

Research



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Author for correspondence:

Luis A. Martinez-Vaquero
e-mail: l.martinez.vaquero@gmail.com

[†]Current address: International Institute for Sustainability, estrada Dona Castorina 124, Rio de Janeiro, Brazil.

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Signalling boosts the evolution of cooperation in repeated group interactions

Luis A. Martinez-Vaquero^{1,†}, Francisco C. Santos² and Vito Trianni¹

¹Institute of Cognitive Sciences and Technologies National Research Council of Italy, via San Martino della Battaglia 44, 00185 Rome, Italy

²INESC-ID Lisboa and Instituto Superior Técnico, Universidade de Lisboa, Lisboa, Portugal

LAM-V, 0000-0001-8194-8757

Many biological and social systems show significant levels of collective action. Several cooperation mechanisms have been proposed, yet they have been mostly studied independently. Among these, direct reciprocity supports cooperation on the basis of repeated interactions among individuals. Signals and quorum dynamics may also drive cooperation. Here, we resort to an evolutionary game-theoretical model to jointly analyse these two mechanisms and study the conditions in which evolution selects for direct reciprocity, signalling, or their combination. We show that signalling alone leads to higher levels of cooperation than when combined with reciprocity, while offering additional robustness against errors. Specifically, successful strategies in the realm of direct reciprocity are often not selected in the presence of signalling, and memory of past interactions is only exploited opportunistically in the case of earlier coordination failure. Differently, signalling always evolves, even when costly. In the light of these results, it may be easier to understand why direct reciprocity has been observed only in a limited number of cases among non-humans, whereas signalling is widespread at all levels of complexity.

1. Introduction

Cooperation and collective action problems are pervasive at all levels of biological complexity, from bacteria [1–4] to the most complex eusocial animals [5] and humans [6]. In many situations, performing a task which is beneficial to an entire group demands a coordinated action of some kind, whereby individuals need to agree upon the action they will perform to survive or fulfil tasks that provide benefits to the group [4,7–13]. Generally speaking, the individual costs associated with collective action, that is, costs incurred by the single to the benefit of the group, may bring forth coordination problems and social dilemmas. And with them, the shadow of free-riding and exploitation, and its direct consequence, the tragedy of the commons [14–16].

The mechanisms and behaviours that support cooperation and collective action vary widely, from the emergence of leaders [17,18] to the evolution of communication and language [19], and are bound to the development of cognitive abilities that suitably balance the costs and benefits related to the collective action outcome. Coordination often requires information transfer through interactions among individuals, which may take many different forms, from indirect stigmergic processes to the direct exploitation of cues or signals [4,20–22]. According to Maynard Smith & Harper [23], a ‘signal’ is defined as ‘an act or structure that alters the behaviour of another organism, which evolved because the receiver’s response has also evolved’. Signals are known to be used as helpers of cooperation, despite they may entail a significant cost to the signaller [4,24]. Other explanations have been proposed to account for the pervasiveness of cooperation in nature [15,25]. Some are based on memory, and direct reciprocity is probably the mechanism that received more attention [26,27]. Direct reciprocity assumes that, when two players meet in a strategic interaction, they may prefer to cooperate if there is a high chance that they meet again. The same

principle can be extended to N -person interactions. While the range of possible conditional strategies can be much larger than in the 2-person case, reciprocity can still efficiently discourage individuals from free-riding in N -person collective [28–32]. Direct reciprocity has also been observed in non-human animals [33]. However, these cases are rare when compared with humans [34,35], possibly due to the complex cognitive abilities required to reciprocate, ecological constraints or evolutionary bootstrapping problems [36–42]. This suggests that, in the presence of other promoters of cooperation (e.g. signalling [4]), natural selection may favour simpler setups than direct reciprocity. On the other hand, repeated interactions may be prone to foster more efficient and honest signalling [43], creating a valuable synergy for the emergence of cooperation.

Evolutionary game theory has successfully been used to study the emergence of cooperation in the presence of both direct reciprocity [25,28,29,44] and signalling [4,11], but the interplay between the two has received little attention [45]. In particular, the evolutionary dynamics emerging from signalling in N -person dilemmas have been thoroughly analysed [11], however without taking into account the possibility of reciprocation. Here, we include this possibility, significantly enlarging the strategy space, investigating to what extent cooperation benefits from the interplay of more than one mechanism known to independently foster it. To do so, we propose a novel evolutionary game-theoretical model in which we combine signalling with the possibility to reciprocate previous actions. We analyse under which conditions one, the other or a combination of them is evolutionarily advantageous, assuming well-mixed populations and pairwise imitation evolutionary dynamics [46]. By doing so, we are able to analyse the complex ecology resulting from the relation between reciprocity and signalling, and their coevolution.

Our results suggest that these two mechanisms, when combined, do not act synergistically to foster higher levels of cooperation. We show that thriving reciprocity strategies are not selected in the presence of signalling and that individuals do better by resorting to costly signalling, neglecting information from past encounters. We find that the combination of signalling and memory-based strategies is undermined by the emergence of a new class of opportunistic strategies that contribute to the common good when the previous attempt of coordination failed and conversely free-ride after a successful cooperation event, overall leading to lower levels of cooperation.

2. Model

We consider a repeated N -person coordination problem, whereby a new round is played with probability ω . A sequence of rounds can be played against either of two opposed ecological conditions [11]: a public goods game G with probability λ —where individuals get a benefit proportional to the number of cooperators if a minimum number of them M has been reached—and a non-public-goods-game \tilde{G} with probability $(1 - \lambda)$ —where all the individuals obtain the same payoff independently of their actions. These ecological conditions can be interpreted as starvation and abundance states [11], where the former corresponds to G (enough individuals should cooperate in order to get any benefit) and the latter to \tilde{G} (the ecological condition does not entail a public goods

problem, so that decisions do not have any influence and all individuals obtain the same payoff). This setting allows for the assessment of the evolutionary dynamics under environmental variation, here associated with adverse or favourable conditions for a collective of individuals. Equivalently, we can imagine a value-sensitive decision-making problem [47] in which G represents a highly valuable public good for which individuals need to spend themselves, and \tilde{G} represents instead an unprofitable condition for which individuals should better avoid investing energies. Notwithstanding the interpretation of the ecological conditions, we consider that individuals interact through a repeated nonlinear public goods problem [10,11], where cooperating individuals incur in a cost c while defectors pay no such cost. In each round, some form of coordination among individuals is needed to achieve a collective benefit. If a minimum number M of cooperators is reached in a round, all individuals receive a benefit $b = rcN_C/N$, where $N_C \geq M$ is the number of cooperators and N the total number of individuals in the group. The multiplication factor is $r > 1$ when in G , and $r = 0$ when in \tilde{G} . Moreover, when signalling is considered, individuals that signal incur in an additional cost c_s (for more details see electronic supplementary material, Extended Methods).

In our model, individuals adopt strategies that are conditional on the past actions and on signals of the group mates, encoding the conditions for which individuals act in one or the other way [11,48–50]. We consider the possibility of signalling as a function of the ecological condition, with two binary choices (s_G and $s_{\tilde{G}}$) indicating if an individual signals (1) or not (0), respectively, in state G or \tilde{G} . Similarly to [11], we do not give any *a priori* meaning to such signals, and let the corresponding actions evolve freely in response to the attainment of a signalling quorum Q : individuals can cooperate (1) or defect (0) as a function of the number of signalling individuals, whether this exceeds the quorum (a_Q) or not ($a_{\bar{Q}}$). Similarly, the memory of past interactions can be exploited at each round: individuals can cooperate or defect as a function of whether the threshold M of cooperators in the previous round was reached (a_M) or not ($a_{\bar{M}}$). Execution errors are introduced for both signals and actions as a small probability ϵ that the individual chooses the opposite option that she intends to. When both signalling and reciprocity are present, individual strategies are represented by six bits: $[s_G, s_{\tilde{G}}; a_{Q,M}, a_{Q,\bar{M}}, a_{Q,M}, a_{Q,\bar{M}}]$, where the first two bits indicate the signalling strategy, and the last four bits indicate the actions corresponding to the attainment of thresholds Q and M .

Evolution is modelled through a stochastic birth–death process [51], considering a well-mixed finite population of Z individuals whose members randomly form groups of size N that play the game previously described. The fitness of each individual is computed averaging over all the possible group configurations she can be part of. Then, randomly selected individuals may adopt the strategy of other random members of the population with a probability that increases with their fitness difference, amplified or reduced by the intensity of selection β [46] (for more details see electronic supplementary material, Extended Methods). Given the large number of strategies, we adopt the so-called rare mutation limit, which allows one to conveniently describe the prevalence of each strategy as a reduced Markov chain [30,52–55]. This approach enables the computation of the invasion diagram among all pairs of strategies, together with the prevalence of each strategy in the long

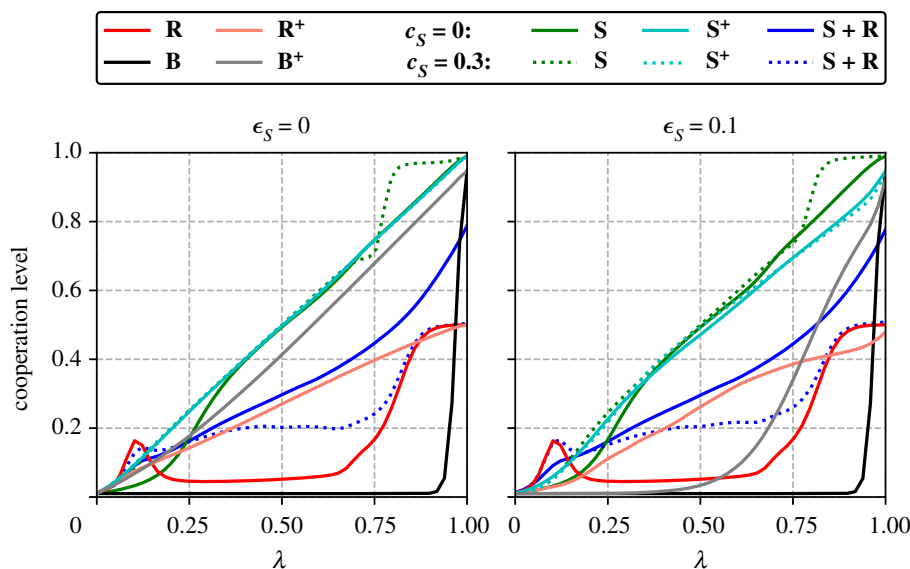


Figure 1. Cooperation level attained under different mechanisms. We tested the following mechanisms: reciprocity (**R**, 2 bits: $[a_M, a_{\bar{M}}]$), signalling (**S**, 4 bits: $[s_G, s_{\bar{G}}; a_Q, a_{\bar{Q}}]$) and the combination of signalling and reciprocity (**S + R**, 6 bits: $[s_G, s_{\bar{G}}; a_{\bar{Q}_M}, a_{\bar{Q}_{\bar{M}}}, a_{Q_M}, a_{Q_{\bar{M}}}]$). The baseline scenario with only pure cooperators and defectors is also included (**B**, 1 bit: $[a]$). For all mechanisms, strategies with the ability to discriminate between G and \bar{G} are also included: **R**⁺ (4 bits: $[a_{\bar{G}_M}, a_{G_M}, a_{\bar{G}_{\bar{M}}}, a_{G_{\bar{M}}}]$), **S**⁺ (6 bits: $[s_G, s_{\bar{G}}; a_{\bar{Q}_G}, a_{\bar{Q}_{\bar{G}}}, a_{Q_G}, a_{Q_{\bar{G}}}]$), **B**⁺ (2 bits: $[a_G, a_{\bar{G}}]$). Different values of the cost of signalling are considered. Cooperation levels have been computed for the combination of both ecological conditions ($G + \bar{G}$, as determined by λ). We assumed $M = 5$, $Q = N/2$, $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$ and $Z = 100$.

run. This framework also allows one to compute an average cooperation level for different parameters of the model.

3. Results

3.1. Signalling versus reciprocity

We first study the cooperation level achieved through signalling (**S**) and reciprocity (**R**) both as separate and coexisting mechanisms (**S + R**; see electronic supplementary material, table S1 for a summary of the different combinations of mechanisms). Figure 1 shows the expected fraction of cooperative actions for those mechanisms together with a baseline (**B**) where only pure cooperation or defection is allowed. We also consider the case in which players can detect the current ecological condition—although with a probability of error ϵ_S —and act accordingly (**B**⁺), possibly together with reciprocity or signalling (**R**⁺ and **S**⁺, respectively; see also electronic supplementary material, table S1). Our analysis is tailored to understand what mechanisms and combinations thereof result in the highest levels of cooperation as a function of the probability of encountering the profitable or unprofitable ecological conditions, determined by λ .

In the absence of any mechanism (baseline condition **B**), defection prevails for almost the entire spectrum of λ . This is because the public good game in G is only marginally advantageous with the selected parameterization, and therefore cooperation is observed only for $\lambda \approx 1$. By providing individuals with the capacity to reciprocate prior outcomes (condition **R**), the overall cooperation level improves, especially when favourable ecological conditions are frequent. A much more effective mechanism is signalling alone (condition **S**), not only when it comes without any cost but also for a moderate one ($c_S = 0.3$). Finally, allowing individuals to use both signalling and reciprocity (condition **S + R**) does not add value to the former: it diminishes the virtue of signalling, reducing the cooperation level to values between those

obtained from signalling and reciprocity considered as separate mechanisms. This result is valid even in the presence of costly signals, in which case the **S + R** strategies attain a cooperation level just above the one scored by **R**.

Cooperation increases when individuals discriminate accurately between the state G and \bar{G} , i.e. when errors in perception of the ecological condition are neglected ($\epsilon_S = 0$). In the case of the baseline condition, the difference between **B** and **B**⁺ is significant, the latter reaching cooperation levels almost as high as the signalling mechanism. When reciprocity is considered, the cooperation level for **R**⁺ also increases over **R**, but remains lower than 0.5, attained when $\lambda = 1$. Finally, when signalling is considered, higher cooperation is registered when individuals can decide how to act as a function of the ecological condition (**S**⁺), increasing over the already good cooperation achieved by simple signalling (**S**) even for small λ . The main reason behind the higher cooperation observed when individuals are able to discriminate the ecological condition resides in the ability to conditionally defect when in \bar{G} while developing a more cooperative strategy when in G , as long as this condition is not too rare (see some examples illustrated in electronic supplementary material, table S2). Nonetheless, when individuals fail to properly discriminate between ecological conditions ($\epsilon_S > 0$), the conditional strategies emerging in **B**⁺, **R**⁺ and **S**⁺ are not that successful any more (see the right panel in figure 1 for $\epsilon_S = 0.1$ and with more detail in electronic supplementary material, figure S1). The cooperation levels for the baseline condition and for the one entailing reciprocity are strongly affected by perception errors, whereas signalling (especially when costly) is able to preserve a high cooperation level. In other words, signalling represents a mechanism capable of correcting the individual perception errors, owing to the aggregation of information from multiple individuals.

One may argue that the cooperation level is not always a fair measure of collective action, given that there is no need to cooperate in the case of abundance (i.e. when in \bar{G}) as this does not lead to additional benefit. Indeed, when the

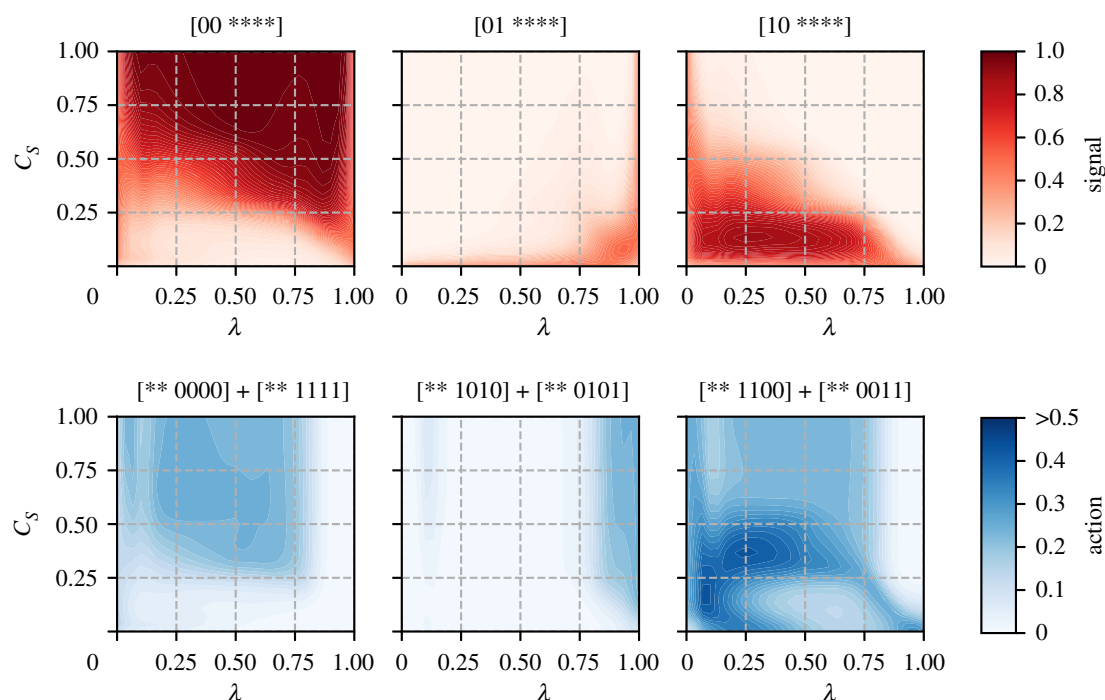


Figure 2. Prevalence of strategies grouped by signalling or acting behaviour. The plots show the aggregated probabilities in the stationary distribution of strategies across the $\{\lambda, c_S\}$ parameter space. In the top row, the signalling behaviour is considered, while the acting behaviour is displayed in the bottom row. Signalling strategies are grouped by the first two bits ($s_G, s_{\bar{G}}$), ignoring the always-signalling group which has negligible prevalence. Concerning the action part, in the bottom row we show groups of strategies that exploit either reciprocity (middle panel) or signalling (right panel), in comparison to strategies that do not use any mechanism (left panel). We assumed $M = 5$, $Q = N/2$, $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$ and $Z = 100$.

discrimination between states is possible, conditions \mathbf{B}^+ , \mathbf{R}^+ and \mathbf{S}^+ all lead to defection in \tilde{G} , as discussed above. Figure 1 also shows that the cooperation level attained when only signalling is allowed is roughly proportional to the frequency of G as given by λ , indicating that signalling favours cooperation mainly when the ecological condition entails a public good game. This is due to the possibility to distinguish the state G from \tilde{G} and to conditionally cooperate as a function of the signalling quorum—if reached—in spite of the coordination problems that can arise when interpreting the meaning of signals. This hypothesis gets support from electronic supplementary material, figure S1, where we compute the cooperation level only for the state G : signalling strategies mostly cooperate in G and do not cooperate when in \tilde{G} . Strategies that only use reciprocity or baseline mechanisms, instead, cannot act conditionally on the state G .

Owing to these results, in the following we focus on the simpler conditions \mathbf{B} , \mathbf{R} , \mathbf{S} and $\mathbf{S} + \mathbf{R}$, as the additional ability to act as a function of the ecological condition does not provide substantial advantages in the presence of perception error. We focus on the emergence and evolution of the behavioural strategies to understand why reciprocity jeopardizes the benefits provided by signalling when the two mechanisms are jointly enabled.

3.2. A new ecology of opportunistic strategies

The low cooperation observed in the presence of both signalling and reciprocity demands an explanation. Why the coexistence of mechanisms that should promote cooperation not only appears unproductive but also jeopardizes the ability to cooperate? Why is reciprocity not just selected out in favour of strategies that use signalling, if that is advantageous?

In figure 2, we show for the $\mathbf{S} + \mathbf{R}$ conditions the prevalence of strategies that resort to signalling (first row) and direct reciprocity (second row) for different values of c_S and λ . If we look at the prevalence of strategies grouped by their signalling behaviour (top row), we note that signalling is significantly used whenever the cost is low. Costly signals are used in situations where cooperation is required, i.e. in the G state ($s_G s_{\bar{G}} = 10$, see the top-right panel), but also to identify a rare condition \tilde{G} ($s_G s_{\bar{G}} = 01$ and high λ , see the middle-top panel). Moreover, the emission of signals does not lead to strategies that just exploit such information, ignoring previous interactions (see figure 2, bottom-right panel). Responses to signals that ignore memory do not dominate, and neither do pure reciprocal strategies (see figure 2, bottom row). Overall, pure signalling strategies are not improved but jeopardized by reciprocity. A similar situation occurs for other values of M (see electronic supplementary material, figure S2).

To fully understand the nuances of the interaction between signalling and reciprocity, we analyse the dynamics among the individual strategies and their emergence and dominance in an evolutionary context. We found that, despite the large strategy space, one can conveniently cluster strategies in a few drifting groups, i.e. strategies that are neutral among each other (for more details see electronic supplementary material, Extended Methods). These drifting groups are identified by distinct colours in figure 3, being characterized by the following properties:

Unconditional strategies (B) When no mechanism is used, like in the baseline condition, the relevant strategies are just *unconditional cooperation* (C) and *unconditional defection* (D).

Reciprocity-based strategies (R) When reciprocity is present, four different strategies are possible, as determined by two bits ($a_M, a_{\bar{M}}$). Besides pure cooperation (C) and pure defection (D),

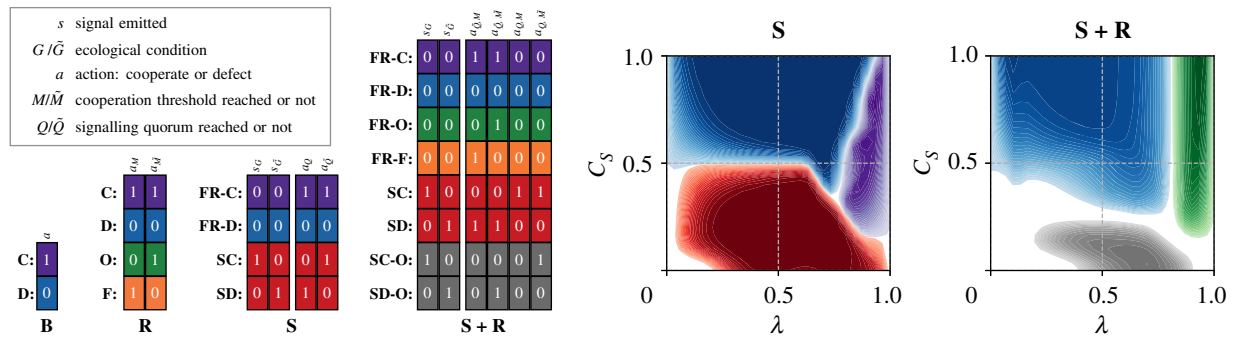


Figure 3. Main groups of strategies. Left: Relevant strategies are displayed for each possible setting, including the baseline setting where no mechanism is involved. Each labelled group is represented by a prototype strategy, and includes mutant strategies that drift with the prototype (for more details see electronic supplementary material, Extended Methods). Strategies are colour-coded in a consistent way indicating coherent resulting behaviours (e.g. red represents those strategy groups that exploit signalling only). Centre and right: Stationary distribution of the drifting groups of strategies in the $\{\lambda, c_s\}$ parameter space when only signalling (S, centre) and reciprocity combined with signalling (S + R, right) are included. The same colour-coding as in the left panel is used. Colour darkness indicates the intensity of the probability in the stationary distribution. Only probabilities higher than 0.5 have been displayed to facilitate the visualization in overlapping areas (see also figure 4). Parameters assumed: $M = 5$, $Q = N/2$, $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$ and $Z = 100$.

we count a strategy that only cooperates if the threshold M was reached and defect otherwise—referred to as *follower* (F)—and the opposite strategy, which cooperates only when the threshold was not reached—referred to as *opportunistic* (O). The former can also be seen as an N-person analogue of Tit-for-Tat, and the latter as the analogue to Anti-Tit-for-Tat, a compensating strategy that only cooperates when the others refuse to do so [56–58].

Signalling-based strategies (S) When only signalling is used, relevant strategies must consider both the signalling and the action components (hence four bits: $s_G, s_{\tilde{G}}, a_Q, a_{\tilde{Q}}$ and 2^4 possible strategies). In this case, we found four well-defined drifting groups, illustrated in figure 3 with a prototypical example for each case. Besides those strategies that free-ride the cost of signalling c_s and just cooperate and defect—referred to as **FR-C** and **FR-D**, respectively—we observe two strategies that signal to indicate when it is better to cooperate or defect as a function of the ecological conditions: **SC** signals to cooperate when in G , while **SD** signals to defect when in \tilde{G} . Both obtain the same net effect, although **SC** prevails over **SD** for most values of λ because paying the cost c_s is better tolerated when a benefit is expected.

Strategies based on reciprocity and signalling (S+R) Finally, when both reciprocity and signalling are present, the full set of 2^6 strategies is available. Nonetheless, as before, only a limited number of drifting groups dominate (see list in figure 3; electronic supplementary material). As before, the possibility to reciprocate leads to the *opportunistic* and *follower* strategies (**FR-O** and **FR-F**, respectively), and the possibility to use signals leads to the observed strategies that signal to cooperate or defect (**SC** and **SD**). More importantly, two additional groups emerge that were not previously found, and that are responsible for the dismissal of cooperation when signalling and reciprocity coexist. These are *opportunistic* strategies that signal either in state G or \tilde{G} , and cooperate accordingly to the signal they emit, but only when the cooperation threshold M was not reached in the previous round. We refer to these strategies as **SC-O** and **SD-O**.

The identified groups allow one to appreciate the prevalence of different types of strategies when the available mechanisms change. Most importantly, we note that opportunistic strategies dominate in a large portion of the parameter space when both signalling and reciprocity are present (condition **S + R**), as shown in the right panel of figure 3.

Specifically, **SC-O** and **SD-O** dominate in those regimes where, in the absence of reciprocity, we would have observed **SC** and **SD** strategies (see condition **S**, centre panel in figure 3). Indeed, opportunistic strategies resort to both information from signals and from the previous round to opportunistically cooperate either in G or in \tilde{G} , leading to lower overall levels of cooperation. Similarly, the reciprocal strategy **FR-O** in **S + R** replaces **FR-C** in **S**, when only signalling is available. Since **FR-O** pays lower costs by cooperating opportunistically, it also reduces the overall levels of cooperation.

Naturally, the prevalence of opportunistic strategies depends on the game parameters. The complete overview of the dominating strategies is provided in figure 4 (see also electronic supplementary material, figure S3, for conditions **B**, **R** and **S**), which reveals how different groups may dominate in different portions of the parameter space when varying the signalling quorum Q and the cooperation threshold M . Generally speaking, we observe that opportunistic strategies are more important when the requirements for cooperation are mild ($M \leq 5$), while higher requirements entail larger usage of signals, even when the related cost is non-negligible. The opportunistic strategies undermine the achievement of high cooperation levels, and can be counteracted only by rising the requirements for cooperation to $M \geq 7$. Under such conditions, a large portion of the parameter space is dominated by pure signalling strategies or unconditional cooperators **FR-C** that free ride on the signals emitted by others, the latter appearing only when the ecological conditions entail a frequent public good game (high λ). Note that the drifting groups of strategies we have identified are evolutionarily robust for a wide range of parameters (see also electronic supplementary material). They are generally not invaded by any other strategy with a probability higher than the one obtained through neutral drift, and when that happens it occurs with a probability much lower than the invasion in the opposite direction (see invasion graphs in electronic supplementary material, figure S4, and preferred directions of invasions [9,52–55] in electronic supplementary material, S4). These results are robust to variations in the number of rounds—as shown in electronic supplementary material, figure S5, where the probability to play an additional round of the iterated game is set to $\omega = 0.9$ —and to the existence of different type of errors, such as the inability of individuals to

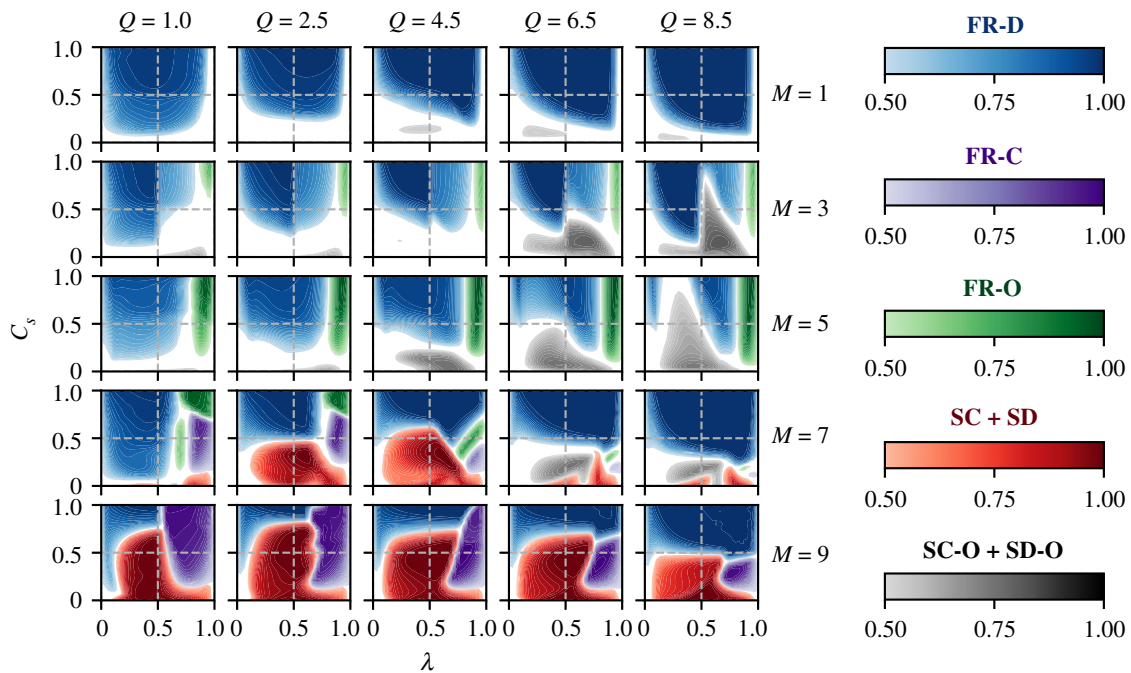


Figure 4. Stationary distribution in the **S + R** condition. Drifting groups of strategies are displayed across the $\{\lambda, c_s\}$ parameter space for all values of thresholds Q and M . Only probabilities larger than 0.5 have been displayed to facilitate the visualization in overlapping areas. Other parameters: $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$ and $Z = 100$.

correctly discriminate the ecological condition ($\epsilon_S > 0$; see electronic supplementary material, figure S6).

3.3. Alternative scenarios

The results discussed so far are valid also for other multiplication factors r and group sizes N . In figure 5, we show the influence of both for intermediate values of M and Q . As expected, low multiplication factors lead to the dominance of defection in the whole parameter space, while higher values promote cooperative strategies, and signalling is exploited widely when $\lambda < 0.5$, i.e. when the G state is rare. In that case, signals are used to identify the need for cooperation when in G , hence avoiding to pay costs with unproductive cooperation when in the \tilde{G} state.

Increasing the size of the groups (N) has a similar effect to reducing the multiplication factor, i.e. prevalence of less cooperative strategies [48], as can be noted by the similar pattern between the case with $r = 10$ and $N = 9$ and the case with $r = 20$ and $N = 18$ in figure 5. This effect has been also identified in other types of nonlinear N -person games [8,10,59], and when the only available mechanism of cooperation was either signalling [11] or reciprocity [28,29]. This dependence, however, may be influenced by how strategies are encoded [60].

Overall, the results of figure 5 confirm that signalling strategies emerge when cooperation is most needed [11], and that mild requirements for cooperation lead to the emergence of signalling strategies that however cooperate opportunistically. Indeed, our results suggest that information about the outcome of previous games is promoting opportunistic behaviours. This can, however, be an effect of the absence of a precise feedback on the outcome of the game, as the cooperation threshold M can be achieved even in the \tilde{G} state, when there is no benefit to compensate the costs of cooperation, hence justifying an opportunistic behaviour that cooperates only half of the times. We, therefore, tested an alternative scenario in which

individuals can base their decision on the actual reception of a benefit in the previous round. We refer to this scenario as the benefit-perceived scenario. This affects only the behaviour in the \tilde{G} state, whether the benefit is unconditionally provided (*abundance*) or unconditionally not provided (*no resource*; for details see electronic supplementary material, Extended Methods). Figure 5 and electronic supplementary material, figure S7, show that when \tilde{G} is frequent ($\lambda < 0.5$) but returns no benefit, and when requirements for cooperation are mild ($M = 5$), the follower strategies **FR-F** dominate. These strategies use memory to identify the G state—the only possibility to obtain a benefit—without the need of signals. Actually, **FR-F** uses knowledge about the obtained benefit as a cue that identifies the ecological condition G , and cooperates accordingly. This mechanism only works if the group is able to reach the threshold M at some point, the reason why this group of strategies disappears for high values of M . Conversely, in case of abundance, pure opportunistic strategies **FR-O** take over a large portion of the parameter space, also dominating signalling strategies (see figure 5; electronic supplementary material, figure S8). Opportunistic strategies can gain in both the G and \tilde{G} state without paying a cost for signalling, but obtain a benefit only half the times when in G . For this reason, **SC** and **SD** still dominate when the cost of signalling c_s is low and λ sufficiently high, as signalling allows to systematically cooperate in G without incurring in errors.

Another reason for the emergence of opportunistic strategies may come from the fact that agents are not aware of the importance of their contribution towards reaching the cooperation threshold M , as the information about how many other agents cooperated in the previous round is not explicitly available. Therefore, attaining M (when this is mild) may well have been possible without the own contribution, hence promoting opportunistic choices. We, therefore, tested what strategies would emerge in such a *self-aware scenario* in which reciprocity is based on the threshold R of individuals other

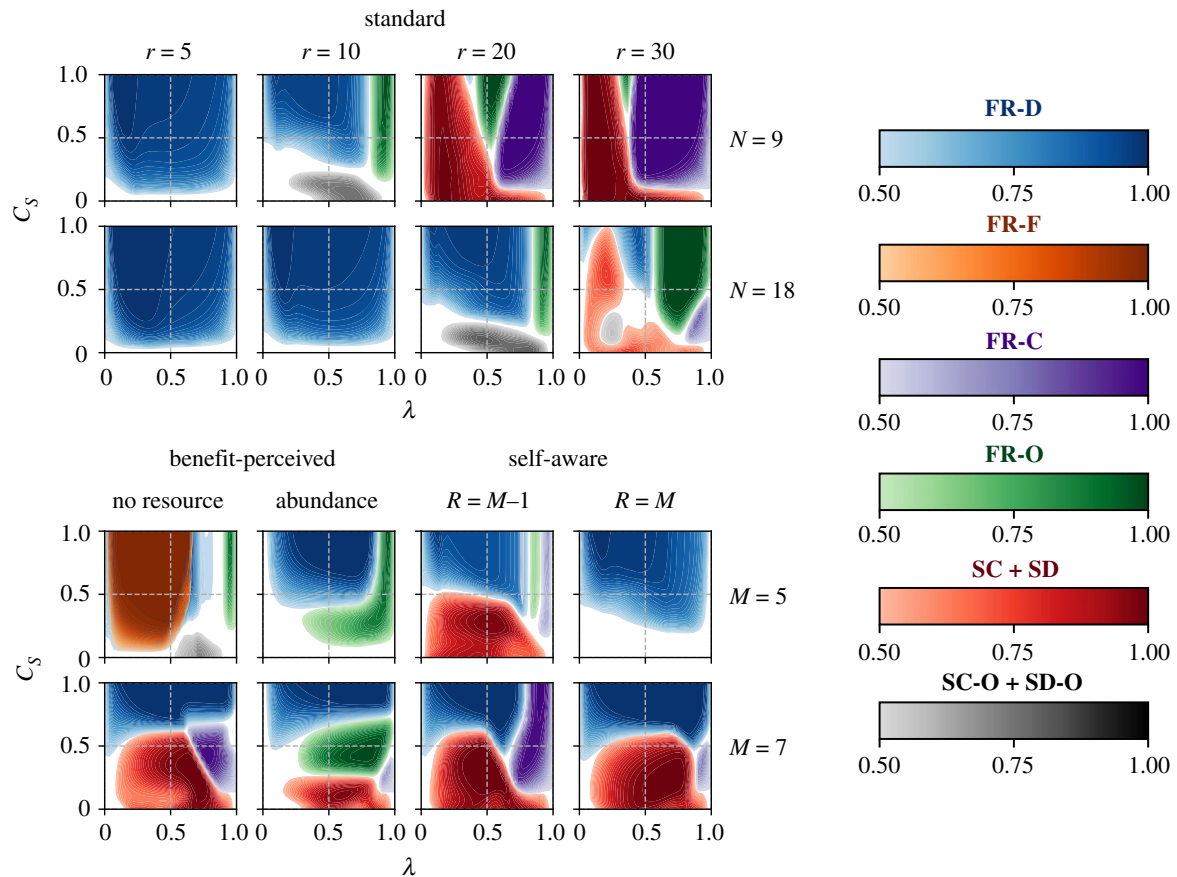


Figure 5. Stationary distribution of the main groups of strategies for different scenarios. Top panels: Effects of different group sizes N and multiplication factor r in the standard scenario, with $M = \frac{5}{9}N$. Note how, within the panel corresponding to $N = 18$ and $r = 30$, one can see a clear transition between **SC-O** and **SC**. Bottom panels: Effects of the benefit-perceived and self-aware scenarios, here with standard parameterization (see also electronic supplementary material for additional cases). In the abundance case, **SC** corresponds to $[10\ 0\ 11]$ while **SD** to $[01\ 110^*]$. In the self-aware scenario, when $R < 5$, **SC** corresponds to $[10\ 001^*]$, **SD** to $[01\ 1^*00]$ and **FR-C** to $[00\ 1^{***}]$. For $R \geq 5$, groups of strategies remain as in the standard scenario. Other parameters assumed unless otherwise indicated: $Q = N/2$, $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$ and $Z = 100$.

than the focal player that cooperated in the previous round (for details see electronic supplementary material, Extended Methods). Figure 5 and electronic supplementary material, figure S9, show, interestingly, that opportunistic strategies are nearly completely wiped out in favour of unconditional defection when $R \geq M$, or of strategies using signals when $R < M$. Indeed, as R is now partially unrelated from the attainment of benefit in G , signalling strategies are more reliable and dominate largely over opportunistic or mixed strategies. Overall, we see that reducing the requirements for group reciprocity actually favours the evolution of signalling strategies.

4. Discussion and conclusion

In a complex collective action problem in which different and contrasting ecological conditions may be encountered, the interplay between mechanisms known to individually promote cooperation, such as signalling and reciprocity, is far from trivial. Our results suggest that successful strategies in the realm of direct reciprocity are not selected in the presence of signalling. Even free-riders, and particularly those that do not pay the cost of emitting signals, make use of the information supplied by others to decide how to act. As a result, reciprocity is relegated to a narrow range of the possible environmental conditions, and when it appears, it does it in combination with signalling. The latter mechanism, on the

other hand, proves more reliable owing to the ability to support the collective discrimination of the ecological context, which is key to support cooperation especially when the problem requirements are tight, being even able to correct errors in the perception on the ecological conditions.

Interestingly, these results are compatible with observations that show how signalling is extensively preferred over reciprocity in non-human living beings [34]. Indeed, it was argued that reciprocity is rare because of cognitive limitations [41,61–63], ecological constraints [64], and an evolutionary bootstrapping problem [39]. Particularly, reciprocity requires an important degree of complexity at the individual level (cognitive skills that allow memory), whereas signalling benefits from the fact that it does not need a large set of repeated interactions to emerge, only relying on the quorum of signals within each group. As already suggested, quorum sensing can be used to precisely identify profitable ecological contexts, whereas reciprocal strategies base their success only on the feedback from others, being successful only on average and in the long run. Additionally, reciprocity hardly evolves when the available information is incomplete [65].

Another reason for the lower prevalence of reciprocity has been identified in the complexity of the ecology of strategies emerging from its combination with signalling. When both signalling and reciprocity are possible, we did not find any synergy, and lower levels of cooperation are reached when compared with, for example, situations in which only signalling is

available. This result remains valid even in the presence of costly signals. In fact, owing to the additional degrees of freedom granted by signals and associated responses in combination with memory-based actions, a new class of opportunistic strategies emerges that prevails in a wide range of parameters, wherein individuals free-ride on the efforts (and signals) of others, but only when their contribution is not decisive. This result highlights the subtle interplay between individuals' strategic complexity and cooperation, suggesting that evolution tends to select simpler heuristics to foster prosociality. This surprising result fits nicely with recent studies in the realm of reputation-based systems [42], where simple moral principles are shown to maximize cooperation, even in complex environments.

Given the size of the strategy space emerging from the combination of signalling and reciprocity, further intricacies were intentionally left out from our model. We assume, for instance, that signalling can come with a cost, whereas memory is cost-free. Here, memory is seen as an intrinsic feature that is not activated deliberately by the individual. However, our results show that reciprocity emerges in a minimal number of scenarios even with cost-free memory; thus, an additional cost would further reduce the chances of reciprocity-based strategies. One could also consider more complex signals [66], individual intentions [67] and reciprocal strategies that react differently for each configuration of the group in terms of the cooperation level observed in the previous round, for instance,

discriminating between a few and many cooperators [29,32]. Such additional features could reveal more complex dynamics for signalling and reciprocity to possibly act in synergy. Future work can explore these interesting paths.

Overall, our framework provides novel insights into the analysis of behavioural dynamics in the presence of multiple cooperation mechanisms, showing how opportunistic behaviour can arise within a complex ecology of behavioural strategies. Under demanding pressures from the collective action problem, our results put forward further explanations on the prevalence of signalling and quorum dynamics as a ubiquitous property in nature, showing how it may prevail even when in direct competition with other cooperation mechanisms that benefit from higher individual cognitive skills.

Data accessibility. This article does not contain any additional data.

Authors' contributions. L.A.M.V. implemented the model. All authors designed the research, analysed the results, wrote and revised the manuscript, gave final approval for publication, and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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