

Evolution of Signaling in Adaptive Networks

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The self-organization of signaling has been a topic of interest in evolutionary theory, due to its ubiquitous presence in nature. Here we show that the entangled evolution of signaling strategies and interaction structure may constitute a key mechanism for the evolution and sustainability of informative signaling. To this end, we propose a novel stochastic population dynamics model — described as a reduced Markov process — which allows us to compute the stationary distribution of signaling strategies in adaptive networks. We show that signal-based partner choice may lead to the evolution of informative signaling, both in the absence and presence of partial conflict, here associated with individuals sometimes benefiting from different actions when interacting. Depending on the level of conflict, signaling can either dominate the population dynamics or arise from a non-trivial interplay with deceivers. These results are shown to remain valid for a wide range of parameters and diverse individual motivations underpinning the time-evolution of the network.

Keywords: signaling, conflict, finite populations, adaptive interaction networks, partner choice

I. INTRODUCTION

Information transfer is a ubiquitous phenomenon, occurring at all levels of complexity, from micro-organisms to humans [1–3]. The fundamental process that supports it is what is usually called signaling: the process through which signal usage carries information about the state of the world. However, the occurrence of signaling systems is nuanced and far from trivial. What is their nature? How do conventions concerning the use of the signals emerge? Here we tackle the evolution of signaling, focusing particularly on the role of time-evolving interaction structures.

It can be tempting to look at signaling systems as a set of static conventions or agreements, in which it is implicitly defined which signals make sense and what is their exact meaning. However, a signaling system should not demand such a formal understanding, since that would require a preexisting language from its users. Focusing on the interactive nature of signaling, a formal approach was initiated by Lewis [4] and borrowed from what at the time was considered the economic field of game theory [5] to create the signaling game. Signaling games are characterized by the existence of two agents: one that has access to private information about the state of the world and signals contingent on it; and another with enough agency to act based on the signals received [4, 6]. On this basis, instead of signals having any innate meaning, they may earn one from usage.

This approach was then extended by the inclusion of evolutionary population dynamics [6–14], inspired by biology. These tools allowed advances in predicting and understanding emergent behavior in evolving populations of interacting agents. In what concerns signaling, the results obtained here seem to depend critically on the agents’ interests. On one hand, if agents in a population

benefit from the same actions, they are said to have common interests, and informative signaling is consistently predicted to emerge [15–19]. On the other hand, agents might be in the presence of partial conflict if they benefit from different actions under part of the states of the world.

Conflict of this form is as much present in real complex systems as signaling itself, some of the most famous examples being nestling feeding, mating quality, and job-market signaling (see these and more examples in [20] for nature, and [21] for economics). This is not trivially explained under evolutionary theory, where several signaling-sustaining features have been proposed to be present, such as costly signals [22–29], kinship [26, 30–32], partial information transfer [31–33], and reciprocity [34]. Most of the literature focuses on the first, despite the significant critiques regarding the lack of incidence of the required high costs on natural systems [35–38].

Contrary to this, time-evolving population structure has been almost systematically neglected in past signaling models where populations are commonly considered static and well-mixed (for an exception under deterministic dynamics, see [39]). This comes off as surprising due to the fact that adaptive networks have been repeatedly pointed out as pervasive over all sorts of complex systems [40–44]. Because of this, signaling is a phenomenon whose intricate dynamics may not be completely disclosed, especially relating the impact of time-evolving population structure on its emergence.

We will be resorting to a set of analytical tools, based on a game-theoretic approach. We start by proposing a signaling game with a novel unifying payoff framework, which will allow the inclusion of partial conflict in the extensively explored Lewis signaling game. We will use stochastic methods on finite populations, an approach commonly overlooked to deterministic models and their stability concepts [7, 9, 10], but already shown to reveal other facets of emerging phenomena [45, 46]. Considering a population of agents who interact with each other under the basis of the signaling game, we will use as a stochas-

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tic update rule the pairwise comparison [11, 47], inspired by the Fermi function and statistical physics. The effect of mutations is taken into consideration, but because of the large size of the state space of the population, we will further use the small mutation limit [12]. By computing the transitions between monomorphic states and consequently, the stationary distribution of the population over them [12, 46, 48–51], we will achieve the values of signaling prevalence. The effect of adaptive interaction networks is considered by using the active linking framework [39, 50, 52–54]. We will develop a partner choice model, which will handily restrain the dynamical parameters of the network. This will allow us to focus on signal-based partner choice norms and briefly explore the potential of outcome-based ones.

Using this framework, we propose to answer the following questions:

- Does signaling emerge under partial conflict?
- What are the main mechanisms affecting the emergence of signaling?
- Can time-evolving population structure generated by partner choice enhance the emergence of signaling?
- Can partner choice emerge from natural selection?

II. RELATED WORK

Game theory formalizes interactions between rational agents, by characterizing the complete set of possible actions that can be performed by them, and how those directly affect the outcomes each of them face. Differently, evolutionary game theory (EGT) provides essential tools for the comprehension of phenomena in complex systems, without requiring any assumption about the rational faculties of the agents present in them. Under its lens, we may study how behaviors such as altruism, cooperation, and signaling, may emerge from natural selection.

An evolutionary model should be able to embody the characteristics needed to observe the process of behavioral selection in a population: the replication of behavior according to the success it represents to its actors, concurrent with the latent possibility of exploring new behaviors. Having this in mind, several models can be used.

The replicator equation [7], and its mutation-extended version, the replicator-mutator equation [8], have been extensively used, both due to their tractability and the simplicity of the analysis of equilibria through concepts such as evolutionarily stable strategy (ESS) [9, 10]. These models have showed that signaling should be expected to emerge under pure common interest, except for some particularly challenging cases [15–19].

Infinite population models may not be adequate for many reasons, between them the fact they do not take into consideration the stochasticity to which most populations are exposed. On these grounds, finite population

dynamics can reveal other facets of emerging phenomena [45]. These methods have been used considerably less to approach signaling and its origins. Their use has relied either on pure common interests under the Lewis SG [17, 18], or rather specific accounts of conflict, such as a version of the battle of sexes [46] and the Sir Philip Sidney game [55].

Under other models, we can see the impact of individual learning in signaling being studied. Agents may have the ability to learn their preferred actions through reinforcement processes [56, 57], neural networks [58, 59], or update of beliefs [1]. Even though these may hold interesting results, they are not contemplated in the approach we intend on doing here.

We know that signaling occurs in complex systems under the presence of partial conflict – see overviews of this topic in the natural world [20] and in human affairs [21]. However, EGT shows that their emergence is not as direct as it would be expected, leaving an open question out of their presence in those systems.

To overcome this complication, a large share of the models on signaling under conflicting interests rely on costly signals. One of the main motivations for this sort of mechanisms is Zahavi’s handicap principle [22]. This principle says that for signals between animals to carry information, agents should incur in a cost when sending them. These costs could surge from factors such as energy spent or increased predation risk and they should translate into signals being sent only by senders to which they are affordable. After the introduction of this mechanism under the signaling game [23], this has been studied to a great extent both in the fields of biology [24–26], and economics [27–29]. However, their usage has been subject to some empirical criticism, as most signals observed in real systems are not costly enough to explain the results obtained [35–38].

Kinship may also be seen as a potential explanation for signaling under conflict [26, 31, 32]. When we consider genes as the evolutionary units and that specimens share a relevant part of them with their kin, their conflicting interests may somehow turn into common ones [30]. We should take into consideration that most models overlap that mechanism with costly signals, and by excluding those we may see signaling systems succumb to deceiving [26]. Besides this, inclusive fitness has been subject to criticisms from the start due to the rigid assumptions it requires, which refrain it from being general enough [60].

Alternative approaches to signaling study how partial information transfer can occur. Individual agents, or populations in equilibrium, may spend a fraction of time signaling and acting accordingly and another fraction not doing it. These equilibria are generally less restrictive than the ones that correspond to optimal information transfer [31, 33]. Similar conclusions are drawn for equilibria where at least one state is properly signaled, while others are pooled, which can happen if the number of relevant states is higher than 2 [32]. Even though these are optimistic scenarios when compared to the difficulty of

expecting the emergence of perfect information transfer, non-null costs still seem to be essential in order to see meaning emerging on evolutionary populations [31–33].

On the other hand, agents having repeated interactions between them is shown to be a feature enough to promote signaling alone, even under cheap talk [34]. As agents interact contingent on the other’s honesty, the short-term benefit of lying is surpassed by the future benefits of maintaining a good relation with their peers. This adapted form of direct reciprocity refreshingly opens the way for new mechanisms to be explored outside costly signaling.

Under all these models, population structure is completely ignored. This feature was repeatedly shown to promote the emergence of cooperative behavior [50, 53, 54, 61–64]. It has also raised distinct implications on signaling emergence under common interests: spatial structure introduces the possibility of regional meaning emergence [65], while small-world networks tend to facilitate the achievement of universal signaling systems in ambitious scenarios not covered by well-mixed models [66].

However, due to the pervasiveness of conflict, we are interested in understanding the impact that population structure has on these settings where signaling emergence is not guaranteed. Adaptive networks have been thoroughly explored in the past decades due to their relevance across all sorts of interactive complex systems [40–44]. By considering populations to consist of adaptive networks of interacting agents, it is shown that signaling systems may be resistant to the fixation of deceivers if the links formed between them have high death rates [39]. This approach used a truncated version of the signaling game, which may provide less restrictive conditions of signaling emergence [19]. The stochastic character of the population was additionally ignored, by using deterministic models of infinite populations, which may hold different outcomes for emerging behavior [45, 46]. By deliberately discarding these choices when studying the role of time-evolving population structure, valuable new insights about signaling emergence may be revealed.

III. MODEL

We propose the game defined by its extensive form in Fig. 1. This formulation introduces a novel payoff framework with two parameters [67], straightforwardly described by the matrix present in equation 1, where payoffs – first the receiver’s and second the sender’s – are represented for each state of the world and action performed. This representation ignores the used signals given they have no direct effect on the payoffs received.

$$\begin{array}{cc} & S_0 & S_1 \\ \begin{array}{c} A_0 \\ A_1 \end{array} & \begin{bmatrix} (a, a) & (0, b) \\ (0, 0) & (a, a - b) \end{bmatrix} \end{array} \quad (1)$$

Parameter a is the reward of successful interactions between the two agents, inspired by the original Lewis game

[4]; and parameter b allows the inclusion of gaugeable partial conflict. Under $b = 0$, this game generates the Lewis signaling game [4], and under $b = a$ a version of the canonical signaling game with partially conflicting interests defined in [33, 39].

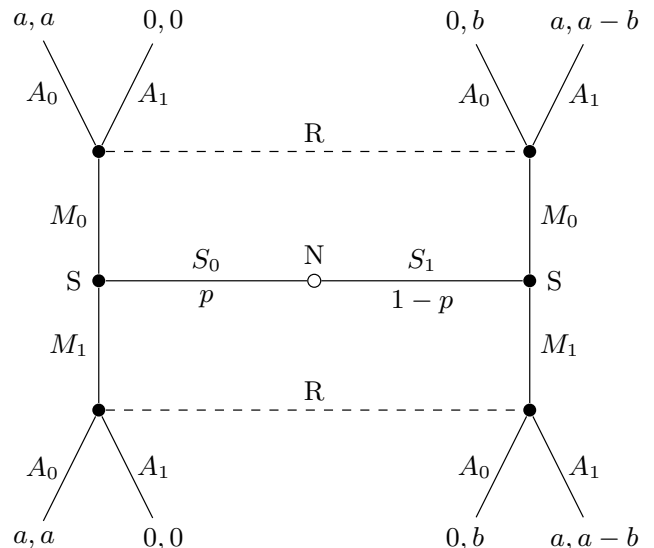


FIG. 1. Signaling game with the proposed unifying payoff framework in extensive form. The payoffs are first the receiver’s, and second the sender’s. The first move is a move by nature (N). It chooses between states of the world S_0 and S_1 with probabilities p and $1 - p$ respectively. Depending on the chosen state, to which the sender (S) has direct access, this agent chooses to send either signal M_0 or M_1 . The receiver (R) receives the chosen signal and, contingent on it, performs one of the acts A_0 or A_1 , without being directly aware of the state of the world. Hence the dashed lines, connecting nodes of equal perception by the receiver.

Since each agent has to choose between a limited amount of signals to send and acts to perform, we can define for each agent a correspondence between what she knows and the probability of choosing any of her prospects. This conditional decision process is what we call the agent’s strategy. We will only take into account pure strategies, under which the decision process becomes deterministic. Those are fully characterized under our symmetric 2 state, 2 signal, 2 act game by four binary variables: {signal sent when state of the world is S_0 ; signal sent when state of the world is S_1 ; act performed when signal received is M_0 ; act performed when signal received is M_1 }. For convenience, let us assume that the signals sent and acts performed are represented by a Boolean variable given by their index. A strategy is then represented by a 4-bits tuple, which can be translated to their decimal numeral (the *strategy index*). Signaling systems (SS) are characterized by agents performing a correspondence between the states of the world and their matching acts through informative signaling, which in this case are strategies 5: {0, 1, 0, 1} and 10: {1, 0, 1, 0}. In relation to these, deceiving would correspond to acting

accordingly, but signaling uninformatively in their own interest, strategies 1: $\{0, 0, 0, 1\}$ and 14: $\{1, 1, 1, 0\}$.

In a population of Z agents, each of them will have encounters with all the other agents according to the interaction defined in Fig. 1. We will consider a symmetrized version [68] of that game, where agents interact half the times as senders and the other half as receivers. One–population and two–population models of the Lewis signaling game have been shown to hold comparable results [15, 19]. The average payoff received by an agent with strategy A when interacting with an agent with strategy B is the following:

$$\pi_{AB} = p \cdot \frac{\pi_{A \rightarrow B}(S_0) + \pi_{A \leftarrow B}(S_0)}{2} + (1-p) \cdot \frac{\pi_{A \rightarrow B}(S_1) + \pi_{A \leftarrow B}(S_1)}{2} \quad (2)$$

where $\pi_{A \rightarrow B}(S_i)$ [$\pi_{A \leftarrow B}(S_i)$] is the payoff received by an agent using strategy A , when interacting as a sender [receiver] with an agent using strategy B under state of the world S_i . The payoffs are defined by the simple matrix from eq. 1, and in reference to the game represented in its extensive form in Fig. 1.

The evolutionary process starts with choosing randomly one agent i in the population. With a probability μ , this agent may undergo a mutation process, where she changes her strategy equiprobably to any of the other 15. With the complementary probability $1-\mu$, another agent j is randomly chosen in the population and they undergo a pairwise comparison [11, 47], where the Fermi function is used as a stochastic update rule (eq. 3)

$$P_i(s(i) \rightarrow s(j)) = \frac{1}{1 + e^{-\beta(\Pi_j - \Pi_i)}} \quad (3)$$

It defines the probability of the first agent i changing from her current strategy $s(i)$ into the one the second agent j is using $s(j)$, based on their fitness Π_i and Π_j defined later. The temperature β accounts for the intensity of selection, which restrains the dispersion around the option that maximizes the individual fitness of agent A . Changing β allows to continuously gauge between neutral drift ($\beta \rightarrow 0$) and deterministic imitation dynamics ($\beta \rightarrow \infty$).

We take into consideration the small mutation limit (SML) [12] $\mu \rightarrow 0$. Under this, the population evolves through successive pairwise comparisons to one of the

monomorphic states, i.e. a state where every agent uses the same strategy. When a mutation occurs, the intruder either fixates on the previously settled strategy, or it succumbs under it. For this reason, the population will spend all of its time with a maximum of two strategies present simultaneously. This allows one to describe the population dynamics in terms of a reduced Markov Chain with a size given by the number of possible strategies (16 in this case) [12, 46, 48–50].

For this approximation to be accurate, it should be confirmed that all the polymorphic states are indeed transient in the non-approximate process [12], otherwise the range of mutation probabilities for which the obtained results hold could be constrainingly small [51]. Under the Lewis Signaling Game ($b = 0$, $p = 0.5$) all non-monomorphic rest points have been shown to be unstable [15, 19]. In the case this does not hold under non-null conflict levels ($b > 0$), the approximation could be extended considering further configurations of interest apart from the monomorphic states, that way achieving more accurate results [51].

Let us consider that a maximum of two strategies are present in a populations (A and B). The probabilities of increasing/decreasing (+/–) by 1 the number k of mutant strategies B in a population with $Z-k$ strategies A is

$$T^\pm(k) = \frac{k}{Z} \frac{Z-k}{Z} \frac{1}{1 + e^{\mp\beta(\Pi_B(k) - \Pi_A(k))}} \quad (4)$$

Fitness values Π_A and Π_B are associated with the average payoff received. For instance, under the SML the fitness of an individual using a strategy A is given by

$$\Pi_A(k) = \frac{k}{Z-1} \pi_{AB} + \frac{Z-1-k}{Z-1} \pi_{AA} \quad (5)$$

Following [69] and using the transition ratio $\lambda_k = T^-(k)/T^+(k)$, we compute the fixation probability $\rho_{A,B}$ of one mutant strategy B on a population using A as it is done in eq. 6. This allows the construction of the transition matrix $M_{n_s \times n_s}$ (eq. 7), which defines the discrete-time Markov Chain of the approximate process. All the matrix elements are numbered from 0 to 15, corresponding to the indexation of the strategy of that monomorphic state.

$$\rho_{A,B} = \left[\sum_{l=0}^{Z-1} \left(\prod_{k=1}^l \lambda_k \right) \right]^{-1} \quad (6)$$

$$M = \begin{bmatrix} 1 - \eta(\rho_{0,1} + \dots + \rho_{0,n_s-1}) & \eta\rho_{0,1} & \dots & \eta\rho_{0,n_s-1} \\ \eta\rho_{1,0} & 1 - \eta(\rho_{1,0} + \rho_{1,2} + \dots + \rho_{1,n_s-1}) & \dots & \eta\rho_{1,n_s-1} \\ \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & 1 - \eta(\rho_{n_s-1,0} + \dots + \rho_{n_s-1,n_s-2}) \end{bmatrix} \quad (7)$$

In the limit of the neutral drift ($\beta = 0$), the fixation probability assumes the constant finite value $\rho = 1/Z$. Due to the stochasticity of the system, this should be valuable as a term of comparison for fixation probabilities [11]. Under this setting, an evolutionarily robust strategy (ERS) [13, 14] is one where all single mutants have fixation probabilities below neutral fixation.

The normalized left eigenvector with eigenvalue 1 of the matrix $\varphi = \varphi M$ provides the stationary distribution of this discrete-time Markov chain [12]. This represents the prevalence of each of the monomorphic states. Because under the SML, transient states are considered to be rare and the time spent in them negligible, signaling prevalence over the evolution is straightforwardly defined as $\sigma = \varphi_5 + \varphi_{10}$.

We introduce the active linking (AL) framework [39, 50, 52–54], under which agents are considered the interacting nodes of an adaptive network. Agents using strategy A have a propensity to form new links α_A , and their links with strategy B have a life expectancy of τ_{AB} , the inverse of their death rate $\gamma_{AB} = \tau_{AB}^{-1}$. Having this in mind, the differential equation for the number of active links X_{AB} between agents using strategies A and B is

$$\dot{X}_{AB} = \alpha_A \alpha_B (N_{AB} - X_{AB}) - \gamma_{AB} X_{AB} \quad (8)$$

where N_{AB} is the total number of possible links between agents with those two strategies. This is $N_{AB} = N_A N_B$ for links between different strategies and $N_{AA} = N_A(N_A - 1)/2$ for links between the same strategies, $N_A(N_B)$ being the number of agents using strategy $A(B)$ in the population.

We consider the typical time of the strategic dynamics to be much larger than the typical time of the linking dynamics $\tau_a \ll \tau_s$, leaving the network in its equilibrium topology at all times [39, 50]

$$X_{AB}^{eq} = \frac{\alpha_A \alpha_B}{\alpha_A \alpha_B + \gamma_{AB}} N_{AB} = \phi_{AB}^{eq} N_{AB} \quad (9)$$

Taking into consideration that only a fraction ϕ_{AB}^{eq} of the original interactions occur, the fitness should weigh the payoffs received in those links with that fraction, therefore turning eq. 5 into eq. 10. Comparing the two, it is concluded that the effect of active linking turns out to be a simple transformation of the strategic payoffs received, where their effective values become $\pi'_{AB} = \pi_{AB} \phi_{AB}^{eq}$.

$$\Pi'_A(k) = \frac{k}{Z-1} \phi_{AB}^{eq} \pi_{AB} + \frac{Z-1-k}{Z-1} \phi_{AA}^{eq} \pi_{AA} \quad (10)$$

It is virtually impossible to do a digestible analysis of the full AL's parameter space as the ones done in [39, 53, 64]. This serves as motivation to develop the concept of partner choice norm, under which the agents'

individual linking preferences are considered. These define the death rate values γ_{AB} under the adaptive interaction network: if both agents are inclined to choose each other, we attribute to that link a slow death rate γ_S ; if none is inclined, we attribute to it a fast one γ_F ; and if their preferences do not match, we attribute the medium value $\gamma_M = (\gamma_S + \gamma_F)/2$. The values of γ_S and γ_F are defined through parameter $\gamma_{F/S} = 0.5 \pm \delta$, where δ represents the degree of discrimination upon which all agents in a population will act when being inclined or not inclined to link. All propensities are left as $\alpha = 1$.

We focus on two forms of signal-based partner choice. Under the Informative norm, agents choose the ones who discriminate between states of the world using different signals and therefore being informative. Under the Convention norm, agents choose others who use the same signals they use for each of the two states of the world. These are just some of the numerous possibilities of existing linking dynamics, and they were chosen based on their supposed logical simplicity [70–72]. They generally assume agents to be able to acknowledge the actions performed by each other, the payoffs received after their encounters, and from there infer the state of the world after interacting as receivers. Additionally, agents are supposed to have repeated interactions, so that they are able to identify each other based on a memory of what occurred in previous encounters.

Additionally, we briefly explore one outcome-based norm [53, 73] relying on distinct information from the encounters, as an alternative to the previous mechanism. Under this, agents choose others if the payoff received when interacting with them is at least equal to the one received between signaling systems in that setting $a - (1-p) \cdot \frac{b}{2}$.

IV. RESULTS AND DISCUSSION

Using the developed evolutionary model, we start by probing the effect of partner choice on signaling emergence, followed by an explanation of the mechanisms underlying the population dynamics. Then the evolutionary likelihood of partner choice will be assessed, by co-evolving it with strategy selection.

In all the partner choice settings exhibited in Fig. 2(a), increasing the conflict level b/a directly decreases the signaling prevalence σ . Under the no norm scenario, signaling prevalence holds values $\sigma > 99\%$ for conflict levels up to $b/a = 0.2$, and signaling remains an evolutionarily robust strategy up until $b/a = 0.4$. As should be expected, there is a plateau where the outcome observed under the Lewis game holds. Beyond that plateau, signaling prevalence drops considerably, eventually attaining its minimum value under $b/a = 1$, where signaling is nonetheless still relevant $\sigma \approx 17\%$. This translates into the existence of three signaling regimes, clear under the no norm scenario: 1) Dominance, when signaling has a prevalence of over 99% – seen under strong alignment of interests; 2)

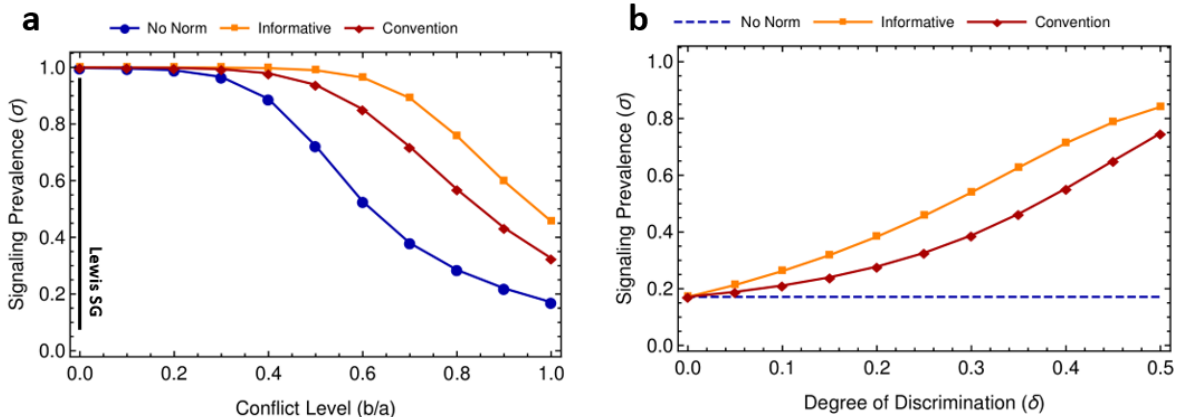


FIG. 2. Signaling prevalence under signal-based partner choice, changing (a) the level of conflict b/a , and (b) the degree of discrimination. The different values of the conflict level b/a were obtained indirectly through the variation of parameter b . On limit $b/a = 0$, this setting becomes the Lewis signaling game; on limit $b/a = 1$, the level of partial conflict becomes maximum. The no norm setting is shown only as a term of comparison and was obtained imposing no discrimination ($\delta = 0$) – hence the dashed horizontal line in (b). Other parameters: (a) $\delta = 0.25$; (b) $b = 1$; (a) and (b) $Z = 50$, $\beta = 1$, $a = 1$, $p = 0.5$.

Prevalence, when signaling is the most prevalent strategy even though prevalence values are lower than 99% – seen under weak alignment and weak partial conflict of interests; 3) and Relevance, when signaling is not the most common strategy but it has a prevalence of over 5% – seen under strong partial conflict of interests.

The two signal-based partner choice settings displayed in Fig. 2 hold systematically better results regarding signaling emergence, than the one without a norm. They prolong the plateau coming from the Lewis game to higher conflict levels than $b/a = 0.5$ and $b/a = 0.3$ under the Informative and Convention norms respectively. They guarantee signaling systems to remain ERS up until conflict levels of $b/a = 0.7$, refraining the system from getting past the prevalence regime under the maximum values of partial conflict. Under the worst-case scenario regarding partial conflict $b/a = 1$, increasing the degree of discrimination δ directly increases the signaling prevalence σ up to values of 84.1% and 74.8% ($\delta = 0.5$) under the Informative and Convention norms (Fig. 2(b)).

We have additionally tested the effects of the outcome-based partner choice, showing that the same conclusions drawn here, hold under that setting. The values obtained for signaling prevalence are comparable to those of the Informative's.

To understand these results, let us closely analyze the evolutionary dynamics underlying the maximum conflict scenario $b/a = 1$. In Fig. 3, we see signaling systems being effectively invaded only by their respective deceptive strategies. Allied with the fact that all the other strategies which signal like them (from the same group) transition to them, SS gain a privileged position in the overall dynamics – second most prevalent set of strategies in Fig. 4(a). Their prevalence is only surpassed by deceivers which fixate not only on SS but on other strategies that signal like them. We may see this juncture as

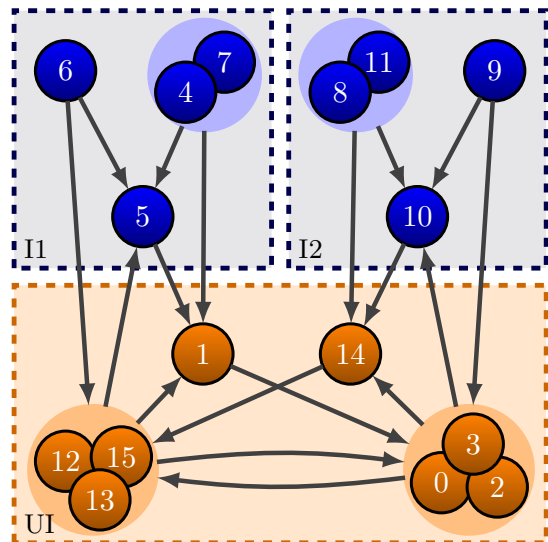


FIG. 3. Graph of the resulting dynamics between the 16 monomorphic states under maximum partial conflict and no norm. The transitions shown correspond to all which are (1) more probable than the neutral fixation, and (2) at least 60% as probable as the most frequent one coming out of the same node. Criterion (2) was included with the aim of assessing the role that every node had on the dynamics, therefore differing from other works where transitions are excluded based on the absolute values of their probabilities leading to some nodes being ignored [46]. The threshold of transition exclusion (60%) was chosen to leave a small but enough number of them coming out from each node. Some of the states are packed for simplicity. All the transitions coming in or out of those states were attributed to their pack. The number of each state follows the numeration of the strategy present in it. These are separated in groups according to the signals sent by them, due to the focus given on signal-based partner choice. Parameters: $\delta = 0$, $Z = 50$, $\beta = 1$, $a = b = 1$, $p = 0.5$.

signalers overthrowing informative strategies who do not harvest the benefits of acting according to their signals; and deceivers using the signals sent by informative strategies to act in their self-benefit, but not providing them with information about the world.

Transition	Fixation Probability ($/\rho_Z$)		
	No Norm	Informative	Convention
5 → 1 10 → 14	7.8	3.8	2.5
6 → 5 9 → 10	14.2	16.5	16.5
6 → 12 9 → 0	13.1	11.5	9.8
6 → 13 9 → 2	18.8	17.6	14.5
6 → 15 9 → 3	13.4	12.1	9.6
4 → 5 8 → 10	7.8	9.2	9.2
4 → 1 8 → 14	7.8	3.8	2.5
7 → 5 11 → 10	7.5	8.9	8.9
7 → 1 11 → 14	7.5	5.9	5.4
1 → 2 14 → 13	1.2	1.1	1.2
1 → 3 14 → 15	1.2	1.1	1.2

TABLE I. Fixation probabilities of the most relevant transitions between monomorphic states. The probabilities are displayed for evolution under three different partner choice settings: no norm ($\delta = 0$), Informative norm and Convention norm. The number of each monomorphic state follows the numeration of the present strategy (see *strategy index* in Model). Strategies are colored according to the group from Fig. 3 to which they belong: blue for I1 or I2 and brown for UI. All transitions are present in Fig. 3. The probabilities are normalized to the neutral fixation probability $\rho_Z = 1/Z$. Parameters: $\delta = 0.25$, $Z = 50$, $\beta = 1$, $a = b = 1$, $p = 0.5$.

In Table I, we have represented the probabilities of some of the transitions on the graph from Fig. 3, where we can observe a pattern. The two forms of signal-based partner choice provoke (1) a decrease in the probability of transitioning between different groups (I1/I2 and UI), by weakening the links connecting them; and (2) an increase in the transition probabilities inside the informative groups (I1 or I2), by reinforcing the links between them. From Fig. 3, we see that the transitions contemplated in (1) are mainly from informative to uninformative states, therefore privileging informative strategies in detriment of uninformative ones. The transitions where (2) applies are from non-SS informative strategies to SS, therefore strengthening the individual prevalence of signaling. This is reflected in, Fig. 4 by the significant decrease of the prevalence of deceiving strategies 1 and 14, and the opposite increase of SS prevalence 5 and 10, when comparing both partner choice settings with the no norm one.

The robustness of these conclusions is proved under a large range of the parameter space, where the existence of other regimes of effectiveness (especially for β , Z , and p) of those two norms has been shown and analyzed. By additionally testing the results under evolutionary settings where partner choice is only performed by signalers [39], we state that the success of the two signal-based norms requires global action, therefore suggesting the mentioned dynamical effects to be crucial.

To assess the evolutionary origins of partner choice and its co-emergence with signaling, the model is extended subjecting this behavior to selection [50, 54]. Each agent is defined by the combination of her linking and strategic behavior. Due to the computational power involved in a freer approach, we only include two types of partner choice in each evolutionary setting: agents choosing others according to a norm, and agents choosing others unconditionally.

Evaluating the inclination of every possible pair of types of agents, and following the already defined procedure to translate this into the death rate of their links, we get the complex 32×32 death rate matrix. Combining this with fixing every propensity values at 1, the linking dynamics are completely set. Additionally considering selection and mutations to happen to the 32 types, sets the strategic dynamics.

In order for populations to adopt partner choice, and therefore sustain structure under this model, they would have to undergo an evolutionary cost. The cost originates from populations being less connected, leading to agents missing encounters and making a lower fitness. A different formulation of the signaling game, where the payoffs received are not constrained to positive values [52] could be a way around this cost and would eventually show different aspects of co-evolution.

Nonetheless, this cost may be justified, since undergoing it must likewise represent a cost to the other agents with whom they miss encounters [50, 55]. The inset panel in Fig. 5 shows that this obstacle is overcome, and partner choice emerges. Both norms have a relevant presence when evolved, which is a fairly positive outcome. This conclusion directly addresses the concerns expressed in [39], about the origin and maintenance of population structure from an evolutionary perspective.

The Convention norm in particular, holds prevalence values twice as high as the Informative norm, showing to have the highest evolutionary likelihood. Exploring a larger fraction of the parameter space, it is found that its prevalence is consistently between 45% and 55%. The lower evolutionary likelihood of the Informative norm may be originated in the special focus it has on uninformative strategies, causing populations in non-informative states to be more disconnected, which should prevent them from evolutionarily adopt the norm. The general emergence of the Convention norm is particularly positive, adding to its success on sustaining signaling emergence. This comes to show that besides partner choice being apt to evolve, it is also attainable that the particular structure evolving from it sustains signaling.

Signaling prevalence increases under the evolution of partner choice behavior, in comparison to the outcome obtained under a population with no norm, as it can be seen in the main panel from Fig. 5. Even though this enhancement was lighter than the one obtained when linking behavior defined by those same norms was fixed, it was consistently observed throughout the explored parameter space. Signaling prevalence under population

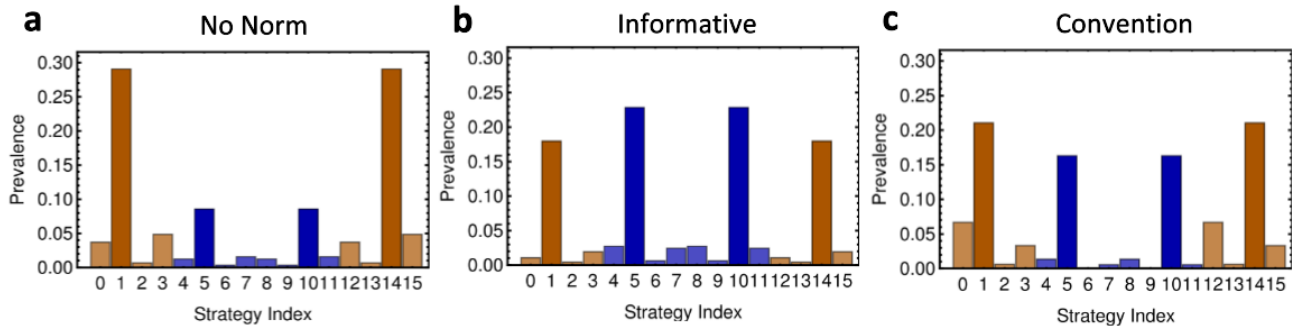


FIG. 4. Prevalence of each strategy, numbered from 0 to 15 (see *strategy index* in Model), under maximum partial conflict. This is a representation of the normalized stationary distribution. Three different partner choice scenarios are presented: no norm ($\delta = 0$), Informative norm ($\delta = 0.25$) and Convention norm ($\delta = 0.25$). Strategies from groups I1 and I2 are represented in blue with signaling systems (5 and 10) highlighted in darker blue. Strategies from group UI are represented in brown with deceivers (1 and 14) in darker brown. See graph in Fig. 3 for a clearer picture of groups. Other parameters: $Z = 50$, $\beta = 1$, $a = b = 1$, $p = 0.5$.

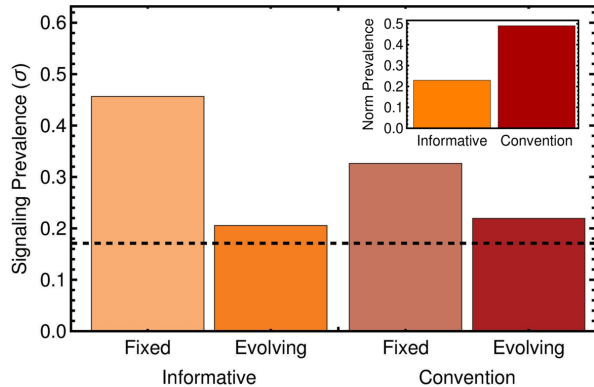


FIG. 5. Comparison between the signaling prevalence results obtained under the initial model – norms are fixed – and the extended model with possible coexistence of different partner choice behavior – norms may evolve. The value obtained under the no norm setting ($\delta = 0$ in the initial model) is shown in a dashed line as a term of comparison. The inset panel shows the prevalence of norm usage over their independent evolution. Parameters: $\delta = 0.25$, $Z = 50$, $\beta = 1$, $a = b = 1$, $p = 0.5$.

structure is therefore said to be mildly enhanced under the co-evolution of the linking behavior creating structure itself. Alternative formulations of the signaling game with negative payoff values could limit the evolutionary cost of partner choice and potentially show an emergence of signaling more robust to this co-evolution.

V. CONCLUSIONS

We have proposed a new model to assess the emergence of signaling under conflict in time-evolving network structures. The stochasticity of populations admitted the relevant evolution of signaling under all levels of partial con-

flict. Even in the scenario where individuals connect with others indiscriminately, signaling ranged from a complete dominance of the evolutionary dynamics under common interests, to the emergence from a non-trivial interplay with deceivers under maximum partial conflict.

We have analyzed different heuristics on partner choice norms, defining individual behavior in regards to the adjustment of their societies. We show that signal-based partner choice is capable of reverting the decrease of signaling prevalence observed under higher conflict levels. This reversion was as strong as the depth of the changes from partner choice on the population structure. This positive effect was explained under the evolutionary dynamics, and its underlying mechanism tested and shown to be robust under average values of population size, intensity of selection, and with states of the world similarly present. Outcome-based partner choice was alternatively shown to have a comparable effect on the emergence of signaling. By subjecting partner choice to selection, it was shown that this behavior was likely to develop, particularly under the case of the Convention norm. This last feature adds that not only is population structure likely to emerge, as it is attainable that the particular structure evolving will enhance signaling. Even though the signaling enhancement enabled by signal-based partner choice was mitigated by its co-evolution, it still emerged consistently. Here, alternative formulations of the signaling game could reveal new facets of co-evolution.

We hope this work is a valuable contribution to the existing literature on signaling. Hitherto, a large part of it has been dedicated to costly signaling as a mechanism to overcome deceiving behavior under partial conflict. We have deliberately tried to diversify this landscape by bringing attention to other features of real populations, such as finiteness and structure, and showing them to have remarkably promising effects on the emergence of signaling.

The developed modeling framework provided the signaling game and its unifying payoff framework as a novel contribution, where the conflict level was used to gauge continuously from the Lewis SG to the canonical SG with partial conflict. Another modeling feature newly proposed was partner choice, which was central to the use of active linking and allowed us to explore adaptive interaction networks under the complete non-truncated 16-strategy game. The extension of this model aiming at co-evolving partner choice behavior was therefore also novel.

This could be further extended to address the new routes and questions opened by the present work. It would be interesting to explore alternative forms of linking behavior, possibly focused on the actions performed by agents, the resemblance between them, or the formation of cliques. Each norm's logical complexity [70, 71] could be assessed formally, as this factor could play a role in the norms' success in promoting signaling [72]. If the computational expenses are overcome, partner choice could be additionally explored subjecting all its possible combinations to natural selection at the same level [74], or under a multi-level selection model [75]. These models could provide valuable insights about both the evolutionary likelihood of this behavior and the co-emergence of signaling. Separating strategic mutations from linking behavior ones by providing each with its independent probability under the co-evolutionary dynamics may alternatively provide distinct emerging outcomes [76].

Two major analytic approximations were used under our model: the small mutation limit [12, 77] and very fast

networks dynamics under active linking [52, 53]. Both approximations could have their validity assessed using agent-based numerical simulations to evaluate changes in the outcome. As an example, this is done under the prisoner's dilemma in [50] for $\mu = Z^{-2}$, and in [53] for linking dynamics under a wide range of τ_a/τ_s . Even though results are shown to hold in both cases, it is not trivial that the same should happen under signaling game dynamics. The SML could be further extended including additional configurations of interest apart from the monomorphic states, to achieve more accurate results [51].

Together with [39], the present work shows that population structure is a theoretically viable and solid alternative to costly signaling theory. We recognize the gap between these results and the experimental data. Therefore, we urge for the need to connect data on signaling from real complex systems from biological and social sciences, with the theoretical results drawn here. This could be done looking for structure in those systems and understanding how it can enhance signaling emergence based on what is shown here, or alternatively using the theoretical framework developed under this work to study the impact of specific network dynamics.

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