Social influence preserves cooperative strategies in the conditional cooperator public goods game on a multiplex network

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(Dated: October 24, 2018)

Numerous empirical studies show that when people play social dilemma games in the laboratory they often cooperate conditionally, and the frequency of conditional cooperators differs between communities. However, this has not yet been fully-explained by social dilemma models in structured populations. Here we model a population as a two-layer multiplex network, where the two layers represent economic and social interactions respectively. Players play a conditional public goods game on the economic layer, their donations to the public good dependent on the donations of their neighbours, and player strategies evolve through a combination of payoff comparison and social influence. We find that both conditional cooperation and social influence lead to increased cooperation in the public goods game, with social influence being the dominant factor. Cooperation is more prevalent both because conditional cooperators are less easily exploited by free-riders than unconditional cooperators, and also because social influence tends to preserve strategies over time. Interestingly the choice of social imitation rule does not appear to be important: it is rather the separation of strategy imitation from payoff comparison that matters. Our results highlight the importance of social influence in maintaining cooperative behaviour across populations, and suggest that social behaviour is more important than economic incentives for the maintenance of cooperation.

PACS numbers: 89.75.Fb 87.23.Ge 02.50.Le

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I. INTRODUCTION

Many important issues can be framed as social dilemmas, or tensions between actions that favour the interests of the individual ('defection' or 'free-riding') and those that favour the group ('cooperation'). Game theory is often used to analyse the prevalence of cooperation in social and biological systems [1, 2], and in particular in social dilemmas [3] including common fisheries [4] and water sources [5]. In standard one-shot social dilemma games players typically choose from two distinct strategies: cooperate or defect. Previous analyses of one-shot games in unstructured populations find that defection dominates the population [6], a result that is at odds with the cooperation widely observed in both social and biological systems [7].

Numerical simulations of single networked populations [8] have been extensively used to examine the reasons that cooperation persists. These networks represent player interactions: network nodes describe players and network edges describe the connections between them. Combinations of networks are also studied, including multiple networks with edges formed between them (interdependent) [9] and multilayered networks where ties between nodes are not necessarily the same on each layer (multiplexes) [10].

The central mechanism through which cooperation is supported on single networks is *network reciprocity*, or the formation of clusters of cooperators that avoid exploitation by surrounding defectors [11–14]. Network reciprocity has been shown to increase on interdependent networks for social dilemmas [15, 16], combinations of different games [17–19], and in games where players' fitness is defined as a weighted sum of their payoffs on each layer [20–26]. On multiplex networks, cooperation is found to be increased [27–29] due to "incoherent" players, who do not play the same strategy across all layers, generating a large enough payoff through defection on some layer(s) to support cooperation on others.

Szolnoki and Perc [30] find that network reciprocity also supports *conditional* cooperators, who decide to cooperate or defect dependent on others' behaviour, along with the standard binary 'cooperate' and 'defect' strategies. Playing explicitly conditional strategies on lattices they found that the conditional strategies shield cooperative clusters from exploitation by free-riders, encouraging cooperation.

Despite network reciprocity providing a key mechanism for the support of cooperation, evidence for it in human laboratory experiments is disputed [31–33]. The most likely explanation for the results in [33] is that some players act as moody conditional cooperators, who are more likely to cooperate if their network neighbours also cooperate. Numerical simulations by Gracia-Lázaro et al. [34] support this hypothesis.

Conditional cooperation can also take the form of continuous strategies, for example where players can decide how much to donate to the public good from a continuous range. Thus while cooperators donate all they have and defectors donate nothing independent of others decisions, conditional cooperators can choose to donate some intermediate amount depending on what others have donated. (Note that this contrasts with the moody conditional cooperation reported in [33] and modelled in [34], where the conditional cooperators have a binary choice either to donate all or to donate none, and it is only the choice of action that depends on how others behave.) There exists a range of empirical evidence that suggest individuals use these kinds of conditional strategies [35], and furthermore, that participants from different backgrounds exhibit different frequencies of conditional cooperation within the population [36–39]. In general, there are two factors that influence how cooperative players are in the laboratory: the first being real-life experiences akin to the public goods game, and the second membership of a group where cooperation is strongly enforced. Members of groups that discourage free-riding in real life cooperate more in the laboratory.

Conditional strategies have been included in a number of models by mapping the group's contribution to the player's by some linear factor. Guttman [40] found that dominant strategies were not unconditional, but included a component that exactly matched group donations in the public goods game. Zhang and Perc [41] represented strategies as a piecewise linear function, finding that the dominant strategy is one that free-rides for low contributions and conditionally cooperates for higher contributions, due to the competing influences of inter- and intra-group competition. Continuous strategies have also been studied in [42].

Mechanisms other than network reciprocity, such as non-payoff-based strategy updates can also lead to an increased prevalence of cooperation. Cimini and Sánchez [43] modelled the evolution of moody conditional cooperation on a network numerically using both payoff-dependent and non-payoff-dependent update rules, including the voter model and reinforcement learning. Interestingly, it is reinforcement learning that generates populations with similar prevalence of cooperation to that observed in the laboratory. Other studies find increased cooperation if certain subsections of the population blindly imitate neighbouring strategies, disregarding their neighbour's payoff either probabilistically [44] or at key points in the network [45]. Lugo and San Miguel [46] updated strategies on a multiplex by considering both the payoff and the number of other players using a given strategy on a given layer, and found that coordination of strategies only occurs when the payoffs are taken into account.

Separating payoff- and non-payoff-based considerations has also been investigated on multiplexes with separate layers representing payoff accumulation and strategy imitation. Wang et al. [47] found reduced cooperation in a two-layer multiplex when one layer connects nodes of similar degree and one layer connects high degree nodes with low degree ones. More recently Amato et al. [48] investigated a model on a two-layer multiplex, where on one layer a 2×2 matrix game is played, while the other acts as the opinion layer, on which it is assumed that cooperation is encouraged. They find that the addition of the opinion layer leads to either full cooperation across the multiplex or polarisation of cooperation and defection across communities, depending on the parameters selected.

Inspired by the laboratory observations highlighting the relevance of conditional cooperators and social influences [35–39], in this article we consider the two themes of conditional cooperation and strategy updates that depend on a mix of economic and societal factors. We investigate the tension between the economic and social influences on conditional cooperators by modelling the population as a set of individuals linked by a multiplex network and playing a repeated version of the public goods game. Through this we seek to understand the importance of social influence on conditional strategies, and the variation of conditional strategies across the community.

The article is structured as follows: in section II we describe the details of the model. Section III presents our results, where we establish the profound impact of both conditional cooperation and societal pressures on levels of cooperation. Our findings support previous empirical discoveries: the dominant factor in the preservation of cooperative strategies is social influence, and this must be considered when modelling cooperation. We explain the mechanisms by which cooperation is preserved by considering outcomes from simulations where social influence either is or is not a factor, and investigate the robustness of our results to the introduction of community structure. We conclude with a discussion in section IV.

II. METHODS

In our model individuals play a public goods game (PGG), each player contributing conditionally to the public good depending on what others have contributed. We divide each generation of the game into two phases: firstly, a sequence of iterations of the conditional PGG resulting in payoff accumulation, and secondly a strategy update phase that depends on both economic factors and social influence. Players are linked by a multiplex network consisting of two layers: one labelled 'economic' and the other 'social'. Payoff accumulation takes place on the economic layer, while both layers can play a part in strategy updates. This structure enables us to vary the strength of economic and social interactions independently. Consequently, for appropriate parameter settings, the model replicates results for the standard PGG and also describes the conditional PGG both with and without social influence.

Section II A describes the structure of the multiplex network. Sections II B and II C set out the the rules for payoff accumulation and strategy updates respectively. Details of the numerical simulations are given in II D.

A. Network structure

The players are placed on nodes in a multiplex Erdős-Rényi network [49] consisting of two layers: the economic layer (mean degree $\langle k_p \rangle$) and the social layer ($\langle k_s \rangle$), with N nodes on each layer. The economic layer defines those with whom each node plays the game to gain a payoff. Each node plays in multiple groups: the group in which the node is focal and the groups in which each of the node's neighbours is focal. The social layer defines those whose strategy the player knows, but does not necessarily play against. Each player is assumed to know the strategy of those with whom it plays the game, and so the payoff network is a subnetwork of the social network. The economic layer is first generated by forming edges between nodes with probability $\frac{\langle k_p \rangle}{N-1}$. Because the economic layer is a subgraph of the social layer, the economic layer is first replicated into the social layer. The social layer is then completed by adding additional edges to each node on the social layer so that the final degree distribution matches that expected of an Erdős-Rényi network with mean degree $\langle k_s \rangle$.

B. Payoff accumulation

During payoff accumulation, each player plays a public goods game that is repeated for L iterations. In each iteration, players make donations based on their conditional strategy and receive payoffs. Each player i has a strategy $a_i \geq 0$ which describes how *conditionally cooperative* they are. Free-riders play strategy $a_i = 0$ whilst very cooperative players play strategies $a_i \gg 0$.

Each player has a maximum of one unit to donate in each group, and possible donations range between zero and one. At each iteration l of the game, player i contributes

$$c_{i,g}(l) = \begin{cases} a_i c_g(l-1) & \text{if } c_g(l-1) < \frac{1}{a_i} \\ 1 & \text{otherwise,} \end{cases} \tag{1}$$

where $c_g(l)$ is the average contribution over all players in the group in iteration l. Critically, the fact that $c_{i,g}(l)$ depends on $c_g(l-1)$ means that players typically do not donate the same amount in every iteration, but instead donate an amount that is conditional on the level of the group contribution in the previous iteration.

As in the standard public goods game, the payoff of player i is calculated by multiplying the average group contribution ($c_g(l)$) by an enhancement factor r, and subtracting the amount donated by player i in that iteration:

$$p_{i,g}(l) = r\frac{c_{i,g}(l) + \sum_{j\in g, i\neq j} c_{j,g}(l)}{G} - c_{i,g}(l) = rc_g(l) - c_{i,g}(l), \tag{2}$$

where $j \in g$ are the players in player i's group, and G is the number of players in the group.

This process of payoff accumulation repeats for a single generation of L iterations. At the beginning of a generation ($l = 1$) it is not known what each member of the group contributed in the last iteration, and so the initial group contribution is set to $c_g(0) = 0.5$. The minimum generation length for a conditional game is therefore two. In the results we report below, we set $L = 2$ since we find that our results are not strongly dependent on the value of $L \geq 2$ (see Fig. A.2).

The total payoff P_i of player i is defined as the sum of their payoffs over the generation length in each group in which they play the game:

$$P_i = \sum_{g=1}^{k_i+1} \sum_{l=1}^{L} p_{i,g}(l), \tag{3}$$

where k_i is the degree of node i and $p_{i,g}(l)$ is the payoff of player i playing in group g at iteration l.

Note that if a player's strategy a_i is smaller than one, then over the generation their donations decrease, and conversely for a strategy higher than one donations increase. Therefore, populations with an average strategy larger than one will donate large amounts, and populations with average strategy smaller than one will donate small amounts.

C. Strategy update rules

Following payoff accumulation players update their strategy using information from the social layer with probability λ, or from the economic layer with probability $1-\lambda$. We call λ the social influence strength.

Updates on the economic layer are designed to mimic a rational self-interest, and therefore a player changes its strategy in an attempt to increase its payoff. Each player (i) in the population selects a neighbour (j) in the economic network at random and compares payoffs derived in the previous generation: if the payoff of the selected player is higher, player i moves its strategy in the direction of player j by a factor θ (known from now on as the imitation strength) and so the updated strategy is

$$a_i(t+1) = a_i(t) + \theta H(P_j > P_i)(a_j(t) - a_i(t)) \quad (4)$$

where t labels the generations and $H(x)$ is the Heaviside step function. Updating on the social layer is designed to mimic a player's desire to adjust their behaviour towards the average of the community. The average behaviour is represented as the mean of the strategies of player i's neighbours in the social network, and updates occur by moving the player's strategy towards the average of the neighbours' strategies on the social layer, $\bar{a}_i$, such that

$$a_i(t+1) = a_i(t) + \theta(\bar{a}_i(t) - a_i(t)), \quad (5)$$

a rule that is similar to Deffuant opinion dynamics [50].

D. Numerical simulations

Our model extends the standard PGG on a network by including both conditional cooperation and social influence. We can tease apart the effect of conditional cooperation and social influence on cooperation by considering different parameter regimes. For example, when $\lambda = 0$ only economic considerations are taken into account during strategy updates, enabling us to study the effect of conditional cooperation alone. However, when $\lambda = 1$ only social influence is important, and Deffuant-like opinion dynamics [50] are recovered. Similarly when $\theta = 1$ players copy each other exactly, and the standard PGG can be recovered when $\lambda = 0$. Table I sets out each of the parameter regimes we will study and the conditions that they describe.

Regime	Social influence, λ	Imitation strength, θ	Initial conditions	Plot colour
Conditional cooperation and social influence	0.1	0.9	Uniform, $0 \leq a_i \leq 5$	Red
Conditional cooperation with economic considerations only	0	0.9	Uniform, $0 \leq a_i \leq 5$	Blue
Standard PGG	0	1	Bimodal, $a_i \in \{0, 5\}$	Black

TABLE I: Parameter regimes for which numerical results are presented, defined in terms of social influence and imitation strengths and initial strategy distributions. The colour used for each regime in subsequent plots is also given.

Unless otherwise stated, in the results reported below, the number of nodes in each layer is $N = 500$, and each run of the dynamics is for $20,000$ generations, or until the dynamics have converged to a single strategy. Here we consider a population to have converged when all members of the population share the same strategy. Due to the form of the strategy imitation rules, and the lack of noise the population will not deviate from this value, and so the simulations are stopped. The mean degree on the economic layer is $\langle k_p \rangle = 4$, and the mean degree of the social layer is $\langle k_s \rangle = 8$. Unless otherwise stated each data point is an average over 20 distinct, randomly initialised runs of the dynamics. Shading indicates a single standard deviation from the mean over the 20 runs.

Two measures of cooperation are used. The first is the mean contribution averaged over players, groups and iterations. If the amount donated by player i in iteration l to group g is $c_{i,g}(l)$, then because a player with degree k_i plays in $k_i + 1$ groups, the average contribution is

$$\langle c \rangle = \frac{\sum_{i=1}^{N} \sum_{m=1}^{k_i+1} \frac{1}{k_i+1} \sum_{l=1}^{L} c_{i,g_{i,m}}(l)}{LN}, \tag{6}$$

where $g_{i,m}$ is the m^{th} group containing player i. The second measure of cooperation is the mean strategy in the population

$$\langle a \rangle = \frac{\sum_{i=1}^{N} a_i}{N}. \quad (7)$$

In the simulations each measure is calculated as an average over the last 2000 generations to give the final average mean contribution and strategy.

III. RESULTS

We present results from numerical simulations for each of the three regimes described in table I, before exploiting the independence of conditional cooperation and social influence to explain the effect of each in turn. In section III A we first illustrate that both conditional cooperation and social influence dramatically increase cooperation at low enhancement factors compared to the standard public goods game. The reasons for the increased cooperation due to conditional strategies is investigated in section III B, before further examining the effect of social influence in section III C. In section III D we consider network structures closer to those described in empirical studies of cooperation in communities [35–39].

A. Comparing the effects of economic and social influences

Fig. 1a plots the mean contribution $\langle c \rangle$ against the scaled enhancement factor $\eta = \frac{r}{\langle k_p \rangle + 1}$ for each of the three regimes described in table I.

As expected, in the standard public goods game (Fig. 1a, black triangles) contributions, and hence cooperation, are maintained on the network at scaled enhancement factors above $\eta = 0.7$ (as in [14]). In contrast, with the introduction of conditional cooperation, (blue circles), cooperation occurs above $\eta = 0.2$, whilst the introduction of social influence results in large contributions for enhancement factors as low as $\eta = 0.05$ (red diamonds).

The differences between the three sets of results are caused by the differences in mean strategies at each enhancement factor, as shown in Fig. 1b. The larger strategies at low enhancement factors for $\lambda = 0.1$ confirm that the inclusion of social influence increases cooperative strategies within the population.

Note that for $\lambda = 0$ and $\lambda = 0.1$, the points where there is rapid change in mean contribution all occur when the mean strategy is close to the the critical value $\langle a \rangle = 1$. As

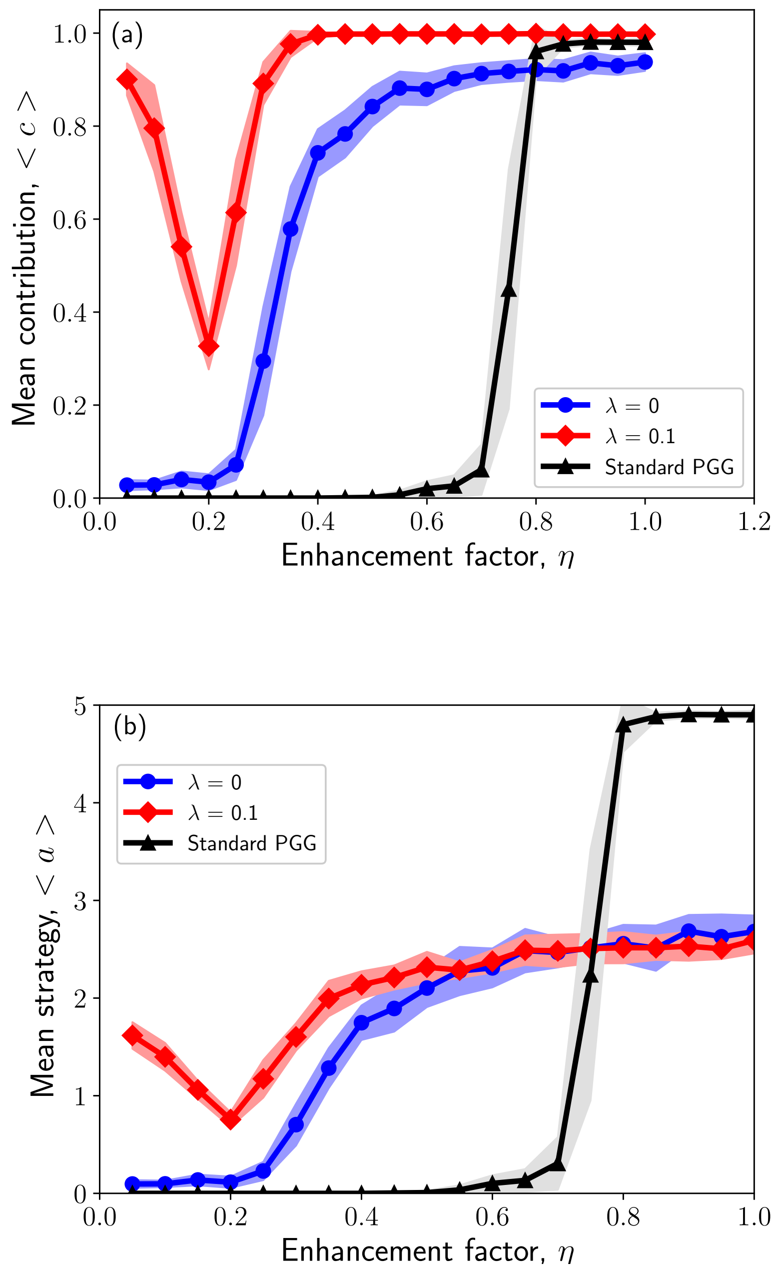

FIG. 1: The mean contribution (a) and strategy (b) plotted against the scaled enhancement factor $\eta = \frac{r}{\langle k_p \rangle + 1}$ for conditional cooperators on the multiplex: economic layer only ($\lambda = 0$, red diamonds) and two-layer multiplex with social influence strength $\lambda = 0.1$ (blue circles). Here, the mean degree on the economic layer is $\langle k_p \rangle = 4$ and on the social layer is $\langle k_s \rangle = 8$; and imitation strength $\theta = 0.1$. Also plotted are results for the standard public goods game (black triangles).

highlighted in section II B, for strategies $a_i > 1$ donations increase over the game iterations, whilst the converse is true for $a_i < 1$, and in general, large mean group strategies result in larger contributions. Consequently, in the neighbourhood of $\langle a \rangle = 1$, a small difference in mean strategy results in a large difference in mean contribution. A striking feature of the $\lambda = 0.1$ results is the dip in cooperation at $\eta \approx 0.2$, a result we explain in section III C.

It is important to note that in Figs. 1a and 1b the probability of strategy update through the social layer is only $\lambda = 0.1$, so the influence of the social behaviour is relatively small. Yet even this low level of influence has a dramatic effect on the amount of cooperation in the system. We confirm the dominance of social influence, varying the generation length and mean social network degree, and finding that neither appears to have much impact on the effect of social influence (appendix A.1, Figs. 7 and 8).

Fig. 2 shows that social influence has an equally dramatic effect on cooperation for two other possible social imitation rules: either targeting the median of the group, or selecting a random social neighbour's strategy (essentially the voter model [50]). The latter is similar to the way in which updates are performed on the economic layer, but on the social layer the payoff of the randomly selected neighbour is not taken into consideration. We observe that which social imitation rule is chosen makes little difference to the mean strategy within the population. Due to the small groups and random initial conditions this is not surprising for the mean and the median rules. However, the fact that on a structured population selecting a neighbour at random on the social layer and blindly imitating it gives the same results as imitating the mean of the social neighbours is interesting. It suggests that it is the separation of strategy imitation from payoff comparison that is important rather than the selection of a particular social imitation rule. We also observe that at low enhancement factors, payoff comparison favours the lowest possible strategy value of zero, and so *any* non-payoff based imitation rule increases the mean population strategy.

B. Isolating the effect of conditional cooperation: restriction to the economic layer ($\lambda = 0$)

As discussed in II D, a measure of the level of cooperation is the mean strategy in the population. In this section we show that the two key factors in determining the strategies at equilibrium are the initial distribution and the enhancement factor. In order to demonstrate

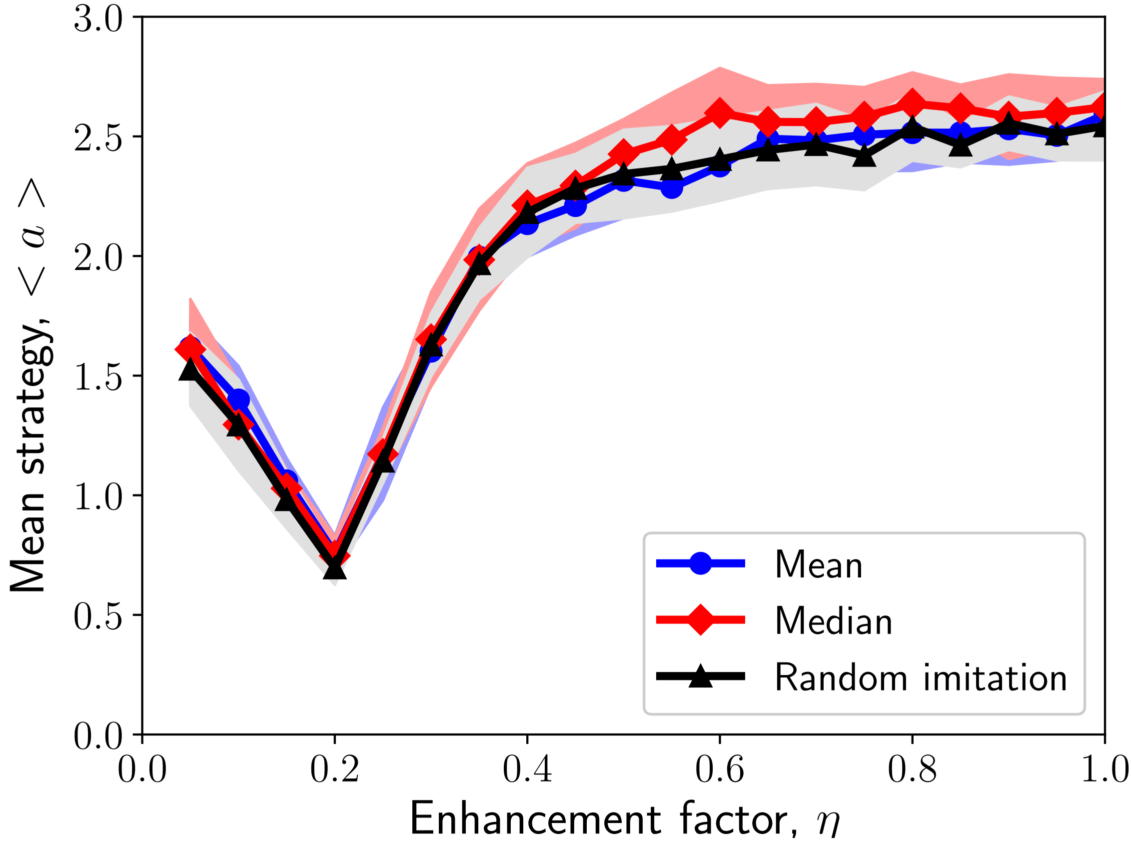

FIG. 2: The mean strategy plotted against the scaled enhancement factor $\eta = \frac{r}{\langle k_p \rangle + 1}$ for conditional cooperators on the multiplex, for three different social imitation rules: targetting the mean of the social neighbourhood (blue circles), targetting the median (red diamonds) and imitation of a random member of the social neighbourhood (black triangles)

this clearly we remove any network effects and consider a well-mixed population initialised with just two strategies, $a_i(0) \in \{a^0(0), a^1(0)\}$, where $a^w(0)$ defines one of two possible strategies that player i may take. As players update their strategies by moving towards that of a better performing player (Eq. 4), we can approximate the subsequent dynamics of the distribution of strategies as two distinct strategies moving towards each other, eventually coalescing at an equilibrium strategy determined by the relative rates of strategy imitation. These rates are defined by the probability that a player with strategy a^v imitates another player with strategy a^w, that is the probability that the total payoff to player w, P_w, is larger than the total payoff to player v, P_v, defined as Q_{vw}. Under the above assumptions using a mean-field approximation we find that the equilibrium strategy $\langle a\rangle(t)$ as $t \to \infty$ depends on the difference in value of the initial strategies $\Delta a(0)$, and the ratio of the probabilities of each strategy imitating the other

$$\lim_{t\to\infty} \langle a\rangle(t) = a^0(0) + \frac{\Delta a(0)}{1 + Q_{10}/Q_{01}}, \tag{8}$$

where $a^0(0)$ is the initial value of the smaller strategy. The derivation of this result is given in Appendix A.5.

The importance of the initial strategy distribution is clearly demonstrated by the presence of $a^0(0)$ and $\Delta a(0)$ in Eq. (8). However, the key to understanding the dynamics of the conditional game is the function Q_{vw}, which depends on the number of possible group compositions where $P_w > P_v$. Due to the form of the public goods game (Eq. (2)), at larger enhancement factors there is a larger number of group compositions in which a more cooperative player gains a higher payoff than in which a less cooperative one does. (See section A.3 for further details.) Hence Q_{01} is increased and Q_{10} is decreased, and therefore according to Eq. (8) increased enhancement factors lead to larger equilibrium strategies.

We further apply the above arguments to explain why conditional cooperation increases cooperation in comparison to the standard PGG. In the conditional game cooperative strategies are less easily exploited, and so the number of cooperative strategies needed in a group for cooperation to flourish at each enhancement factor is lower, leading to higher frequencies of cooperation in the conditional game in comparison to the standard PGG (as observed in Fig. 1b).

Returning to the conditional cooperator game on a network, it is the relative probabilities of one strategy imitating another, along with network reciprocity that explain the results in the absence of social influence ($\lambda = 0$). (See the appendix for further details.)

C. The effect of social influence ($\lambda = 0.1$)

We now explain the difference in cooperation between parameter regimes (Fig. 1b) by considering the combination of the mean strategies on the two layers. Taking each layer separately, the dynamics on the social layer attract the population towards the initial mean strategy, owing to the Deffuant-like strategy update rule (Eq. (5)), whereas updating strategies on the economic layer shifts them towards a value dependent on the enhancement factor.

Competition between the dynamics on the two layers results in the equilibrium mean strategy observed for each value of λ.

At each enhancement factor in Fig. 1b the initial population mean strategy ($\langle a\rangle(0) = 2.5$) is higher than the equilibrium strategy found by the economic layer dynamics alone. Thus at low enhancement factors the introduction of social pressure increases the mean strategy above one, and so the contribution to the public good is dramatically increased. This effect is less pronounced for higher enhancement factors because the difference between the equilibrium strategies with and without social influence is reduced, and at some enhancement factors the equilibrium strategy without social influence is higher. We illustrate this effect by plotting strategy distributions for a single run of the dynamics in Fig. 3, where we observe that for dynamics where social influence is included ($\lambda = 0.1$, red histogram) the mean strategy is closer to the initial population mean and the strategy distribution is much narrower than for $\lambda = 0$.

The differing equilbrium strategies on the two layers also explain the split in behaviour of the mean strategy above and below $\eta = 0.2$ (Figs. 1b, 2, 4b, 7 and 8). Eq (A.17) in section A.4 shows that the critical enhancement factor above which *any* positive strategy performs better than a free-rider in direct competition is $\eta_c = 0.2$. Above this enhancement factor, previous arguments that the mean strategy is a combination of economic and social equilbrium strategies hold. However, below it the equilibrium strategy on the economic layer is decoupled from the enhancement factor (as the equilibrium strategy on the economic layer is zero for all $\eta < 0.2$). Furthermore, at enhancement factor $\eta = 0$, payoffs on the economic layer are given by the negative of the player's contribution (2). Owing to the distribution of initial strategies many players contribute $c = 1$ initially, so there is no difference between them in economic payoff and thus social influence dominates strategy imitation halting the slide to free-riding that would otherwise occur. As the enhancement factor increases from zero, the economic payoff gradually becomes more strongly coupled to strategy through the increasing importance of the group contribution (Eq. (2)), and so the overall equilibrium strategy is attracted towards the economic equilibrium strategy.

The importance of social influence in shifting the mean strategy towards the initial population mean is further supported by comparing results for a smaller range of initial strategies with a lower initial mean (uniform distribution, $0 < a_i < 2$, Fig. 4), with the results in Fig. 1a (uniform distribution, $0 < a_i < 5$).

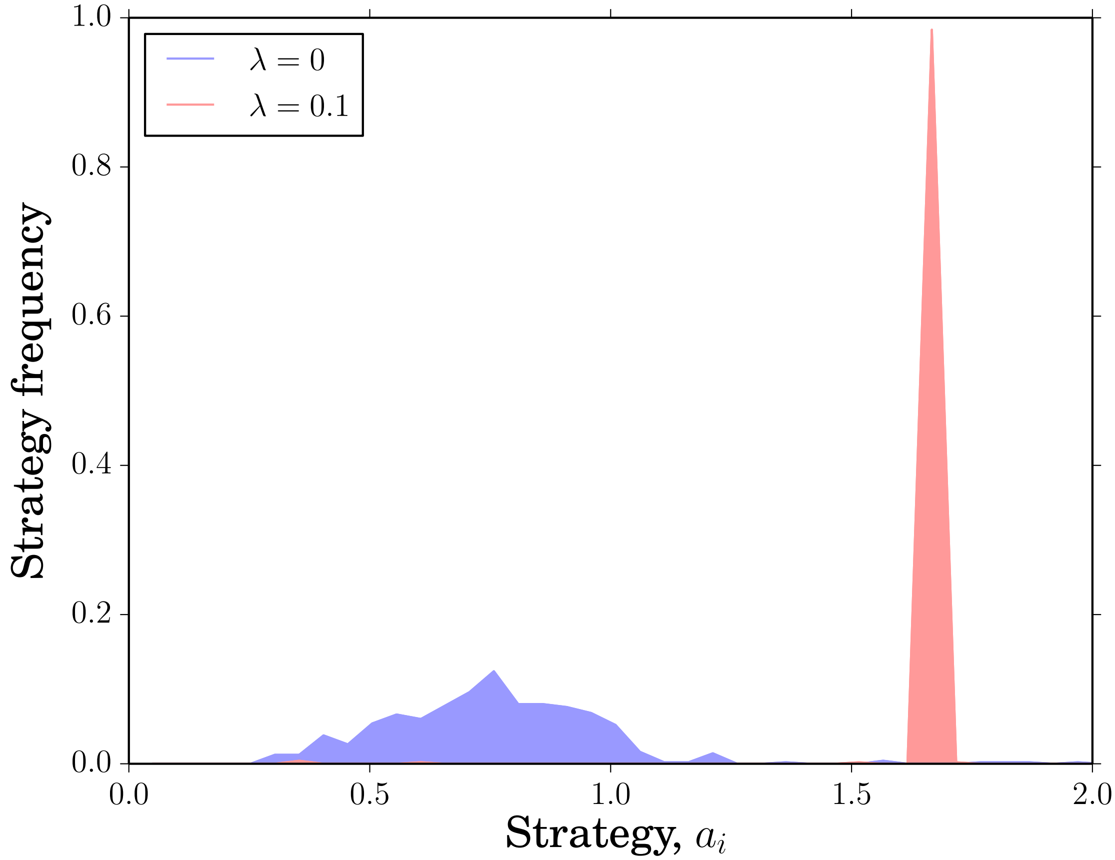

FIG. 3: The distribution of strategies after $t = 1000$ generations. Plotted from a single run of the dynamics updating using the economic layer only ($\lambda = 0$, blue line) and social influence ($\lambda = 0.1$, red line) for enhancement factor $\eta = 0.3$, mean economic degree $\langle k_p \rangle = 4$ and mean social degree $\langle k_s \rangle = 8$.

Comparing the contribution for the high and low mean initial distributions (Figs. 1a and 4a respectively) the mean contribution for low mean initial conditions is lower for all enhancement factors compared to the high mean initial conditions. As might be expected, social influence slightly depresses the mean strategy and consequent contributions at high enhancement factors for the low mean initial conditions, because it entrenches the impact of initial strategies that are lower on average than the purely economic equilibrium strategy for higher enhancement factors. The lower mean strategies and cooperation in Fig. 4 compared to Fig. 1 confirm the importance of the initial distribution of strategies, as also observed in Eq. (8).

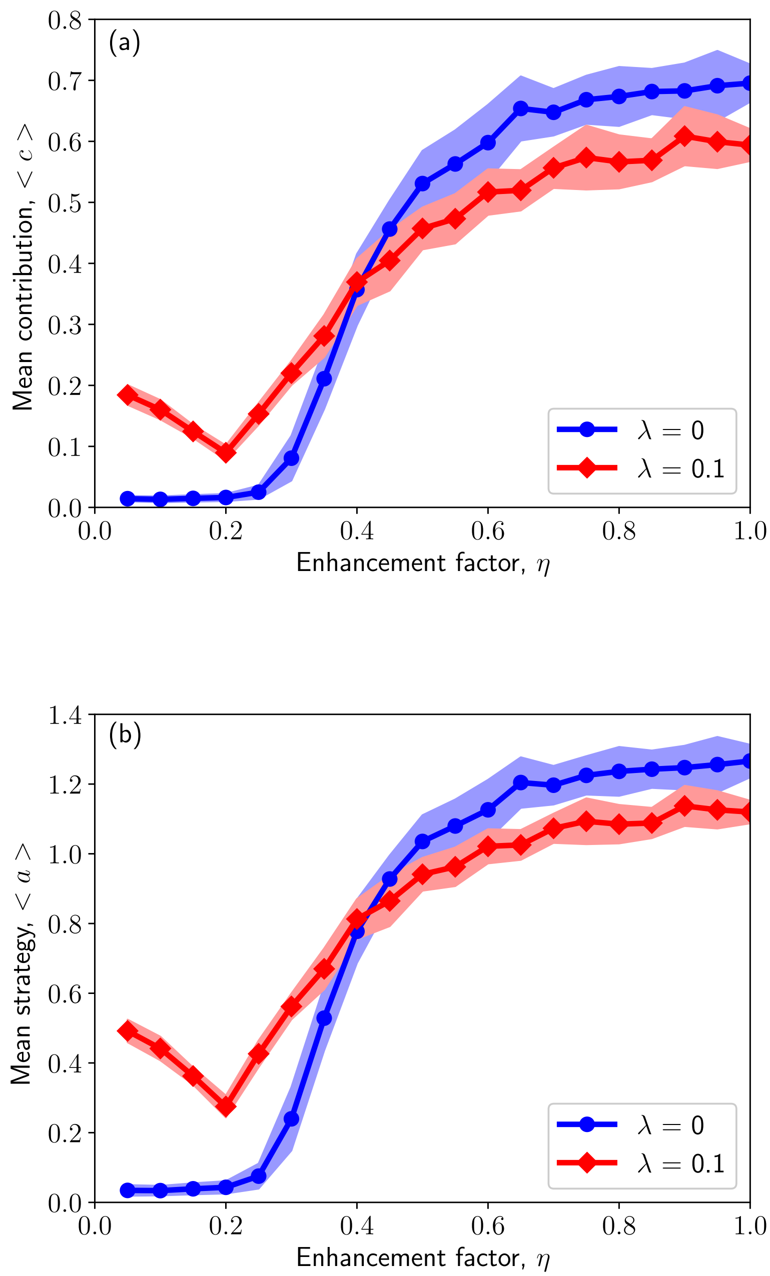

FIG. 4: The mean contribution (a) and strategy (b) plotted against the scaled enhancement factor $\eta = \frac{r}{\langle k_p \rangle + 1}$ for conditional cooperators on the multiplex. The mean strategy is compared for the economic layer only ($\lambda = 0$, blue circles) and the two-layer multiplex with social influence strength $\lambda = 0.1$ (red diamonds), with initial strategies selected at random from a unifom distribution $0 < a_i < 2$. The dynamics are run for mean degree $\langle k_p \rangle = 4$ on the economic layer and $\langle k_s \rangle = 8$ on the social layer, and imitation strength $\theta = 0.1$.

D. The effect of community structure

In this section we study the behaviour of the model on a network designed to resemble the populations observed in empirical investigations [35–39]. These communities tend to be small, with a large number of connections between people and so we use the block network [51] structure to model them. We first create the economic layer by building a number of complete networks, or 'communities'. Edges between nodes in different communities are formed on the economic layer with probability $p_{BR} = p_e \; \forall B, R$ where B and R label the communities. The social layer is a replica of the economic layer. An example of the economic network used in this section is shown in Fig. 5.

We run our model dynamics on a community network, and find that for disconnected communities the distribution of strategies mimics those observed in the empirical studies. The economic network consists of $N = 40$ nodes divided at random into six economic communities, with community sizes selected at random, whilst ensuring that each community has at least two members. To understand the effect of the community network structure, we compare the strategy distribution on the community networks with that on a random network. We generate Erdős-Rényi networks of an equal size and mean degree as the community networks ($\langle k_p \rangle$=7.3 for $p_e = 0$ and $\langle k_p \rangle$=7.9 for $p_e = 0.01$). Mean degrees were calculated by averaging the mean network degree across 100 community networks. We plot the distribution of final strategies for 100 runs of the dynamics for both the community and Erdős-Rényi networks in Fig. 6. The dynamics are run for 5000 generations with an initial group contribution of $c_g(0) = 0.5$. Strategies are selected from a uniform distribution $0 \leq a_i \leq 5$, the enhancement factor is $\eta = 0.5$, the social influence strength is $\lambda = 0.1$, and the mean strategy is averaged over the last 500 generations.

Figure 6 shows that the model dynamics in this community structure result in a wide distribution of strategies, and in both Fig. 6a and Fig. 6b the strategies found on the community networks are lower than those on random ones.

When no edges are formed between communities ($p_e = 0$, green line in Fig. 6a) strategies range between approximately 0 and 2, mimicking results found in [35–39], where strategies tend to vary from free-riding to conditionally cooperative, with a few players that donate more than the group average at each iteration.

The low strategies in the community networks in Fig. 6a are explained by considering the

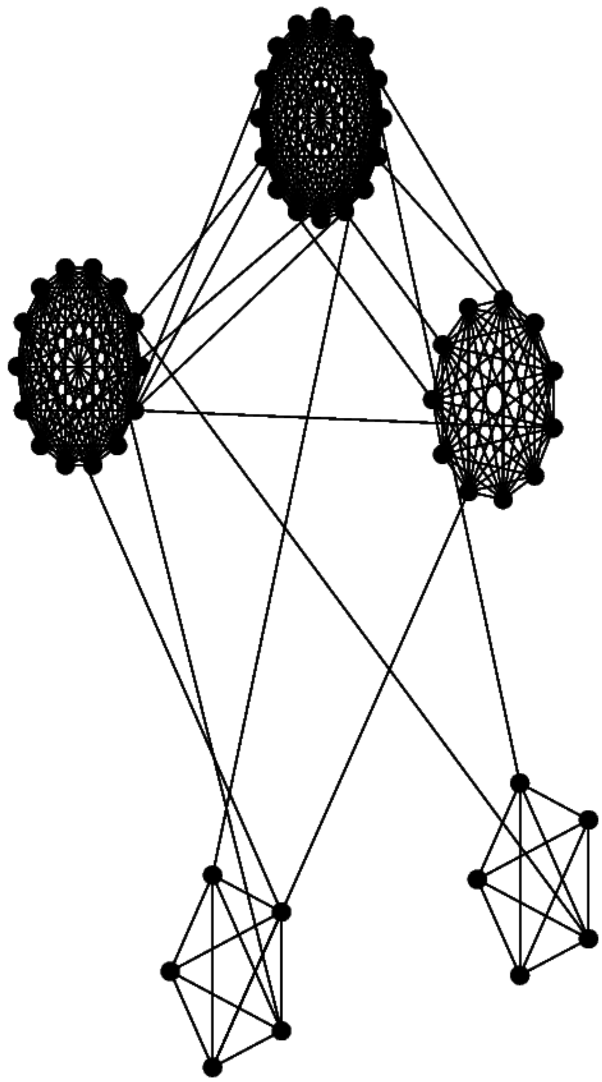

FIG. 5: An example of the network of communities. Here the probability of forming an edge between nodes not in the same community is $p_e = 0.01$.

behaviour of a single community on the economic layer. The community is a fully connected network, so each individual gains the same from the public good, c_g. However, players with larger strategies donate more, thereby lowering their payoff (see Eq. 2). Updates on the economic layer therefore tend to the lowest strategy in the community. Since strategies are initialised randomly, the lowest strategy is not necessarily zero and so strictly positive strategies are observed. Based on our results in section III C we expect that social influence is also helping to maintain strategies at a higher level than they would be in its absence.

On the Erdős-Rényi network players donate to multiple groups of different sizes, reducing

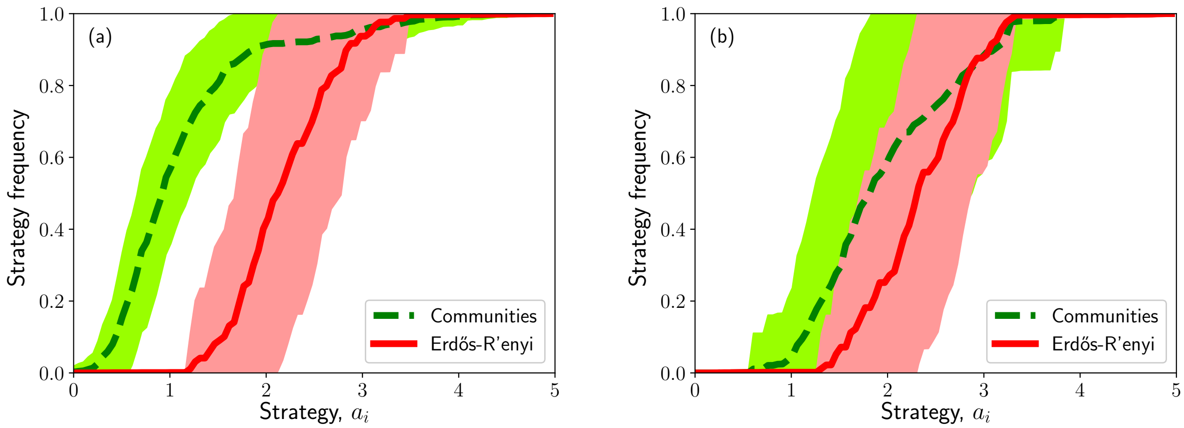

FIG. 6: The cumulative distribution of strategies on community networks after 5000 generations for 100 runs of the dynamics, with updates with no inter-community edges (a, $p_e = 0$) and with inter-community edges (b, $p_e = 0.01$). Initial strategies are distributed uniformly on the interval [0,5]. The enhancement factor is $\eta = 0.5$, the social influence is $\lambda = 0.1$ and the initial group contribution is $c_g(0) = 0.5$.

the strict relationship of a low strategy to a high payoff, and thereby preserving larger strategies than in the community networks. The same effect, but to a lesser extent, causes the observed strategy increase on community networks between $p_e = 0$ and $p_e = 0.01$ (the green lines in Figs. 6a and 6b respectively).

IV. DISCUSSION AND CONCLUSION

We have introduced a model inspired by a number of empirical observations of human cooperation in the real world. We sought to understand how non-payoff based imitation alters cooperation in the conditional public goods game, and whether non-payoff based rules could account for the variation in conditional cooperation observed within communities.

Both conditional cooperation and social influence on strategy updates can have a considerable effect on the amount contributed to the public good, even when social influence operates as little as 10% of the time. Similar effects are observed for a range of social imitation rules, suggesting that it is the decoupling of imitation dynamics from economic payoffs that is important rather than the particular choice of social imitation rule.

Conditional cooperation increases contributions compared to the standard public goods game through two mechanisms: the resilience of conditional strategies to free-riding; and network reciprocity.

In general, social influence in the conditional public goods game homogenises the final distribution of strategies across the population. This homogenisation is very strong, and remains unaffected by changes in the social network degree, or the number of game iterations. Whether social influence leads to an increase in cooperation is heavily dependent on the initial strategies in the population. If strategies are initially highly cooperative on average, then social influence will increase cooperation in the system at very low enhancement factors. However, if initial strategies are insufficiently cooperative, then social updates do not affect the amount donated greatly at low enhancement factors, and can decrease contributions at high enhancement factors. One possible reason for the sensitivity to the initial conditions may be that global dynamics are sensitive to local arrangements of particular strategies. However, we do not believe this is the case for two reasons: the variation in mean strategies and contributions in Fig. 1 are small between each randomly initialised run; and preliminary investigations of additional noise (not included) result in little change in the mean strategy for reasonable values of noise.

Since the least cooperative strategy in the public goods game, namely free-riding, is the most economically advantageous at low enhancement factors, we emphasise that *any* social influence rule that does not favour free-riding will result in more cooperative strategies at low enhancement factors than evolve under purely economic considerations. This may be relevant to the finding of a review of empirical studies comparing the efficacy of economic and social interventions aimed at increasing cooperative behaviour, that social interventions prove more successful [52].

Our findings lend support to other studies showing that conditional cooperation in the public goods game leads to an increase in overall cooperation, that players evolve to play conditionally [40, 41], and that an update rule that does not take the payoff into account results in more cooperative strategies [34, 44, 53]. We have extended these results by studying conditional strategies on networked populations, and considering empirically motivated strategies within the context of non-payoff based update rules on the multiplex. In contrast to [48], in our model there is no need to explicitly encourage cooperation on the social layer in order to mimic the cooperation found in the real world. The results presented are also supported by previous theoretical work [54–56], demonstrating that non-payoff based, asymmetric imitation rules result in larger frequencies of cooperation.

We have also studied networks designed to resemble the structure of real communities that manage renewable resources described in a number of empirical studies. When our model dynamics are run on such community networks the final distribution of strategies mimic those observed in real-life communities, ranging from free-riding to conditional cooperation.

We were motivated to understand the variation of conditional cooperation across real communities. However, within our model there is no penalty for an entire community that chooses to free-ride, i.e. there is no minimum payoff required for survival, no minimum resource that must be harvested. To make our model more realistic in this respect, we could extend it to include a minimum payoff threshold for survival. Our work could also be extended to investigate the importance of social influence on more complex strategies, such as the piecewise linear responses to group contributions studied in [41].

We conclude that social influence should be taken into account when modelling cooperation in social systems. In our model social influence leads to a large increase in cooperation, as long as cooperative individuals are already present in the population. Thus any intervention to increase cooperation should take account of existing social norms in the population, and the current prevalence of cooperative behaviour, rather than attempt to increase cooperation purely through economic incentives.

ACKNOWLEDGEMENTS

This work was supported by the Engineering and Physical Sciences Research Council [grant number EP/H021779/1] (Evolution and Resilience of Industrial Ecosystems, ERIE). The code used for the numerical simulations can be found at 10.5281/zenodo.801737.

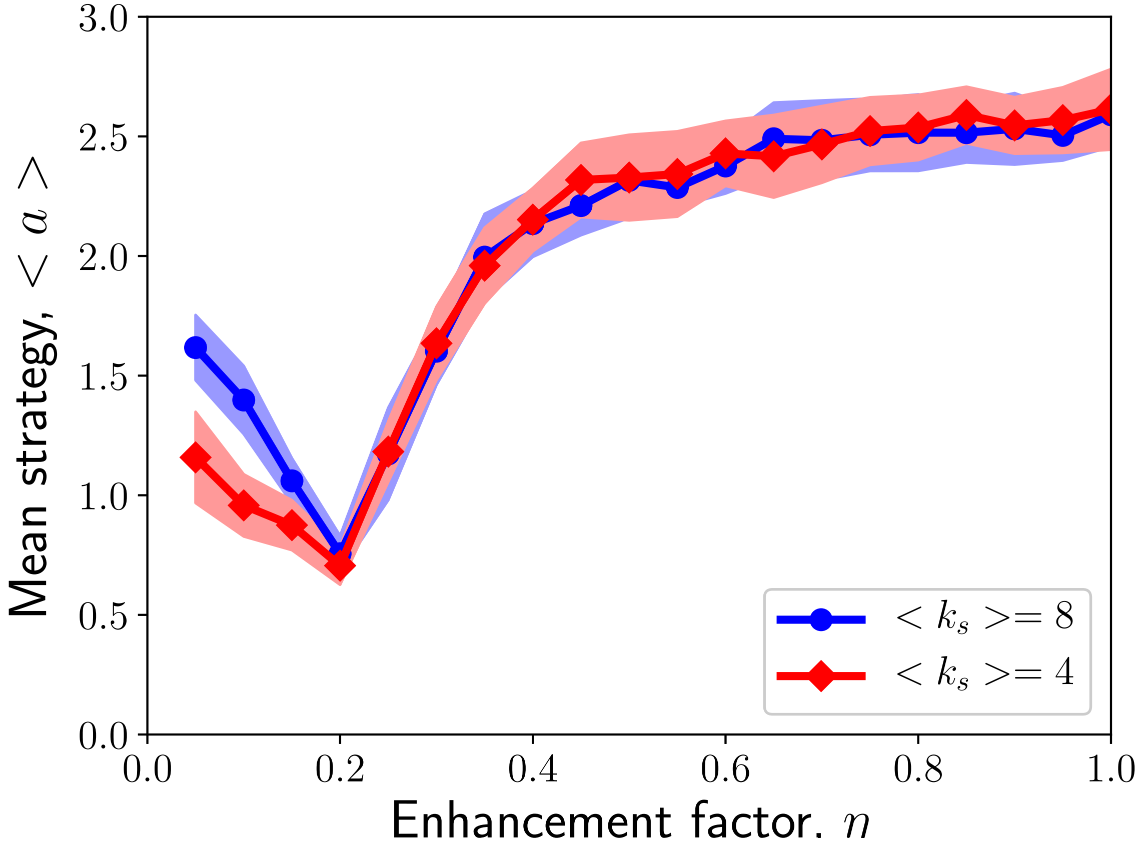

FIG. 7: The mean strategy plotted against the scaled enhancement factor $\eta = \frac{r}{\langle k_p \rangle + 1}$ for conditional cooperators on the multiplex. The mean strategy is compared for different degrees on each layer ($\langle k_s \rangle = 8$, $\langle k_p \rangle = 4$, blue circles) and equal degrees ($\langle k_s \rangle = \langle k_p \rangle = 4$, red diamonds).

APPENDIX

A.1. SIMULATION RESULTS FOR VARYING GENERATION LENGTH AND MEAN SOCIAL NETWORK DEGREE

We compare results for different generation lengths (L) and different mean degrees on the social network ($\langle k_s \rangle$). Figure 7 compares two different mean degrees on the social layer ($\langle k_s \rangle = 8$ and $\langle k_s \rangle = 4$), whilst figure 8 compares two different generation lengths ($L = 10$ and $L = 2$). The mean strategy is plotted against the scaled enhancement factor $\eta = \frac{r}{\langle k_p \rangle + 1}$ for conditional cooperators on the multiplex. The number of nodes is $N = 500$.

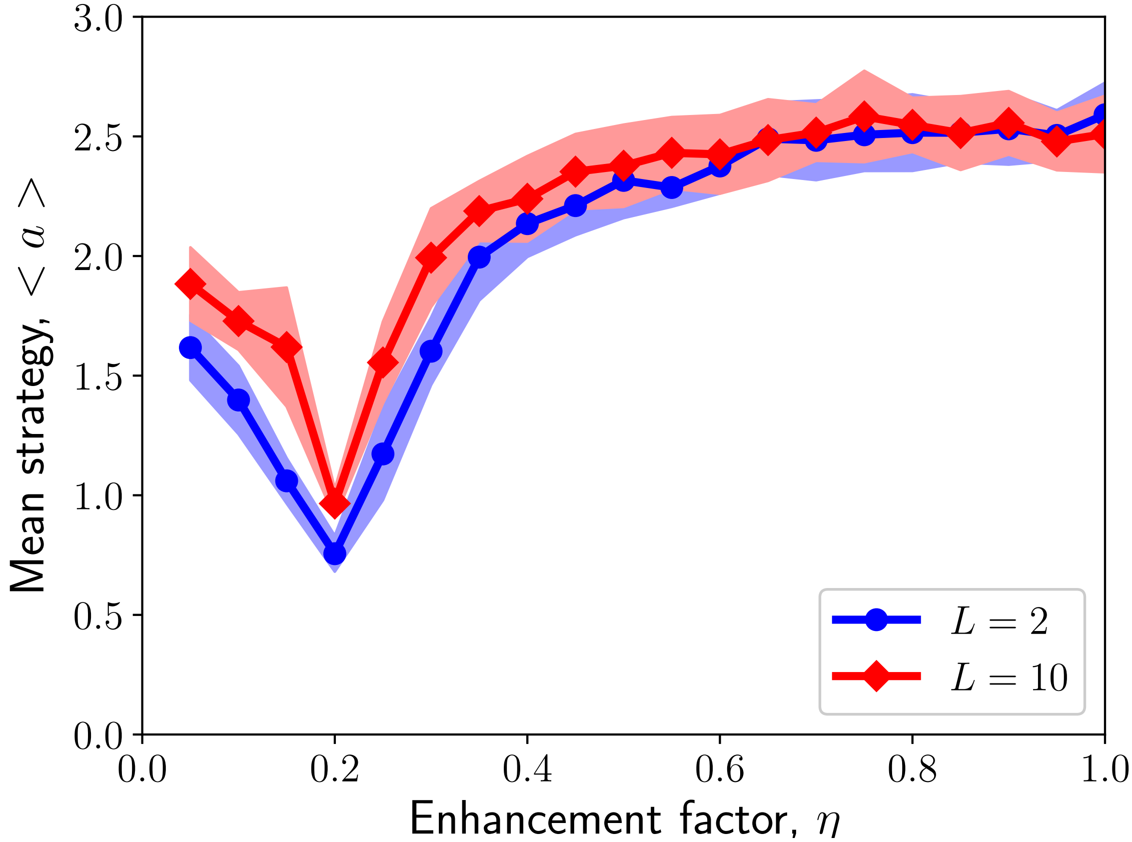

FIG. 8: The mean strategy plotted against the scaled enhancement factor $\eta = \frac{r}{\langle k_p \rangle + 1}$ for conditional cooperators on the multiplex. The mean strategy is compared for long generation lengths ($L = 10$, red diamonds) and short generation lengths ($L = 2$, blue circles).

A.2. CALCULATION OF THE PAYOFF

We show how to calculate analytically the total payoff over a single generation in a single group for small donations. For sufficiently small initial contributions $c_g(0)$ players always donate less than one. Recall from Eq. (2) that player i, with strategy a_i calculates their payoff from group g in iteration l of the game as

$$p_{i,g}(l) = rc_g(l) - c_{i,g}(l), \tag{A.1}$$

where $c_g(l)$ is the group contribution at this iteration and $c_{i,g}(l)$ is player i's contribution to this group. When players only contribute conditionally the contribution in group g with size G at iteration l is then

$$c_g(l) = \frac{\sum_{i\in g} a_i c_g(l-1)}{G} = a_g c_g(l-1), \tag{A.2}$$

where $a_g = \frac{1}{G}\sum_{i\in g} a_i$, and as long as $c_g(0) < 1$ for all l the group mean contributions are therefore given by

$$c_g(l) = a_g^l c_g(0). \tag{A.3}$$

The payoff at each iteration is thus

$$\begin{aligned} p_{i,g}(l) &= r a_g^l c_g(0) - c_{i,g}(l) && \text{(A.4)}\\ &= r a_g^l c_g(0) - a_i a_g^{l-1} c_g(0) && \text{(A.5)}\\ &= c_g(0) a_g^{l-1}\left(r a_g - a_i\right), && \text{(A.6)}\end{aligned}$$

and the total payoff for player i over a generation is

$$\begin{aligned} P_{i,g} &= \sum_{l=1}^{2} c_g(0) a_g^{l-1}\left(r a_g - a_i\right) && \text{(A.7)}\\ &= c_g(0)\left(\frac{1-a_g^2}{1-a_g}\right)\left(r a_g - a_i\right) && \text{(A.8)}\\ &= c_g(0)\left(1+a_g\right)\left(r a_g - a_i\right). && \text{(A.9)}\end{aligned}$$

A.3. PROBABILITY OF ONE STRATEGY IMITATING ANOTHER

We calculate the probability of one strategy imitating another in a population where each player plays one of two strategies a^0 or a^1 (as defined in section III B). Player i with strategy a^0 imitates player j with strategy a^1 if P_j is greater than P_i, and using Eq. (A.9) this occurs when

$$\begin{aligned} &\left(1+\frac{n_1 a^0 + (G-1-n_1)a^1 + a^1}{G}\right)\left(r\frac{n_1 a^0 + (G-1-n_1)a^1 + a^1}{G} - a^1\right)\\ &> \left(1+\frac{n_0 a^0 + (G-1-n_0)a^1 + a^0}{G}\right)\left(r\frac{n_0 a^0 + (G-1-n_0)a^1 + a^0}{G} - a^0\right)\end{aligned} \tag{A.10}$$

where r is the enhancement factor and n_0 and n_1 are the numbers of a^0 strategies in players i and j's groups respectively. Both groups are of size G. This condition can be written

$$f(a^1, a^0, n_1, n_0) > 0, \tag{A.11}$$

where

$$f(a^1, a^0, n_1, n_0) = (G + n_1 a^0 + (G-1-n_1)a^1 + a^1)(r(n_1 a^0 + (G-1-n_1)a^1 + a^1) - Ga^1) \\ - (G + n_0 a^0 + (G-1-n_0)a^1 + a^0)(r(n_0 a^0 + (G-1-n_0)a^1 + a^0) - Ga^0). \tag{A.12}$$

The probability that a player with strategy a^0 imitates a randomly selected player with strategy a^1 is the probability of selecting a player with strategy a^1 multiplied by the probability that the selected player has a larger payoff, or

$$Q_{01} = \rho_1 \sum_{n_0=0}^{G-1} \sum_{n_1=0}^{G-1} q(n_0) q(n_1) H(f(a^1, a^0, n_1, n_0)) \tag{A.13}$$

where again $H(x)$ is the Heaviside step function and $q(n)$ is the probability of a group forming with n strategy a^0 players in the rest of the group. As the rest of the group is formed at random from a bimodal distribution in the well-mixed case

$$q(n) = \binom{G-1}{n} \rho_0^n (1-\rho_0)^{G-1-n}, \tag{A.14}$$

where ρ_0 is the density (fraction) of strategy a^0 players in the population.

A similar calculation can be made to determine Q_{10}, the probability that a player with strategy a^1 imitates a randomly selected player with strategy a^0.

A.4. CRITICAL ENHANCEMENT FACTOR

The minimum enhancement factor, $\eta_c = \frac{r_c}{G}$, at which positive strategies generate higher payoffs than free-riders is the enhancement factor at which the minimum payoff of a strategy a^1 player is larger than the maximum payoff of an $a^0 = 0$ player. The maximum possible payoff is when all other group members play strategy a^1, whilst the minimum is when all other players play a^0. Therefore from Eq. (A.12) we have

$$f(a^1, 0, G-1, 0) = (G + (G-1)a^1 + a^1)(r((G-1)a^1 + a^1) - Ga^1) \\ - (G + (G-1-(G-1))a^1)(r((G-1-(G-1))a^1)) \tag{A.15}$$

$$= G^2 a^1 (1 + a^1)(r-1). \tag{A.16}$$

The critical enhancement factor occurs when $f(a^1, 0, G-1, 0) = 0$, or $r_c = 1$, and therefore

$$\eta_c = \frac{1}{G} \tag{A.17}$$

A.5. EQUILIBRIUM STRATEGY IN A WELL-MIXED BIMODAL POPULATION

We derive an expression for the mean strategy at equilibrium in a well-mixed bimodal population in terms of the probability of strategy a^v imitating strategy a^w, $Q_{vw}(t)$, and demonstrate that this is determined by the initial strategies and the rate at which each of the bimodal peaks approaches the other. We assume that the probability of one strategy imitating the other remains constant across generations for both strategies so that $Q_{vw}(t) = Q_{vw}(0) = Q_{vw}$, and use this to calculate the equilibrium strategy $\langle a \rangle$ as $t \to \infty$. Treating each strategy as independent and coherent, and using Eq. (4) the updated strategy in generation $t+1$ is given by

$$a^v(t+1) = a^v(t) + \theta Q_{vw}(t)(a^w(t) - a^v(t)). \tag{A.18}$$

Thus the expected mean strategy of a population consisting of two strategies a^0 and a^1 evolves according to

$$\langle a \rangle(t+1) = \rho_0 a^0(t+1) + \rho_1 a^1(t+1) \tag{A.19}$$

$$= \langle a \rangle(t) + \theta(a^1(t) - a^0(t))(\rho_0 Q_{01}(t) - \rho_1 Q_{10}(t)), \tag{A.20}$$

where ρ_0 and ρ_1 are the fractions of the population playing strategies a^0 and a^1 respectively. The difference between two strategies $a^1(t)$ and $a^0(t)$ in the next genetation is

$$a^1(t+1) - a^0(t+1) = a^1(t) - a^0(t) + \theta Q_{10}(a^0(t) - a^1(t)) - \theta Q_{01}(a^1(t) - a^0(t)) \tag{A.21}$$

$$= (a^1(t) - a^0(t))\,(1 - \theta Q_{10} - \theta Q_{01}) \tag{A.22}$$

and substituting $\Delta a(t) = a^1(t) - a^0(t)$ gives

$$\Delta a(t+1) = \Delta a(t)\,(1 - \theta Q_{10} - \theta Q_{01})\,. \tag{A.23}$$

Writing

$$\beta = 1 - \theta Q_{10} - \theta Q_{01} \tag{A.24}$$

we have

$$\Delta a(1) = \beta \Delta a(0), \tag{A.25}$$

which by induction gives

$$\Delta a(t) = \beta^t \Delta a(0). \tag{A.26}$$

Using $\rho_0 + \rho_1 = 1$, this gives the mean strategy as

$$\langle a\rangle(t+1) = \rho_0 a^0(t) + \rho_1 a^1(t) + \theta(a^1(t) - a^0(t))(\rho_0 Q_{01} - \rho_1 Q_{10}) \tag{A.27}$$

$$= a^0(t) + \Delta a(t)(\rho_1 + \theta(\rho_0 Q_{01} - \rho_1 Q_{10})) \tag{A.28}$$

Substituting Eq. (A.26) and letting $\gamma = \rho_1 + \theta(\rho_0 Q_{01} - \rho_1 Q_{10})$ gives

$$\langle a\rangle(t+1) = a^0(t) + \beta^t \Delta a(0)\gamma. \tag{A.29}$$

We rewrite Eq. (A.18) to give

$$a^0(t+1) = a^0(t) + \theta Q_{01}\Delta a(t) \tag{A.30}$$

$$= a^0(t) + \delta\Delta a(t), \tag{A.31}$$

where $\delta = \theta Q_{01}$. The value of the smaller strategy after one generation is then

$$a^0(1) = a^0(0) + \delta\Delta a(0), \tag{A.32}$$

and therefore after t generations is

$$a^0(t) = a^0(0) + \delta\Delta a(0)(1 + \beta + \beta^2 + ... + \beta^{t-1}) \tag{A.33}$$

$$= a^0(0) + \delta\Delta a(0)\left(\frac{1-\beta^t}{1-\beta}\right). \tag{A.34}$$

We combine this with Eq. (A.29) to give

$$\langle a\rangle(t+1) = a^0(0) + \delta\Delta a(0)\left(\frac{1-\beta^t}{1-\beta}\right) + \beta^t \Delta s(0)\gamma. \tag{A.35}$$

Since we have $\theta > 0$, $0 < Q_{vw} < \rho_w$ and $\rho_0 + \rho_1 = 1$, then from Eq. (A.24) we must also have $0 < \beta < 1$, and so we find

$$\langle a\rangle(\infty) = \lim_{t\to\infty}\langle a\rangle(t) = a^0(0) + \frac{\delta\Delta a(0)}{1-\beta}. \tag{A.36}$$

Substituting β and δ as defined above into this Eq. gives

$$\langle a\rangle(\infty) = a^0(0) + \frac{\theta Q_{01}\Delta a(0)}{1-(1-\theta Q_{10} - \theta Q_{01})} \tag{A.37}$$

$$= a^0(0) + \frac{\Delta a(0)}{1 + Q_{10}/Q_{01}} \tag{A.38}$$

From this equation we see that the final equilibrium mean strategy depends on the ratio of the probabilities of each strategy imitating the other, and the initial strategies.

We confirm that Eq. (A.38) is a good fit by plotting the mean strategy at equilibrium, for both numerics and Eq. (A.38), against the scaled enhancement factor η in figure 9. Once again the initial strategies are $a^1(0) = 5$ and $a^0(0) = 0$.

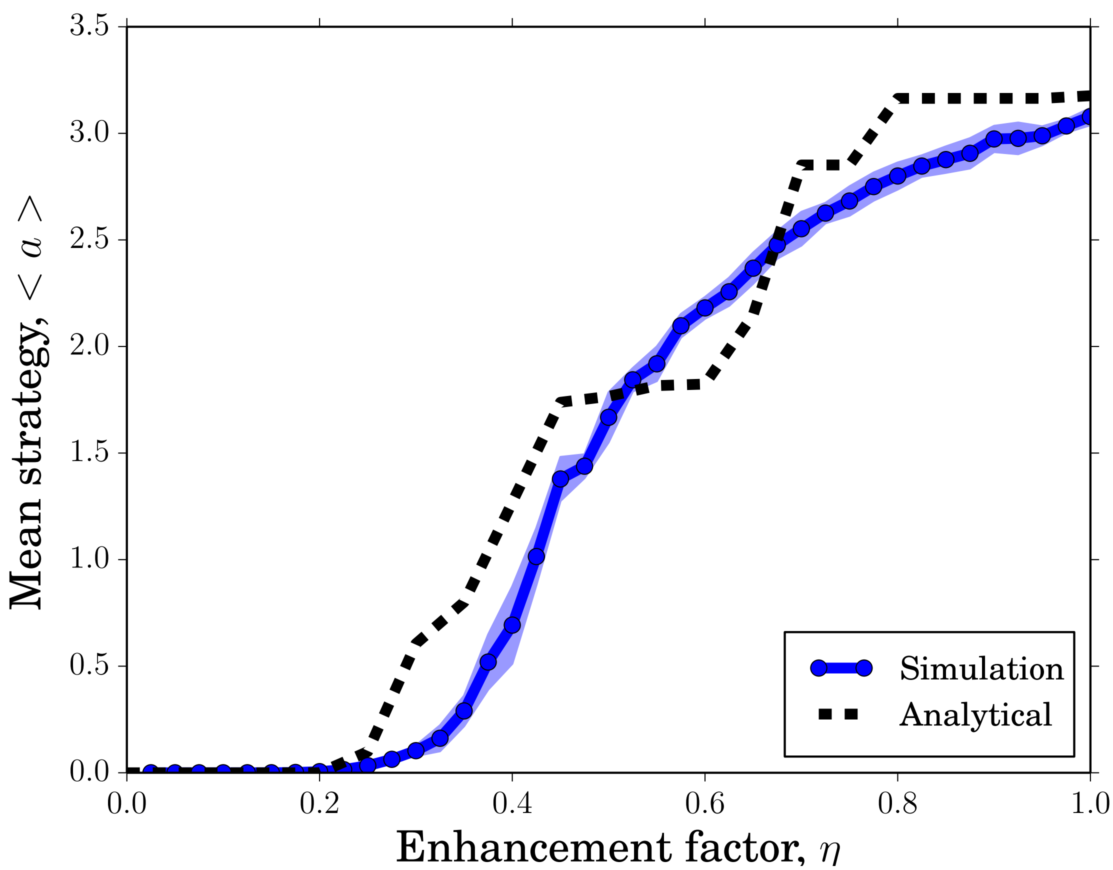

FIG. 9: The mean strategy plotted against the scaled enhancement factor η with bimodal initial conditions $a^0(0) = 0$ and $a^1(1) = 5$ for numerics (single points) and analytics (dashed lines from Eq. (A.38)). The imitation strength is $\theta = 0.1$ and the group size is $G = 5$.

A.6. NETWORK RECIPROCITY

Network reciprocity is confirmed by plotting the strategy of each player against the mean strategy of the player's neighbours (Fig. 10). Strategy segregation (network reciprocity) does indeed emerge over time: at early times (Fig. 10, top row) the player and neighbour strategies are not strongly correlated, and many of the extreme strategies have not changed. After $t = 50$ generations, however, a very strong correlation between a player's strategy and that of its neighbours emerges (bottom rows), with correlation coefficient 0.71 for $\eta = 0.5$.

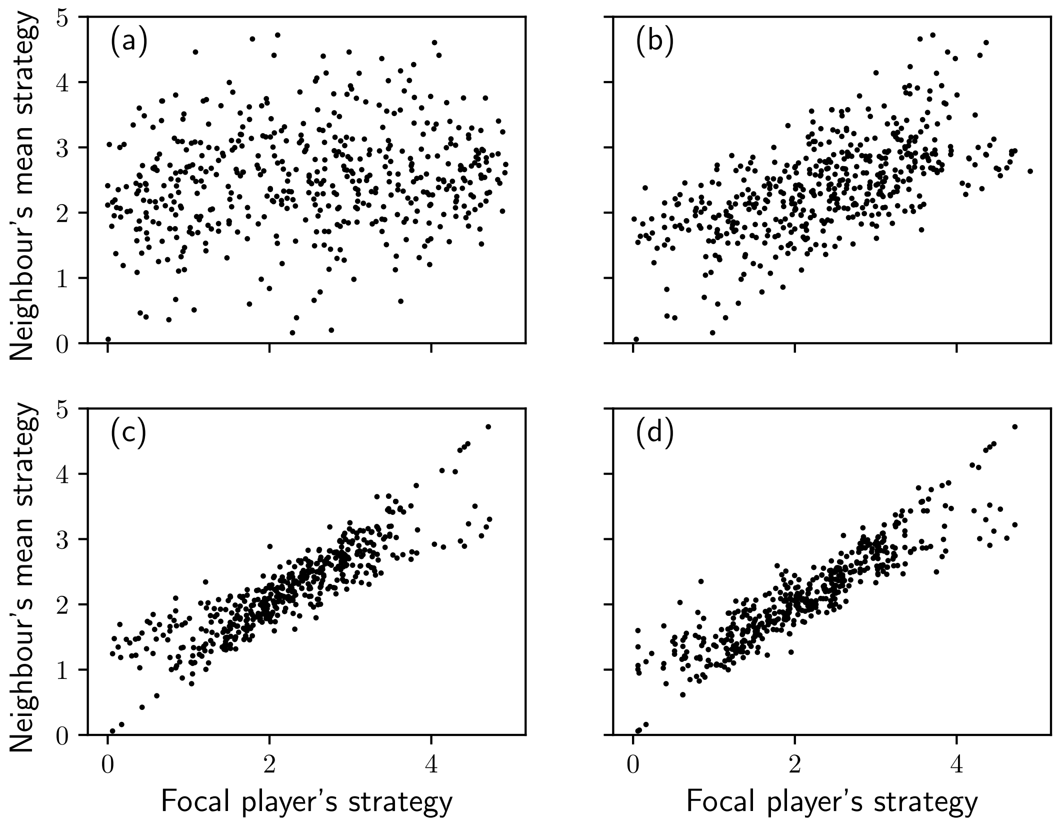

FIG. 10: The mean strategy of a node's neighbours plotted against that node's strategy in the network for scaled enhancement factor $\eta = 0.5$. Plots are for figure a) at generation $t = 1$ with Pearson correlation coefficient between the node's strategy and the mean strategy of its nearest neighbours 0.15, b) at generation $t = 10$ with correlation 0.51, c) at generation $t = 50$ with correlation 0.71 and d) at generation $t = 500$ with correlation 0.75.

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