Signalling boosts the evolution of cooperation in repeated group interactions

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Abstract

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 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.

Keywords

Cooperation, evolutionary dynamics, game theory, signalling, reciprocity, public good games

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 fulfill tasks that provide benefits to the group [4, 7–13]. Generally speaking, the individual costs associated to 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 and 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 (EGT) has successfully been used to study the emergence of cooperation both in the presence of 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 which 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 evolutionary 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 co-evolution.

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 \( \omega \). A sequence of rounds can be played against either of two opposed ecological conditions [11]: a public goods game \( G \) with probability \( \lambda \)—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 \cite{47} in which \(G\) represents a highly valuable public good for which individuals need to spend themselves, and \(G\) 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 non-linear public goods problem \cite{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 \(c_s\) (see Extended Methods in Supplementary Material for details).

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 \cite{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 \cite{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 \((\tilde{a}_Q)\). 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 \((\tilde{a}_M)\). Execution errors are introduced for both signals and actions as a small probability \(\epsilon\) 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: \([s_G, s_{\tilde{G}}; a_{\tilde{Q}}, a_M, a_{Q}, a_{\tilde{Q}}, a_M]\), 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 \cite{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 \(\beta\) \cite{46} (see Extended Methods in Supplementary Material for details). 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 \cite{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-run. This framework also allows to compute an average cooperation level for different parameters of the model.

3 Results

Signalling versus reciprocity

We first study the cooperation level achieved through signalling \((S)\) and reciprocity \((R)\) both as separate and coexisting mechanisms \((S+R, \text{see Table S1 for a summary of the different combinations of mechanisms})\). Fig 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 \(\epsilon_S\)—and act accordingly \((B^+)\), possibly together with reciprocity or signalling \((R^+\) and \(S^+\), respectively, see also 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 \(\lambda\).

In the absence of any mechanism (baseline condition \(B\)), defection prevails for almost the entire spectrum of \(\lambda\). This is because the public good game in \(G\) is only marginally advantageous with the selected parameterisation, 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 $\tilde{G}$, 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 levels 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 $\lambda$. 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 $\tilde{G}$ while developing a more cooperative strategy when in $G$, as long as this condition is not too rare (see some examples illustrated in 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 Fig 1 for $\epsilon_s = 0.1$ and with more detail in Fig 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 G) as this does not lead to additional benefit. Indeed, when the discrimination between states is possible, conditions B+, R+, and S+ all lead to defection in G, as discussed above. Fig 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 G̃ 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 Fig S1, where we compute the cooperation level only for the state G: signalling strategies mostly cooperate in G and do not cooperate when in G̃. 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 B, R, S, and S+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 jeopardises the benefits provided by signalling when the two mechanisms are jointly enabled.

**A new ecology of opportunistic strategies**

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

In Fig 2, we show for the S+R conditions the prevalence of strategies that resort to signalling (first row) and direct reciprocity (second row) for different values of cS 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 (sGS̃G = 10, see the top-right panel), but also to identify a rare condition G̃ (sGS̃G = 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 Fig 2, bottom-right panel). Response to signals that ignore memory do not dominate, and neither pure reciprocal strategies do (see Fig 2, bottom row). Overall, pure signalling strategies are not improved but jeopardised by reciprocity. A similar situation occurs for other values of M (see Fig 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 (see Extended Methods in Supplementary Material for details). These drifting groups are identified by distinct colours in Fig 3, being characterised 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 (aM, aNG). Besides pure cooperation (C) and pure defection (D), 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: sG, s̃G, ãQ, aQ and 2^4 possible strategies). In this case, we
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 \((s_G, s_{\tilde{G}})\), 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 \( Z = 100 \).

found four well-definite drifting groups, illustrated in Fig 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 \( \text{FR-C} \) and \( \text{FR-D} \), respectively—we observe two strategies that signal to indicate when it is better to cooperate or defect as a function of the ecological conditions: \( \text{SC} \) signals to cooperate when in \( G \), while \( \text{SD} \) signals to defect when in \( \tilde{G} \). Both obtain the same net effect, although \( \text{SC} \) prevails over \( \text{SD} \) for most values of \( \lambda \) 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 \( 2^n \) strategies is available. Nonetheless, as before, only a limited number of drifting groups dominate (see list in Fig 3 and Supplementary Material). As before, the possibility to reciprocate leads to the opportunistic and follower strategies (\( \text{FR-O} \) and \( \text{FR-F} \), respectively), and the possibility to use signals leads to the observed strategies that signal to cooperate or defect (\( \text{SC} \) and \( \text{SD} \)). More importantly, two additional groups emerge that were not previously found, and that are responsible for the dismiss of cooperation when signalling and reciprocity co-exist. 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 \( \text{SC-O} \) and \( \text{SD-O} \).

The identified groups allow 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 \( \text{S+R} \)), as shown in the right panel of Fig 3. Specifically, \( \text{SC-O} \) and \( \text{SD-O} \) dominate in those regimes where, in the absence of reciprocity, we would have observed \( \text{SC} \) and \( \text{SD} \) strategies (see condition \( \text{S} \), center panel in Fig 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 fewer 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 Fig 4 (see also Fig 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 $\lambda$). Note that the drifting groups of strategies we have identified are evolutionarily robust for a wide range of parameters (see also 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 Fig S4 and preferred directions of invasions [9, 52–55] in the Section S4 of the Supplementary Material). These results are robust to variations in the number of rounds—as shown in Fig 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 correctly discriminate the ecological condition ($c_s > 0$, see Fig S6).

**Alternative scenarios**

The results discussed so far are valid also for other multiplication factors $r$ and group sizes $N$. In Fig 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 Fig 5. This effect has been also identified in other types of non-linear 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 Fig 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, see Extended Methods in Supplementary Material) for details. Fig 5 and Fig 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, 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
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 to SC. Bottom panels: Effects of the benefit-perceived and self-aware scenarios, here with standard parameterisation (see also Supplementary Material for additional cases). In the abundance case, SC corresponds to $[10011]$ while SD to $[01100]$. In the self-aware scenario, when $R < 5$, SC corresponds to $[10001]$, SD to $[01100]$ and FR-C to $[001111]$. 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 $Z = 100$.

space, also dominating signalling strategies (see Fig 5 and Fig 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 costs of signalling $c_s$ is low and $\lambda$ 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 than the focal player that cooperated in the previous round (see Extended Methods in Supplementary Material for details). Fig 5 and Fig 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 Conclusions

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 [65]. 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 [66].

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 to, e.g., 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 pro-sociality. 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 where 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 [67], individual intentions [68], 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 feature 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.
Author Contributions

LAMV 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.

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References

[1] Miller MB, Bassler BL. Quorum sensing in bacteria. Annual Reviews in Microbiology. 2001;55(1):165–199.
[2] Cornforth DM, Sumpter DJT, Brown SP, Brännström Å. Synergy and Group Size in Microbial Cooperation. The american naturalist. 2012;180(3):296–305.
[3] Nadell CD, Drescher K, Foster KR. Spatial structure, cooperation and competition in biofilms. Nature Publishing Group. 2016; p. 1–12.
[4] Skyrms B. Signals: Evolution, learning, and information. Oxford University Press; 2010.
[5] Queller DC. Relatedness and the fraternal major transitions. Philosophical Transactions of the Royal Society B: Biological Sciences. 2000;355(1403):1647–1655.
[6] Smith EA. Communication and collective action: language and the evolution of human cooperation. Evolution and Human Behavior. 2010;31(4):231–245.
[7] Skyrms B. The Stag Hunt and Evolution of Social Structure. Cambridge: Cambridge University Press; 2003.
[8] Souza MO, Pacheco JM, Santos FC. Evolution of cooperation under N-person snowdrift games. J Theor Biol. 2009;260(4):581–588.
[9] Kurokawa S, Ihara Y. Emergence of cooperation in public goods games. Proceedings of the Royal Society B: Biological Sciences. 2009;266(1660):1379–1384.
[10] Pacheco JM, Santos FC, Souza MO, Skyrms B. Evolutionary dynamics of collective action in N-person stag hunt dilemmas. Proceedings of the Royal Society of London B: Biological Sciences. 2009;276(1655):315–321.
[11] Pacheco JM, Vasconcelos VV, Santos FC, Skyrms B. Co-evolutionary dynamics of collective action with signaling for a quorum. PLoS computational biology. 2015;11(2):e1004101.
[12] Peña J, Nöldeke G, Lehmann L. Evolutionary dynamics of collective action in spatially structured populations. Journal of Theoretical Biology. 2015;382(C):122–136.
[13] Gavrilets S, Richerson PJ. Collective action and the evolution of social norm internalization. Proceedings of the National Academy of Sciences. 2017;114(23):6068–6073.
[14] Hardin G. The tragedy of the commons. science. 1968;162(3859):1243–1248.
[15] Rand DG, Nowak MA. Human cooperation. Trends in cognitive sciences. 2013;17(8):413–425.
[16] Gardner A, Foster KR. The Evolution and Ecology of Cooperation – History and Concepts. In: Ecology of Social Evolution. Berlin, Heidelberg: Springer, Berlin, Heidelberg; 2008. p. 1–36.
[17] King AJ, Johnson DDP, Van Vugt M. The Origins and Evolution of Leadership Minireview. CURBIO. 2009;19(19):R911–R916.
[18] Johnstone RA, Manica A. Evolution of personality differences in leadership. Proceedings of the National Academy of Sciences of the United States of America. 2011;108(20):8373–8378.
[19] Hauser MD, Chomsky N, Fitch WT. The faculty of language: What is it, who has it, and how did it evolve? Science. 2002;298(5598):1569–1579.
[20] Wilson EO. Sociobiology: The New Synthesis. Cambridge, MA: Belknap Press; 1975.
[21] Maynard Smith J, Szathmary E. The Major Transitions in Evolution. Oxford: Freeman; 1995.
[22] Theraulaz G, Bonabeau E. A Brief History of Stigmergy. Artificial Life. 1999;5(2):97–116.
[23] Maynard Smith J, Harper D. Animal signals. Oxford University Press; 2003.
[24] Gintis H, Smith EA, Bowles S. Costly signaling and cooperation. Journal of theoretical biology. 2001;213(1):103–119.
[25] Nowak MA. Five rules for the evolution of cooperation. Science. 2006;314:1560–1563.
[26] Trivers RL. The evolution of reciprocal altruism. Q Rev Biol. 1971;46:35–57.
[27] Axelrod R. The Evolution of Cooperation. New York: Basic Books; 1984.
[28] Van Segbroeck S, Pacheco JM, Lenaerts T, Santos FC. Emergence of fairness in repeated group interactions. Physical review letters. 2012;108(15):158104.
[29] Pinheiro FL, Vasconcelos VV, Santos FC, Pacheco JM. Evolution of all-or-none strategies in repeated public goods dilemmas. PLoS computational biology. 2014;10(11):e1003945.
[30] Hilbe C, Martinez-Vaquero LA, Chatterjee K, Nowak MA. Memory-n strategies of direct reciprocity. Proceedings of the National Academy of Sciences. 2017;114(18):4715–4720.
[31] Martinez-Vaquero LA, Cuesta JA, Sánchez A. Generosity Pays in the Presence of Direct Reciprocity: A Comprehensive Study of 2×2 Repeated Games. PLoS ONE. 2012;7:e35135.
[32] Kurokawa S, Wakano JY, Ihara Y. Evolution of groupwise cooperation: Generosity, paradoxical behavior, and non-linear payoff functions. Games. 2018;9(4):100.
[33] Milinski M. Tit for tat in sticklebacks and the evolution of cooperation. Nature. 1987;325(6103):433–435.
[34] Hammerstein P. Why is reciprocity so rare in social animals? A protestant appeal. In: Hammerstein P, editor. Genetic and Cultural Evolution of Cooperation (Dahlem Workshop Report 90). Cambridge, Massachusetts: MIT Press; 2003. p. 83–93.
[35] Clutton-Brock T. Cooperation between non-kin in animal societies. Nature. 2009;462(7103):433–435.
[36] Dunbar R. Grooming, gossip, and the evolution of language. Harvard University Press; 1998.
[37] Hauser M, McAllufle K, Blake PR. Evolving the ingredients for reciprocity and spite. Philosophical Transactions of the Royal Society B: Biological Sciences. 2009;364(1533):3255–3266.
[38] Whitlock MC, Davis BH, Yeaman S. The costs and benefits of resource sharing: reciprocity requires resource heterogeneity. Journal of Evolutionary Biology. 2007;20(5):1772–1782.

[39] André JB. Mechanistic constraints and the unlikely evolution of reciprocal cooperation. Journal of Evolutionary Biology. 2014;27(4):784–795.

[40] Taborsky M, Frommen JG, Riehl C. Correlated pay-offs are key to cooperation. Phil Trans R Soc B. 2016;371(1687):20150084.

[41] Moreira J, Vukov J, Sousa C, Santos FC, d’Almeida AF, Santos MD, et al. Individual memory and the emergence of cooperation. Animal Behaviour. 2013;85(1):233–239.

[42] Santos FP, Santos FC, Pacheco JM. Social norm complexity and past reputations in the evolution of cooperation. Nature. 2018;555(7695):242.

[43] Rich P, Zollman KJ. Honesty through repeated interactions. Journal of theoretical biology. 2016;395:238–244.

[44] Hilbe C, Chatterjee K, Nowak MA. Partners and rivals in direct reciprocity. Nature Human Behaviour. 2018; p. 1.

[45] Lotem A, Fishman MA, Stone L. From reciprocity to unconditional altruism through signalling benefits. Proceedings of the Royal Society of London Series B: Biological Sciences. 2003;270(1511):199–205.

[46] Traulsen A, Nowak MA, Pacheco JM. Stochastic dynamics of invasion and fixation. Phys Rev E. 2006;74:011909.

[47] Pais D, Hogan PM, Schlegel T, Franks NR, Leonard NE, Marshall JAR. A Mechanism for Value-Sensitive Decision-Making. PLoS ONE. 2013;8(9):e73216.

[48] Boyd R, Richerson PJ. The evolution of reciprocity in sizable groups. J Theor Biol. 1988;132:337–356.

[49] Kurokawa S, Wakano JY, Ihara Y. Generous cooperators can outperform non-generous cooperators when replacing a population of defectors. Theoretical population biology. 2010;77(4):257–262.

[50] Santos FC, Pacheco JM, Skyrms B. Co-evolution of pre-play signaling and cooperation. Journal of Theoretical Biology. 2011;274(1):30–35.

[51] Nowak MA, Sasaki A, Taylor C, Fudenberg D. Emergence of cooperation and evolutionary stability in finite populations. Nature. 2004;428(6983):646.

[52] Fudenberg D, Imhof LA. Imitation processes with small mutations. J Econ Theory. 2006;131:251–262.

[53] Imhof LA, Fudenberg D, Nowak MA. Evolutionary cycles of cooperation and defection. Proceedings of the National Academy of Sciences of the United States of America. 2005;102(31):10797–10800.

[54] Vasconcelos VV, Santos FP, Santos FC, Pacheco JM. Stochastic Dynamics through Hierarchically Embedded Markov Chains. Phys Rev Lett. 2017;118:058301.

[55] Omidshafiei S, Tuyls K, Czarnecki WM, Santos FC, Rowland M, Connor J, et al. Navigating the Landscape of Multiplayer Games. arXiv:200501642. 2020;

[56] Baek SK, Jeong HC, Hilbe C, Nowak MA. Comparing reactive and memory-one strategies of direct reciprocity. Scientific reports. 2016;6:25676.

[57] Do Yi S, Baek SK, Choi JK. Combination with anti-tit-for-tat remedies problems of tit-for-tat. Journal of theoretical biology. 2017;412:1–7.
[58] Domingos EF, Grujić J, Burguillo JC, Kirchsteiger G, Santos FC, Lenaerts T. Timing uncertainty in collective risk dilemmas encourages group reciprocation and polarization. arXiv:200307317. 2020.

[59] Santos FC, Pacheco JM. Risk of collective failure provides an escape from the tragedy of the commons. Proceedings of the National Academy of Sciences USA. 2011;108(26):10421–10425.

[60] Takezawa M, Price ME. Revisiting “The Evolution of Reciprocity in Sizable Groups”: Continuous reciprocity in the repeated n-person prisoner’s dilemma. Journal of theoretical biology. 2010;264(2):188–196.

[61] Stevens JR, Hauser MD. Why be nice? Psychological constraints on the evolution of cooperation. Trends in cognitive sciences. 2004;8(2):60–65.

[62] Stevens JR, Cushman FA, Hauser MD. Evolving the psychological mechanisms for cooperation. Annu Rev Ecol Evol Syst. 2005;36:499–518.

[63] Hauser M, McAuliffe K, Blake PR. Evolving the ingredients for reciprocity and spite. Philosophical Transactions of the Royal Society of London B: Biological Sciences. 2009;364(1533):3255–3266.

[64] Whitlock M, Davis B, Yeaman S. The costs and benefits of resource sharing: reciprocity requires resource heterogeneity. Journal of evolutionary biology. 2007;20(5):1772–1782.

[65] André JB. Mechanistic constraints and the unlikely evolution of reciprocal cooperation. Journal of evolutionary biology. 2014;27(4):784–795.

[66] Kurokawa S. Evolutionary stagnation of reciprocators. Animal Behaviour. 2016;122:217–225.

[67] de Melo CM, Terada K. The interplay of emotion expressions and strategy in promoting cooperation in the iterated prisoner’s dilemma. Scientific Reports. 2020;10(1):1–8.

[68] Han TA, Santos FC, Lenaerts T, Pereira LM. Synergy between intention recognition and commitments in cooperation dilemmas. Scientific Reports. 2015;5.
Supplementary Material

Signalling boosts the evolution of cooperation in repeated group interactions

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In this Supplementary Material we further elaborate on the methods and results discussed in the main text. In Section S1, we provide an additional details on the analytical and numerical procedures employed. In Section S2, we detail the nature of the strategies in each drifting group. We show further evidence of the robustness of our conclusions in Section S3, providing extended analyses and discussion of the whole parameter space. Finally, in Section S4 we deduce analytically the conditions under which some significant strategies are more likely to be invaded by others.

S1. Extended Methods

As detailed in the main text, we consider a finite population of $Z$ individuals, which form random groups of size $N$. Within each group, individuals interact through a non-linear and stochastic $N$-player iterated game. As we detail in the following sections, we present a finite population model of evolution, in which the proportion of time spent at equilibria can be explicitly calculated. We consider that individuals revise their behaviour by social learning, such that individuals with higher fitness will tend to be imitated more often. Here, fitness is given by the average payoff obtained from a large number of $N$-player interactions. Given the large number of different strategies ($2^S$ for $S+R$), our analysis can be simplified by adopting the limit of rare mutations, corresponding to maximal reduction of configurations of interest in a hierarchy of possible approximations [1, 2, 3, 4]. Under a process of imitation dynamics, only a new mutation can introduce a new strategy and, whenever mutations are rare, new strategies will either invade a resident population or become extinct. Thus, assuming that mutations take place much slower than the reproductive or imitation dynamics, as we describe later, there exist a maximum number of two strategies $A$ and $B$ at the same time in the population. We denote as $N_\Lambda$ and $Z_\Lambda$ the number of individuals of type $\Lambda \in \{A, B\}$ in the group and population, respectively, such as $N_A + N_B = N$ and $Z_A + Z_B = Z$.

Game payoffs and strategy space

We first assume that the ecological context is in one of two states $L$: a public good game state $G$ with probability $\lambda$ and a non public good game $\tilde{G}$ with probability $1 - \lambda$. In each round, individuals may decide to contribute a value to a common pool (to Cooperate, C) or refuse to contribute (to defect, D). In the $G$ state, a collective benefit is produced to the extent that at least $N_C \geq M$ individuals contributed to the public good, where $M$ represents a coordination threshold. In this case, each member of the group obtains a benefit $b = rcN_C/N$, with $c$ the cost of cooperating, $N_C$ the number of cooperators, and $r > 1$ the multiplication factor. If $N_C < M$ no collective benefit is produced, and all receive 0.

In $S+R$, behavioural strategies represent under what condition individuals will act in one or another way. We assume that individuals make two decisions within each round of the game:

- **Signalling**. First individuals decide if they signal ($S$) or not ($\tilde{S}$). Signalling comes with a cost $c_S$. This decision is only based on the current ecological context, hence it is encoded by two bits in the strategy.
space $s_\alpha$, with $\alpha \in \{G, \tilde{G}\}$. If more than a given number $Q$ of individuals in the group signal, we say that the quorum was reached and the group is signalling.

- **Acting.** After the signalling phase, individuals decide whether to cooperate ($C$) or defect ($D$). Cooperation comes with an individual cost $c$, whereas defecting is free. In this phase, the decision is made taking into account if the group reached the signalling quorum and if at least $M$ individuals cooperated in the previous round. Therefore four bits characterise this decision in the strategy space $a_{\gamma\gamma'}$, with $\gamma \in \{Q, \tilde{Q}\}$ and $\gamma' \in \{M, \tilde{M}\}$ representing all combinations from the achievement—or not—of the signalling quorum ($\gamma$) and the attainment—or not—of the cooperation threshold ($\gamma'$). Note that in the count of individuals that cooperated is also included the focal player; we also analysed the scenario where the focal player excludes herself from this count (see below).

In summary, strategies are given by six bits $\{s_G, s_{\tilde{G}}; a_{\tilde{Q}, M}, a_{Q, \tilde{M}}, a_{Q, M}, a_{\tilde{Q}, \tilde{M}}\}$. We restrain our analysis to pure strategies, i.e. $s_\alpha, a_{\gamma\gamma'} \in \{\epsilon, 1-\epsilon\}$, where $\epsilon$ represents the small probability that an individual commits an error, that is, chooses the opposite option that she intends to. To make easier the notation we will write strategies just using 0 and 1 instead of $\epsilon$. For example, an individual playing the strategy $[100101]$ signals only when in $G$ and cooperates only if the group was signalling (no matter if the threshold $M$ was reached in the previous round); on the contrary an individual with the strategy $[001010]$ never signals but cooperates if enough individuals $M$ cooperated in the previous round, neglecting signals.

The payoff that each individual obtains in a given round of the repeated game is the sum of the benefit (if any) and the costs of signalling and cooperating (if she decides to do so). Since a game is played for multiple rounds, the action of a player in a round may be influenced by the actions of the group in the previous round. If we consider two strategies, $A$ and $B$, the iterative process can be described as a Markov chain with a stochastic matrix $A$ whose elements $A_{ij}$ represent the transition probabilities between states $i$ and $j$ in a group formed by $N_A$ and $N_B$ individuals. Each state represents the number of individuals of each type that cooperates in a given round $(N_{C,A}(i), N_{C,B}(i))$ (with $N_{C}(i) = N_{C,A}(i) + N_{C,B}(i)$) and then the parameter space can be written as $\{0, \ldots, N_A\} \times \{0, \ldots, N_B\}$.

Given the stochastic nature of this repeated game and errors associated, for a large number of rounds (i.e. the probability of playing a new round is $\omega = 1$), initial conditions are not important since all possible states are eventually visited. In this situation, the probability $p^L$ that the system is found in state $a_i$ for a given ecological context $L$ just corresponds to the normalised eigenvector associated with the first eigenvalue of $A^L$ [5]. On the other hand, if the number of rounds are finite ($\omega < 1$), the probability $p^L$ is computed as follows:

$$p^L = (1 - \omega) p^0 (I - \omega A^L)^{-1}$$

(1)

where $I$ is the identity matrix and $p^0$ the vector with the probabilities of the initial states. The length of each dimension of these matrices and vectors are $(N_A + 1)(N_B + 1)$. We assume that the initial conditions in this game is $p^0_j = \epsilon N_{C}(i) + (1 - \epsilon)(N - N_{C}(i))$ independently of the ecological context. In other words, all individuals begin defecting (except for errors). This choice—although seemingly arbitrary—represents the case where $\gamma$ is presented with a new instance of the problem and has no prior knowledge to exploit. In such conditions, agents cannot rely on any memory about the outcome of previous interactions, equivalent to the state in which the cooperation threshold was not reached.

The transition probabilities $A_{ij}$ can be expressed as

$$A_{ij} = Pr^A(i, j) Pr^B(i, j),$$

(2)

where $Pr^A(i, j)$ stands for the probability that $N_{C,A}(j)$ individuals cooperate out of the $N_A$ that are in the group, corresponding then to the probability mass function of the binomial distribution:

$$Pr^A(i, j) = \binom{N_A}{N_{C,A}(j)} p_A^i N_{C,A}(j) (1 - p_A^i)^{N_A - N_{C,A}(j)},$$

(3)

which is a function of the probability $p_A^i(i)$ that an individual following strategy $A$ cooperates when in state $i$. This probability depends on whether the thresholds $Q$ and $M$ were reached and how the individual reacts according to her strategy:

$$p_A^i(i) = \Theta(N_S - Q) \Theta(N_C(i) - M) a_{Q,M}^A$$
$$+ \Theta(N_S - Q) [1 - \Theta(N_C(i) - M)] a_{Q,\tilde{M}}^A$$
$$+ [1 - \Theta(N_S - Q)] \Theta(N_C(i) - M) a_{\tilde{Q},M}^A$$
$$+ [1 - \Theta(N_S - Q)] [1 - \Theta(N_C(i) - M)] a_{\tilde{Q},\tilde{M}}^A,$$

(4)
where \( \Theta(x) \) stands for the Heaviside step function, i.e., \( \Theta(x) = 1 \) if \( x \geq 0 \) and 0 otherwise. Note that \( A \) is different if individuals exclude themselves in the count of the threshold for reaching the cooperation threshold \( M \) (see below for an alternative).

The average payoff per round that a \( k \)-strategist obtains in the group under the ecological context is \( W^L_A(N_A, N_B) = w^L_A \cdot \mathbf{p}^L \), where \( w_A \) corresponds to the vector with the payoffs of each possible state for the player with strategy \( A \):

\[
w^L_A,i = rc \frac{N_C(i)}{N} \Theta(N_C(i) - M) - c \frac{N_{C,k}(i)}{N_A} - c_s s^\Lambda_i.
\]

(5)

Finally, the average payoff of an individual with strategy \( A \) taking into account both ecological contexts is \( W_A(N_A, N_B) = \lambda W^G_A(N_A, N_B) + (1 - \lambda) W^L_A(N_A, N_B) \).

**Evolutionary dynamics**

Once the average payoff per round \( W_A(N_A, N_B) \) is obtained, we compute the average payoff \( \Pi_A \) over all the possible group combinations [6, 7, 8, 9]:

\[
\Pi_A = \sum_{N_\Lambda=1}^{\min(N,Z_\lambda)} H(N_\Lambda - 1, N - 1, Z_\Lambda - 1, Z - 1) W_\Lambda(N_A, N_B),
\]

(6)

where the hypergeometric distribution can be expressed as

\[
H(N_\Lambda, N, Z_\Lambda, Z) = \frac{\binom{Z_\lambda}{N_\Lambda} \binom{Z - Z_\lambda}{N - N_\Lambda}}{\binom{Z}{N}}.
\]

(7)

In order to simplify the evolutionary dynamics analysis, we adopt the small mutation approximation [1]. Under this approximation, whenever a mutant (an invasor) appears in a resident population, two possible final scenarios occur before any other mutation takes place: the mutant trait fixates in the population (it is imitated by all residents) or mutants are expelled (they imitate the resident strategy). In either case, the final state is monomorphic and no mixed state is considered, which could lead to a much more complex ecosystem of strategies [10, 4]. The transition probability between pairs of strategies is determined as a fixation probability, i.e. the probability that a single mutant with a strategy \( j \) invades a population formed by \( Z - 1 \) individuals that follow a strategy \( i \) [11, 1, 2]:

\[
\rho_{ij} = \left( 1 + \sum_{m=1}^{Z-1} \prod_{k=1}^{m} \frac{T^-(k)}{T^+(k)} \right)^{-1},
\]

(8)

where \( T^+(k) \) is the probability that an individual of the resident strategy \( i \) imitates a mutant \( j \) and \( T^-(k) \) is the probability that an individual of the mutant strategy \( j \) imitates a resident \( i \) in a population of \( k \) individuals playing the resident strategy. Assuming a Fermi probability function for pairwise strategy imitation [12], these probabilities are given by

\[
T^\pm(k) = \frac{k(Z - k)}{Z^2} \left( 1 + e^{\pm \beta |\Pi_i(k) - \Pi_j(k)|} \right)^{-1},
\]

(9)

where \( \beta \) represents the intensity of selection, i.e., the strength individuals base their decision to imitate the others.

In the case of neutral drift, the fixation probability among all pairs of strategies is \( \rho_{ij} = \eta = 1/Z \). The probabilities defined by Eq (8) determine a transition matrix of a Markov chain among strategies, assuming a sufficiently low mutation rate [13]. The non-diagonal elements of this matrix are \( T_{ij} = \rho_{ij} \nu^{-1} \), and the diagonal is \( T_{ii} = 1 - \sum_j T_{ij} \), where \( \nu \) is the total number of strategies. The normalised eigenvector associated with the first eigenvalue of that matrix provides the stationary distribution \( D_i \) of strategies [14, 1], which represents the relative time the population spends adopting strategy \( i \). The transition probability \( G_{g_i,g_j} \) between two groups of strategies \( g_i \) and \( g_j \) is computed as:

\[
G_{g_i,g_j} = \sum_{i \in g_i,j \in g_j} T_{ij} \frac{D_i}{\sum_{k \in g_i} D_k}
\]

(10)

**Drifting groups**

In order to analyse the specific dynamics and success of the different strategies, we identify groups of strategies that show equivalent behaviour. Strategies [00 **α1α2] and [11 α1α2**] formed 8 groups (for each combination of \( \alpha_i \), and varying * within each group) whose strategies show neutral drift among them if the noise in signal is
low enough. Specifically, when approximately \( \epsilon < Q/N \) and \( \epsilon < 1 - Q/N \) for the first and second set of groups, respectively, since the actual average number of individuals that signal in a group is \( N_S - (2N_S - N)\epsilon \) when \( N_S \) of them intend to do it. In our analysis we assume \( \epsilon = 0.01 \), therefore the previous groups are drifting groups (except for \( Q = N \) for the second set of groups). This does not mean that the probabilities of the strategies within a drifting group in the stationary distribution are the same, since, as we show, there usually exist some strategies that are able to invade others more successfully.

Since the initial conditions of the iterated game assume that all individuals begin defecting, except because of noise, strategies \([\alpha_1 \alpha_2 10 \alpha_3 \alpha_4]\) are equivalent to \([\alpha_1 \alpha_2 00 \alpha_3 \alpha_4]\), and \([\alpha_1 \alpha_2 0 \alpha_3 \alpha_4 10]\) to \([\alpha_1 \alpha_2 0 \alpha_3 \alpha_4 00]\), if the noise is low and the threshold \( M \) is high enough to prevent that the bit that differentiates them plays any role. The probability that less than \( M \) individuals commit an error acting due to noise in one round follows the binomial cumulative distribution function:

\[
Pr_i(< M) = \sum_{k=0}^{M-1} \binom{N}{k} \epsilon^k (1 - \epsilon)^{N-k}. \tag{11}
\]

The probability that this happens in every round of the game (except the last one, in which case it would not have any effect) is \([Pr_i(< M)])^{R-1}\), where \( R = (1 - \omega)^{-1} \) is the average number of rounds of the game. Note that it would be possible that in a round \( M \) is reached but in the next, again due to errors, individuals that would have started to cooperate defect again, correcting the first errors. This is the reason why, even when \( \omega = 1 \) and all the states can be reached, these drifting groups still appear, as we have seen in our analysis.

**Alternative scenarios**

Our model includes strategies that can decide their action taking into account if the number of individuals that cooperated in the past is higher or lower than the threshold \( M \). We also analysed a scenario where—instead of using memory of past interactions—individuals base their decision on the actual reception of a benefit. We refer to this case as the benefit-perceived scenario. The model remains the same, except when the ecological context is \( \tilde{G} \). There exist two main possible interpretations of \( \tilde{G} \): a scenario without resources or a scenario with abundance. In the former, individuals are not obtaining any benefit (equivalent in the regular scenario to consider that \( M \) was not reached), whereas in the latter every individual obtains a benefit (equivalent to consider that \( M \) is always reached).

A second alternative scenario is introduced to study the effects of self-awareness. So far, we have assumed that individuals can base their action on the number of individuals that cooperated within the group in the previous round (i.e., if the threshold \( M \) was reached) without removing themselves from this counting. In the self-aware scenario, we introduce another parameter \( R \in [1, N - 1] \), that stands for the number of individuals other than the focal player that cooperated in the previous round, and serves as a threshold for the individuals to decide their current action. As a consequence, \( R \) can be different from \( M \), which represents the number of individuals needed to obtain the benefit. The strategy space is modified in its acting module as \( a_{\gamma', \gamma} \), where now \( \gamma' = \{ R, \tilde{R} \} \). As a consequence, \( A \) also changes since \( Pr^k(i,j) \) corresponds now to the probability mass function of the Poisson binomial distribution [15], i.e., the probability that \( N_{C,k}(j) \) -individuals cooperate among the total \( N_k \) in the group, considering that the probability of cooperation of each individual is \( Pr^k(i) \) for \( N_{C,k}(i) \) of them and \( Pr^k_{C,D}(i) \) for the remaining \( N_k(i) - N_{C,k}(i) \) ones, where

\[
P_{C,i}^k = \Theta (N_S - Q) \Theta (N_C(i) - 1 - R) \ a_{Q,R}^k \\
+ \Theta (N_S - Q) (1 - \Theta (N_C(i) - 1 - R)) \ a_{Q,\tilde{R}}^k \\
+ (1 - \Theta (N_S - Q)) \Theta (N_C(i) - 1 - R) \ a_{Q,R}^k \\
+ (1 - \Theta (N_S - Q)) \Theta (N_C(i) - 1 - R) \ a_{Q,\tilde{R}}^k \tag{12}
\]

S2. Representative groups of strategies

Among all the possible strategies that can use signalling and reciprocity (condition \( S+R \)), we have identified the strategies and drifting groups of strategies (i.e, groups in which strategies show neutral drift among them)
that are the most representative in the stationary distributions for a wide range of parameters. Here we describe these groups with more detail (see the main text for a summary):

- **Signalling to cooperate (SC):** strategy [100011] signals under state $G$ and cooperates when the group signals. Strategies [101011] joins the prototype in a drifting group if $M$ is high enough.

- **Signalling to defect (SD):** strategy [011100] signals under state $\tilde{G}$ and only cooperates if the group is not signalling. SD is symmetric to SC, and in a similar way, strategy [101110] forms a drifting group with it for high values of $M$.

- **Signalling to cooperate and opportunistic (SC-O):** strategy [100001] is similar to the prototype of SC, but when it is time to cooperate, it only does it if $M$ was not reached previously.

- **Signalling to defect and opportunistic (SD-O):** strategy [010100] shows the same relation with SD as SC-O with SC.

- **Free-riding in signalling but using the lack of signalling to cooperate (FR-C):** strategy [001100] acts similarly as SD but does not signal under any circumstance. It constitutes a drifting group with [0011**] strategies.

- **Free-riding in signalling and pure defecting (FR-D):** strategy [000000] is the pure defector; it does not signal neither cooperates. It is part of the drifting group [0000**].

- **Free-riding in signalling and opportunistic (FR-O):** strategy [001000] behaves as SD-O without signalling. Its drifting group is [0001**].

- **Free-riding in signalling and following (FR-F):** strategy [001000] do not signal and cooperates only if the group was also not signalling and the $M$ was previously reached. Its drifting group is [0001**]. This group also drifts with FR-C when $M$ is low, and with FR-D when $M$ is high enough. It only appears independently under the benefit-perceived scenario.

One can see that all these important groups use the information from signals to decide how to act (except the full defector FR-D). However only some of them contribute actively using signals under $G$ or $\tilde{G}$ (SC, SD, SC-O, and SD-O); the rest just exploit signals for action, without paying the costs of signalling (FR-C, FR-D, FR-O, and FR-F). Some of these strategies combine this information with reciprocity (SC-O, SD-O, FR-O and FR-F), but none of them use only reciprocity to make their decisions.

### S3. Influence of parameters of the model

**Emergence of signalling strategies.** For moderate $c_S$, signalling is exploited and acquires a clear meaning, standing for the identification of rare ecological conditions. This is clearly visible in Fig. 2 of the main text for $M = 5$ (see also Fig. S2 for $M = 7$), which shows the prevalence of all the signalling strategies within the $\{\lambda, c_S\}$ parameter space, while the dominating groups are displayed in Fig. 4 of the main text and also Fig. S5 for a finite number of rounds ($\omega = 0.9$). When $c_S$ is negligible, strategies that exploit signals to cooperate (i.e., SC or SC-O) and to defect (SD or SD-O) dominate equally. This is also visible in the invasion graphs from Fig. S4a and S4b, in which we note also that the two signalling strategies do not invade each other, as a result of the different meaning associated to signals which prevents their coexistence. When $c_S$ takes a non-null but low value, SC and SC-O prevail for lower values of $\lambda$, while SD and SD-O dominate for higher ones, since it is less costly to signal for the less frequent ecological condition. However this symmetry is quickly broken: whereas SC and SC-O continue dominating when $\lambda \leq 0.5$, SD and SD-O disappear quickly (see also the invasion graphs in Fig. S4c and S4d). Interestingly, unless $\lambda$ is close to an extreme, SC and SD never invade each other, neither do SC-O and SD-O (at least not with a probability higher than the neutral drift): the success of one or the other are the result of the interaction with other strategies, especially those that free-ride the signalling costs (see Fig. S4). The asymmetric benefit for different environmental conditions result in asymmetries in the strategies, so that signalling for the unprofitable conditions results in lower advantage, and is therefore subsumed by strategies that mostly cooperate but free ride the signalling cost (see below). Given that coexistence of signals with different meaning is not possible, different signalling strategies mostly appear in isolation.
Free-riding on signalling costs. When $c_S$ takes high values, strategies that dominate do not signal under any circumstance and only specify their actions, coherently, when the quorum in signalling was not reached. Depending on the frequency of each ecological condition, these actions may differ. When $\lambda$ is not high, SC and SC-O eventually become too expensive and FR-D (full defection) takes their place, since cooperation becomes a cost not worthy to be paid for the few chances of obtaining a benefit in the $G$ state (see also Fig. S4e). On the other hand, FR-C prevails over SD even for moderate values of $c_S$, because both employ the same strategy to act (i.e., cooperate when there is no signal), but the former does not pay any cost for signalling (see Fig. S4h). FR-D cannot exploit SC in the same way because the latter cooperates only when the signalling quorum is attained, while in the absence of signalling, no benefit is obtained. Hence, FR-D cannot obtain any benefit by only free-riding the costs of signalling, and dominates only when $c_S$ is too high. Note that FR-D hardly ever invades SC in Fig. S4. On the contrary, SC does invade FR-D for moderate-low values of $c_S$, as discussed before. In between FR-C and FR-D, there appears the opportunistic strategy FR-O. An individual playing FR-O within a cooperative group acts as a defector. Conversely, among defectors, FR-O cooperates. It may look like a counter-intuitive behaviour, but this strategy allows to exploit cooperators, recognising when the own contribution is not necessary to obtain the benefit, and if not enough individuals cooperate, FR-O makes an effort to sum up enough cooperators. This elaborated behaviour has the objective to maximise the number of times a benefit is obtained, but working for it as less as possible. When individuals of an homogeneous population follow this strategy, they will cooperate half of the time. This behaviour only pays when the $G$ state appears with a high frequency, otherwise defectors FR-D take over (see also Fig. S4f and S4g). Overall, a general pattern among strategies that share the same signalling behaviour can be found: FR-O can invade FR-C and FR-D can invade both, but never in the opposite direction (see Fig. S4). The same happens with SC-O invading SC, and SD-O invading SD. As observed in other studies based on public good games, there exist an evolutionary tendency to defection when the benefits-cost trade-off is not benign. Cooperative strategies become successful when they can invade other strategies with a different signalling behaviour, keeping defectors at bay without directly invading defectors that share the same signalling behaviour.

Cooperation threshold and signalling quorum. Thresholds $M$ and $Q$ have a significant role in the dynamics of the system. Fig. 4 in the main text and Fig. S5 show how $M$ plays a fundamental role. Cooperation is favoured with the increase of $M$: cooperative strategies (SC, SD, and FR-C) dominate over their opportunistic counterparts (namely, SC-O, SD-O and FR-O) when $M > 5$, while full defection (FR-D) dominates across large portions of the parameter space for low values of $M$. Indeed, higher values of $M$ impose stronger constraints for cooperation in order to receive a benefit. In such conditions, SC-O and SD-O are not able to invade SC and SD, respectively, since an unconditional cooperative strategy that is based on signalling only is more advantageous than the conditional counterpart. The impact of the threshold $Q$ is less important. Intermediate values of $Q$ are better for SC. The presence of SC-O, on the other hand, increases with $Q$ when the requirements for cooperation are mild ($3 \leq M \leq 7$). This happens when the system has enough time to self-organise, but not when the number of rounds is limited, as shown in Fig. S5. Both FR-C and FR-O lose importance against defectors playing FR-D when $Q$ increases since it is more difficult that the signalling quorum is reached when $Q$ is high.

As already suggested in the discussion above, the thresholds $M$ and $Q$ are strongly related the probability of making errors with respect to what dictated by the strategy. For instance, $M$ can be interpreted as the effectiveness of cooperation against errors. An increase in the error probability can be represented by an increase of the cooperation threshold $M$, because individuals that cooperate may not effectively contribute to reach the threshold due to frequent errors in their actions. Under this interpretation, FR-O is less successful because higher cooperation thresholds/errors jeopardise the positive contribution towards reaching the threshold, leading to less occasions for opportunistic behaviour and overall lower payoff. In the same way, when individuals commit errors in assessing the signalling behaviour, reaching the signalling quorum $Q$ is more difficult, hence we can interpret higher errors as a larger quorum. When $Q$ is low, the signalling quorum may be reached due to errors even when in $G$, leading SC and SC-O to cooperate without obtaining any benefit. With signalling, we can consider also another source of error, that is, using the signal in the wrong ecological condition. This error $\epsilon_S$ represents the inability of individuals to correctly discriminate $G$ from $\bar{G}$, so that a signal is produced with probability $(1 - \epsilon_S)s_S + \epsilon_Ss_a$. This type of error could undermine the success of SC or SD, which trust in the correct assessment of the ecological context to decide whether or not to cooperate. However, results show that the signalling strategies are rather robust against this kind of error, thanks to the aggregation of information from multiple individuals and to the quorum mechanism. As a matter of fact, a rather high value of $\epsilon_S$ is necessary to observe some effect, as can be seen in Fig. S6.
S4. Invasibility preference

The evolutionary process leading to the emergence of one or the other strategy is very complex, as shown by the invasibility graphs in Fig. S4, because every strategy plays a role, even when its probability in the stationary distribution is low. In spite of this, it is possible to deduce the conditions under which a given strategy is more likely to replace another strategy than vice versa. Due to the complexity of the strategies themselves, we focus only on the conditions on $c_S$ and $\lambda$ for those pairs of strategies where both members emerge for the same combination of the other parameters. The preference on the direction of the invasibility between two strategies does not guarantee that the preferred strategy has higher probability in the stationary distribution due to the influence of the rest of the strategies. Therefore this analysis should be taken as a way to corroborate the results that were already discussed.

In the limit of large population size $Z$, strategy $A$ replaces $B$ in the population if

$$\sum_{N_A=1}^N W_A(N_A, N_B) > \sum_{N_A=0}^{N-1} W_B(N_A, N_B),$$

(13)

where $W_A(N_A, N_B)$ is the payoff that a focal player following strategy $\Lambda$ obtains in a group of size $N$ formed by $N_A$ individuals playing strategy $A$ and $N - N_B$ playing strategy $B$ [16]. We apply this condition for some significant pairs of strategies $(A, B)$ assuming that $\epsilon \to 0$, $M, Q = \{1, \ldots, N-1\}$ are integers (the closest greater integer is taken when the original parameter was not an integer), $\omega = 1$, and $c = 1$, obtaining the following conditions:

- **(SC, FR-D):** $c_S < \left(\frac{r}{N} - 1\right) + \left(\frac{Q-1}{N}\right)$
- **(SC-O, FR-D):** $c_S < \frac{1}{2} \left(\frac{r}{N} - 1\right) + \left(\frac{Q-1}{N}\right) - \frac{\max\{0, M-Q\}}{N}$
- **(FR-C, FR-D):** $\lambda > \frac{N}{r}$
- **(FR-O, FR-D):** $\lambda > \frac{N + M - 1}{r}$
- **(SC, SC-O) and (SD, SD-O):** $r - 2N + M > 0$
- **(SC, FR-C):** $\frac{1}{\lambda} - c_S > \frac{2(N-Q) + 1}{N}$
- **(SD, FR-C):** $c_S < \frac{1}{N}$
- **(FR-O, FR-C):** $\lambda < \frac{2N - M}{r}$
- **(SC, SD):** $\left(\lambda - \frac{1}{2}\right)c_S < \frac{2Q - N - 1}{2N}$

These conditions generally match the qualitative behaviour observed in Fig. S4 and discussed in Section S3. Quantitative differences, when present, are justified by the approximations taken and by the fact that this analysis considers only single strategies—chosen as the prototype for each drifting group (see Section S2)—while the invasion graphs in Fig. S4 take the entire drifting group into account.

References

[1] Fudenberg D, Imhof LA. Imitation processes with small mutations. J Econ Theory. 2006;131:251–262.
[2] Imhof LA, Fudenberg D, Nowak MA. Evolutionary cycles of cooperation and defection. Proceedings of the National Academy of Sciences of the United States of America. 2005;102(31):10797–10800.
[3] Hilbe C, Martinez-Vaquero LA, Chatterjee K, Nowak MA. Memory-n strategies of direct reciprocity. Proceedings of the National Academy of Sciences. 2017;114(18):4715–4720.
[4] Vasconcelos VV, Santos FP, Santos FC, Pacheco JM. Stochastic Dynamics through Hierarchically Embedded Markov Chains. Phys Rev Lett. 2017;(118):058301.
[5] Sigmund K. The Calculus of Selfishness. Princeton: Princeton University Press; 2010.

[6] Hauert C, Michor F, Nowak MA, Doebeli M. Synergy and discounting of cooperation in social dilemmas. Journal of theoretical biology. 2006;239(2):195–202.

[7] Pacheco JM, Santos FC, Souza MO, Skyrms B. Evolutionary dynamics of collective action in N-person stag hunt dilemmas. Proceedings of the Royal Society of London B: Biological Sciences. 2009;276(1655):315–321.

[8] Souza MO, Pacheco JM, Santos FC. Evolution of cooperation under N-person snowdrift games. J Theor Biol. 2009;260(4):581–588.

[9] Pinheiro FL, Vasconcelos VV, Santos FC, Pacheco JM. Evolution of all-or-none strategies in repeated public goods dilemmas. PLoS computational biology. 2014;10(11):e1003945.

[10] Martinez-Vaquero LA, Cuesta JA, Sánchez A. Generosity Pays in the Presence of Direct Reciprocity: A Comprehensive Study of 2×2 Repeated Games. PLoS ONE. 2012;7:e35135.

[11] Nowak MA, Sasaki A, Taylor C, Fudenberg D. Emergence of cooperation and evolutionary stability in finite populations. Nature. 2004;428(6983):646.

[12] Traulsen A, Nowak MA, Pacheco JM. Stochastic dynamics of invasion and fixation. Phys Rev E. 2006;74:011909.

[13] Wu B, Gokhale CS, Wang L, Traulsen A. How small are small mutation rates? Journal of mathematical biology. 2012;64(5):803–827.

[14] Imhof LA, Fudenberg D, Nowak MA. Evolutionary cycles of cooperation and defection. Proc Natl Acad Sci USA. 2005;102:10797–10800.

[15] Hong Y. On computing the distribution function for the Poisson binomial distribution. Computational Statistics & Data Analysis. 2013;59:41–51.

[16] Kurokawa S, Ihara Y. Emergence of cooperation in public goods games. Proceedings of the Royal Society B: Biological Sciences. 2009;276(1660):1379–1384.
### Table S1. Summary of the combination of mechanisms analysed.

For each combination of mechanism exploited, we provide the possible input variables (ecological condition $G/\tilde{G}$, attainment of the signalling quorum $Q/\tilde{Q}$ and achievement of the cooperation threshold $M/\tilde{M}$), which determine the possibility to signal ($s$) and/or to act ($a$). The total number of resulting strategies for each experimental condition is also shown.

| Mechanism | Ecological conditions | Signalling quorum | Memory on cooperation | Number of strategies |
|-----------|-----------------------|-------------------|-----------------------|---------------------|
| B         | -                     | -                 | -                     | 2                   |
| B⁺        | -                     | -                 | -                     | 2²                  |
| R         | -                     | -                 | $a$                   | 2²                  |
| R⁺        | -                     | -                 | $a$                   | 2⁴                  |
| S         | $s$                   | $a$               | -                     | 2⁴                  |
| S⁺        | $s, a$                | $a$               | -                     | 2⁶                  |
| S+R       | $s$                   | $a$               | $a$                   | 2⁶                  |

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**Figure S1. Cooperation level attained under different evolutionary conditions.** Similarly to Fig. 1 in the main text, we consider reciprocity (R), signalling (S), the combination of them (S+R), the baseline scenario (B), and strategies with the ability to discriminate between $G$ and $\tilde{G}$ ($R^+, S^+$, and $B^+$, respectively). Different values of the cost of signalling are considered. The first row displays the level of cooperation attained when both states $G$ and $\tilde{G}$ are considered, and corresponds to Fig. 1 in the main text. The second row shows the level of cooperation when only the $G$ state is considered. Model parameters: $M = 5$, $Q = N/2$, $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$, and $Z = 100$. 

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Figure S2. Prevalence of strategies grouped by signalling or acting behaviour. Similarly to Fig. 2 in the main text, the plots show the aggregated probabilities in the stationary distribution of strategies across the \( \{\lambda, cS\} \) parameter space. Here, the behaviour for \( M = 7 \) is displayed. Signalling strategies (top row) are grouped by the first two bits \( (s_G, s_{\tilde{G}}) \), ignoring the always-signalling group which has negligible prevalence. Concerning the action part (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). Model parameters: \( Q = N/2, \omega = 1, \beta = 1, r = 10, c = 1, \epsilon = 0.01, N = 9, \) and \( Z = 100. \)

Figure S3. Stationary distribution in the B, R and S condition. The baseline B and the reciprocity R conditions are displayed in the leftmost column, and only signalling S is shown with varying quorum \( Q \) in the remaining panels. For B and R, the column shows the probabilities of all the possible strategies for different thresholds \( M \). The other panels show the stationary distribution of the most successful group of strategies when signalling is the sole mechanism available (condition S), and for different values of \( M \) and \( Q \). Only probabilities higher than 0.5 have been displayed to facilitate the visualisation in overlapping areas. Model parameters: \( \omega = 1, \beta = 1, r = 10, c = 1, \epsilon = 0.01, N = 9, \) and \( Z = 100. \).
Table S2. Stationary distribution under every mechanism separately. Stationary distribution of the main strategies or group of strategies that emerge under conditions B, B⁺, R, R⁺, S, and S⁺ for different values of \( \lambda \) assuming that there is no error in perceiving the ecological context (\( \epsilon_s = 0 \)). Strategies under B⁺, R⁺, and S⁺ are shown as the composition of two strategies between parenthesis; individual chooses the first strategy when under \( \hat{G} \) and the second when under \( \tilde{G} \). Numbers on the right of each strategy indicate their probability in the stationary distribution. Parameters of the model: \( M = 5, Q = N/2, \omega = 1, \beta = 1, r = 10, c = 1, \epsilon = 0.01, N = 9, \) and \( Z = 100 \).
Figure S4. Graphs of invasion among the most representatives groups of strategies. Each panel shows the invasion graph for different combinations of $\lambda$, $c_S$ and $M$. The node size is proportional to probabilities in the stationary distribution. The arrow size and numbers above them correspond to the logarithm of the normalised transition probability among groups of strategies $G(\nu \eta)^{-1}$. Parameters of the model: $Q = N/2$, $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$, and $Z = 100$. 

Parameters of the model: $Q = N/2$, $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$, and $Z = 100$. 

(a) $\lambda = 0.5$, $c_S = 0$, $M = 5$

(b) $\lambda = 0.5$, $c_S = 0$, $M = 7$

(c) $\lambda = 0.5$, $c_S = 0.1$, $M = 5$

(d) $\lambda = 0.3$, $c_S = 0.3$, $M = 7$

(e) $\lambda = 0.5$, $c_S = 0.5$, $M = 5$

(f) $\lambda = 0.8$, $c_S = 0.3$, $M = 7$

(g) $\lambda = 0.9$, $c_S = 0.5$, $M = 5$

(h) $\lambda = 0.9$, $c_S = 0.3$, $M = 7$
Figure S5. Stationary distribution of the main groups of strategies for $\omega = 0.9$. Note that reducing the number of rounds does not change in general the results. The main difference with respect to Fig. 4 in the main text takes place when $Q$ is high and $M$ intermediate-low. In this case, one can detect the reduction of the success of SC-O and FR-O strategies for a high cost of signalling $c_S$. Model parameters: $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$, and $Z = 100$.

Figure S6. Stationary distribution of the main groups of strategies for different values of $\epsilon_S$. Model parameters: $Q = N/2$, $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$, and $Z = 100$. 
Figure S7. Stationary distribution of the main groups of strategies for the benefit-perceived scenario under no resource. Model parameters: $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$, and $Z = 100$.

Figure S8. Stationary distribution of the main groups of strategies for the benefit-perceived scenario under abundance. Group of strategies SC and SD corresponds to $[100^*11]$ and $[0110^*]$, respectively. Model parameters: $\omega = 1$, $\beta = 1$, $r = 10$, $c = 1$, $\epsilon = 0.01$, $N = 9$, and $Z = 100$. 
Figure S9. Stationary distribution of the main groups of strategies for the self-aware scenario. Group of strategies change as follows: SC corresponds to \([10 001^*]\) when \(R < 5\) and to \([10 011]\) otherwise; SD corresponds to \([01 100^*]\) when \(R < 5\), and to \([01 110]\) otherwise; FR-C corresponds to \([00 111]\) when \(R < 5\), and to \([00 111]\) otherwise. Model parameters: \(Q = N/2\), \(\omega = 1\), \(\beta = 1\), \(r = 10\), \(c = 1\), \(\epsilon = 0.01\), \(N = 9\), and \(Z = 100\).