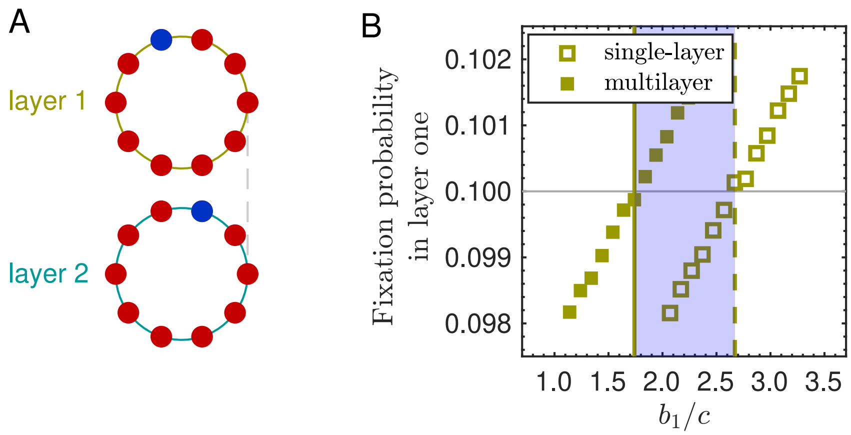

Figure 3: Multilayer games can promote cooperation. (A) We consider a "ring network" in each layer, with each node connected to two neighboring nodes. Nodes that occupy the same position in both layers represent the same individual, as indicated by the dashed line. The initial strategy configuration contains one cooperative individual in layer one (blue) and one cooperative individual in layer two (blue). (B) The probability that cooperation will eventually fix in layer one. We compare two scenarios: when the layers operate independently (open squares) versus when the two layers are coupled (solid squares). Cooperation in layer one is favored by selection if it fixes with a greater probability than in the absence of selection (horizontal line). According to our analytical prediction, cooperation will be favored whenever the benefit-to-cost ratio (b_1/c) exceeds a critical value, indicated by the solid vertical line (for coupled layers) and by the dashed vertical line (for independent layers). For the benefit-to-cost ratios indicated in light blue, coupling between layers promotes cooperation in layer one even though it would be disfavored by selection under evolution in layer one alone. Dots indicate results from 10^7 replicate Monte Carlo simulations. Parameters: $b_2 = 10$, $c = 1$, and $\delta = 0.02$.

disfavored by selection in each layer alone, cooperation can nonetheless be favored in both layers simultaneously when they are coupled.

In the two-layer ring network, for any configuration with only one cooperator in layer one and one cooperator in layer two, we have derived a simple formula to calculate the critical benefit-to-cost ratio $(b_1/c)^*$ required to favor cooperation (see Methods). For more complicated initial configurations we can still resort to the general condition (equation (2)) to obtain theoretical predictions, although the expressions are more complicated. Even among these simple graphs we find a diverse range of scenarios in which multiplayer coupling promotes cooperation (see SFig. 4).

Coupled heterogeneous networks For ring networks, cooperation is favored in each layer alone provided the benefit-to-cost ratio exceeds some critical value. Coupling between layers can reduce the critical value and thereby promote cooperation. However, the prospects for cooperation may be far worse in other population structures. In fact, there are many single-layer population structures in which cooperation is never favored in a social dilemma, no matter how large the

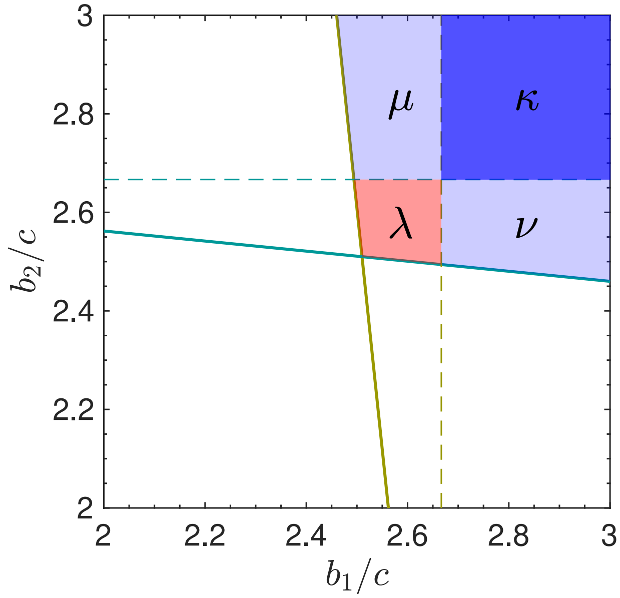

Figure 4: When coupling promotes cooperation. We analyze a two-layer ring network with the initial strategy configuration shown in Fig. 3A. If the population evolves in layer one alone, then cooperation is favored by selection only when b_1/c exceeds the olive dashed line. Coupling with layer two facilitates the evolution of cooperation in layer one, decreasing the required benefit-to-cost ratio from the olive dashed line to the olive solid line. If the population evolves in layer two alone, cooperation is favored by selection only when b_2/c exceeds the blue dashed line. Coupling with layer one facilitates the evolution of cooperation in layer two, decreasing the required benefit-to-cost ratio to the blue solid line. Without coupling, selection favors cooperation in both layers only in region κ. But coupling extends that region to $\kappa\mu\lambda\nu$. Note that in region λ, cooperation is disfavored in each layer on its own, but it is favored in both layers when they are coupled.

benefit-to-cost ratio[11,23,24].

The star graph is an example of a population structure that always suppresses cooperation. The graph consists of a central hub and $N-1$ leaf nodes. Regardless of the initial strategy configuration, no finite value of the benefit-to-cost ratio can selectively favor cooperation (i.e. $(b_1/c)^* = \infty$). Nonetheless, if we couple two stars in a certain way (Fig. 5A) then selection favors cooperation in both stars simultaneously provided b_1/c and b_2/c exceed $\left(18N^4 - 55N^3 + 64N^2 - 33N + 6\right) / \left(4N^3 - 2N^2\right)$ (see Supporting Information for detailed derivations). The region λ in Fig. 5A depicts the benefit-to-cost ratios that favor cooperation in these two-layer graphs.

An even more striking example occurs on the wheel network, shown in Fig. 5B. For any initial strategy configuration on such networks, the critical benefit-to-cost ratio is negative, $(b_1/c)^* < 0$ – meaning that selection actually favors spite, an antisocial behavior where an indi-

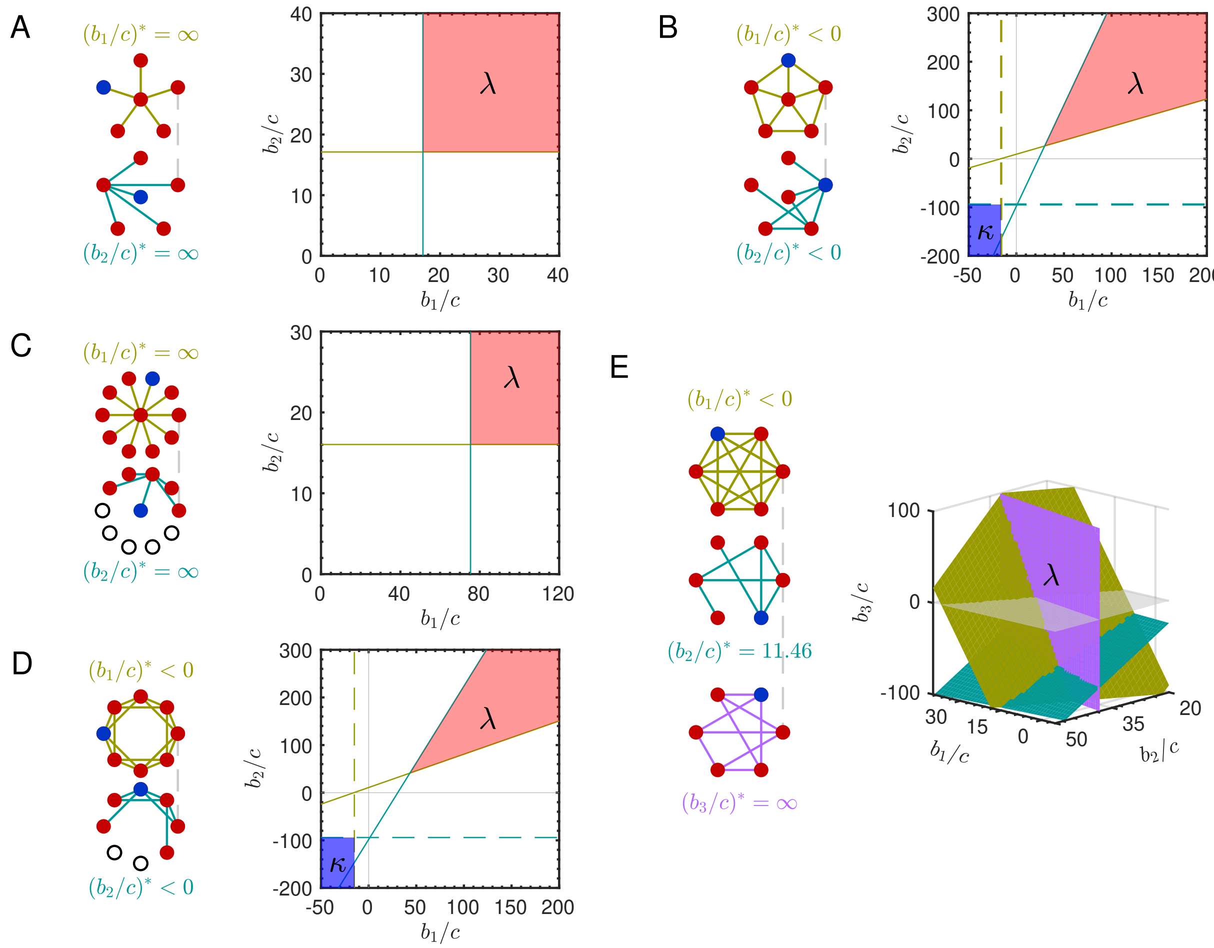

Figure 5: Multilayer coupling can promote cooperation even when cooperation is disfavored in individual layers. We present five representative examples. (A) In each layer alone, the critical benefit-to-cost ratio is infinite, i.e. $(b_1/c)^* = (b_2/c)^* = \infty$. As a result, cooperation is never favored by selection, regardless of how large the benefit-to-cost ratio is. Nevertheless, when the two layers are coupled, selection then favors cooperation in both layers, provided b_1/c and b_2/c fall within the region λ. (B) In each layer alone, the critical benefit-to-cost ratio is negative, i.e. $(b_1/c)^*, (b_2/c)^* < 0$. These negative ratios indicate that selection can favor the fixation of spite in each layer alone—so that an individual will pay a cost of $c > 0$ to *decrease* his partner's payoff. Nevertheless, when the two layers are coupled, selection then favors cooperation in both layers, provided b_1/c and b_2/c fall within the region λ. Multilayer networks can also rescue cooperation when there are different population sizes in different layers (C, D), or for populations with more than two layers (E). In (C) and (D), open circles indicate absence of a node in that layer.

vidual pays a cost to decrease her neighbor's payoff. But if we couple one wheel network with another, as shown in Fig. 5B, cooperation can be favored on both layers, provided b_1/c and b_2/c lie in region λ. Together with the star network, this example shows that coupling can promote cooperation in multiple layers, even if selection always disfavors cooperation in each layer alone.

Our framework also applies to mutilayer populations with different population sizes in different layers. That is, a player may have social interactions in layer one, but no social interactions in layer two (see examples in Fig. 5C and D) – corresponding, for example, to an individual who forgoes online social networking altogether. Figure 5C and D confirm that in such cases coupling can still allow cooperation to be favored in both layers, even if cooperation is disfavored in each layer alone for any benefit-to-cost ratio. In such populations with different population sizes in different layers the general rule for the evolution of cooperation is analogous to equation (2) (see Supporting Information).

Our framework also applies to multilayer populations with an arbitrary number of layers. Figure 5E illustrates an example of three-layer population. When the three layers evolve independently, cooperation is favored neither in layer one ($(b_1/c)^* < 0$) nor in layer three ($(b_3/c)^* = \infty$). Coupling the three layers allows selection to favor cooperation, provided benefit-to-cost ratios lie in the three-dimensional region λ. In particular, coupling not only makes it possible for cooperation to be favored in layer one and layer three, but it also reduces the value of b_2/c required for cooperation being favored in layer two. Therefore, the coupling of more layers can provide more opportunities for the evolution of cooperation. In Supporting Information, we derive the general condition for selection to favor cooperation on population structures with an arbitrary number of layers.

Small multilayer populations To study behavioral dynamics across a variety of structures, we have systematically analyzed all two-layer networks of size $N = 3, 4, 5, 6$ and all initial configurations of a single cooperator in each layer (see Methods for details). We first report the proportion of single-layer networks and strategy configurations in which cooperation can be favored in layer one alone for some choice of benefit-to-cost ratio (i.e. $(b_1/c)^* > 0$, blue bars in Fig. 6). Coupling layer one with a randomly chosen network and strategy configuration in layer two can significantly increases the frequency of structures on which selection favors cooperation in layer one, for some values $b_1/c > 0$ and $b_2/c > 0$ (red bar). Coupling layer one with a deliberately designed network and configuration in layer two can further increase the frequency of cooperation (green bar). In a large proportion of these cases, coupling to either a random or a designed network in layer two, selection actually favors cooperation in both layers simultaneously (SFig. 5). Therefore, in a systematic analysis of all small structures, multilayer networks have a significant positive impact on prospects for cooperation.

Larger multilayer populations The networks explored above are all relatively small, but they nonetheless exhibit a diverse range of behavioral dynamics and surprising effects induced by multilayer coupling. To study behavior on larger networks we sampled many two-layer Erdös-Rényi random networks[40] and two-layer scale-free networks[41] of size $N = 50$ individuals. We

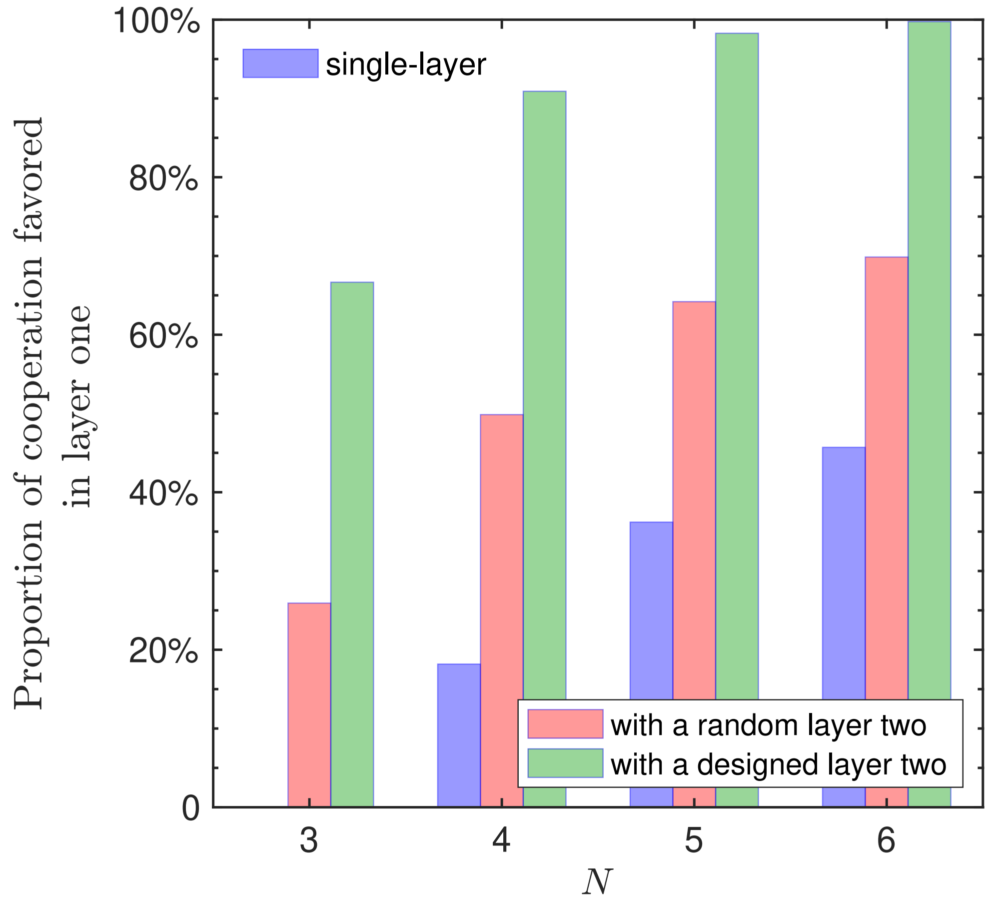

Figure 6: Proportion of small networks that permit the evolution of cooperation. We systematically analyzed all networks of size $N = 3, 4, 5, 6$, including all initial configurations containing a single cooperator. Blue bars indicate the proportion of single-layer networks and mutant configurations in which selection can favor cooperation in layer one for some benefit-to-cost ratio, i.e. $(b_1/c)^* > 0$. For $N = 3$, selection does not favor cooperation for any network and configuration, for any value of b_1/c. Coupling layer one with a randomly chosen network and strategy configuration in layer two increases the frequency of selection for cooperation (i.e. selection favors cooperation in layer one for some choice of $b_1/c > 0$ and $b_2/c > 0$, shown in red). Coupling layer one with a deliberately designed network and strategy configuration in layer two further increases the frequency of cooperation in layer one (green). In a majority of these cases, coupling to either a random or a designed network in layer two, selection actually favors cooperation in both layers simultaneously (see SFig. 5).

sampled such networks across a diverse range of average node degrees in layer one and in layer two (see Fig. 7A). In each two-layer network we placed a single mutant cooperator in each layer and analyzed all $50 \times 50 = 2,500$ initial strategy configurations. Figure 7A and B report the frequency of structures for which selection can favor cooperation in both layers for some positive values of b_1/c and b_2/c. Compared with the corresponding frequencies when the two layers evolve separately (see SFig. 6), we find that coupling two layers is broadly conducive to selection for cooperation, as shown in the highlighted area in Fig. 7A and B. In particular, in the random networks with average degree greater than 26, cooperation is never favored for any benefit-to-cost ratio. Coupling such networks to a random network in layer two can often rescue cooperation (dark red area in Fig. 7A). Figure 7C and D show examples of random and scale-free two-layer networks that favor the evolution of spite on each layer alone, but that can favor cooperation on both layers when coupled (see also SFig. 7 and SFig. 8 for further analysis and examples).

Empirical multilayer populations We also studied six real-world examples of communities engaged in multiple domains of social interaction. The six empirical two-layer networks[28–32] range from online and offline relationships among members of the Computer Science Department at Aarhus University, to the marriage and business relationships among prominent families in renaissance Florence, and they range in population size from $N = 21$ to $N = 71$ (Fig. 8). We analyzed the prospects for cooperation when individuals play donation games in each layer, including all initial configurations with a single cooperator in each layer. In all of these empirical networks, even if two layers evolve separately cooperation can be favored in each layer provided the benefit-to-cost ratios are sufficiently large. Coupling the two layers can nonetheless reduce the benefit-to-cost ratios required to support cooperation. Figure 8A shows the proportions of initial configurations for which coupling facilitates cooperation in this way. Figure 8C shows an example of this phenomenon, using the two-layer network of socio-emotional and professional relationships among customers surveyed in a Zambian tailor shop; coupling these two domains of social interaction facilitates cooperation in both domains, by reducing the benefit-to-cost ratios required to favor prosocial behavior.

The behavioral outcome in one layer may be more important than in another layer, such as when more individuals appear in one layer, or when prosociality in one domain is more important for the overall welfare of a society. To study this in the context of real-world multilayer networks, we analyzed to what degree the benefit-to-cost ratio for cooperation to be favored in layer one alone can be reduced. (In these analyses the prospect for cooperation in the second layer is left uncontrolled, and so cooperation might be disfavored in layer two.) We find that in all six empirical two-layer networks, and for nearly all initial configurations, a proper choice of benefits and costs in layer two can serve to lower the critical benefit-to-cost ratio required for the evolution of cooperation in layer one (Fig. 8B). Remarkably, we find that the critical benefit-to-cost ratio in layer one can sometimes be reduced to zero by coupling (SFig. 9), which indicates that cooperation can be favored in layer one despite providing no immediate benefit in that domain at all. This dramatic effect of coupling occurs for more than 25% initial configurations in the six empirical networks. The spatial arrangement of cooperators strongly affects whether the required benefit-to-cost ratio can be reduced all the way to zero by coupling. In general, the closer two initial cooperators, one in each layer, the more likely that coupling can catalyze cooperation in layer one even without providing any immediate layer-one benefit (SFig. 10). Aside from the

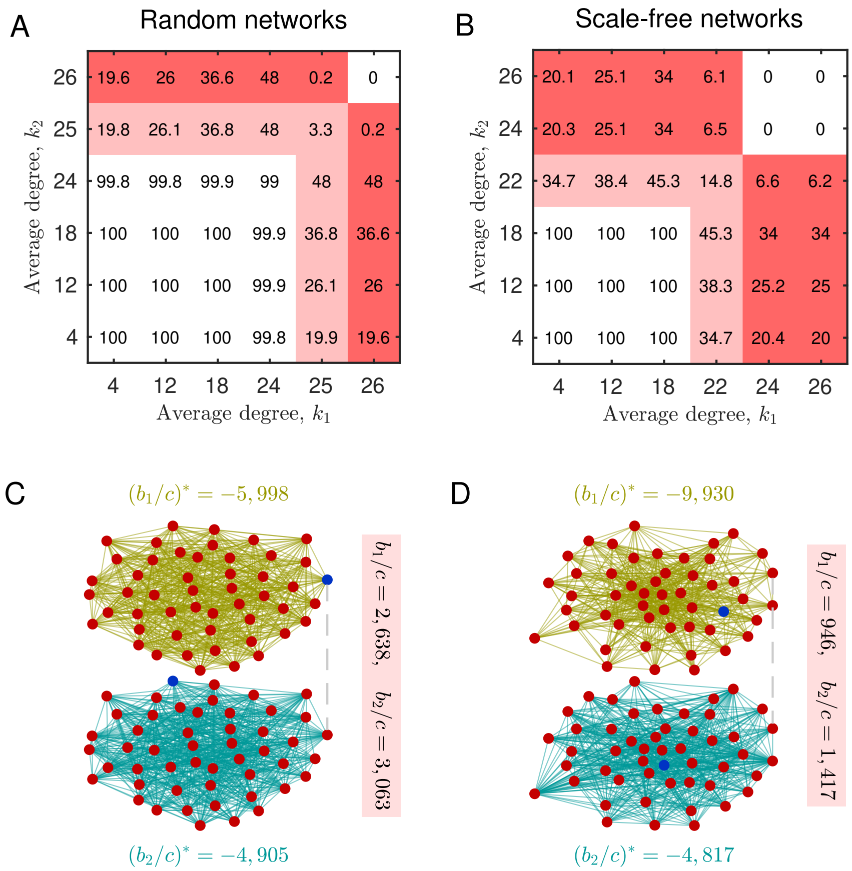

Figure 7: Multilayer coupling can catalyze the evolution of cooperation in random and scale-free populations. We sampled 100 two-layer Erdös-Rényi random networks of size $N = 50$, and 100 two-layer scale-free networks of size $N = 50$, for each pair of average node degrees, k_1 and k_2, in layers one and two, respectively. For each two-layer network we analyzed all 2,500 initial configurations consisting of a single mutant cooperator in each layer. (A) The proportion (percentage) of sampled two-layer random networks and initial configurations in which selection can favor cooperation in both layers, for some positive values of b_1/c and b_2/c. Highlighted entries indicate regimes when coupling increases the frequency of selection for cooperation in both layers compared to independent evolution in each layer. Coupling can have a dramatic effect—e.g. favoring cooperation in both layers for nearly 50% of sampled networks, compared to virtually never favoring cooperation without coupling (see SFig. 6). For some regimes, coupling permits selection for cooperation in both layers even though one or both layers oppose its selection in the absence of coupling (dark red). (B) The proportion (percentage) of sampled two-layer scale-free networks and initial configurations in which selection can favor cooperation in both layers; highlighted entries indicate regimes when coupling increases the frequency of selection for cooperation in both layers compared to independent evolution in each layer. (C) and (D) Examples of two-layer random and scale-free networks, respectively, in which spite is favored on each layer evolving independently, but cooperation is favored in both layers when coupled.

six empirical networks, we also illustrate this phenomenon in two-layer random networks and two-layer scale-free networks (SFig. 11 and 12).

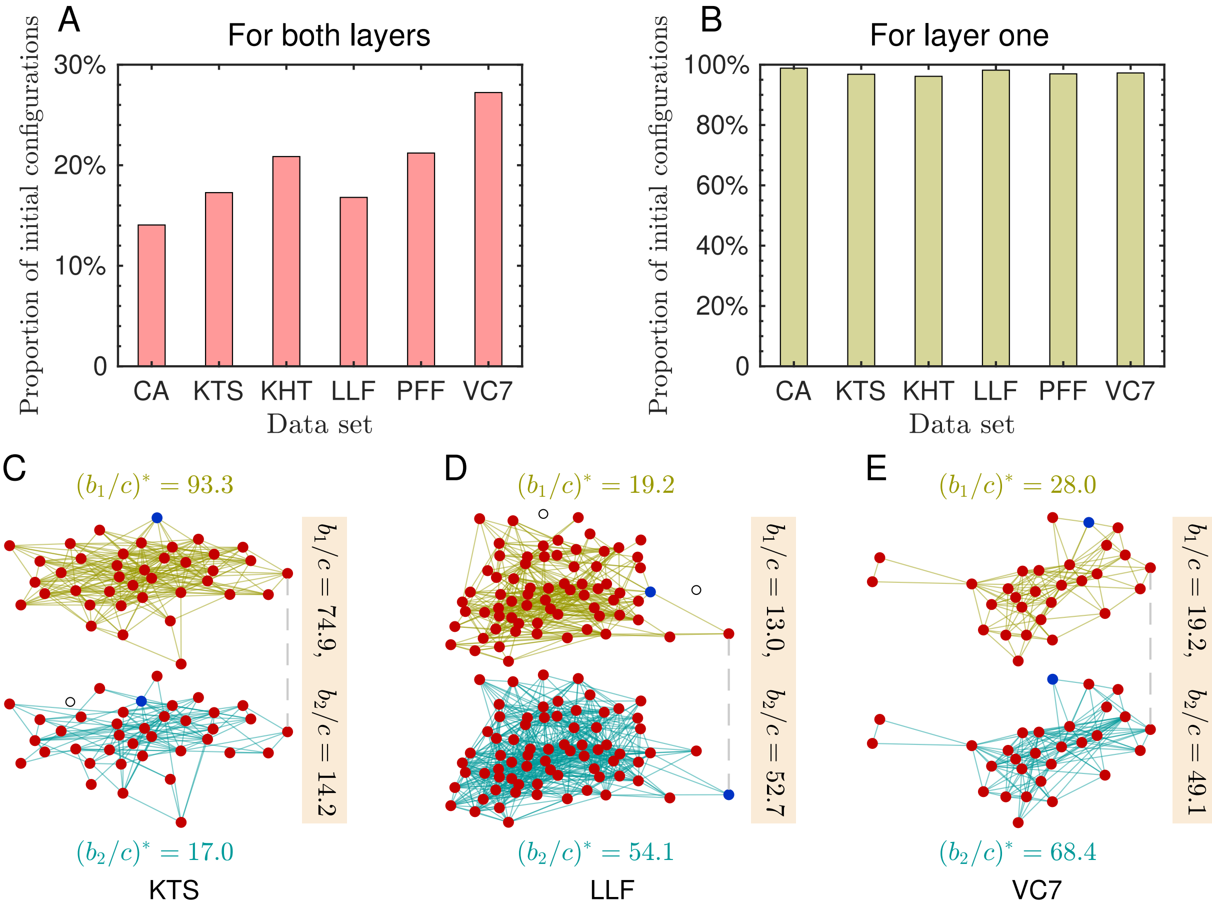

Figure 8: Evolution of cooperation in six real-world two-layer networks. We analyzed networks of online and offline relationships among 61 employees of the Computer Science Department at Aarhus University (CA)[28]; social-emotional and professional relationships among 39 customers surveyed in a Zambian tailor shop (KTS)[29]; friendship and professional relationships among 21 managers at a high-tech company (KHT)[30]; friendship and professional relationships among 71 partners at the Lazega Law Firm (LLF)[31]; marriage and business relationships among 16 families in renaissance Florence (PFF)[32]; and friendship and scholastic relationships among 29 seventh-grade students in Victoria, Australia (VC7). We considered all initial configurations with a single mutant cooperator in each layer, where individuals play the donation game. (A) Proportion of configurations in which coupling layers reduces benefit-to-cost ratios required for cooperation to be favored in both layers, relative to when layers evolve independently. (B) Proportion of initial configurations in which coupling layers reduces the benefit-to-cost ratio required for cooperation to be favored in layer one. (C-E) Three example configurations with a single mutant cooperator (blue) among defectors (red), where open circles indicate isolated individuals. In these examples, selection favors cooperation in each layer alone provided the benefit-to-cost ratio exceeds a critical value, e.g. $(b_1/c)^* = 93.3$ in KTS layer one. Coupling layers reduces the benefit-to-cost ratio required for cooperation to evolve in one or both layers. For example, when $b_1/c = 74.9$ and $b_2/c = 14.2$, selection favors cooperation in both layers of the coupled KTS network.

Discussion

One of the many complexities of human societies is the structure of our social interactions. Structure is not confined to a single type of interaction, but includes the distinct domains of relationships in which we interact. This feature would not complicate the problem of understanding behavior if interactions and standing in one domain had no influence on other domains. But that is emphatically not the case. A person with a large online following, for example, can leverage this for success and appeal in professional relationships; and someone with success in business can garner support in politics or even religion. The empirical impact of coupling between domains can be dramatic, as exemplified by the famous Medici family of renaissance Florence[32], but also in modern times. Understanding coupling between domains of social interaction is therefore critical to understanding what drives prosocial and selfish behavior in societies.

We have modelled the evolution of prosocial behaviors across domains using multilayer networks, where each individual uses separate strategies and plays distinct games in different layers. An individual's total payoff across domains determines his or her influence over peers. We find that the threshold for selection to favor cooperation in a multilayer population can be much lower than it is in a single-layer population[19,23]. For a large portion of multilayer populations, coupling can promote cooperation in all layers, even when cooperation is disfavored in each layer alone. And so the prospects for cooperation are fundamentally changed when social interactions occur in distinct, but coupled, domains.

Our results have been derived in a completely general mathematical framework, whose power we have illustrated through systematic analysis of all small networks, as well as extensive sampling of larger random and scale-free networks. We have also analyzed six empirical two-layer networks across diverse real-world communities, where we find that coupling promotes the spread of prosocial behavior, especially by strategic design of incentives in one layer. Our analysis of these six empirical networks has been confined to the simple donation game, which is not a perfectly accurate description of the all the real-world social interactions that occur in these empirical settings. But this simple model hopefully captures the key, qualitative tension between prosocial, selfish, and even antisocial behavior[11,12,15,19,23,27]. The qualitative conclusions we draw from it are driven by the empirical network structures and the behavioral dynamics that arise when individuals garner influence across domains.

Our work has several implications for the evolution of prosocial behavior, both in theory and practice. The first noteworthy implication is the importance of coordinating benefit-to-cost ratios between layers (i.e. b_1/c and b_2/c). If selection favors cooperation for some positive benefit-to-cost ratio in a single-layer network, then it does so for any larger ratio. In a multilayer network, however, the condition for cooperation to be favored depends on benefit-to-cost ratios in both layers (equation (2)). Increasing b_1/c unilaterally can actually result in selection against cooperation. Intriguingly, we find that in up to 40% of the two-layer networks we examined, cooperation can be favored in layer one even when there is no immediate benefit of cooperation in that layer (b_1/c

near zero), provided the benefits in layer two are sufficiently large.

Another important implication concerns how to design or modify interactions in one domain in order to promote cooperation in another, or in both. Indeed, not every multilayer structure is beneficial for cooperation, and so one can ask whether it is possible to slightly modify interactions in one layer to promote cooperation in both layers. Although this question is quite deep and difficult for full mathematical analysis, we have analyzed it systematically in all two-layer networks of size 6 (See SFig. 13). In these cases we find that adding or severing a small number of connections in layer two, if done properly, can rescue cooperation in both layers. Investigating this question in greater generality is a worthwhile avenue for future study, with clear practical implications.

Several prior studies have demonstrated that selection cannot favor cooperation in a single-layer structured population under birth-death or pairwise-comparison updating[19,42–44]. More recent studies have found that game transitions[45] and heterogeneous distributions of social goods[25] can catalyze cooperation under these update rules. Here, too, we find that a simple coupling of layers works efficiently to make cooperation favored by selection under birth-death or pairwise-comparison updating (see SFig. 14). In practice, there may be considerable cultural differences between domains, it is not unreasonable to expect that the mechanisms of imitation and learning differ between layers. The multilayer approach also allows for such a mixture of update rules in different layers (see Supporting Information).

The literature on evolutionary game theory commonly assumes that new types (innovations or mutations) appear uniformly at random within a population. This assumption simplifies the mathematical analysis of population dynamics, and it is also scientifically reasonable when death rates are uniform and mutants are initially rare[12–16,19,23]. However, non-uniform arrangements of mutants can lead to completely different outcomes. For example, one arrangement might favor cooperation while another suppresses it[46], as we have seen in the multilayer context as well. More generally, we have proven that when the mutant in a layer is introduced randomly and uniformly, then the threshold required for cooperation to be favored is independent of the other layers (see SFig. 15 and Supporting Information). In other words, averaging the dynamics over a uniform initial mutant distribution obscures the effects of one layer on another. And so we conclude that the common assumption used in the field turns out to be pathological special case that is not representative of the effects of mutation in general.

Our study of multilayer games has used single-layer networks as the primary reference point for comparison. However, there are substantial similarities between the process we study here and evolutionary set theory[12], a framework in which different sets represent different social categories (or different types of social relationships), and each individual falls into one or more of these sets. The crucial difference between evolutionary set theory and multilayer networks is that, in the former, individuals adopt a single strategy and apply it against all other members of his or her set(s); and set membership can change in time. In our setting, on the other hand, domain membership is fixed but we allow for separate behaviors in different domains of interactions. In this sense, the framework of multilayer networks is orthogonal to evolutionary set theory. Moreover, in the context of multilayer games it is not the strategy one uses in a layer that determines your influence in that layer; rather, all your strategies matter.

The last two decades have seen extensive investigation into the effects of spatial structure on evolutionary games[10]. Most of these studies are based on a single (one-layer) population structure, limited to one of a few different update rules. While the use of multilayer networks in evolutionary dynamics is not new[35,36], to our knowledge our work provides the first rigorous mathematical results on evolution in multilayer populations. These results are applicable to an arbitrary number of layers and any connectivity structure within each layer, and so they allow for efficient exploration of diverse multilayer structures. They also apply to a broad class of evolutionary update rules, including mixtures across layers. Many questions remain for future work in this area, including the effects of different interaction and replacement structures in each layer; the dynamics of producers of other kinds of social goods; the implications of strategy "spillover" from one layer to another; and dynamic social categories that can change over time. As modeling techniques grow more sophisticated to reflect the complexity of human and non-human societies, a better empirical understanding of interdependence of social domains will be crucial for predicting the dynamics of prosocial behaviors.

Methods

Here we briefly summarize our theoretical results on weak selection in multilayer populations, and we refer to Supporting Information for detailed derivations. We consider a population structure described by a two-layer network of size N, with edge weights $\left(w_{ij}^{[1]}\right)_{i,j}$ in layer one and $\left(w_{ij}^{[2]}\right)_{i,j}$ in layer two. All edges are symmetric, i.e. $w_{ij}^{[1]} = w_{ji}^{[1]}$ and $w_{ij}^{[2]} = w_{ji}^{[2]}$, and self loops are not allowed. The weighted degree of node i is $w_i^{[1]} = \sum_{j=1}^{N} w_{ij}^{[1]}$ in layer one and $w_i^{[2]} = \sum_{j=1}^{N} w_{ij}^{[2]}$ in layer two. The relative weighted degree of node i is thus $\pi_i^{[1]} = w_i^{[1]} / \sum_{j=1}^{N} w_j^{[1]}$ in layer one and $\pi_i^{[2]} = w_i^{[2]} / \sum_{j=1}^{N} w_j^{[2]}$ in layer two. Under death-birth updating, the relative weighted degree of i in a given layer corresponds to the so-called reproductive value of i in that layer[24,47,48], which represents the contribution of i to future generations, in the absence of selection.

The evolutionary dynamics of death-birth updating in network-structured populations can be described in terms of random walks on networks[23]. Here, too, random walks come into play, but since we are dealing with multilayer networks we need to be clear about their definitions. In a two-layer network, we define a random walk as follows. In layer one (resp. two), starting at node i, a one-step walk terminates at node j with probability $p_{ij}^{[1]} = w_{ij}^{[1]}/w_i^{[1]}$ (resp. $p_{ij}^{[2]} = w_{ij}^{[2]}/w_i^{[2]}$). Let $\left(p^{[1]}\right)_{ij}^{(n)}$ denote the probability that a walker starting at node i terminates at node j after an n-step random walk in layer one. We define an (n,m)-step random walk to be an n-step walk in layer one followed by an m-step walk in layer two, where the beginning of the second random walk corresponds to the end of the first. Let $\left(p^{[1,2]}\right)_{ij}^{(n,m)}$ denote the probability that a walker starting at node i terminates at node j after an (n,m)-step walk.

The effects of selection depend on the assortment of strategies within the network. In a two-layer network, the spatial assortment involves not only strategies within the same layer but also those in the other layer. Let β_{ij} denote the probability that, in layer one, both nodes i and j are cooperators under neutral drift. Similarly, let γ_{ij} be the probability that both nodes i in layer one and node j in layer two are cooperators. When $i = j$, we let β_i denote β_{ij} and γ_i denote γ_{ij}. For a formal mathematical description of the underlying distribution, see Supporting Information.

If $\boldsymbol{\xi}$ is any initial strategy configuration, then $\xi_i^{[L]}$ denotes is the strategy of node i in layer L. The quantity then $\widehat{\boldsymbol{\xi}}^{[L]} = \sum_{i=1}^{N} \pi_i^{[L]} \xi_i^{[L]}$ represents the fixation probability of cooperators in layer L under neutral drift ($\delta = 0$)[24]. In Supporting Information, we show that one can obtain β_{ij} and γ_{ij} by solving the following linear system of equations,

$$\begin{cases} \beta_{ij} = & \frac{N}{2}\left(\xi_i^{[1]}\xi_j^{[1]} - \widehat{\boldsymbol{\xi}}^{[1]}\right) + \frac{1}{2}\sum_{k=1}^{N} p_{ik}^{[1]}\beta_{kj} + \frac{1}{2}\sum_{k=1}^{N} p_{jk}^{[1]}\beta_{ik}, \\ \\ \beta_i = & N\left(\xi_i^{[1]} - \widehat{\boldsymbol{\xi}}^{[1]}\right) + \sum_{k=1}^{N} p_{ik}^{[1]}\beta_k, \\ \\ \gamma_{ij} = & \frac{N^2}{2N-1}\left(\xi_i^{[1]}\xi_j^{[2]} - \widehat{\boldsymbol{\xi}}^{[1]}\widehat{\boldsymbol{\xi}}^{[2]}\right) + \frac{1}{2N-1}\sum_{k_1,k_2=1}^{N} p_{ik_1}^{[1]} p_{jk_2}^{[2]}\gamma_{k_1k_2} \\ & +\frac{N-1}{2N-1}\sum_{k_1=1}^{N} p_{ik_1}^{[1]}\gamma_{k_1j} + \frac{N-1}{2N-1}\sum_{k_2=1}^{N} p_{jk_2}^{[2]}\gamma_{ik_2}, \end{cases} \tag{3}$$

together with the additional constraints $\sum_{i=1}^{N} \pi_i^{[1]}\beta_i = 0$ and $\sum_{i=1}^{N} \pi_i^{[1]}\gamma_i = 0$.

Using these quantities, we let $\theta_n = \sum_{i,j=1}^{N} \pi_i^{[1]} \left(p^{[1]}\right)_{ij}^{(n)} \beta_{ij}$, which means the probability that both the starting and the ending nodes of an n-step random walk in layer one are cooperators, where the starting node i is selected based on the reproductive value, $\pi_i^{[1]}$. Analogously, for the inter-layer random walk defined previously, we let $\phi_{n,m} = \sum_{i,j=1}^{N} \pi_i^{[1]} \left(p^{[1,2]}\right)_{ij}^{(n,m)} \gamma_{ij}$. This quantity represents the probability that the beginning of the walk in layer one and the end of the walk in layer two both correspond to cooperators. Substituting θ_n and $\phi_{n,m}$ into equation (2) then gives the condition for selection to favor cooperation. In Supporting Information, we give examples illustrating how one can use network symmetry to obtain explicit expressions for these quantities in simple multilayer populations. For general multilayer networks, we also provide code for determining θ, ϕ, and evaluating equation (2).

Rule for evolutionary dynamics in a two-layer ring network We now consider an example on a two-layer ring network, where *(i)* in each layer, a node is connected to two other nodes; and *(ii)* node i is connected to j in layer one if and only if i's associated node is connected to j's associated node in layer two (see Fig. 3A). We study the initial strategy configuration of a single mutant cooperator in each layer. Let d be the shortest distance between these two cooperator nodes. That is, if i is a cooperator in layer one and j is a cooperator in layer two, then d is the length of the shortest path from i to j on the ring. When a node in layer one and its associated node in layer two are cooperators, $d = 0$. The configuration shown in Fig. 3A is an example with $d = 1$.

We find that cooperation is favored in the two-layer ring network only if equation (2) holds, where $\theta_1 = -\left(N-1\right)/2$, $\theta_2 = -\left(N-2\right)/2$, $\theta_3 = -3\left(N-2\right)/4$,

$$\phi_{0,1} = -\sum_{\ell=1}^{N-1} \frac{\cos\frac{2\pi\ell d}{N}}{2N-1+\cos\frac{2\pi\ell}{N}}, \tag{4}$$

$$\phi_{2,0} = \begin{cases} -2\left(N-1\right)\phi_{0,1} - N + 1 & d = 0, \\ \\ -2\left(N-1\right)\phi_{0,1} + 1 & d \geqslant 1, \end{cases} \tag{5}$$

and

$$\phi_{2,1} = \begin{cases} \left(4N^2-6N+3\right)\phi_{0,1} + 2N^2 - 4N + 3 & d = 0, \\ \\ \left(4N^2-6N+3\right)\phi_{0,1} - \frac{5}{2}N + 3 & d = 1, \\ \\ \left(4N^2-6N+3\right)\phi_{0,1} - 2N + 3 & d \geqslant 2. \end{cases} \tag{6}$$

Small multilayer populations When mutant appearance is stochastic, the average fixation probability is used to measure which spatial structure facilitates cooperation. For example, many prior studies have relied on the assumption that a mutant cooperator appears in every node with the equal probability. By averaging over all initial locations with respect to a fixed mutant-appearance distribution, the remaining variables are population structure and the update rule. In addition to these two components, we also consider a more fine-grained approach that takes into account the mutants' initial positions within the population. In other words, we study the effects of spatial structure, update rule, and the initial strategy configuration on evolutionary dynamics[26,46].

We call the combination of a population structure and a mutant configuration a "profile." In a single-layer network, two profiles G and H are isomorphic if there is a bijection $f : V(G) \to V(H)$ between the node sets of G and H such that *(i)* any two nodes i and j of G are adjacent if and only if $f(i)$ and $f(j)$ are adjacent in H; and *(ii)* strategies of any node u of G and $f(u)$ of H are identical. Otherwise, the two profiles are non-isomorphic.

Similarly, a pair of two-layer profiles G and H are isomorphic if there is a bijection $f : V(G) \to V(H)$ between the node sets of G and H such that *(i)* in each layer, any two nodes i and j of G are adjacent if and only if in the same layer $f(i)$ and $f(j)$ of H are adjacent ; and *(ii)* in each layer, the state of any node u of G and $f(u)$ of H are identical. Otherwise, the two profiles are non-isomorphic. Table SI.1 shows the number of non-isomorphic single-layer and non-isomorphic two-layer profiles for networks of size $N = 3, 4, 5, 6$. Note that the total number of non-isomorphic profiles is far greater for two-layer networks than single-layer ones. For example, for $N = 3$ there are 26 non-isomorphic two-layer profiles compared to 3 such single-layer profiles; and for $N = 6$ there are $36,394,472$ non-isomorphic two-layer profiles compared to 407 such single-layer profiles.

We analyze all non-isomorphic single-layer profiles for $N = 3, 4, 5, 6$ to obtain the proportion of profiles in which cooperation can be favored for some $b_1/c > 0$ (blue bars in Fig. 6). When randomly choosing two single-layer profiles, there are $407 \times 407 = 165,649$ combinations. We take one as layer one and another as layer two. Since there are many ways for a node in layer one to correspond to a node in layer two (i.e. a multilayer "superposition"), each combination can actually produce many two-layer non-isomorphic profiles. Assuming that such a combination generates X two-layer non-isomorphic profiles, and of them Y profiles make cooperation favored for some positive b_1/c and b_2/c, we say coupling such two single-layer profiles makes cooperation favored with probability Y/X. Analyzing all such combinations, we obtain the proportion of couplings of a single-layer profile to a random single-layer profile that favor cooperation in both layers (see red bar in Fig. 6).

References

1. Darwin, C. *On the Origin of Species, 1859* (John Murray, London, UK, 2004).

2. Block, P. *et al.* Social network-based distancing strategies to flatten the COVID-19 curve in a post-lockdown world. *Nature Human Behaviour* **4**, 588–596 (2020).

3. López, L. & Rodó, X. The end of social confinement and COVID-19 re-emergence risk. *Nature Human Behaviour* **4**, 746–755 (2020).

4. Jacquet, J. *et al.* Intra- and intergenerational discounting in the climate game. *Nature Climate Change* **3**, 1025–1028 (2013).

5. Keohane, R. O. & Victor, D. G. Cooperation and discord in global climate policy. *Nature Climate Change* **6**, 570–575 (2016).

6. Hamilton, W. D. The Evolution of Altruistic Behavior. *The American Naturalist* (1963).

7. Trivers, R. L. The Evolution of Reciprocal Altruism. *The Quarterly Review of Biology* (1971).

8. Nowak, M. A. Five Rules for the Evolution of Cooperation. *Science* **314**, 1560–1563 (2006).

9. Nowak, M. A. & May, R. M. Evolutionary games and spatial chaos. *Nature* **359**, 826–829 (1992).

10. Lieberman, E., Hauert, C. & Howak, M. A. Evolutionary dynamics on graphs. *Nature* **433**, 312–316 (2005).

11. Tarnita, C. E., Ohtsuki, H., Antal, T., Fu, F. & Nowak, M. A. Strategy selection in structured populations. *Journal of Theoretical Biology* **259**, 570–581 (2009).

12. Tarnita, C. E., Antal, T., Ohtsuki, H. & Nowak, M. A. Evolutionary dynamics in set structured populations. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 8601–8604 (2009).

13. Chen, Y. T. Sharp benefit-to-cost rules for the evolution of cooperation on regular graphs. *Annals of Applied Probability* **23**, 637–664 (2013).

14. Débarre, F., Hauert, C. & Doebeli, M. Social evolution in structured populations. *Nature Communications* **5**, 3409 (2014).

15. Allen, B. & Nowak, M. Games on graphs. *EMS Surveys in Mathematical Sciences* **1**, 113–151 (2014).

16. Su, Q., Li, A., Wang, L. & Stanley, H. E. Spatial reciprocity in the evolution of cooperation. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20190041 (2019).

17. Li, A. *et al.* Evolution of cooperation on temporal networks. *Nature Communications* (2020).

18. Santos, F. C. & Pacheco, J. M. Scale-free networks provide a unifying framework for the emergence of cooperation. *Physical Review Letters* **95**, 98104 (2005).

19. Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. A. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441**, 502–505 (2006).

20. Hadjichrysanthou, C., Broom, M. & Rychtář, J. Evolutionary Games on Star Graphs Under Various Updating Rules. *Dynamic Games and Applications* **1**, 386–407 (2011).

21. Maciejewski, W., Fu, F. & Hauert, C. Evolutionary Game Dynamics in Populations with Heterogenous Structures. *PLoS Computational Biology* **10**, e1003567 (2014).

22. Rand, D. G., Nowak, M. A., Fowler, J. H. & Christakis, N. A. Static network structure can stabilize human cooperation. *Proceedings of the National academy of Sciences of the United States of America* **111**, 17093–17098 (2014).

23. Allen, B. *et al.* Evolutionary dynamics on any population structure. *Nature* **544**, 227–230 (2017).

24. Allen, B. & McAvoy, A. A mathematical formalism for natural selection with arbitrary spatial and genetic structure. *Journal of Mathematical Biology* **78**, 1147–1210 (2019).

25. McAvoy, A., Allen, B. & Nowak, M. A. Social goods dilemmas in heterogeneous societies. *Nature Human Behaviour* **4**, 819–831 (2020).

26. McAvoy, A. & Allen, B. Fixation probabilities in evolutionary dynamics under weak selection. *arXiv* **1908.03827** (2019).

27. Fotouhi, B., Momeni, N., Allen, B. & Nowak, M. A. Conjoining uncooperative societies facilitates evolution of cooperation. *Nature Human Behaviour* **2**, 492–499 (2018).

28. Matteo, M., Barbora, M. & Luca, R. Combinatorial Analysis of Multiple Networks. *arXiv* **1303.4986** (2013).

29. Heath, A. Strategy and Transaction in an African Factory. *Sociology* (1974).

30. Krackhardt, D. Cognitive social structures. *Social Networks* (1987).

31. Emmanuel, L. *The Collegial Phenomenon: The Social Mechanisms of Cooperation Among Peers in a Corporate Law Partnership* (Oxford University Press, 2001).

32. Padgett, J. F. & Ansell, C. K. Robust Action and the Rise of the Medici, 1400-1434. *American Journal of Sociology* **98**, 1259–1319 (1993).

33. Kivelä, M. *et al.* Multilayer networks. *Journal of Complex Networks* **2**, 203–271 (2014).

34. Boccaletti, S. *et al.* The structure and dynamics of multilayer networks. *Physics Reports* **544**, 1–122 (2014).

35. Wang, Z., Szolnoki, A. & Perc, M. Evolution of public cooperation on interdependent networks: The impact of biased utility functions. *Europhysics Letters* **97**, 48001 (2012).

36. Wang, Z., Wang, L., Szolnoki, A. & Perc, M. Evolutionary games on multilayer networks: a colloquium. *European Physical Journal B* **88**, 124 (2015).

37. Nowak, M. A., Sasaki, A., Taylor, C. & Fudenherg, D. Emergence of cooperation and evolutionary stability in finite populations. *Nature* **428**, 646–650 (2004).

38. Wu, B., Altrock, P. M., Wang, L. & Traulsen, A. Universality of weak selection. *Physical Review E* **82**, 46106 (2010).

39. Wu, B., García, J., Hauert, C. & Traulsen, A. Extrapolating Weak Selection in Evolutionary Games. *PLoS Computational Biology* (2013).

40. Erdős, P. & Rényi, A. On the evolution of random graphs. *The Structure and Dynamics of Networks* **9781400841**, 38–82 (2011).

41. Goh, K. I., Kahng, B. & Kim, D. Universal Behavior of Load Distribution in Scale-Free Networks. *Physical Review Letters* **87**, 278701–278701–4 (2001).

42. Taylor, P. D., Day, T. & Wild, G. Evolution of cooperation in a finite homogeneous graph. *Nature* **447**, 469–472 (2007).

43. Traulsen, A., Pacheco, J. M. & Nowak, M. A. Pairwise comparison and selection temperature in evolutionary game dynamics. *Journal of Theoretical Biology* **246**, 522–529 (2007).

44. Allen, B., Lippner, G. & Nowak, M. A. Evolutionary games on isothermal graphs. *Nature Communications* **10** (2019).

45. Su, Q., McAvoy, A., Wang, L. & Nowak, M. A. Evolutionary dynamics with game transitions. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 25398–25404 (2019).

46. Chen, Y. T., McAvoy, A. & Nowak, M. A. Fixation Probabilities for Any Configuration of Two Strategies on Regular Graphs. *Scientific Reports* **6**, 39181 (2016).

47. Taylor, P. D. Allele-Frequency Change in a Class-Structured Population. *The American Naturalist* **135**, 95–106 (1990).

48. Maciejewski, W. Reproductive value in graph-structured populations. *Journal of Theoretical Biology* (2014).

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Author contributions.

Q.S. and A.M. conceived the project and derived analytical results; Q.S. performed numerical calculations; Q.S., A.M., Y.M. and J.B.P. analyzed the data; Q.S., A.M. and J.B.P. wrote the main text; Q.S. and A.M. wrote the supplementary information.

Competing Interests. The authors declare no competing interests.

Figures

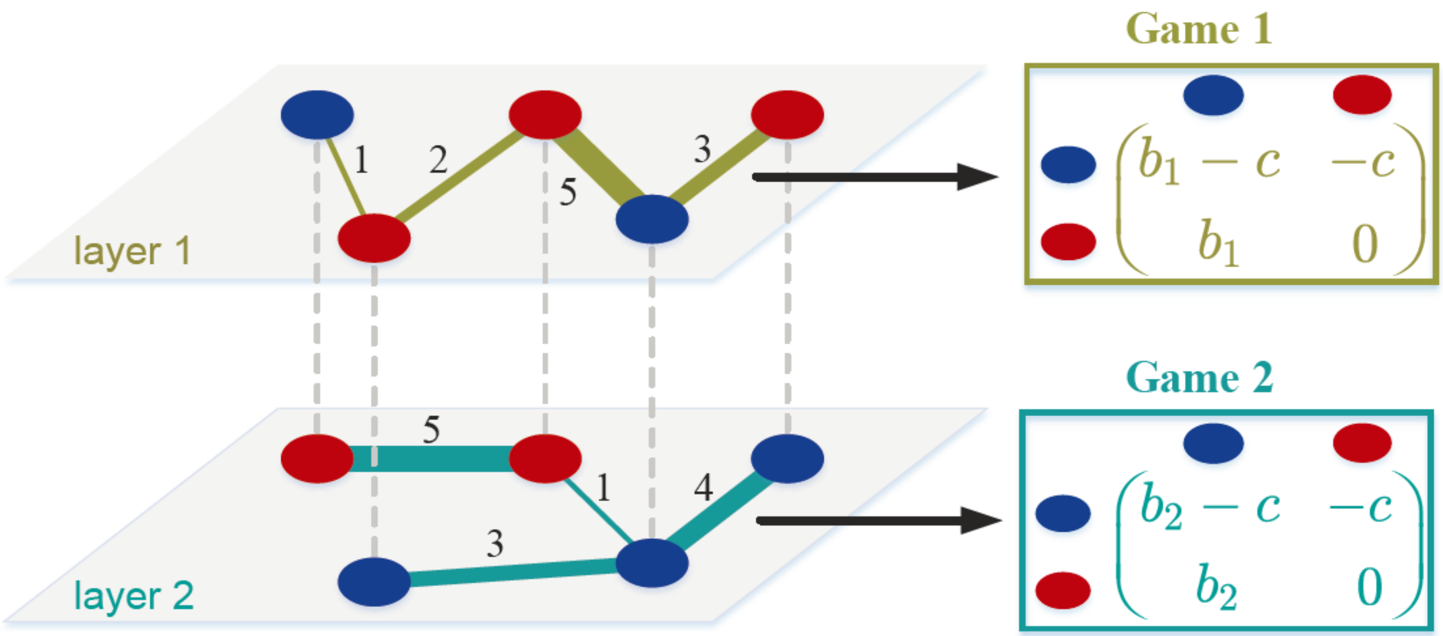


Figure 1

Evolutionary games in multilayer populations. A population with two domains of social interaction is described by a two-layer network, with edge weights wi[j1] in layer one and wi[j2] in layer two (see numbers next to edges for this example). Each player occupies a node in layer one and an associated node in layer two, as indicated by dashed lines. Each player adopts a (possibly different) strategy in each layer, such as cooperation (blue) or defection (red). In each successive time step, each player i plays game one with all her neighbors in layer one and derives an average payoff ui[1] in layer one; the player also plays game two with all her neighbors in layer two and obtains average payoff ui[2]. Player i's total payoff is the sum across layers, ui = ui[1] + ui[2], which determines her reproductive rate, fi = exp (δui). After all social interactions occur, a random player i is selected to update her strategy in layer one by copying that of a random neighbor j with probability proportional to j's total fitness wi[j1] fj (i.e. preferential copying of successful individuals). At the same time, a (possibly different) player k updates his strategy in layer two, by copying that of a random neighbor h proportional to w[k2h] fh. We focus our analysis on donation games, in which each player chooses whether to pay a cost (c) to provide a benefit to her neighbor. The benefit may be different in layer one (b1) than in layer two (b2).

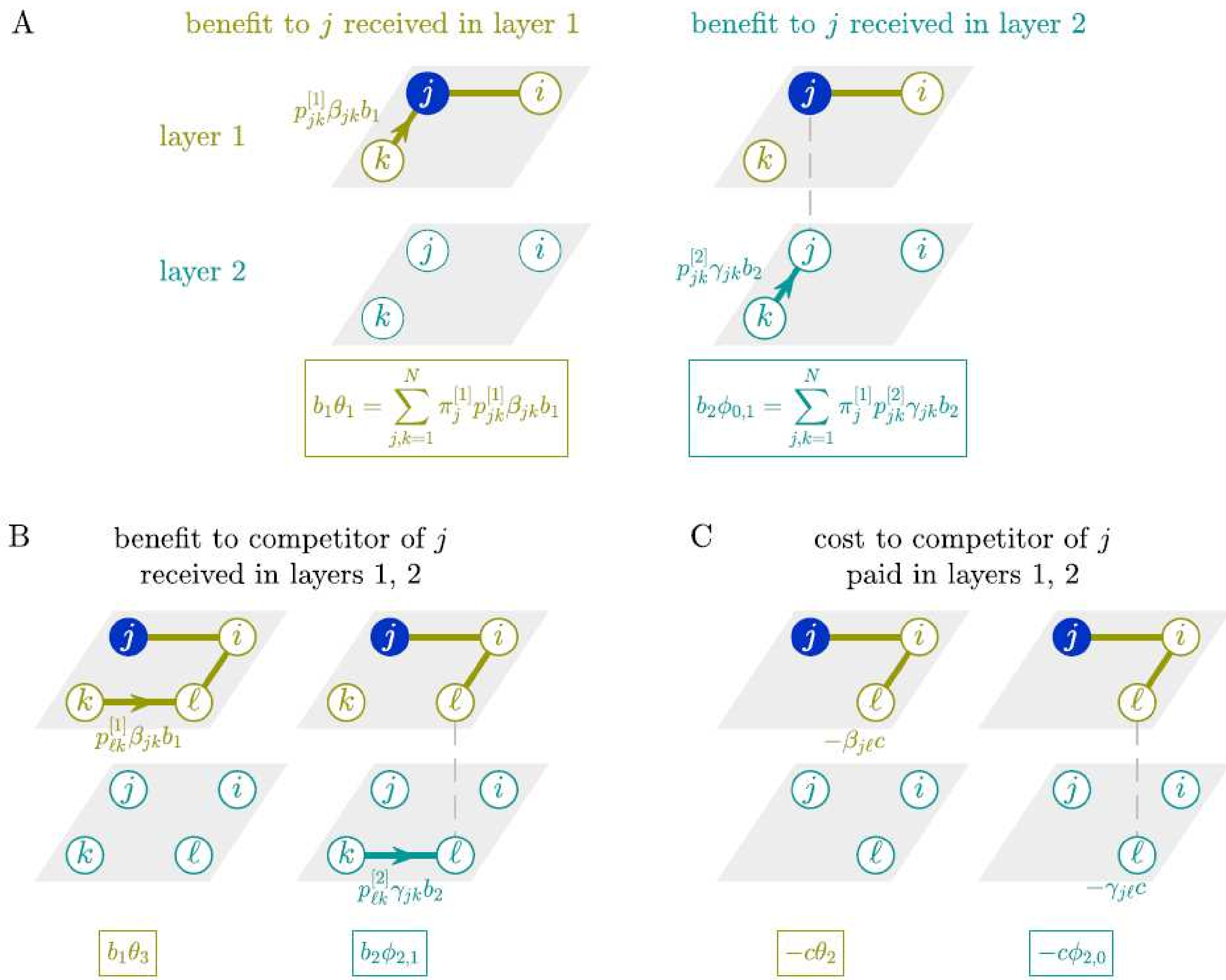


Figure 2

General rule for the evolution of cooperation in multilayer populations. We consider what happens when individual i is chosen to update her strategy in layer one, and her neighbors compete to have their strategy copied. Cooperation will be selectively favored in layer one if a cooperative neighbor, node j, has greater expected payoff than a random neighbor, node l. Node j receives an average benefit b1θ1 from its own one-step neighbors in layer one (panel A, left). Node j also receives an average benefit b2φ0,1 from its own one-step neighbors in layer two (panel A, right). The expression for θ1 (respectively φ0,1) accounts for the probability p[j1k] (p[j2k]) that a random walk moves from node j to k in layer one (layer two); and for the probability βjk (γjk) that node k has the same strategy in layer one (layer two) as node j has in layer one (see also Supporting Information). Node j pays the cost cθ0 as a cooperator in layer one and cφ0,0 in layer two. Node j's net payoff is therefore θ1b1 + φ0,1b2 − (θ0c + φ0,0c). Any competitor of j, such as node l, is also vying to have its strategy copied. Note that in layer one, node ℓ is two steps away from node j. Node l receives an average benefit b1θ3 (respectively b2φ2,1) from its one-step neighbors in layer one (layer two), who are three steps away in layer one (two steps away in layer one and one step away in layer two) from node j, as shown in panel B. Whenever l is a cooperator she pays cost c, leading to an average cost θ2c in layer one and φ2,0c in layer two (panel C). Node l's net payoff is therefore θ3b1 + φ2,1b2 − (θ2 + φ2,0)c. Selection will favor cooperation only if θ1b1 + φ0,1b2 − θ0c − φ0,0c > θ3b1 + φ2,1b2 − (θ2 + φ2,0)c.

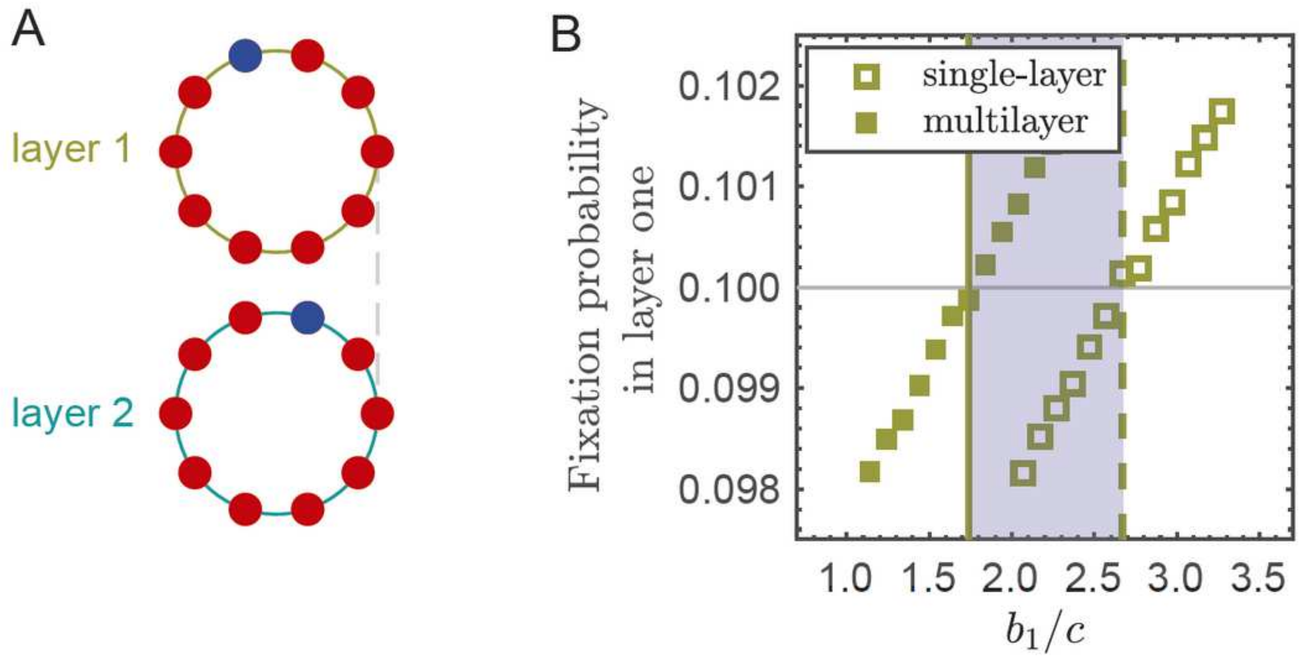


Figure 3

Multilayer games can promote cooperation. (A) We consider a "ring network" in each layer, with each node connected to two neighboring nodes. Nodes that occupy the same position in both layers represent the same individual, as indicated by the dashed line. The initial strategy configuration contains one cooperative individual in layer one (blue) and one cooperative individual in layer two (blue). (B) The probability that cooperation will eventually fix in layer one. We compare two scenarios: when the layers operate independently (open squares) versus when the two layers are coupled (solid squares). Cooperation in layer one is favored by selection if it fixes with a greater probability than in the absence of selection (horizontal line). According to our analytical prediction, cooperation will be favored whenever the benefit-to-cost ratio (b1/c) exceeds a critical value, indicated by the solid vertical line (for coupled layers) and by the dashed vertical line (for independent layers). For the benefit-to-cost ratios indicated in light blue, coupling between layers promotes cooperation in layer one even though it would be disfavored by selection under evolution in layer one alone. Dots indicate results from 107 replicate Monte Carlo simulations. Parameters: b2 = 10, c = 1, and δ = 0.02.

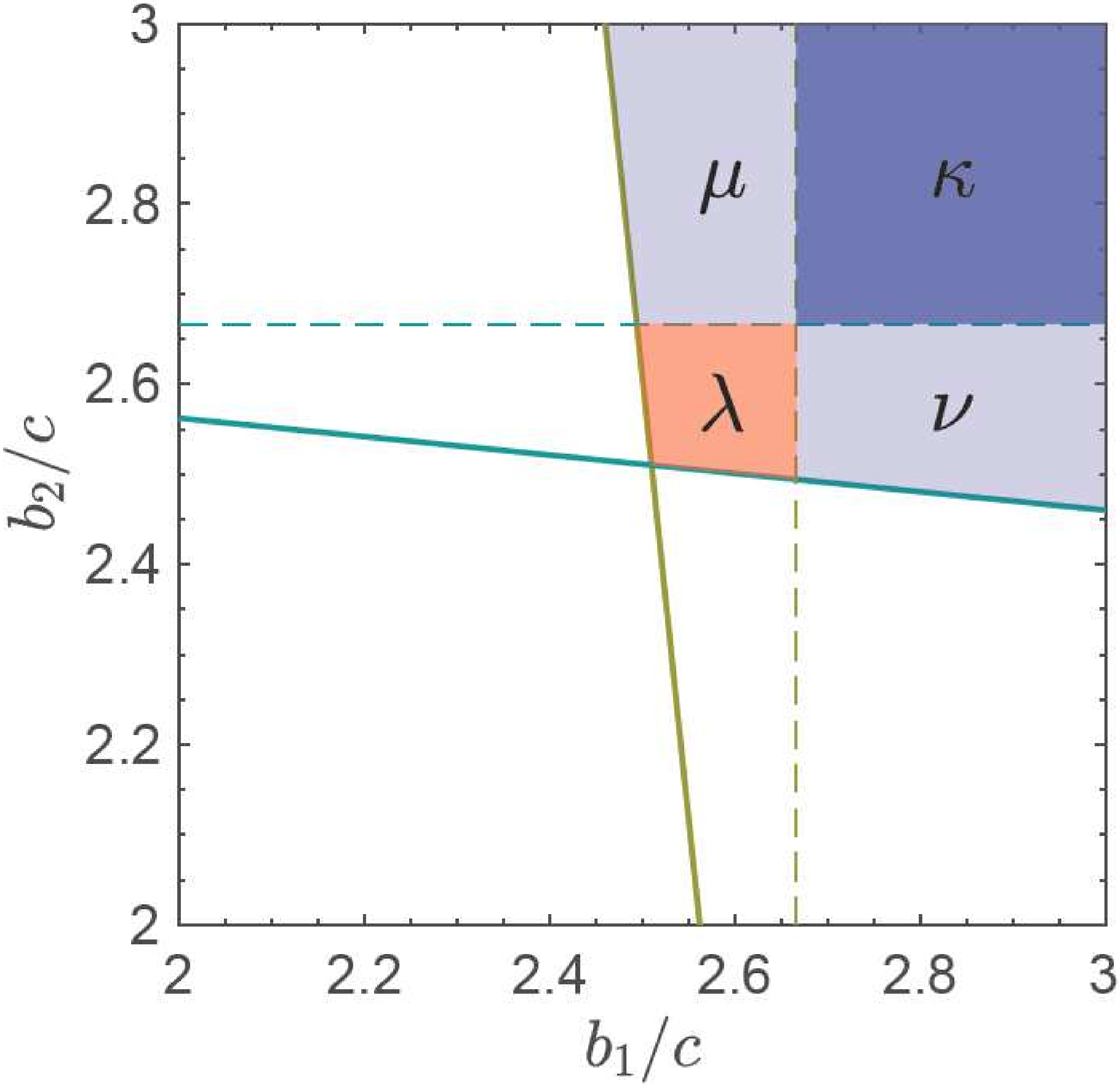


Figure 4

When coupling promotes cooperation. We analyze a two-layer ring network with the initial strategy configuration shown in Fig. 3A. If the population evolves in layer one alone, then cooperation is favored by selection only when b1/c exceeds the olive dashed line. Coupling with layer two facilitates the evolution of cooperation in layer one, decreasing the required benefit-to-cost ratio from the olive dashed line to the olive solid line. If the population evolves in layer two alone, cooperation is favored by selection only when b2/c exceeds the blue dashed line. Coupling with layer one facilitates the evolution of cooperation in layer two, decreasing the required benefit-to-cost ratio to the blue solid line. Without coupling, selection favors cooperation in both layers only in region κ. But coupling extends that region to κμλν. Note that in region λ, cooperation is disfavored in each layer on its own, but it is favored in both layers when they are coupled.

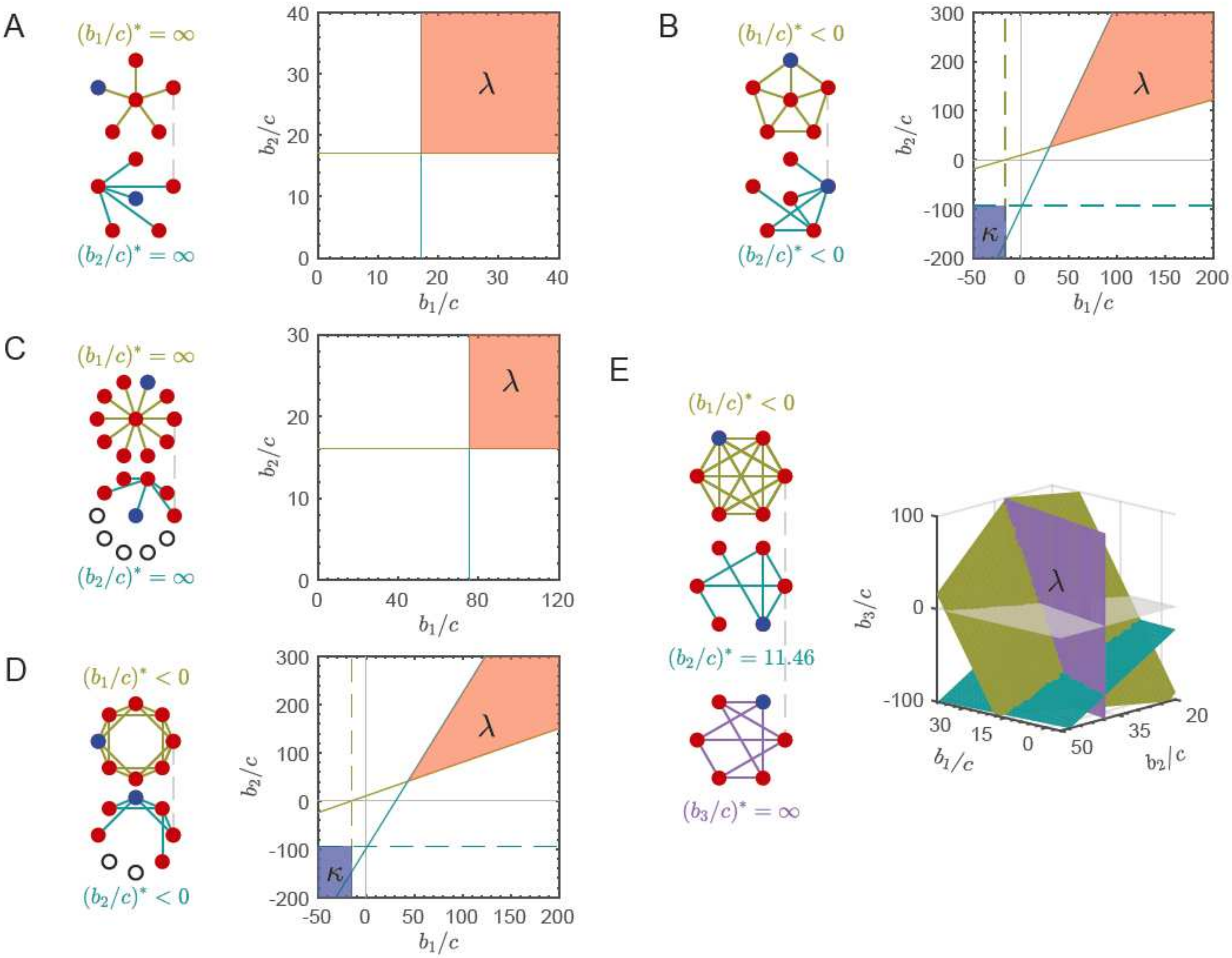


Figure 5

Multilayer coupling can promote cooperation even when cooperation is disfavored in individual layers. We present five representative examples. (A) In each layer alone, the critical benefit-to-cost ratio is infinite, i.e. $(b1/c)^* = (b2/c)^* = \infty$. As a result, cooperation is never favored by selection, regardless of how large the benefit-to-cost ratio is. Nevertheless, when the two layers are coupled, selection then favors cooperation in both layers, provided b1/c and b2/c fall within the region λ. (B) In each layer alone, the critical benefit-to-cost ratio is negative, i.e. $(b1/c)^*$, $(b2/c)^* < 0$. These negative ratios indicate that selection can favor the fixation of spite in each layer alone—so that an individual will pay a cost of $c > 0$ to decrease his partner's payoff. Nevertheless, when the two layers are coupled, selection then favors cooperation in both layers, provided b1/c and b2/c fall within the region λ. Multilayer networks can also rescue cooperation when there are different population sizes in different layers (C, D), or for populations with more than two layers (E). In (C) and (D), open circles indicate absence of a node in that layer.

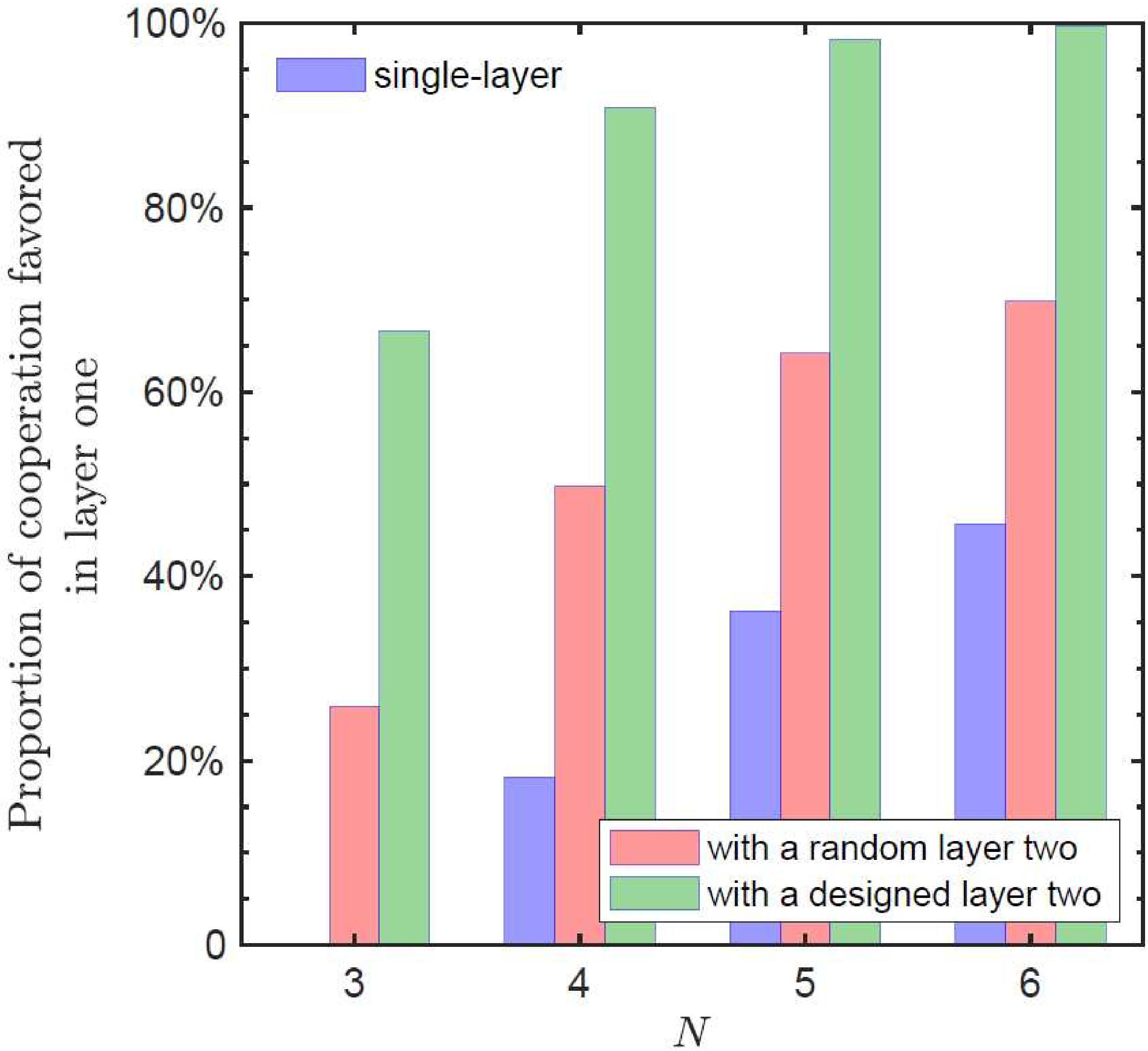
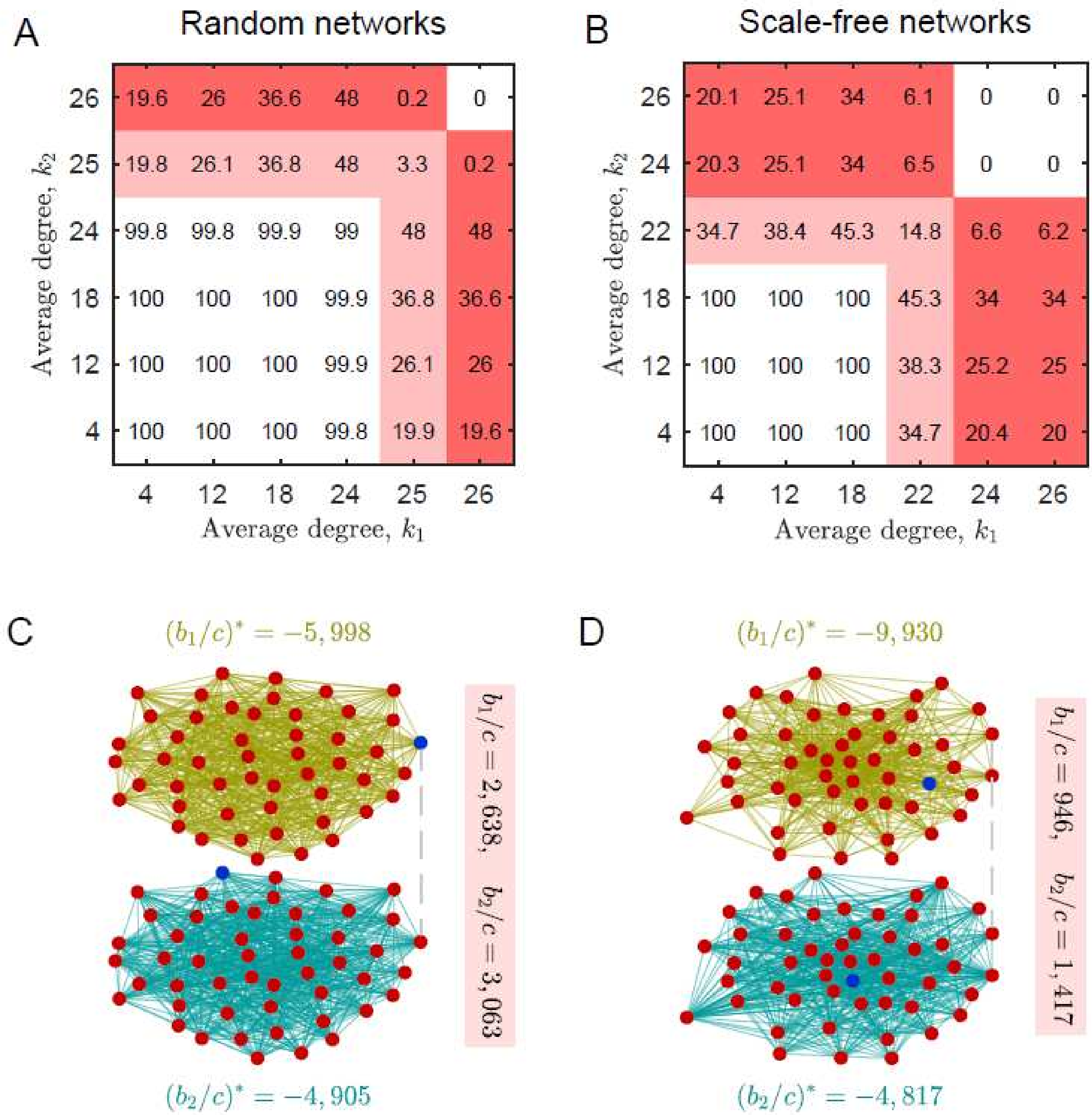


Figure 6

Proportion of small networks that permit the evolution of cooperation. We systematically analyzed all networks of size N = 3, 4, 5, 6, including all initial configurations containing a single cooperator. Blue bars indicate the proportion of single-layer networks and mutant configurations in which selection can favor cooperation in layer one for some benefit-to-cost ratio, i.e. (b1/c) > 0. For N = 3, selection does not favor cooperation for any network and configuration, for any value of b1/c. Coupling layer one with a randomly chosen network and strategy configuration in layer two increases the frequency of selection for cooperation (i.e. selection favors cooperation in layer one for some choice of b1/c > 0 and b2/c > 0, shown in red). Coupling layer one with a deliberately designed network and strategy configuration in layer two further increases the frequency of cooperation in layer one (green). In a majority of these cases, coupling to either a random or a designed network in layer two, selection actually favors cooperation in both layers simultaneously (see SFig. 5).



k_2 \ k_1 (A)	4	12	18	24	25	26
26	19.6	26	36.6	48	0.2	0
25	19.8	26.1	36.8	48	3.3	0.2
24	99.8	99.8	99.9	99	48	48
18	100	100	100	99.9	36.8	36.6
12	100	100	100	99.9	26.1	26
4	100	100	100	99.8	19.9	19.6

k_2 \ k_1 (B)	4	12	18	22	24	26
26	20.1	25.1	34	6.1	0	0
24	20.3	25.1	34	6.5	0	0
22	34.7	38.4	45.3	14.8	6.6	6.2
18	100	100	100	45.3	34	34
12	100	100	100	38.3	25.2	25
4	100	100	100	34.7	20.4	20

Figure 7

Multilayer coupling can catalyze the evolution of cooperation in random and scale-free populations. We sampled 100 two-layer Erd¨os-R´enyi random networks of size N = 50, and 100 two-layer scale-free networks of size N = 50, for each pair of average node degrees, k1 and k2, in layers one and two, respectively. For each two-layer network we analyzed all 2,500 initial configurations consisting of a single mutant cooperator in each layer. (A) The proportion (percentage) of sampled two-layer random networks and initial configurations in which selection can favor cooperation in both layers, for some positive values of b1/c and b2/c. Highlighted entries indicate regimes when coupling increases the frequency of selection for cooperation in both layers compared to independent evolution in each layer. Coupling can have a dramatic effect—e.g. favoring cooperation in both layers for nearly 50% of sampled net-works, compared to virtually never favoring cooperation without coupling (see SFig. 6). For some regimes, coupling permits selection for cooperation in both layers even though one or both layers oppose its selection in the absence of coupling (dark red). (B) The proportion (percentage) of sampled two-layer scale-free networks and initial configurations in which selection can favor cooperation in both layers; highlighted entries indicate regimes when coupling increases the frequency of selection for cooperation in both layers compared to independent evolution in each layer.(C) and (D) Examples of two-layer random and scale-free networks, respectively, in which spite is favored on each layer evolving independently, but cooperation is favored in both layers when coupled.

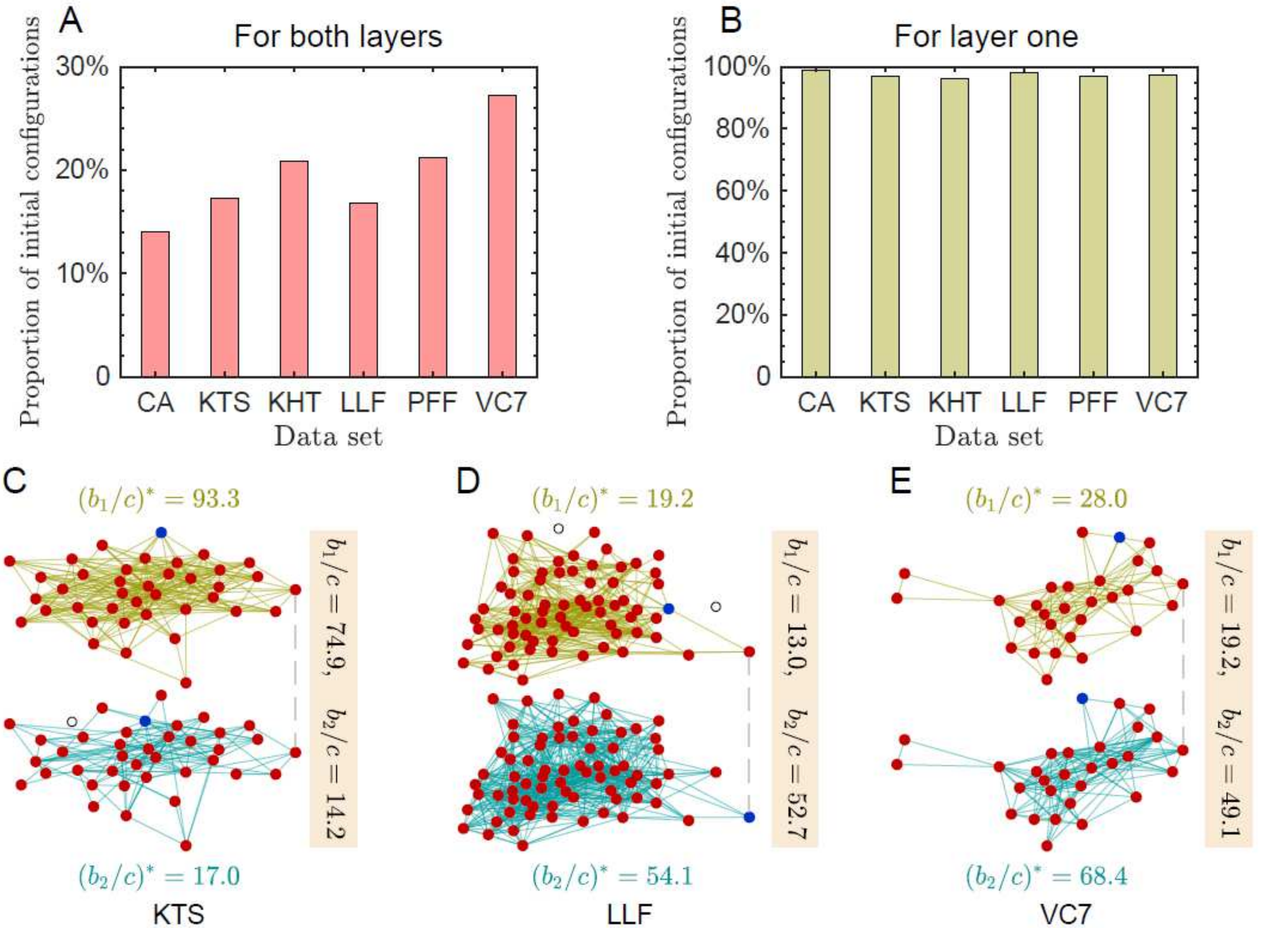


Figure 8

Evolution of cooperation in six real-world two-layer networks. We analyzed networks of online and offline relationships among 61 employees of the Computer Science Department at Aarhus University (CA)[28]; social-emotional and professional relationships among 39 customers surveyed in a Zambian tailor shop (KTS)[29]; friendship and professional relationships among 21 managers at a high-tech company (KHT)[30]; friendship and professional relationships among 71 partners at the Lazega Law Firm (LLF)[31]; marriage and business relationships among 16 families in renaissance Florence (PFF)[32]; and friendship and scholastic relationships among 29 seventh-grade students in Victoria, Australia (VC7). We considered all initial configurations with a single mutant cooperator in each layer, where individuals play the donation game. (A) Proportion of configurations in which coupling layers reduces benefit-to-cost ratios required for cooperation to be favored in both layers, relative to when layers evolve independently. (B) Proportion of initial configurations in which coupling layers reduces the benefit-to-cost ratio required for cooperation to be favored in layer one. (C-E) Three example configurations with a single mutant cooperator (blue) among defectors (red), where open circles indicate isolated individuals. In these examples, selection favors cooperation in each layer alone provided the benefit-to-cost ratio exceeds a critical value, e.g. $(b_1/c)^*$ = 93.3 in KTS layer one. Coupling layers reduces the benefit-to-cost ratio required for cooperation to evolve in one or both layers. For example, when b_1/c = 74.9 and b_2/c = 14.2, selection favors cooperation in both layers of the coupled KTS network.

Supplementary Files

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