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Evolution of prosocial behaviours in multilayer populations

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Human societies include diverse social relationships. Friends, family, business colleagues and online contacts can all contribute to one's social life. Individuals may behave differently in different domains, but success in one domain may engender success in another. Here, we study this problem using multilayer networks to model multiple domains of social interactions, in which individuals experience different environments and may express different behaviours. We provide a mathematical analysis and find that coupling between layers tends to promote prosocial behaviour. Even if prosociality is disfavoured in each layer alone, multilayer coupling can promote its proliferation in all layers simultaneously. We apply this analysis to six real-world multilayer networks, ranging from the socio-emotional and professional relationships in a Zambian community, to the online and offline relationships within an academic university. We discuss the implications of our results, which suggest that small modifications to interactions in one domain may catalyse prosociality in a different domain.

The scale and sophistication of global human societies are due in no small part to cooperation. Altruistic behaviour 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 behaviours 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 infectious diseases[2,3], to efforts to combat climate change[4,5], cooperation is a critical precursor to social prosperity.

At the same time, the emergence and stability of prosocial behaviours 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 tested empirically in laboratory experiments[22]. The latest mathematical results allow for extensive analysis of large families of heterogeneous population structures[23–25] and arbitrary initial configurations of individuals[26]. A large portion of population structures favour 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 or strangers 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 behaviour 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.

Altruistic acts in different domains often involve different costs and benefits, 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 behaviours in distinct domains. These complexities of human social life violate the classic assumptions made in most prior game-theoretic studies of prosocial behaviour, which typically focus on a single domain of interaction or assume that individuals use the same strategy against all opponents[9–21,23–27]. Compared with a growing literature on the dynamics and structural analysis of multiple-domain coupling[33,34], the evolution of prosocial behaviour has received less attention and has been investigated only through numerical simulations in specific cases[35–39]. The general question of how coupling between domains influences behaviour in a population, for an arbitrary number of domains each with arbitrary spatial structure and potentially different pay-offs, remains unresolved and outside the scope of simulations studies[35–39]. Although numerical simulations are useful for rapid exploration within a set of parameters, the notion of 'generalizability', which is important for progress in the social and behavioural sciences[40], demands that theoretical results be established mathematically so that the extent of their generality is known. However, mathematical results on this topic remain absent, so far, 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 a given domain, and players can adopt different behavioural strategies in different domains. An individual's behaviour 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 (that is, 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

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cooperation. If cooperation is disfavoured in each layer alone, or even if layers individually favour 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.

Results

Model. We model a population of N 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 pay-off 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 Supplementary Information section 2.3.2 for analysis of more than two layers). Interactions within layer one occur along weighted edges $w_{ij}^{[1]}$ ($w_{ij}^{[1]} > 0$); and interactions in layer two occur along weighted edges $w_{ij}^{[2]}$ ($w_{ij}^{[2]} > 0$). 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 neighbours 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 neighbours in layer one, and she plays game two with all her neighbours in layer two. Each player i obtains edge-weighted average pay-off $u_i^{[1]}$ in layer one and $u_i^{[2]}$ in layer two, given by

$$u_i^{[1]} = -cs_i^{[1]} + b_1 \sum_{j=1}^{N} p_{ij}^{[1]} s_j^{[1]},$$
$$u_i^{[2]} = -cs_i^{[2]} + b_2 \sum_{j=1}^{N} p_{ij}^{[2]} s_j^{[2]}, \quad (1)$$

where $p_{ij}^{[1]} = w_{ij}^{[1]}/w_i^{[1]}$ and $p_{ij}^{[2]} = w_{ij}^{[2]}/w_i^{[2]}$. Player i's total pay-off is the sum of those obtained in each layer, namely $u_i = u_i^{[1]} + u_i^{[2]}$. The total pay-off across layers determines the rate at which a player's strategy spreads (that is its 'reproductive rate'), $f_i = \exp(\delta u_i)$, where $0 < \delta < 1$ is the intensity of selection[41]. The regimes $\delta \ll 1$ corresponds to weak selection[42,43] 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 analyse other mechanisms such as pairwise-comparison updating, birth–death updating and a mixture of the two (that is, different update rules for different layers; see Supplementary Information section 2.1).

General rule for the evolution of cooperation in multilayer populations. 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; for example, cooperation in layer one and defection in layer two. In general, selection can favour cooperation provided the benefit-to-cost ratio, b/c, is sufficiently large[19]. Here, we analyse how the critical benefit-to-cost ratio to support cooperation in layer one, $(b_1/c)^*$, depends on coupling with a second layer.

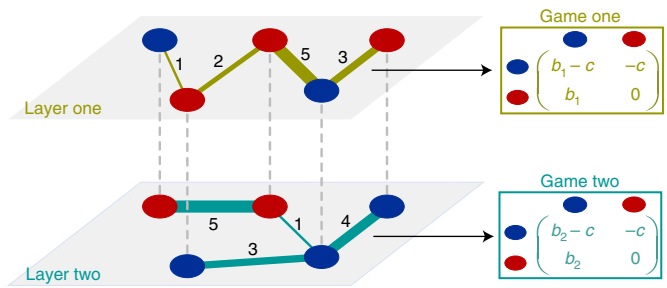

Fig. 1 | Evolutionary games in multilayer populations. A population with two domains of social interaction is described by a two-layer network, with edge weights $w_{ij}^{[1]}$ in layer one and $w_{ij}^{[2]}$ in layer two (see numbers next to edges for this example). Each player occupies a node in layer 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 neighbours in layer one and derives an average pay-off $u_i^{[1]}$ in layer one; the player also plays game two with all her neighbours in layer two and obtains average pay-off $u_i^{[2]}$. Player i's total pay-off 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 neighbour j with probability proportional to j's total fitness $w_{ij}^{[1]} f_j$ (that is 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 neighbour 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 neighbour. The benefit may be different in layer one (b_1) than in layer two (b_2).

Let $\rho_C^{[1]}$ denote the probability that all players eventually cooperate in layer one, starting from some fixed configuration of co-operators and defectors. We use $\left(\rho_C^{[1]}\right)^{\circ}$ to denote this probability under neutral drift, that is when $\delta = 0$. Selection is said to favour 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[10,19,41]. We focus primarily on the probability that cooperation will fix under weak selection, compared to neutral drift. We also compare the fixation probability of cooperation with the fixation probability of defection, and we find qualitatively similar results using this relative measure (Supplementary Information section 1).

To analyse 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 (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 neighbouring nodes in layer one. Similarly, we

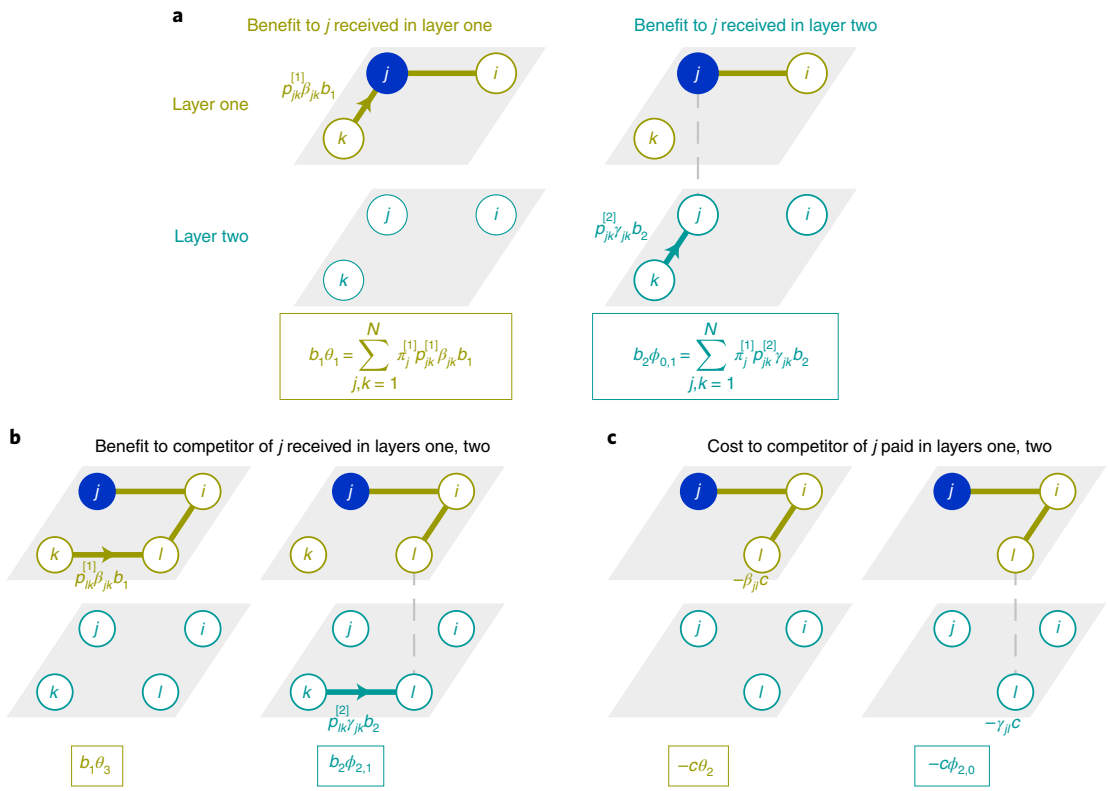

Fig. 2 | General rule for the evolution of cooperation in multilayer populations. a–c, We consider what happens when individual i is chosen to update her strategy in layer one, and her neighbours compete to have their strategy copied. Cooperation will be selectively favoured in layer one if a cooperative neighbour, node j, has greater expected pay-off than a random neighbour, node l. Node j receives an average benefit $b_1\theta_1$ from its own one-step neighbours in layer one (**a**, left). Node j also receives an average benefit $b_2\phi_{0,1}$ from its own one-step neighbours in layer two (**a**, right). The expression for θ_1 (respectively $\phi_{0,1}$) accounts for the probability $p_{jk}^{[1]}$ ($p_{jk}^{[2]}$) 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 is cooperative in layer one (layer two) as node j in layer one (Supplementary Information section 2.1.1). Node j pays the cost $c\theta_0$ as a co-operator in layer one and $c\phi_{0,0}$ in layer two. Node j's net pay-off 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 neighbours 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 (**b**). Whenever ℓ is a co-operator she pays cost c, leading to an average cost $\theta_2 c$ in layer one and $\phi_{2,0} c$ in layer two (**c**). Node l's net pay-off is therefore $\theta_3 b_1 + \phi_{2,1} b_2 - (\theta_2 + \phi_{2,0})c$. Selection will favour cooperation if $\theta_1 b_1 + \phi_{0,1} b_2 - \theta_0 c - \phi_{0,0} c > \theta_3 b_1 + \phi_{2,1} b_2 - (\theta_2 + \phi_{2,0})c$.

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 neighbour in layer two. We can obtain θ_n and $\phi_{n,m}$ by solving systems of $O(N^2)$ linear equations (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 favoured by selection:

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

Informally, this condition states that a cooperative neighbour of a node in layer one must have a higher pay-off than a random neighbour. The four terms on the left side quantify the benefits and costs to a cooperative neighbour, 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 neighbour, 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 favours 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 us to study how multiple domains of social interactions influence the prospects for cooperation, in arbitrary interaction networks. In the following, we focus on unweighted 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 neighbours in each layer. Initially, a single individual in each layer is cooperative, and the co-operator in layer one is connected to the co-operator in layer two (Fig. 3a). When the two layers evolve independently, or in the absence of layer two, cooperation is favoured by selection in layer one 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 pay-offs obtained in that layer, but also on her interactions in the other layer. In this case, the co-operator in layer one is being exploited by two neighbouring defectors, as seen in Fig. 3a, but nonetheless she receives an extra benefit from a cooperative neighbour in layer two, who increases her fitness and promotes the spread of her (cooperative) strategy in layer one (see also Supplementary Fig. 1 for further details).

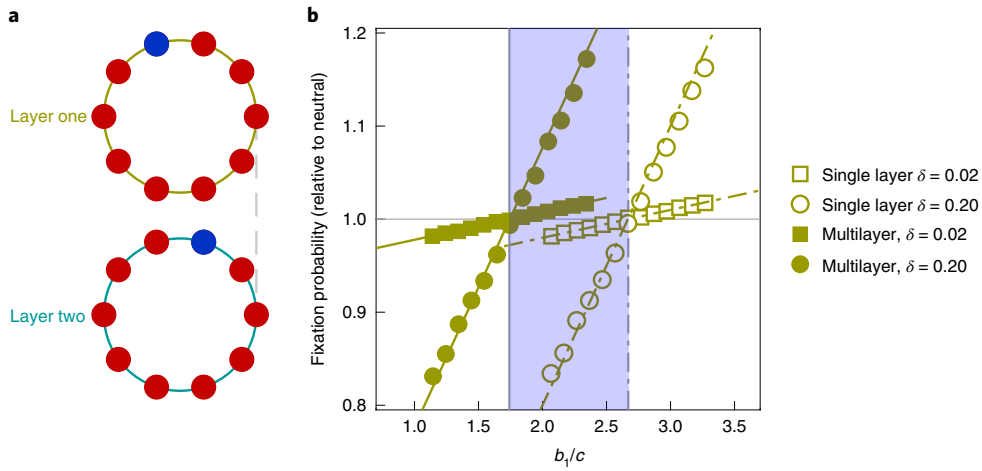

Fig. 3 | Multilayer games can promote cooperation. a, We consider a 'ring network' in each layer, with each node connected to two neighbouring nodes. Nodes that occupy the same position in both layers represent the same individual, as indicated by the dashed line. The initial strategy configuration contains 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, $\rho_C^{[1]}$, relative to the fixation probability under neutral drift, $\left(\rho_C^{[1]}\right)^{\circ}$. We compare two scenarios: when the layers operate independently versus when the two layers are coupled. Cooperation in layer one is favoured by selection if it fixes with a greater probability than in the absence of selection (horizontal line). Squares (for $\delta = 0.02$) and circles (for $\delta = 0.20$) indicate fixation probabilities estimated from 10^7 replicate Monte Carlo simulations, and lines indicate analytical predictions. Our analysis under weak selection predicts that cooperation will be favoured 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 disfavoured by selection under evolution in layer one alone. Parameters: $b_2 = 10$, $c = 1$.

Coupling layers can have a substantial effect on the probability that cooperation will spread and overtake a population, even in regimes where selection disfavours cooperation in the absence of coupling. For the example shown in Fig. 3, when the selection intensity is very small, for example $\delta = 0.02$, the fixation probability of cooperation can be increased by a small amount (3%) relative to the case of independent layers; but when the selection intensity is moderate, such as $\delta = 0.20$, the effect size can be as large as 27.76% (Fig. 3b). Although the absolute increase in fixation probability is always small, for weak selection, it makes sense to quantify the effect size relative to neutrality.

Figure 4 illustrates more generally how multilayer coupling affects evolutionary dynamics in ring networks. When the two layers evolve separately, cooperation is favoured in layer one only if b_1/c exceeds the olive dashed line; cooperation is favoured in layer two only if b_2/c exceeds the blue dashed line. Selection thus favours cooperation in both layers only when b_1/c and b_2/c lie in region κ. Coupling layers moves the benefit-to-cost ratio required for cooperation in layer one to the olive solid line, and it moves the benefit-to-cost ratio required in layer two to the blue solid line—in both cases expanding the parameter range of costs and benefits that favour cooperation. In particular, the region λ reveals the remarkable fact that even if cooperation is disfavoured by selection in each layer alone, cooperation can nonetheless be favoured in both layers simultaneously when they are coupled.

In the two-layer ring network, for any configuration with only one co-operator in layer one and one co-operator in layer two, we have derived a simple formula to calculate the critical benefit-to-cost ratio $(b_1/c)^*$ required to favour cooperation (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 multilayer coupling promotes cooperation (Supplementary Fig. 2).

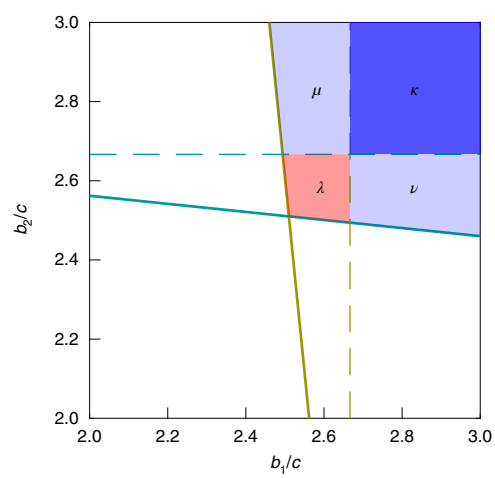

Fig. 4 | When coupling promotes cooperation. We analyse a two-layer ring network with the initial strategy configuration shown in Fig. 3a. If the population evolves in layer one alone, then cooperation is favoured by selection only when b_1/c exceeds the olive dashed line. Coupling with layer two facilitates 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 favoured 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 favours 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 disfavoured in each layer on its own, but it is favoured in both layers when they are coupled.

Coupled heterogeneous networks. For ring networks, cooperation is favoured 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

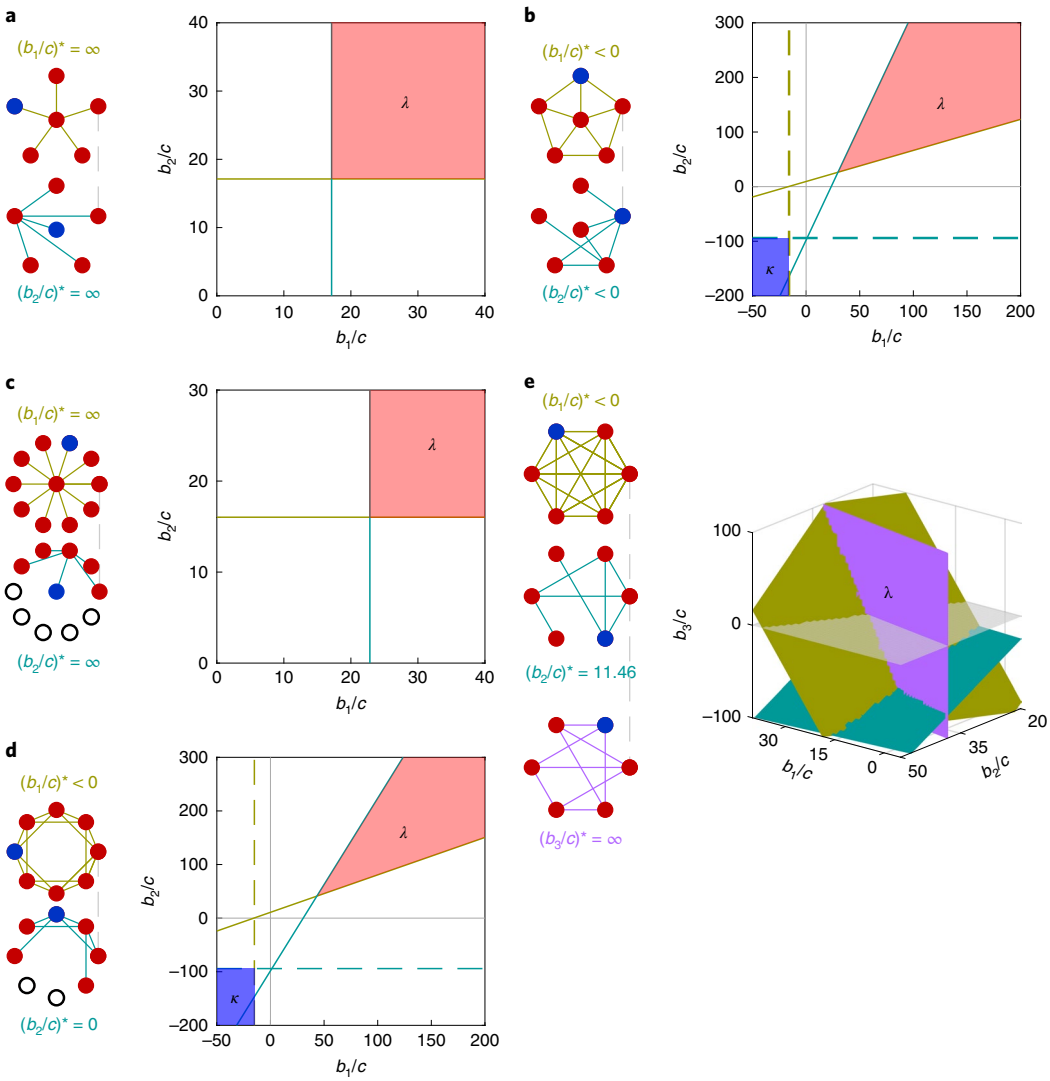

Fig. 5 | Multilayer coupling can promote cooperation even when cooperation is disfavoured in individual layers. We present five representative examples. **a**, In each layer alone, the critical benefit-to-cost ratio is infinite, that is $(b_1/c)^* = (b_2/c)^* = \infty$. As a result, cooperation is never favoured by selection, regardless of how large the benefit-to-cost ratio is. Nevertheless, when the two layers are coupled, selection then favours 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, that is $(b_1/c)^*, (b_2/c)^* < 0$. These negative ratios indicate that selection can favour the fixation of spite in each layer alone—so that an individual will pay a cost of $c > 0$ to *decrease* his partner's pay-off. Nevertheless, when the two layers are coupled, selection then favours cooperation in both layers, provided b_1/c and b_2/c fall within the region λ. **c**–**e**, 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**). Open circles in **c** and **d** indicate the absence of a node in that layer.

which cooperation is never favoured in a social dilemma, no matter how large the 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 favour cooperation (that is $(b_1/c)^* = \infty$). Nonetheless, if we couple two stars in a certain way (Fig. 5a) then selection favours 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 Supplementary Information section 2.2.2 for detailed derivations). The region λ in Fig. 5a depicts the benefit-to-cost ratios that favour 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 favours spite, an antisocial behaviour in which an individual pays a cost to decrease her neighbour's pay-off. But if we couple one wheel network with another, as shown in Fig. 5b, cooperation can be favoured 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 disfavours cooperation in each layer alone.

Our framework also applies to multilayer 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,d)—corresponding, for example, to an individual who forgoes online social networking altogether. Figure 5c,d confirms that in such cases, coupling can still allow cooperation to be favoured in both layers, even if cooperation is disfavoured 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) (Supplementary Information section 2.3.1).

Our framework also applies to multilayer populations with an arbitrary number of layers. Figure 5e illustrates an example of a three-layer population. When the three layers evolve independently, cooperation is favoured neither in layer one ($(b_1/c)^* < 0$) nor in layer three ($(b_3/c)^* = \infty$). Coupling the three layers allows selection to favour 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 favoured in layer one and layer three, but it also reduces the value of b_2/c required for cooperation to be favoured in layer two. In Supplementary Information section 2.3.2, we derive the general condition for selection to favour cooperation on population structures with an arbitrary number of layers. Although coupling of layers can provide more opportunities for the evolution of cooperation, some choices of benefits and costs in layers may lead to negative effects. In the example shown in Fig. 5e, if b_1/c and b_3/c are selected beyond the region λ, then coupling domains may increase the critical benefit-to-cost ratio $(b_2/c)^*$, making it harder for cooperation to evolve in layer two.

Small multilayer populations. To study behavioural dynamics across a variety of structures, we systematically analysed all two-layer networks of size $N=3$, 4, 5 and 6, and all initial configurations of a single co-operator in each layer (see Methods for details). We first report the proportion of single-layer networks and strategy configurations in which cooperation can be favoured in layer one alone for some choice of benefit-to-cost ratio (that is, $(b_1/c)^* > 0$, blue bars in Fig. 6). Coupling layer one with a randomly chosen network and strategy configuration in layer two can increase the frequency of structures on which selection favours 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 favours cooperation in both layers simultaneously (Supplementary Fig. 3). Therefore, in a systematic analysis of all small structures, multilayer networks have a 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 behavioural dynamics and surprising effects induced by multilayer coupling. To study behaviour on larger networks, of size $N=50$, we sampled many two-layer Erdös–Rényi (ER) random networks[44] and many two-layer Goh–Kahng–Kim (GKK) networks[45] generated with exponent $\gamma=2.5$. We sampled these networks across a diverse range of average node degrees in layer one and in layer two (Fig. 7a). The two classes of networks differ in their node degree distribution. For example, for average degree 4, the maximum node degree is 10 in ER random networks and up to 28 in GKK networks we study. In each two-layer network we placed a single mutant co-operator in each layer and analysed all $50\times50=2{,}500$ initial strategy configurations. Figure 7a,b reports the frequency of structures for which selection can favour 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 (Supplementary Fig. 4), we find that coupling two layers is broadly conducive to cooperation, as shown in the highlighted area in Fig. 7a,b. In particular, in the random networks with average degree >26, cooperation is never favoured for any benefit-to-cost ratio, whereas coupling such networks to a random network in layer two can often rescue cooperation (dark red area in Fig. 7a). Figure 7c,d shows examples of random two-layer networks that favour the evolution of spite on each layer alone, but that can favour cooperation on both layers when coupled (see also Supplementary Figs. 5 and 6 for further analysis and examples).

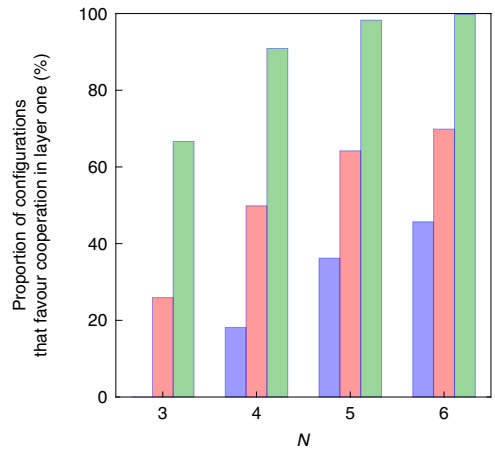

Fig. 6 | Proportion of small networks that permit the evolution of cooperation. We systematically analysed all networks of size $N=3$, 4, 5 and 6, including all initial configurations containing a single co-operator. Blue bars indicate the proportion of single-layer networks and mutant configurations in which selection can favour cooperation in layer one for some benefit-to-cost ratio, that is $(b_1/c)^* > 0$. For $N=3$, selection does not favour 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 (that is, selection favours 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 (shown in green). In a majority of these cases, coupling to either a random or a designed network in layer two, selection actually favours cooperation in both layers simultaneously (Supplementary Fig. 5).

We also investigated larger networks, with size up to $N=300$ and average degree $\bar{k}_1=\bar{k}_2=4$, generated by the Goh–Kahng–Kim algorithm with exponent $\gamma=2.5$ and, alternatively, by the Barabási–Albert algorithm[46]. These networks exhibit broad distributions of node degree (Supplementary Fig. 7). For each two-layer network, we randomly sampled 500 initial strategy configurations. Among the GKK networks, in 99.23% of cases coupling layers decreases the benefit-to-cost ratio required for cooperation in layer one; furthermore, in 10.15% of cases, coupling promotes cooperation in both layers simultaneously. Among the Barabási–Albert networks, in 99.26% of cases coupling layers decreases the benefit-to-cost ratio required for cooperation in layer one; and in 11.24% of cases, coupling promotes cooperation in both layers simultaneously.

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 $N=71$ (see Supplementary Information section 2.4 for details of network description and analysis). We analysed the prospects for cooperation when individuals play donation games in each layer, including all initial configurations with a single co-operator in each layer. In all of these empirical networks, even if two layers evolve separately, cooperation can be favoured 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

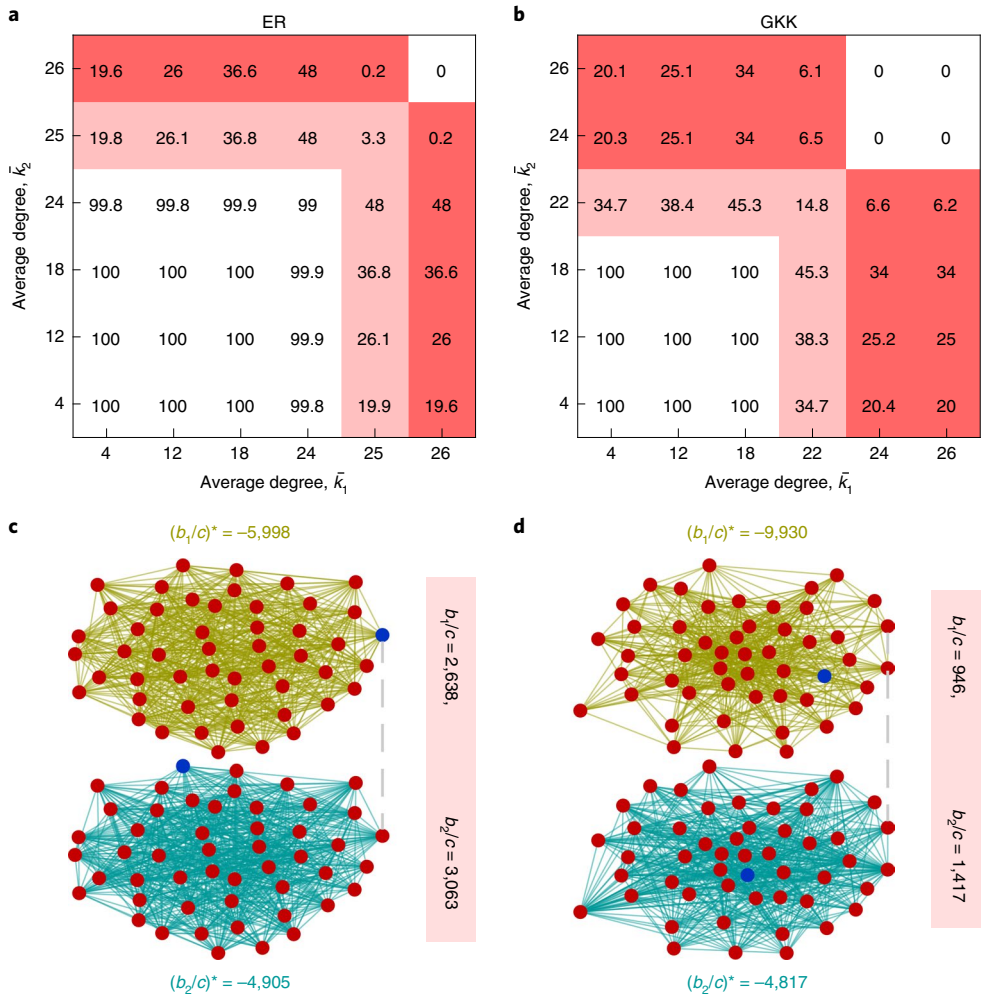

Fig. 7 | Multilayer coupling can catalyse the evolution of cooperation in random networks. We sampled 100 two-layer ER random networks of size $N=50$, and 100 two-layer GKK networks generated by the Goh–Kahng–Kim algorithm[45] of size $N=50$, for each pair of average node degrees, $\bar{k}_1$ and $\bar{k}_2$, in layers one and two, respectively. For each two-layer network we analysed all 2,500 initial configurations consisting of a single mutant co-operator in each layer. **a**, The proportion (percentage) of sampled two-layer ER networks and initial configurations in which selection can favour 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 with independent evolution in each layer. Coupling can have a dramatic effect—for example, favouring cooperation in both layers for nearly 50% of sampled networks, compared with virtually never favouring cooperation without coupling (Supplementary Fig. 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 GKK networks and initial configurations in which selection can favour cooperation in both layers; highlighted entries indicate regimes when coupling increases the frequency of selection for cooperation in both layers compared with independent evolution in each layer. **c**,**d**, Examples of two-layer ER (**c**) and GKK (**d**) networks in which spite is favoured on each layer evolving independently, but cooperation is favoured in both layers when coupled.

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 favour prosocial behaviour.

In practice, the behavioural outcome in one layer may be more important than in another layer, such as when more individuals interact 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 analysed to what degree the benefit-to-cost ratio for cooperation to be favoured 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 disfavoured 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).

The effect size of one layer on another can be substantial. In the case of the empirical networks of social and professional interactions in a Zambian tailor shop, for example, if interactions occur in a single layer (social interactions only), then the benefit-to-cost ratio required for cooperation to spread is unreasonably large: $(b_1/c)^* = 93.3$. And yet, when behaviour is coupled with professional interactions, by setting $b_2/c=30$ the benefit-to-cost ratio to favour cooperation in social interactions is dramatically reduced to $(b_1/c)=53.6$; at the same time, the fixation probability of cooperation in that layer is increased by 135.2% relative to neutrality (for selection intensity $\delta=0.2$), which is a measure of the effect size of coupling.

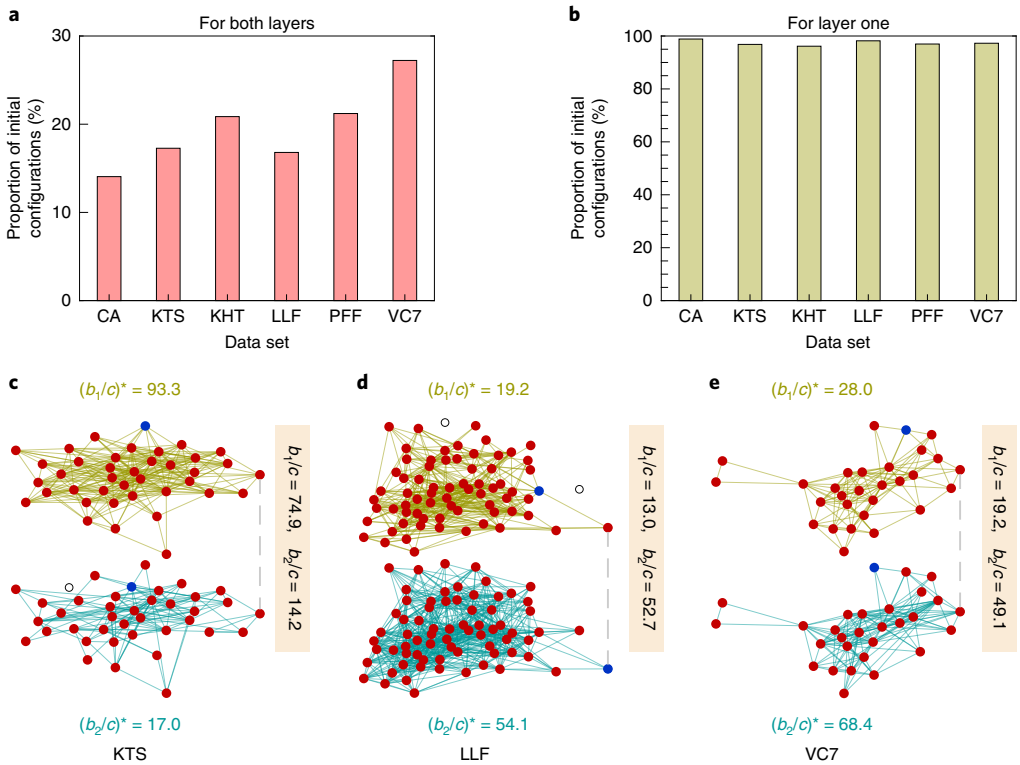

Fig. 8 | Evolution of cooperation in six real-world two-layer networks. We analysed networks of online and offline relationships among 61 employees of the computer science department at Aarhus University (CA)[28]; social–emotional and professional relationships among 39 customers surveyed in a Zambian 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 co-operator 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 favoured 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 favoured in layer one. **c**–**e**, Three example configurations, KTS (**c**), LLF (**d**) and VC7 (**e**), with a single mutant co-operator (blue) among defectors (red), where open circles indicate isolated individuals. In these examples, selection favours cooperation in each layer alone provided the benefit-to-cost ratio exceeds a critical value, for example $(b_1/c)^* = 93.3$ 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 favours cooperation in both layers of the coupled KTS network.

Remarkably, the critical benefit-to-cost ratio in layer one can sometimes be reduced to zero by coupling to a second layer (Supplementary Fig. 8), which indicates that cooperation can be favoured 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 co-operators 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 co-operators, one in each layer, the more likely that coupling can catalyse cooperation in layer one even without providing any immediate layer-one benefit (Supplementary Fig. 9). Aside from analysing six empirical networks, we also illustrate this phenomenon in two-layer random networks with different degree distributions (Supplementary Figs. 10 and 11). So far, we have assumed that individuals in each layer use averaged (edge-weighted) pay-offs. We find similar, cooperation-promoting effects of coupling layers when pay-offs are accumulated across interactions (Supplementary Information section 2.1.7).

Discussion

One of the many complexities of human societies is the structure of social interactions. Structure is not confined to a single type of interaction, but includes the distinct domains of relationships in which humans interact. This feature would not complicate the problem of understanding behaviour 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 behaviour in societies.

We have modelled the evolution of prosocial behaviours across domains using multilayer networks, where each individual uses separate strategies and plays distinct games in different layers. An individual's total pay-off across domains determines his or her influence over peers. We find that the threshold for selection to favour 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 disfavoured in each layer alone. And so the prospects for cooperation are fundamentally changed when social interactions occur in distinct, but coupled, domains.

Our work has several potential implications for the evolution of prosocial behaviour. The first noteworthy implication is that

coupling between layers can often facilitate cooperation by proper coordination of the benefit-to-cost ratios between the two layers (equation (2)). In practice, the benefit-to-cost ratio required for cooperation to spread in a single-layer network may be unreasonably large, as exemplified by the social interaction network measured in a Zambian tailor shop. But when coupled to the layer of professional interactions (layer two), an appropriate choice of the benefit-to-cost ratio in layer two can reduce the ratio required to support cooperation in layer one by as much as 40%, while also increasing the probability that cooperation fixes in layer one by over 130%. More generally, we find that in up to 40% of the two-layer networks we examined, cooperation can be favoured 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 potential implication concerns how interactions may be engineered or modified in one domain to promote cooperation in another, or in both. Indeed, not every multilayer structure is beneficial for cooperation; and even if the structure can favour cooperation, the benefit-to-cost ratio required may be unreasonably large. But it may be possible to slightly modify interactions in one layer to promote cooperation in both layers. Although modifying in-person interactions may be unfeasible, online interactions are often amenable to oversight or control. Although this question is quite deep and difficult for full mathematical analysis, we have analysed it systematically in all two-layer networks of size 6 (Supplementary Fig. 12). In these cases we find that adding or severing a small number of connections in one layer, if chosen properly, can rescue cooperation in both layers (see Supplementary Fig. 12 for intuition). Investigating this question in greater generality is a worthwhile avenue for future study.

Several prior studies have demonstrated that selection cannot favour cooperation in a single-layer structured population under birth–death or pairwise-comparison updating[19,47–49]. More recent studies have found that game transitions[50] and heterogeneous distributions of social goods[25] can catalyse cooperation under these update rules. Here, too, we find that a simple coupling of layers works efficiently to make cooperation favoured by selection under birth–death or pairwise-comparison updating (Supplementary Fig. 13). In practice, there may be considerable cultural differences between social domains, and it is not unreasonable to expect that the mechanisms of imitation and learning differ between layers. The multilayer approach allows for such a mixture of update rules in different layers (Supplementary Information, section 2.1).

Because our aim has been to analyse multilayer populations in a mathematically rigorous manner, our study has several limitations. Because the population structures are fixed as traits evolve, there is an implicit assumption that networks change much more slowly than behaviours. Although this is a common assumption in the literature, it does exclude interesting cases involving dynamic topologies. Our analysis also requires weak selection. Stronger selection can complicate the formal analysis of evolutionary models in structured populations[51], but it is nonetheless an important aspect of natural populations and should be considered in future models of multilayer populations. The method we have employed for weak selection is computationally feasible for populations of moderate size, but calculations become more cumbersome in large populations (at least when allowing for arbitrarily complicated network topologies). Generally, for an L-layer network of size N, the complexity of computing fixation probabilities is bounded by solving a linear system of size $O\left(L^2N^2\right)$. Furthermore, our metric for evolutionary success, fixation probability, is a long-term measure and does not capture the timescale of evolutionary processes as the population sojourns through transient states. Fixation probabilities themselves are relevant only when mutations appear sufficiently infrequently, which may or may not be true–especially in settings of cultural evolution in which 'mutation' is interpreted as 'exploration.' So while our analysis reveals many interesting properties of multilayer populations, there is fertile ground for future theoretical investigations.

Methods

Here, we briefly summarize our theoretical results on weak selection in multilayer populations, and we refer to Supplementary Information section 1 for detailed derivations. We consider a population structure described by a two-layer network of size N, with edge weights $w_{ij}^{[1]}$ in layer one and $w_{ij}^{[2]}$ in layer two. All edges are symmetric, that is $w_{ij}^{[1]} = w_{ji}^{[1]}$ 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[24,52,53], 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 because 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 (respectively two), starting at node i, a one-step walk terminates at node j with probability $p_{ij}^{[1]} = w_{ij}^{[1]}/w_i^{[1]}$ (respectively $p_{ij}^{[2]} = w_{ij}^{[2]}/w_i^{[2]}$). 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 co-operators under neutral drift. Similarly, let γ_{ij} be the probability that both nodes i in layer one and node j in layer two are co-operators. 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 Supplementary Information section 1.

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 $\widehat{\xi}^{[L]} = \sum_{i=1}^N \pi_i^{[L]}\xi_i^{[L]}$ represents the fixation probability of co-operators in layer L under neutral drift ($\delta=0$)[24]. In Supplementary Information section 1, we show that one can obtain β_{ij} and γ_{ij} by solving the following linear system of equations,

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

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

$$\phi_{n,m} = \sum_{i,j=1}^N \pi_i^{[1]}\left(p^{[1,2]}\right)_{ij}^{(n,m)}\gamma_{ij},$$

which means the probability that both the starting and the ending nodes of an n-step random walk in layer one are co-operators, where the starting node i is selected based on the reproductive value, $\pi_i^{[1]}$. Analogously, for the interlayer 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 co-operators. Substituting θ_n and $\phi_{n,m}$ into equation (2) then gives the condition for selection to favour cooperation. In Supplementary Information section 2.2.2, 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: (1) in each layer, a node is connected to two other nodes; and (2) 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 (Fig. 3a). We study the initial strategy configuration of a single mutant co-operator in each layer. Let d be the shortest distance between these two co-operator nodes. That is, if i is a co-operator in layer one and j is a co-operator 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 co-operators, $d=0$. The configuration shown in Fig. 3a is an example with $d=1$.

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

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

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

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 co-operator appears in every node with 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[26,54].

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: (1) any two nodes i and j of G are adjacent if and only if $f(i)$ and $f(j)$ are adjacent in H; and (2) strategies of any node u of G and $f(u)$ of H are identical. Otherwise, the two profiles are non-isomorphic (see examples in Supplementary Fig. 14).

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: (1) 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 (2) 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. Supplementary Table 1 shows the number of non-isomorphic single-layer and non-isomorphic two-layer profiles for networks of size $N=3$, 4, 5 and 6. Note that the network in each layer is required to be connected. The total number of non-isomorphic profiles is far greater for two-layer networks than for single-layer ones. For example, for $N=3$ there are 26 non-isomorphic two-layer profiles compared with 3 such single-layer profiles; and for $N=6$ there are 36,394,472 non-isomorphic two-layer profiles compared with 407 such single-layer profiles.

We analyse all non-isomorphic single-layer profiles for $N=3$, 4, 5 and 6 to obtain the proportion of profiles in which cooperation can be favoured for some $b_1/c>0$ (or equivalently, the critical benefit-to-cost satisfies $0 < (b_1/c)^* < \infty$; see blue bars in Fig. 6). When randomly choosing two single-layer profiles, for $N=6$, there are $407 \times 407 = 165{,}649$ combinations. We take one as layer one and another as layer two. Because there are many ways for a node in layer one to correspond to a node in layer two (that is 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 favoured for some positive b_1/c and b_2/c (or equivalently, the region $(b_1/c, b_2/c)$ constrained by equation (2) partially overlaps with the first quadrant), we say coupling such two single-layer profiles makes cooperation favoured with probability Y/X. Analysing all such combinations, we obtain the proportion of couplings of a single-layer profile to a random single-layer profile that favour cooperation in both layers (see red bar in Fig. 6 and Supplementary Table 2).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All the network datasets used in this paper are freely and publicly available at https://manliodedomenico.com/data.php

Code availability

All code has been deposited into the publicly available GitHub repository at https://github.com/qisu1991/MultilayerPopulations

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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. analysed 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.

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