

# Social Context and the Evolution of Empathy

## Abstract

*Human societies differ in the social context of their economic interactions: whereas hunter-gatherers depend primarily on familiars for their subsistence, people in market societies depend primarily on strangers. This variation raises a critical question: How does social context influence the evolution and behavioral expression of empathy? Experimental evidence consistently shows that empathy increases with social closeness. Using evolutionary game theory, I examine how empathy evolves in various social-economic ecologies. I situate the evolutionary game on a network with distinct social and economic layers and define empathy as cooperating conditional on social proximity. The results reveal that when interactions occur among both familiars and strangers, discriminatory empathy outperforms unconditional cooperation, but when interactions occur only among strangers, empathy produces no cooperation. These findings highlight the behavioral consequences of modern human ecologies characterized by anonymity and provide insights for designing institutions and structuring human ecologies that better foster cooperation.*

We are a social species. Our aptitude for cooperation and social learning has enabled us to adapt to a wide variety of ecosystems and organize into diverse sociocultural configurations. This array of human ecologies gives rise to cooperation problems that range in scale and scope from mammoth hunts to climate change. Simultaneously, human ecology shapes the evolution and expression of cooperative behaviors such as empathy. In this paper, ecology refers to the pattern of relationships between individuals and their environments<sup>1</sup>, cooperation refers to any action that is individually costly but collectively beneficial<sup>2</sup>, and empathy refers to an internal state that motivates cooperative action contingent on social proximity<sup>3</sup>. The social context of economic interactions constitutes an important dimension of human ecology that varies across different societies. Whereas hunter-gatherers know most of those whom they depend upon for subsistence, the constituents of market societies depend primarily on strangers. In this paper, I explore the effects of social context on the evolution and behavioral expression of empathy.

Empirical evidence indicates that cooperation increases with the sociality of the interaction context. Game theoretic experiments have demonstrated this effect by manipulating social context in various ways. Reducing anonymity by identifying subjects by name or photograph or by conducting the game in a face-to-face setting tends to promote cooperation<sup>4–17</sup>, and so does permitting discussion among subjects before the game<sup>4,18–23</sup>. Revealing the group identities of subjects tends to prompt in-group cooperation<sup>24–27</sup>. Most notably, in non-anonymous games, social distance between interaction partners in their real-world social networks correlates negatively with cooperation<sup>11,28–31</sup>. Similarly, questionnaires of hypothetical choices suggest that cooperation increases with subjective relational closeness<sup>32–40</sup>.

Psychologists also expound the importance of relational context in understanding cooperative behavior<sup>32,41</sup>, especially in the literature on empathy. Although empathy has been defined in a number of ways<sup>3,42</sup>, the concept generally refers to a cognitive, affective, and/or behavioral response of one individual to the state of another<sup>3,43</sup>. Empathic responses are mediated by psychological and social context<sup>3,44–48</sup>. Namely, empathy increases with familiarity, similarity, past experience, and salience<sup>43,44,46,48–50</sup>. These effects of “psychological distance”<sup>3</sup> or “relationship closeness”<sup>45</sup> encapsulate the general observation that the strongest empathic responses occur between close friends or family and the weakest between out-group strangers<sup>3</sup>. The internal cognitive and affective aspects are often associated with cooperative behavior<sup>3,20,21,42–</sup>

<sup>47,49,51–55</sup>. In game theoretic experiments, encouraging perspective-taking in the game instructions increases cooperation<sup>20,21,23,54,56</sup>. Measures of dispositional empathy sometimes correlate with cooperation<sup>55,57,58</sup>, and sometimes do not<sup>14,58–62</sup>, but notably, all those experiments that did not demonstrate an effect were conducted in anonymous settings.

These experimental findings suggest we are more prone to empathize and cooperate in situations that are more saliently social and with individuals who are socially closer to us. How might this strategy of cooperating conditional on social proximity have evolved? And how does the social context of interactions influence its evolution?

Whereas situational effects of sociality on cooperation are readily observable in experimental settings, evolutionary effects are not. Evolutionary game theory provides a framework for analyzing evolutionary dynamics by modelling the persistence and spread of behavioral strategies in a population as a function of the relative payoffs the strategies yield in intrapopulation game interactions. The human behavioral repertoire (including cooperation) is a product of interacting genetic and cultural evolution<sup>63–65</sup>. Genes persist and spread via survival and reproduction of the carrier. Cultural traits spread via social learning. Given the long history of misuse and misinterpretation of evolutionary concepts applied to humans<sup>1</sup>, it is important to distinguish between explanation and justification: evolution is not synonymous with progress nor is fitness synonymous with desirability.

Cooperation poses an evolutionary puzzle given the separation of the actor from the benefits of their action. If individuals interact randomly with each other and employ unconditional strategies (always cooperate or never cooperate), those who never cooperate inevitably accumulate a higher payoff than those who always cooperate. Cooperation can only evolve if the benefits of cooperation are sufficiently concentrated among cooperators, such that the average cooperation benefits received by cooperators exceed the cooperation costs they pay. This logic applies to both cultural and genetic evolution and can thus produce both learned and innate cooperative traits. Hamilton's rule expresses this logic in mathematical form:  $rb > c$ , where  $b$  and  $c$  represent, respectively, the benefits and costs of cooperation and  $r$ , the relatedness coefficient, represents the proportion of cooperation benefits received by cooperators<sup>66–69</sup>. This concentration of benefits among cooperators can occur through assortment due to the coincidence of behavioral transmission and interaction ecologies as in the cases of kin selection<sup>67</sup>, group selection<sup>66</sup>, and

static networks<sup>70</sup>, or it can arise through conditional behavior as in the cases of direct and indirect reciprocity<sup>71–73</sup>, parochial altruism<sup>66</sup>, altruistic punishment<sup>63</sup>, and choice of interaction partners (which results in assortment)<sup>74</sup>. These evolutionary mechanisms may manifest in a variety of proximate behavioral motives including social emotions<sup>3,43,44,51,66</sup> and internalized or externally enforced social and moral norms<sup>63,66,75–77</sup>.

To analyze the effects of social context on the evolution of cooperative behaviors, I develop a model consisting of an evolutionary game situated on a network with distinct social and economic layers (Fig. 1,2). The game interactions occur on the economic layer, and behavioral strategy transmission occurs on the social layer. In this way, I can vary the social context of the evolutionary game by varying the social-economic overlap of the network. Earlier studies have found that in the case of a single-layer network where both game interactions and strategy transmission occur, unconditional cooperation can persist and spread if the gains from cooperation are larger than the number of interaction and transmission neighbors<sup>78</sup>. The network structure in these models results in strategy assortment, thereby promoting the evolution of cooperation. Separating the loci of strategy transmission and game interactions can undermine the evolution of unconditional cooperation by lessening the assortment of strategies<sup>79–81</sup>. In the case of genetic evolution, the strategy transmission network represents a network of kin; in the case of cultural evolution, it represents a network of social learning. This suggests that unconditional cooperation can evolve only when the interaction context is highly social. But what if cooperation is conditioned on social proximity?

I define empathy as the strategy of cooperating with those within a certain range in the social network and defecting against everyone further away. While several others have operationalized empathy in a utility function or as a game theoretic strategy<sup>82,83</sup>, the social distance conditionality is novel. Each of the situational and relational mediating factors associated with increased empathy in the psychology literature<sup>46</sup> can be related to proximity in a social network: familiarity by the definition of a social relation, similarity due to network homophily<sup>84</sup>, past experience from durable social relationships, and salience in the context of face-to-face interactions. To analyze the evolutionary viability and stability of empathy, I estimate fixation probabilities numerically by running simulations of my evolutionary game model, and I apply the method of pair approximation<sup>85</sup> to obtain an analytical rule for the evolution of empathy. The numerical and

analytical results show that discriminatory empathy is adaptive when interactions occur among both familiars and strangers, but as anonymity increases, empathy results in less cooperation.

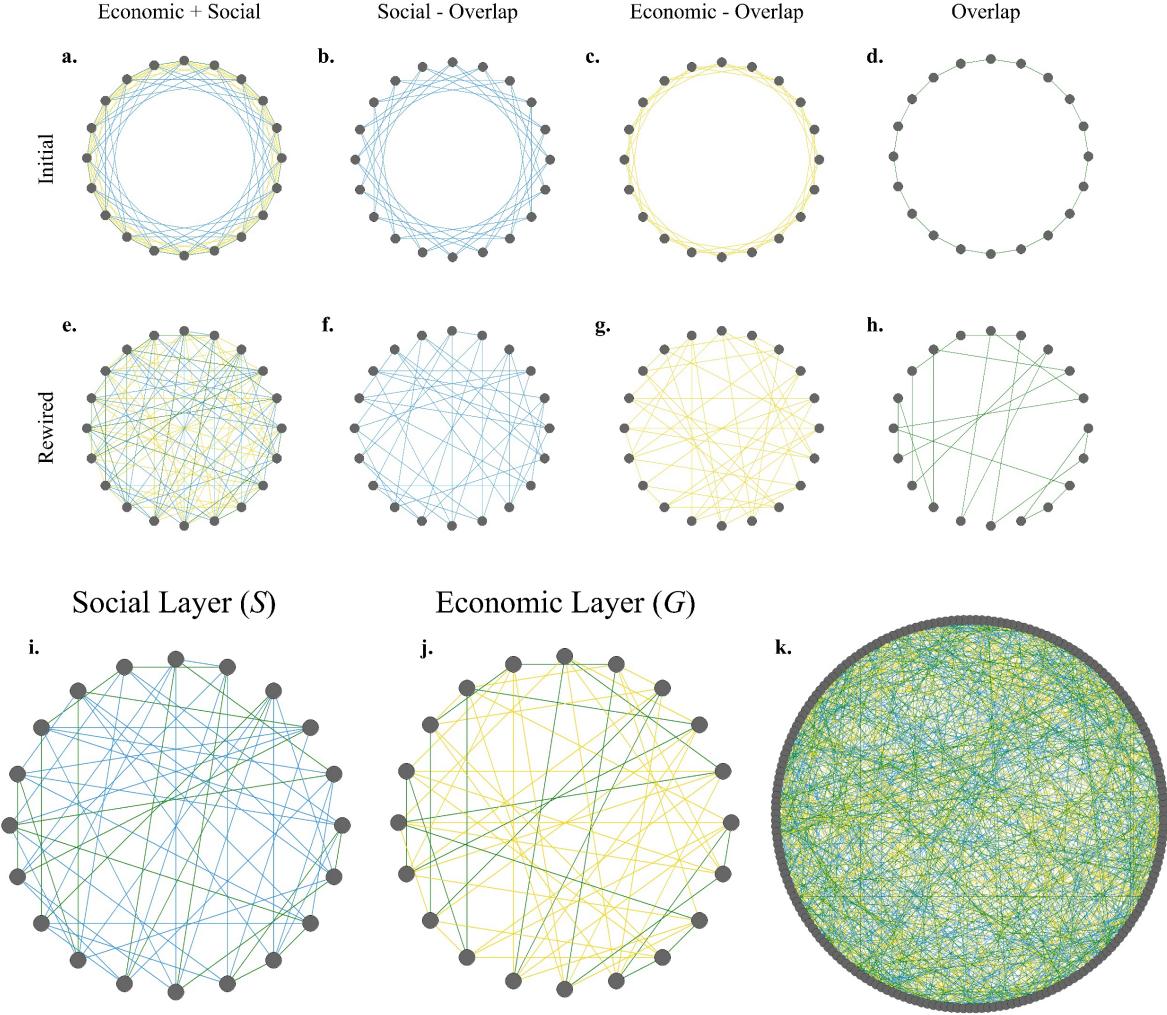
## Results

### Model

The model I develop consists of a prisoner’s dilemma game, the competing strategies for playing the game, the fitness function dictating how strategies spread, and the multilayer network on which the evolutionary game dynamics occur. I run evolutionary game simulations and apply a technique called pair approximation to derive numerical and analytical results describing the impact of social context on the evolution of empathy.

The two-layer network structures the interactions among the population of  $N$  nodes. The game occurs on the economic layer ( $G$ ), and the strategy updating occurs on the social layer ( $S$ ). The overlap network ( $O$ ) is obtained from the intersection of the edge sets of  $G$  and  $S$ . The economic, social, and overlap networks are all regular degree: Every node has  $g$  economic neighbors and  $s$  social neighbors,  $o$  of which are both social and economic neighbors. (The term “regular” refers to the constant number of neighbors or “degree”.) The sociality of the interaction context is represented by the overlap degree divided by the economic degree  $\frac{o}{g}$ , which indicates the proportion of interactions which occur among familiars. To generate a random regular multilayer network from the set of all possible regular multilayer networks given the parameters  $N$ ,  $g$ ,  $s$ , and  $o$ , I construct a circulant network of degree  $g + s - o$ , partition the edges into  $(G - O)$ ,  $(S - O)$ , and  $O$ , stochastically rewire the edges of each partitioned edge set, and reconstruct  $G$  and  $S$ . Figure 1 illustrates this network generation algorithm, which I developed by modifying the Watts-Strogatz model<sup>86</sup>. A detailed description can be found in Supplementary Information.

**Fig. 1: Generating a multilayer network**



*Notes:* The evolutionary game takes place on a random regular  $N$ -node multilayer network with distinct social and economic layers. Both layers are random regular networks, and the intersection of the layers is also a random regular network, so every node has the same number of economic neighbors ( $g$ ), the same number of social neighbors ( $s$ ), and the same number of social-economic neighbors ( $o$ ). The random regular multilayer networks used in the simulations are constructed by partitioning and rewiring circulant networks. **a.–h.** depict the rewiring of the circulant union network,  $S \cup G$ , and each of its partitioned subsets:  $S - O$ ,  $G - O$ , and  $O$  ( $N = 20$ ,  $g = s = 4$ ,  $o = 2$ ). **i.** depicts the social layer obtained from  $S = S - O + O$  (i.e. from the union of **f.** and **h.**). **j.** depicts the economic layer obtained from  $G = G - O + O$  (i.e. from the union of **g.** and **h.**). **k.** depicts an example of a multilayer network used in the actual simulations ( $N = 200$ ,  $g = s = 8$ ,  $o = 4$ ) with the edges of  $S - O$ ,  $G - O$ , and  $O$  colored blue, yellow, and green, respectively.

The nodes of this network interact and update their strategies in a series of rounds. During each round, every node plays a one-shot game with each of their economic neighbors. In these games, each player chooses to either cooperate or defect (Fig. 2). The act of cooperation consists of paying a cost  $c$  to convey a benefit  $b$  to the other player, where  $c > 0$  and  $b > c$ . The act of defection

is costless and conveys no benefit to the other. The game defined by these actions and payoffs is an example of a prisoner's dilemma.

**Fig. 2: Game payoffs**

		Cooperate	Defect
		Cooperate	$b - c$
Cooperate	Cooperate	$b - c$	$b$
	Defect	$-c$	0
Defect	Cooperate	$b$	0
	Defect	$-c$	0

*Notes:* Each round, every node plays a one-shot prisoner's dilemma with each of its economic neighbors, accumulating payoffs according to the payoff matrix shown.  $b$  and  $c$  denote the benefits and costs of cooperation, respectively.

Each node plays the game according to their inherited or learned behavioral strategy. This strategy is defined by an empathetic range variable,  $x_i \in \mathbb{N}$ , which indicates that node  $i$  will cooperate with every economic neighbor who is  $x_i$  or fewer social edges away and defect against all others. In other words,  $i$  will cooperate with  $j$  if and only if  $d_{i,j} \leq x_i$ , where  $d_{i,j}$  is the distance between  $i$  and  $j$  in the social layer of the multilayer network. If  $x_i = 0$ , node  $i$  defects unconditionally. If  $x_i \geq \text{diameter}(S)$ , node  $i$  cooperates unconditionally. If  $x_i \in (0, \text{diameter}(S))$ , node  $i$  cooperates conditional on social proximity. Throughout this paper, I refer to these three types as defectors, unconditional cooperators, and empathizers, respectively. Note that empathizers who cooperate only with social neighbors ( $x_i = 1$ ) behave identically to unconditional cooperators in the context of full sociality ( $\frac{o}{g} = 1$ ) but behave identically to defectors in the absence of sociality ( $\frac{o}{g} = 0$ ).

The prevalence of cooperation in a population of empathizers thus depends directly on the sociality of the interaction context. I demonstrate in Supplementary Information how this behavioral

strategy defined by  $x_i$  can be obtained from a utility function with an other-regarding component that decays with social distance.

Each round, each node,  $i$ , accumulates a total payoff from the games played with their economic neighbors:

$$\Pi_i = \sum_{m \in N_i(G)} \pi_{i,m} \quad (1)$$

$N_i(G)$  denotes the set of economic neighbors of  $i$ . The fitness of node  $i$  (i.e.  $i$ 's propensity to spread its behavioral strategy) is then calculated from this total payoff according to the following equation<sup>78,79</sup>:

$$f_i = 1 - w + w \cdot \Pi_i \quad (2)$$

where  $w \in [0,1]$  is the strength of selection. This parameter specifies the importance of payoffs in the updating dynamic. When  $w = 0$ , strategies spread according to neutral drift (i.e. they spread stochastically and independently from payoffs); when  $w = 1$ , strategies spread according to the relative size of the payoffs reaped by the strategy-bearing nodes.

Each round, after all games have been played, one node is selected randomly from the population to update their strategy by emulating one of their social neighbors. This updating mechanism is called the death-birth rule<sup>79</sup>. The updating node,  $i$ , adopts the strategy of any one of their social neighbors,  $j$ , with a probability proportionate to  $j$ 's relative fitness:

$$P(i \text{ emulates } j) = \frac{f_j}{\sum_{m \in N_i(S)} f_m} \quad (3)$$

where  $N_i(S)$  is the set of social neighbors of  $i$ .

I analyze the evolutionary properties of cooperation in this model by employing two different approaches, one numerical and the other analytical. For the first, I run simulations to estimate fixation probabilities (the probability of a single invading strategies spreading to the entire population). For the second, I apply the technique of pair approximation to derive an analytical rule describing the game and network conditions under which cooperation can spread.

## Numerical results

Simulations begin with one invading strategy placed in a population of another strategy and run until one of the two competing strategies has fixated (i.e. eliminated its competitor). I estimate cooperator fixation probabilities by running 8000 simulations and calculating the proportion of these simulations that end in cooperator fixation. I am interested not only in the conditions under which cooperators might invade a population of defectors (viability) but also the conditions under which a population of cooperators might fend off invading defectors (stability). Both cooperative and non-cooperative equilibria can be found in any society, so understanding how cooperation is maintained is just as important as understanding how it is initially fostered. And as the results show (Fig. 3, 4), viability and stability are not symmetric since cooperators rely on assortment for their fitness advantage.

To run one of these simulations, I must specify network parameters,  $N$ ,  $g$ ,  $s$ , and  $o$ , game parameters,  $b$  and  $c$ , and the selection strength,  $w$ . I limit the  $N$  to 200 and  $g$  and  $s$  to 8 in my main numerical analysis (Fig. 4), and my analytical results suggest little generality is lost in this specification. I vary the overlap degree,  $o$ , from 0 to 8 by steps of 2 to analyze the evolutionary dynamics under various social contexts. (The step size is constrained by the network generation algorithm.) I vary the relative gains from cooperation,  $\frac{b}{c}$ , around a median value of 8 to capture the interactive effects of network structure and game payoffs on the evolutionary dynamics. Earlier findings by Ohtsuki et al.<sup>78,79</sup> as well as my own numerical and analytical results suggest that the boundary of the evolutionary feasibility of cooperation lies in this region of the game-network parameter space (where  $\frac{b}{c}$  is close to  $g$  and  $s$ ). I vary  $\frac{b}{c}$  by varying  $b$  and holding  $c$  constant at  $c = 1$ . Multiplying both  $b$  and  $c$  by a scalar alters the payoff of every outcome by the same factor. Scaling the payoffs up or down in this manner is equivalent to altering the strength of selection ( $w$ ). I conduct my primary analyses under conditions of weak selection ( $w = 0.1$ ) in accordance with much of the theoretical literature on the evolution of cooperation on networks<sup>78–81,87,88</sup>. In Supplementary Information, I discuss selection strength more extensively and analyze its impact on the evolution of cooperation (see Supplementary Figures 2 and 3).

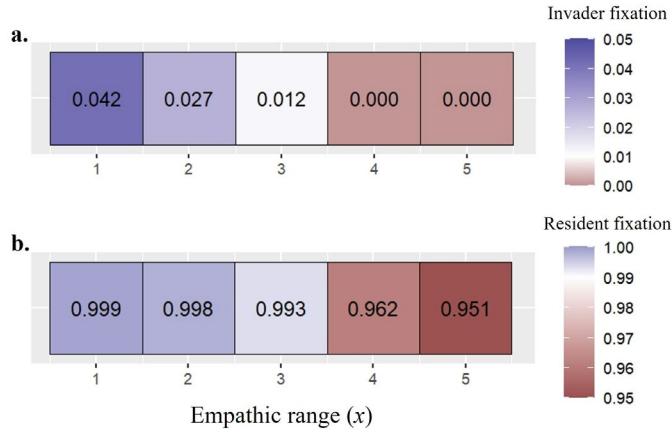
The fixation probability estimates of the evolutionary game simulations indicate that whereas unconditional cooperation relies on a highly social interaction context to evolve, empathy

(cooperation conditional on social proximity) can persist and spread when this sociality is low as long as the relative gains from cooperation are sufficiently large (Fig. 4). In other words, the numerical results suggest that conditioning cooperation on social proximity is adaptive when interactions occur among both familiars and strangers.

A strategy is selected for if its fixation probability is larger than that of a neutral mutant  $\left(\frac{1}{N}\right)$ . In Figures 3 and 4, fixation probability estimates for invading cooperators larger than (smaller than)  $\frac{1}{N}$  are colored blue (red). Similarly, fixation probability estimates for resident cooperators larger than (smaller than)  $1 - \frac{1}{N}$  are colored blue (red). Thus, blue (red) cells indicate game and network conditions under which cooperation is selected for (against). Note that in the absence of sociality ( $o = 0$ ), empathizers are no different from defectors, so their fixation probability estimates hover around those of neutral mutants, and in the context of full sociality ( $o = g$ ), empathizers are no different than unconditional cooperators, so their fixation probability estimates align.

Figure 3 reports the fixation probability estimates for empathizers with different empathic ranges ( $x = 1, 2, 3, 4, 5$ ) competing against defectors in the context of partial sociality  $\left(\frac{o}{g} = 0.5\right)$  when the gains from cooperation are slightly larger than the social and economic degrees  $\left(\frac{b}{c} = 6 > g = s = 4\right)$ . These conditions select for all empathy variants with  $x \leq 3$ . More generally, fitness decreases with empathic range.

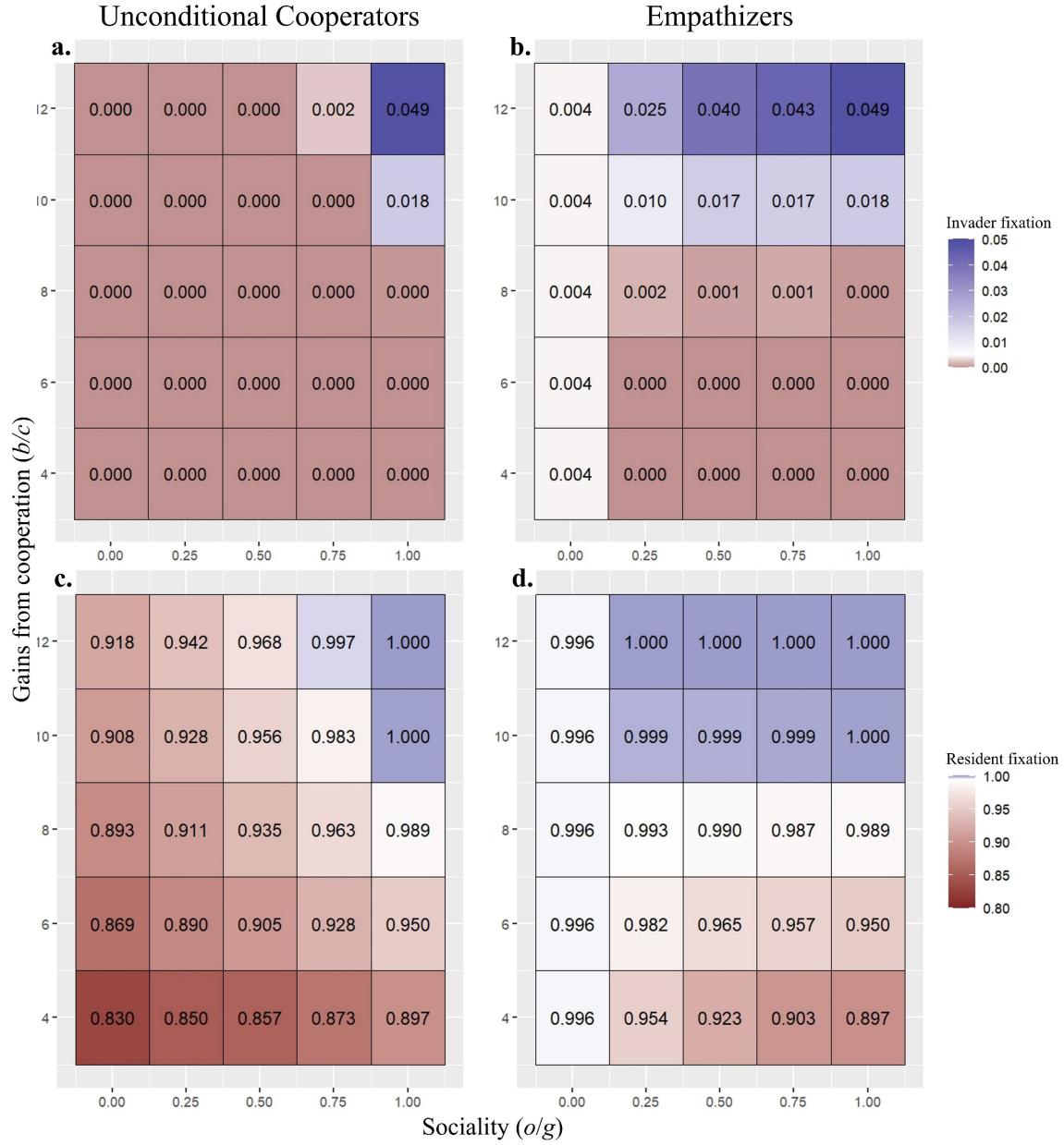
**Fig. 3: The evolutionary advantage of conditioning cooperation on social proximity**



*Notes:*  $N = 100$ ,  $g = s = 4$ ,  $o = 2$ ,  $w = 0.1$ ,  $b = 6$ ,  $c = 1$ , 8000 simulations per estimate. In the case of partial sociality ( $o/g = 0.5$ ), evolutionary game simulations suggest that conditioning cooperation on social proximity is adaptive. Fitness appears to decrease with empathetic range. **a.**, The fixation probability estimates for empathizers with different ranges introduced into a population of defectors (viability). **b.**, The fixation probability estimates for resident empathizers with different ranges fending off invading defectors (stability). Empathizers with a range of 1 cooperate only with social neighbors whereas empathizers with a range of 5 cooperate with almost everyone. If a cell is blue (red), the empathizers are selected for (against).

Figure 4 reports the fixation probability estimates for unconditional cooperators ( $x \geq \text{diameter}(S)$ ) and empathizers ( $x = 1$ ) competing against defectors under various conditions of sociality and gains from cooperation. The fitness of unconditional cooperators increases with gains from cooperation as well as sociality. Empathizer fitness increases with gains from cooperation, but its relation to social context is more complex. In the context of partial sociality ( $\frac{o}{g} > 0$ ) and when the gains from cooperation exceed the degrees of the social and economic layers ( $\frac{b}{c} > 8 = s = g$ ), empathizers are selected for (viability fixation probability estimates exceed  $\frac{1}{N}$ , and stability fixation probability estimates exceed  $1 - \frac{1}{N}$ ). Below this  $\frac{b}{c}$  threshold, empathizers are selected against. Viability fixation probability estimates increase with sociality when  $\frac{b}{c} > 8$ , but stability fixation probability estimates decrease with sociality when  $\frac{b}{c} < 8$ . The explanation is this: as sociality increases, empathizers cooperate more, and when the gains from cooperation are sufficiently high, this increases their average fitness relative to competing defectors, but when the gains from cooperation are low, this decreases their average fitness relative to competing defectors.

**Fig. 4: The impact of social context on the evolution of cooperation**



*Notes:*  $N = 200$ ,  $g = s = 8$ ,  $w = 0.1$ ,  $c = 1$ , 8000 simulations per estimate. Unconditional cooperation relies on high sociality and gains from cooperation to evolve, but discriminatory empathy can persist and spread even when sociality is low as long as the gains from cooperation are sufficiently large. **a, b**, The fixation probability estimates for cooperators invading a population of defectors (viability). **c, d**, The fixation probability estimates for resident cooperators fending off invading defectors (stability). **a, c**, The estimates for unconditional cooperators. **b, d**, The estimates for empathizers who cooperate only with social neighbors. If a cell is blue (red), the cooperators are selected for (against).

## Analytical results

In their 2007 paper<sup>79</sup>, Ohtsuki, Nowak, and Pacheco apply the technique of pair approximation to an evolutionary game model on a multilayer network and find that unconditional cooperation is favored by selection when  $\frac{b}{c} > \frac{g \cdot s}{o}$ . I apply this technique to replicate this rule for the evolution of unconditional cooperation and to derive a similar rule for the evolution of empathy:  $\frac{b}{c} > s$ . This analytical result aligns with the numerical results. Both suggest that discriminating on the basis of social distance mitigates the damage low sociality inflicts on the evolutionary feasibility of cooperation.

Pair approximation comprises a method for approximating evolutionary dynamics and equilibrium conditions on networks by focusing on the dynamics as they occur among node pairs<sup>85</sup>. This abstraction away from the complex geometry of the full network makes possible the derivation of differential equations that describe the essential dynamics of the model. In the context of the model in this paper, pair approximation shows that when selection strength is weak ( $w \ll 1$ ), the local density of strategies on the network equilibrates faster than the global density of strategies. The strategy with the higher fitness in this local strategy density equilibrium is likely to prevail in the simulation.

Let  $p_A$  be the prevalence of strategy A in the entire population, and let  $q_{A|B}^{(*)}$  be the probability that any \* neighbor of a B-strategy node is an A-strategy node (i.e.  $q_{A|B}^{(*)}$  represents the local density of A around B in the \* layer). Then, in a population of competing A and B strategies, the following identities always hold:

$$q_{A|A}^{(G-O)} = q_{A|B}^{(G-O)} = p_A \quad (4)$$

$$q_{*|*}^{(O)} = q_{*|*}^{(S)} \quad (5)$$

On the network of edges belonging only to the economic layer ( $G - O$ ), the probability of a neighbor of either strategy being an A player is equal to the global prevalence of that strategy. The local strategy densities on the social ( $S$ ) and overlap ( $O$ ) layers are identical since the overlap layer is a subset of the social layer.

In the case of weak selection,  $q_{A|A}^{(S)}$  equilibrates before  $p_A$  does. This local strategy density equilibrium approximates the state of the population in the simulations while  $p_A \in \left(\frac{1}{N}, 1 - \frac{1}{N}\right)$ . In this equilibrium, the following relationship holds:

$$q_{A|A}^{(S)} - q_{A|B}^{(S)} = \frac{1}{s-1} \quad (6)$$

In words, A nodes are more likely than B nodes to be social neighbors with other A nodes. This strategy homophily (i.e. clustering of strategies) arises on the social layer because social neighbors may, at some point, have acquired their current strategies from one another. The mathematical derivation can be found in Supplementary Information.

To compare the fitness of two strategies competing for emulation in this equilibrium, I must compare their payoffs, and to compare their payoffs, I must compare their expected economic neighborhoods. But since  $q_{A|A}^{(G-O)} = q_{A|B}^{(G-O)} = p_A$ , the difference in economic neighborhoods is the same as the difference in overlap neighborhoods. Let  $A_A$  be the number of A nodes in the overlap neighborhood of an A node and  $A_B$  be the number of A nodes in the overlap neighborhood of a B node. From the local strategy density equilibrium relationship (Supplementary Information), I find that

$$E(A_A - A_B) = \frac{o}{s} \quad (7)$$

Thus, the expected difference in total round payoffs between an unconditional cooperator ( $C$ ) and a defector ( $D$ ) competing for emulation is given by

$$E(\Pi_C - \Pi_D) = (b \cdot C_C - c \cdot g) - (b \cdot C_D) = \frac{b \cdot o}{s} - c \cdot g \quad (8)$$

which is positive when

$$\frac{b}{c} > \frac{g \cdot s}{o} \quad (9)$$

This inequality—originally derived by Ohtsuki et al.<sup>79</sup>—specifies the conditions of sociality and gains from cooperation under which unconditional cooperation is selected for.

In the case of empathizers who cooperate only with social neighbors ( $x = 1$ ), the expected difference in total round payoffs between an empathizer ( $M$ ) and a defector ( $D$ ) competing for emulation is given by

$$E(\Pi_M - \Pi_D) = (b \cdot M_M - c \cdot o) - (b \cdot M_D) = \frac{b \cdot o}{s} - c \cdot o \quad (10)$$

which is positive when

$$\frac{b}{c} > s \quad (11)$$

This inequality specifies that empathy is selected for as long as the gains from cooperation exceed the degree of the social layer.

The numerical estimates from the simulations corroborate the analytical rules for both unconditional cooperators and empathizers.

The evolutionary success of any strategy in the simulations depends firstly on its capacity to duplicate before being eliminated (Supplementary Fig. 3) and secondly on its relative fitness in the local strategy density equilibrium. Under weak selection, cooperators invading a population of defectors may survive to the local density equilibrium; then, if the network and game conditions satisfy the relevant analytical rule, the invading cooperators reap a higher average payoff and are therefore likely to spread. Similarly, under weak selection, defectors invading a population of cooperators may survive to the local density equilibrium; then, if the network and game conditions satisfy the relevant analytical rule, the resident cooperators reap a higher average payoff and are therefore likely to fend off the defectors.

## Discussion

In this paper, I developed an evolutionary game model on a multilayer network to explore the impact of social context on the evolution of cooperation. The main results are intuitive: when we interact with both familiars and strangers, it is adaptive to cooperate with the former but not the latter. Low sociality impedes the evolution of unconditional cooperation but not the evolution of socially-contingent cooperation—i.e. empathy. However, if empathy spreads to the whole

population (i.e. fixates), the prevalence of cooperative behavior depends directly on the degree of sociality.

Empathy, as I have defined it, combines the evolutionary tactics of discrimination and assortment to concentrate the benefits of cooperation among cooperators: empathizers cooperate with those who, due to the strategy transmission process, are more likely than chance to also be empathizers. The limiting factor then becomes the degree of the social layer which dictates the “relatedness” of overlap neighbors—i.e. the likelihood they share the same strategy. This interpretation is embodied in the analytical rule for the evolution of empathy, which can be rewritten as  $\left(\frac{1}{s}\right)b > c$ , such that  $\frac{1}{s}$  corresponds with the relatedness coefficient of Hamilton’s rule<sup>66,67,69</sup>.

The basic insight here is that if behavioral strategies spread among familiars (via biological reproduction or social learning), then familiarity functions as a proxy for behavioral relatedness. Thus, conditioning cooperation on familiarity concentrates the benefits of cooperation among cooperators, allowing cooperative behavior to spread. Importantly, this logic does not depend on the unrealistic assumption that social and economic networks are static and homogeneous in structure. Nor does it depend on the assumption of weak selection or the death-birth updating rule.

Studies of empathy and socially-contingent cooperation have most often explained the evolution of this form of conditional cooperation with reference to Hamilton’s theory of kin selection<sup>67</sup> and Trivers’ theory of reciprocal altruism<sup>71</sup>, since social proximity may coincide with genetic relatedness and interaction duration<sup>34,36,43,49,51,53,82</sup>. If we interpret the dynamics and results of the model in the context of genetic evolution, then the social layer, where the strategies spread, is a kin network, and social distance corresponds to genetic relatedness. The strategy of empathy in this case is identical to discriminatory kin-based altruism: cooperate with close kin; defect with others. And this strategy is an evolutionary improvement over unconditional cooperation when individuals interact with both kin and non-kin. If, instead, we interpret the dynamics and results of the model in terms of cultural evolution, then social distance corresponds to cultural rather than genetic relatedness, and the evolutionary mechanism illustrated is more closely related to parochial altruism<sup>66</sup> than kin selection. Both genetic and cultural interpretations of the model align with the evidence that relational closeness correlates with cooperation between kith and between kin<sup>34</sup>.

These dual interpretations also align with the evidence that individuals' cooperative proclivities are products of both heredity and socialization<sup>89,90</sup>.

The model suggests that modern human ecologies may impact cooperative behavior through two distinct channels: first, through the context-dependent expression of our evolutionary inheritance, and second, through cultural evolution itself. Since genetic evolution occurs at a much slower rate than cultural evolution (due to the different means of transmission), our genetic inheritance may reflect ancient human ecologies while our cultural inheritance may reflect modern human ecologies<sup>63</sup>. Consequently, our innate behaviors may be maladaptive to large-scale, anonymous market societies. Whereas empathy may effectively foster cooperation in big game hunts and childcare, it is poorly suited to address climate change and international conflict. The effects of social context on cultural evolution may also hinder the resolution of modern cooperation problems. The results of the model suggest that asocial human ecologies could erode the evolutionary feasibility of unconditional cooperation and select for non-cooperative behavior (either in the form of unconditional defection or vestigial empathy).

The insights the model provides into the behavioral ecology of cooperation suggest cooperation problems might be solved either by altering individual incentives to align self-interest with collective welfare or by changing the social context to better select for and provoke cooperative behavior. The most effective solution depends on the nature of the specific cooperation problem. If the context is unavoidably asocial, the incentive approach might be justified by the reality of self-interested actors. This case is exemplified by a carbon tax implemented to mitigate climate change. Here, the tax brings the cost individuals impose on the global population back into their own self-interested calculation, thus relieving the need for any internally motivated cooperation. In other contexts, it may be possible to increase the sociality of interactions, thus provoking more cooperation. This case is exemplified by the management of local resource commons<sup>91–93</sup>. Here, the delegation of commons governance to local communities that depend on the resource may function well on the basis of empathy without any top-down policy solution tailored to self-interested actors<sup>94,95</sup>.

More broadly, the model developed here exemplifies how the mathematical tools of evolutionary game theory and multilayer networks lend themselves to modelling the evolution of context-dependent behaviors. Such theoretical models provide important insights into the nuance and

dynamism of human behavioral ecology<sup>1</sup>, which could prove key to navigating the complex social and environmental problems we face today<sup>96</sup>.

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