Evolutionary consequences of behavioral diversity

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Iterated games provide a framework to describe social interactions among groups of individuals. Recent work stimulated by the discovery of “zero-determinant” strategies has rapidly expanded our ability to analyze such interactions. This body of work has primarily focused on games in which players face a simple binary choice, to “cooperate” or “defect”. Real individuals, however, often exhibit behavioral diversity, varying their input to a social interaction both qualitatively and quantitatively. Here we explore how access to a greater diversity of behavioral choices impacts the evolution of social dynamics in finite populations. We show that, in public goods games, some two-choice strategies can nonetheless resist invasion by all possible multi-choice invaders, even while engaging in relatively little punishment. We also show that access to greater behavioral choice results in more “rugged” fitness landscapes, with populations able to stabilize cooperation at multiple levels of investment, such that choice facilitates cooperation when returns on investments are low, but hinders cooperation when returns on investments are high. Finally, we analyze iterated rock-paper-scissors games, whose non-transitive payoff structure means unilateral control is difficult and zero-determinant strategies do not exist in general. Despite this, we find that a large portion of multi-choice strategies can invade and resist invasion by strategies that lack behavioral diversity – so that even well-mixed populations will tend to evolve behavioral diversity.

Diversity in social behaviors, not only in humans but across all domains of life, presents a daunting challenge to researchers who work to explain and predict individual social interactions or their evolution in populations. Iterated games provide a framework to approach this task, but determining the outcome of such games under even moderately complex, realistic assumptions – such as memory of past interactions [1–7], signaling of intentions, indirect reciprocity or identity [8–15], or a heterogeneous network of interactions [16–24] – is exceedingly difficult.

The discovery of zero-determinant (ZD) strategies [2] has stimulated rapid advances in our ability to analyze iterated games [1,3,26–29,31–33], leading to new understanding of how one individual can influence the longterm outcome of a pairwise social interaction, the evolutionary potential for cooperation, the prospects for generosity and extortion among groups, and the role of memory in social dynamics [34–38]. These advances all rest on a key mathematical insight: the outcome of iterated games can be easily understood when players’ strategies, even those of startling complexity [3,28,33], are viewed in the right coordinate system. This coordinate system was suggested by the discovery of ZD strategies and developed fully by Akin [26] and others [1,3,28,31,32]. ZD strategies have also been generalized to two-player games with arbitrary actions spaces [31]. Here, we study evolutionary dynamics in the full space of memory-1 strategies in a population of players with access to multiple behavioral choices, including games for which no ZD strategies exist at all.

Many game-theoretic studies of social behavior, although by no means all [31,39,40], constrain players to a binary behavioral choice such as “cooperate” or “defect” [41,42]. Other studies, particularly those looking at social evolution, constrain players to a single type of behavioral strategy, but allow for a continuum of behavioral choices – e.g. the option to contribute an arbitrary amount of effort to an obligately
cooperative interaction \([39][40]\). In general, and especially in the case of human interactions, individuals have access to both a wide variety of behavioral choices, and to a complex decision making process among these choices. Here we bridge this gap and study how the diversity of behavioral choices impacts the evolution of decision making in a replicating population, focusing on the prospects for cooperation and for the maintenance of behavioral diversity.

We develop a framework for analyzing iterated games in which players have an arbitrary number of behavioral choices and an arbitrary memory-1 strategy for choosing among them. We apply this framework to study the effect of a large behavioral repertoire on the evolution of cooperation in public goods games. We show that increasing the number of investment levels available to a player can either facilitate or hinder the evolution of cooperation in a population, depending on the ratio of individual costs to public benefits in the game. We apply the same framework to study games with non-transitive payoff structures, such as rock-paper-scissors, and we show that, while ZD strategies in general do not exist for such games, nonetheless memory-1 strategies exist that ensure the maintenance of behavioral diversity, in which players make use of all the choices available to them.

Methods and Results

Players in an iterated game repeatedly choose from a fixed set of possible actions. Depending on the choice she makes, and the choices her opponents make, a player receives a certain payoff each round. The process by which a player determines her choice each round is called her strategy. A strategy may in general take into account a wide variety of information about the environment, memory of prior interactions between players, an opponent’s identity, his social signals etc \([1–6,10,12–15,19–24]\). Here we restrict our analysis to two-player, simultaneous infinitely iterated games in which a player chooses from among \(d\) possible actions using a memory-1 strategy, which takes account only the immediately preceding interaction between her and her opponent. Although memory-1 strategies may seem restrictive, in fact a strategy that is a Nash equilibrium or evolutionary robust against all memory-1 strategies is also robust against all longer memory strategies as well (see SI and \([1–3,33]\)).

A memory-1 strategy is specified by choosing \(d^2\) probabilities for each possible action \(i\), denoted \(p^i_{jk}\), which specify the chance the player executes that action in a round of play, given that she made choice \(j\) and her opponent made choice \(k\) in the preceding round. Each probability can be chosen independently, save for the constraint that the sum across actions \(\sum_{i=1}^{d} p^i_{jk} = 1\) must hold. We study the evolution of social behavior by analyzing the composition of such strategies in a replicating population over time. In an evolving population the reproductive success of a player depends on the total payoff she receives in pairwise interactions with other members of the population \([43]\). We study how strategy evolution is affected by the number and by the types of behavioral choices available to individuals.

We study two qualitatively different behavioral choices that players can make: different sizes of contributions and different types of contributions to social interactions (Figure 1). If players can vary the size of the contribution they make to a social interaction, this means that they alter the degree of their participation but not the qualitative nature of the interaction. For example, in a public goods game, a player may choose to contribute an amount \(C\) to the public good, or \(2C\), or \(3C\) etc. In contrast, when players can vary the type of contribution they make, this can change the qualitative nature of the social interaction. For example, in a game of rock-paper-scissors the different behavioral choices result in qualitatively different social interactions – rock beats scissors, but scissors beats paper, etc. Such qualitative differences can lead to non-transitive payoffs and correspondingly complex social and evolutionary dynamics \([44][50]\).

Here we study both kinds of behavioral choice, differences in size and type, and their effects on the evolution of strategies in a population. We analyze well-mixed, finite populations of \(N\) players reproducing according to a copying process, in which a player \(X\) copies her opponent \(Y\)’s strategy with probability \(1/(1 + \exp[\sigma(S_x - S_y)])\) where \(\sigma\) scales the strength of selection and \(S_x\) is the average payoff received by player \(X\) from her social interactions with each of the \(N-1\) other members of the population \([41][43]\), which
corresponds to the fitness associated with the strategy given the current composition of the population. For a single invader \( Y \) in a population otherwise composed of strategy \( X \), this means \( S_y = S_{yx} \) and \( S_x = \frac{N-2}{N-1}S_{xx} + \frac{1}{N-1}S_{xy} \)

![Diagram showing choice of contribution size and type](image)

Figure 1: Two ways to expand the behavioral repertoire in iterated games. (Top) In a public goods game a player contributes to a public pool at some cost to herself, and she receives a benefit based on the contributions of all players in the game. In a simple two-choice game, such as the Prisoner’s Dilemma, players face a binary choice, to cooperate and contribute cost \( C \) or to defect and contribute nothing. At the other extreme, in a continuous game, players have an unlimited number of options and may contribute any amount. What happens to the evolution of social behavior as the numbers of choices increases? Is it beneficial for a population to have access to more choices in a public goods game? (Bottom) Players may also choose between qualitatively different types of contributions to social interactions. For example, unicellular organisms may produce pathogens, social signals, public goods or all three [44,55–57]. Qualitatively different behavioral options produce complex payoff structures, such as the non-transitive rock-paper-scissors interactions [44–47]. What happens to the evolution of social behavior as the types of contributions to social interactions expand? Is it better to maintain a diversity of behavioral options, or to restrict to a single type of contribution?

The outcome of an infinitely iterated \( d \)-choice game:

To analyse social evolution in multi-choice iterated games we must first calculate the expected longterm payoff \( S_{xy} \) of an arbitrary player \( X \) facing an arbitrary opponent \( Y \). To do this, we will generalize an approach used for two-choice two-player games, in which a player’s memory-1 strategy \( p \) is represented in an alternate coordinate system [26], so that the outcome of the repeated game can be determined with relative ease. For a \( d \)-choice two-player game, the probability that a focal player chooses action \( i \), given that she played action \( j \) and her opponent action \( k \) in the preceding round, is denoted \( p_{ijk} \). For each action \( 1 \leq i < d \) there are \( d^2 \) independent probabilities, corresponding to each possible outcome of the preceding round. In the alternate coordinate system we construct (see SI), the probabilities \( p_{ijk} \) are written as linear combinations of the payoff \( R_{jk} \), the focal player received in the preceding round, times a coefficient \( \chi^i \); the payoff \( R_{kj} \) her opponent received, times a coefficient \( \phi^i \); the number of times she played action \( i \) within her memory (which is one or zero for a memory-1 strategy); a baseline rate of playing action \( i \), denoted \( \kappa^i \); and \( d^2 - 3 \) additional terms that depend on the specific outcome of the preceding round, denoted \( \lambda_{ijk} \).
This choice of coordinate system enforces the following relationship between the longterm average payoffs received by the two players:

\[ \phi^i S_{yx} - \chi^i S_{xy} - (\phi^i - \chi^i) \kappa^i + \sum_{j=1}^{d} \sum_{k=1}^{d} \lambda_{jk}^i v_{jk} = 0 \]  

(1)

where \( v_{jk} \) denotes the equilibrium rate of action \( jk \), and where we fix the values of three of the \( \lambda_{jk}^i \) to ensure a system of \( d^2 \) coordinates (see SI). Note there are \( d - 1 \) such equations, one for each behavioral choice \( 1 \leq i < d \). A ZD strategy of the type studied in [31] can be recovered by setting all \( \lambda_{jk}^i = 0 \).

Choosing how much to contribute to a public good:

We will use the relationship between two players scores (Eq. 1) to analyse the evolution and stability of cooperative behaviors in multi-choice public goods games, played in a finite population. In the two-player public goods game each player chooses an investment level, \( C \), which produces a corresponding amount of public benefit that is then shared equally between both players, regardless of their investment choices. In general, if a player invests \( C_j \) and her opponent \( C_k \) the public benefit produced is determined by a function \( B(C_j + C_k) \), so that her net payoff is \( B(C_j + C_k)/2 - C_j \) while her opponent’s payoff is \( B(C_j + C_k)/2 - C_k \).

Two-choice public goods games have been studied extensively, producing a clear understanding of the cooperative equilibria that exist in populations [1,3,26,27,34–36]. A wide variety of evolutionary robust memory-1 strategies exist for two-choice public goods games. The character and evolvability of these strategies have been explored in detail [1,3,34,36,51–53]. But the assumption of only two investment levels – of two behavioral choices – is unrealistic for many applications. Even if a player adopts such a two-choice strategy, there is in general no reason for her opponent to do the same. Thus we begin our analysis by asking whether a cooperative, two-choice, memory-1 strategy resident in a population can resist invasion against players who can make arbitrary investment choices.

For simplicity, we will focus here on a linear relationship between costs and benefits of investment in the public good, so that \( B = rC \) where values \( 1 < r < 2 \) produce a social dilemma in which mutual cooperation is beneficial but each player has an incentive to defect. The more general case, with non-linear functional relationships, is described in the Supporting Information.

For linear benefits, a two-choice strategy is completely defined by

\[ p_{1i} = 1 - ((\phi - \chi)(r(C_1 + C_i)/2 - \kappa) - \phi C_i + \chi C_1 + \lambda_{1i}) \]
\[ p_{2i} = -((\phi - \chi)(r(C_2 + C_i)/2 - \kappa) - \phi C_i + \chi C_2 + \lambda_{2i}) \]

where the index \( i \) corresponds to an opponent who invests \( C_i \), which in general can take any non-negative value. Here we choose the boundary conditions \( \lambda_{11} = \lambda_{22} = 0 \) and \( \lambda_{12} = \lambda_{21} \), and from Eq. 1 we obtain the following relationship between two players’ longterm payoffs

\[ \phi S_{yx} - \chi S_{xy} - (\phi - \chi)\kappa + \lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^{d} (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) = 0 \]

When player \( Y \) is constrained to the same two choices as player \( X \), then this relationship reduces precisely to the relationship for two-player, two-choice games discussed in [1,2,26,36]. However, we will consider the more general case when player \( Y \) has access to different, and possibly more, investment choices than
X. In general, a strategy X resident in a population of N players can resist selective invasion by a mutant Y if

\[ S_{yx} < \frac{N-2}{N-1} S_{xx} + \frac{1}{N-1} S_{xy} \]

where \( S_{xx} \) is the longterm payoff of the resident strategy against itself. A cooperative two-choice strategy by definition has \( S \) ability to choose different investment levels. \( C \) level when resident in a population, and that resists invasion by any invader, regardless of the invader’s

If (and only if) Eq. 3 is satisfied, then there exists a two-choice strategy that enforces cooperation at some

where we have set \( c = C_1/C_2 \) and \( c^* = C_2/C_1 \). All four of these inequalities are hardest to satisfy when \( c^* = 0 \), i.e. when an invader does not invest at all in the public good (although this is not necessarily the case when benefits vary non-linearly with costs – see Supporting Information). Using this fact, alongside the requirement that a strategy be viable (i.e. \( p_{ij} \in [0,1], \ \forall i,j \)), we can derive the following necessary and sufficient condition for the existence of a two-choice strategy that is universally robust:

\[ \frac{C_1}{C_2} < \frac{r-1}{\frac{r}{2} + \frac{1}{N-2}} \]  

If (and only if) Eq. 3 is satisfied, then there exists a two-choice strategy that enforces cooperation at some level when resident in a population, and that resists invasion by any invader, regardless of the invader’s ability to choose different investment levels.

Eq. 3 offers insight into the degree of punishment that a resident cooperative strategy must be prepared to wield, in order to remain robust against all invaders (Fig. 2). A resident strategy can punish a non-cooperative invader by reducing her investment in the public good from \( C_2 \) to \( C_1 \). If \( C_1 \) is only slightly smaller than \( C_2 \) then the resident strategy has a limited capacity to punish invaders. Whereas if \( C_1 \) is much less than \( C_2 \) the resident strategy has a greater capacity for punishment. The critical question is how much capacity for punishment, quantified by the ratio of \( C_1 \) and \( C_2 \), is required to ensure that the resident cooperator can be robust against all invaders (who can make arbitrary investments, outside of those available to the resident). The answer to this question is shown in Figure 2, which quantifies the minimum reduction in public investment that a cooperative two-choice strategy must make in order to be universally robust. As might be expected from Eq. 3, larger ratios of public benefit to individual cost \( r \) and larger population sizes \( N \) mean that smaller reductions in public investment are sufficient for universal robustness of the resident cooperator. And as Fig. 2 shows, for a wide range of parameters a population can enjoy robust cooperation using a simple two-choice strategy with only moderate threat of punishment, e.g. \( C_1 \) no less than than one-half of \( C_2 \).
Figure 2: When are simple two-choice strategies robust against all multi-choice invaders in public goods games? We considered the evolutionary robustness of two-choice strategies, in which players iteratively choose to invest amount $C_1$ or $C_2 > C_1$ to produce a public benefit $B$ proportional to the total investment of both players, $B = rC$. Cooperative strategies limited to two investment choices can be evolutionary robust against all invaders, who may invest an arbitrary amount $C \neq C_1, C_2$, provided the strategy has sufficient opportunity to punish a defector—that is, provided $C_1$ is sufficiently smaller than $C_2$. We determined (Eq. 4) the largest ratio of investment levels, $C_2/C_1$, that permits universally robust cooperative two-choice strategies, as a function of the the population size, $N$, and the public return on individual investment, $r$. Colors are gradated in 10% intervals, so that the light blue region indicates a two-choice player can choose a strategy that maintains robust cooperation while engaging in relatively little punishment, by reducing her investment to only 90% of its maximum. The bright red region indicates that a two-choice player must have access to a high degree of punishment, $C_1$ much less than $C_2$, in order to maintain cooperation. As described in Eq. 4, the figure can alternatively be interpreted as the proportion of pairs of investment levels used by a $d$-choice player that produce a robust sub-optimal fitness peak, and thus represents a lower bound on the “ruggedness” of the fitness landscape experienced by a population of $d$-choice players.

Evolutionary consequences of multiple investment choices:

We now turn our attention to the implications of these results for an evolving population of players who can make $d > 2$ choices for investment in the public good. We assume a discrete series of $d + 1$ investment levels, from 0 to the maximum $C_{\text{max}}$, so that subsequent levels of investment differ by $C_{\text{max}}/d$. When $d$ is large, players have more options for investment, between the fixed minimum value zero and fixed maximum value $C_{\text{max}}$.

Because all two-choice strategies form a subset of $d$-choice strategies, an evolving population of $d$-choice players has access to, at minimum, all evolutionary robust two-choice strategies. Thus, unlike in the two-choice case, where there are only three qualitatively distinct types of evolutionary robust strategies [1], a $d$-choice population may result in many different classes of evolutionary robust outcomes, most of which are sub-optimal in the sense that they produce less public good than the global maximum, $rC_{\text{max}}$.

We can place a lower bound on how many such sub-optimal, but evolutionary robust, outcomes are possible when players have $d + 1$ choices. Any given pair of investment levels $C_i$ and $C_j$, with $i > j$, can be a robust two-choice strategy provided $C_i$ and $C_j$ satisfy Eq. 4. Thus all pairs of investment levels $j < \frac{r-1}{r + \frac{1}{N-2}} i$ have viable robust two-choice strategies associated with them; and for a $d + 1$-choice game the total number of such evolutionary robust but sub-optimal strategies, $P_r$, satisfies

$$P_r > \left( \frac{r - 1}{r + \frac{1}{N-2}} \right) \frac{d(d + 1)}{2}. \quad (4)$$
Thus the number of sub-optimal evolutionary robust outcomes grows at least quadratically with the number of investment levels available to individuals.

Fig. 2 can now be re-interpreted as showing the proportion of pairs of investment levels that can produce a robust, sub-optimal two-choice strategy for a population of \( d + 1 \)-choice players. To put these results in perspective, if players are allowed \( d = 100 \) investment choices, with return on investment \( r = 3/2 \), then in a population size \( N = 1,000 \) there are at least \( 3.6 \times 10^3 \) robust strategies that fail to maximize the total public good – resulting in an extremely “rugged” fitness landscape and a large number of sub-optimal evolutionary outcomes. By contrast, with only \( d = 2 \) choices, there are at most two sub-optimal evolutionary robust outcomes [1].

We have seen that increasing the number of available choices to players, between a fixed minimum and maximum investment level, has the potential to produce sub-optimal but evolutionary robust outcomes. To test how the number of available choices impacts evolutionary dynamics in a population, we ran evolutionary simulations under weak mutation [36], with mutants drawn uniformly from all \( d \)-choice memory-1 strategies. We compared the mean payoffs received by populations constrained to \( d = 2 \) choices, to the mean payoffs in populations with access to \( d = 11 \) choices (Figure 3). The results are striking: when ratios of public benefit to individual cost are low, so that robust strategies are rare (Eqs. 2-3), the population that has \( d = 11 \) investment choices evolves a higher mean payoff than the \( d = 2 \) choice population – because a greater number of robust cooperative strategies provides an advantage. But when ratios of public benefit to individual cost are higher, so that robust strategies are more common, the \( 11 \)-choice population evolves a lower mean payoff than the \( 2 \)-choice population – because the huge number of sub-optimal robust strategies causes the \( 11 \)-choice population to “get stuck” and fail to maximize its evolutionary potential. Thus, increasing the number of investment options, between a fixed minimum and maximum, can either facilitate or hinder cooperative interactions in a population.

**Non-transitive payoff structures:**

So far we have focused on multiple options for investment and its impact on the evolution of cooperative behaviors in public goods games. But the co-ordinate system we have introduced for studying multi-choice iterated games, and the resulting relationship between two players’ scores (Eq. 1), applies generally, and so it can be applied to study many other questions in evolutionary game theory. Among the most interesting questions occur with only \( d = 3 \) choices, but with non-transitive payoffs, where the evolutionary dynamics are complex and the impact of repeated interactions remains unclear [44][50].

Games with non-transitive payoff structures, such as rock-paper-scissors, describe social dynamics without any strict hierarchy of behaviors. Individuals can invest in qualitatively different types of behavior, which dominate in some social interactions but lose out in others. Such non-transitive interactions have been observed in a range of biological systems, from communities of *Escherichia coli* species [44], to mating competition among male side-blotched lizards *Uta stansburiana* [45]. Rock-paper-scissors interactions are well known in ecology as having important consequences for the maintenance of biodiversity: in well mixed populations playing the one-shot game, diversity is often lost, whereas in spatially distributed populations multiple strategies can be stably maintained [46][47]. Here we analyse the equivalent problem for the maintenance of diversity in evolving populations of players who engage in iterated non-transitive interactions.

We will assess the potential for maintaining behavioral diversity in a population playing an iterated rock-paper-scissors game – that is, we look for strategies that can resist invasion by players who employ a single behavioral choice (1=rock, 2=paper or 3=scissors). We assume that, in any given interaction, a fixed benefit \( B \) is at stake, and players invest a cost \( C_1, C_2 \) or \( C_3 \) to execute the corresponding behavioral choice. Under the rock-paper-scissors game we then have payoffs \( R_{13} = B - C_1 \), \( R_{21} = B - C_2 \), \( R_{32} = B - C_3 \), \( R_{31} = -C_3 \), \( R_{12} = -C_1 \) and \( R_{23} = -C_2 \). When two players make the same choice we assume they receive equal payoff: \( R_{11} = B/2 - C_1 \), \( R_{22} = B/2 - C_1 \) and \( R_{33} = B/2 - C_1 \).
We evolved a well-mixed population of $N = 100$ haploid, asexual individuals reproducing according to the copying process [43] with an individual’s fitness determined by playing pairwise iterated public goods games. We calculated ensemble mean fitness across $10^5$ replicate populations, each evolved under weak mutation for at least $10^6$ fixation events. We compared populations with only two investment choices available, $C_1 = 0$ and $C_2 = 1$, versus populations in which players could choose among 11 levels of investment, between 0 and 1 in increments of 0.1. In both cases evolution occurred on the full set of memory-1 strategies. When the ratio of public benefit to individual cost is small, two-choice populations evolve to low mean fitness and exhibit little cooperation, whereas 11-choice populations evolve higher fitness and higher levels of investment in the public good. However, when the ratio of public benefit to individual cost is higher two-choice populations evolve strategies that maximize the public good, whereas 11-choice populations are less cooperative and receive roughly 10% payoff reduction compared to the two-choice case. Thus, a larger repertoire of behavioral options can either facilitate or impede the evolution of cooperation, depending upon the public return on individual investment.

We first consider the case of a completely symmetric game of rock-paper-scissors, with $C_1 = C_2 = C_3 = C$. In this case a given round of the game has only three distinct outcomes for a player: win (+), lose (-) or draw (o). A player’s memory-1 strategy can be thought of as the probability that she plays, for example, a move that would have won in the preceding round, given that she lost. We write this probability $p^+$. Similarly $p^-$ is the probability she plays the same move that lost the preceding round; and $p^o$ is the probability that she plays the move that would have resulted in a draw. This symmetric strategy is thus composed of 9 probabilities, which are written in our alternative coordinate system as:

\[
\begin{align*}
p^o_o & = 1 - (\phi - \chi)(B/2 - C - \kappa) \\
p^-_o & = 1 - (\phi(B - C) + \chi C - (\phi - \chi)\kappa) \\
p^+_o & = 1 + (\phi C + \chi(B - C) + (\phi - \chi)\kappa) \\
p^+_+ & = \lambda^+_o + (\phi C + \chi(B - C) + (\phi - \chi)\kappa) \\
p^-_+ & = \lambda^-_+ - (\phi - \chi)(B/2 - C - \kappa) \\
p^+_+ & = \lambda^+_+ - (\phi(B - C) + \chi C - (\phi - \chi)\kappa) \\
p^-_+ & = \lambda^-_+ + (\phi C + \chi(B - C) + (\phi - \chi)\kappa) \\
p^+_o & = \lambda^+_o - (\phi - \chi)(B/2 - C - \kappa) \\
p^-_o & = \lambda^-_o - (\phi - \chi)(B/2 - C - \kappa)
\end{align*}
\]

where we have set $\lambda^+_o = \lambda^-_+ = \lambda^-_o = 0$ as a boundary condition. We see immediately from this that there
exists no viable ZD strategy, for which \( \lambda^i_j = 0 \), \( \forall i, j \), unless we also set \( \kappa = \chi = \phi = 0 \) to produce the singular “repeat” strategy \(^2\). Nonetheless, we can still analyse the outcome of iterated rock-paper-scissors games using this coordinate system.

### Maintaining behavioral diversity in a game of rock-paper-scissors:

The symmetric, iterated rock-paper-scissors game is simple to analyse, because payoff is conserved, meaning that the sum of two interacting players’ payoffs is constant, \( S_{xy} + S_{yx} = B - 2C \). Thus the expected fitness of a population is independent of the strategy that is resident, and \( S_{xx} = B/2 - C \) holds for all strategies \( X \). It might seem unlikely, then, that behavioral diversity offers any advantage in this situation. After all, a player who uses a strategy that employs only rock, paper or scissors produces no higher mean fitness at the population level than a player who always uses rock. To determine whether this intuition is correct, and non-transitive payoffs lead inevitably to a loss of behavioral diversity, we evaluated the conditions for a strategy to resist selective invasion by a player who always uses the same move. Such strategies do indeed exist, and satisfy the following inequality:

\[
p_o (1 - p_- - p_+) > p_o (1 - p_+ - p_-). \tag{5}
\]

As one might hope, strategies that tend to switch to the move that would have won in the preceding round – corresponding to larger values of \( p_+^+, \ p_-^+ \) and smaller values of \( p_0^-, \ p_-^-, \ p_+^- \) – tend to be evolutionary robust. However Eq. 6 also provides a more valuable insight, if we calculate the overall robustness of memory-1 strategies to the loss of behavioral diversity. To do this we calculate the probability that a randomly drawn memory-1 strategy satisfies Eq. 6, which reveals that fully 50% of such strategies maintain behavioral diversity in the completely symmetric rock-paper-scissors game (Figure 4). Furthermore, due to symmetry, the condition for a new strategy to invade a resident is simply \( S_{yx} > S_{xy} \) (see SI). And so if a resident can resist invasion against a particular invader, it can also invade a population in which that invader is resident. Thus 50% of strategies can successfully invade in a population that lacks behavioral diversity – so that behavioral diversity is both highly evolvable and easy to maintain in the iterated rock-paper-scissors game, even in a well-mixed population – in sharp contrast to the one-shot game.

We can also assess the robustness of behavioral diversity when the symmetry of the game is broken, so that \( C_1 \neq C_2 \neq C_3 \). In Figure 4a we numerically calculate the overall robustness of randomly drawn strategies as a function of the costs \( C_1/C_3 \) and \( C_2/C_3 \) keeping \( B \) and \( C_3 \) fixed. We find that, for a wide range of costs, including in some cases with \( B < C \), behavioral diversity can be maintained with relative ease in an evolving population (Fig. 4).

### Discussion

We have studied how the repertoire of behavioral options influences the prospects for cooperation, and the maintenance of behavioral diversity, in evolving populations. Our analysis has relied on the theory of iterated games and, in particular, on a coordinate system we developed to describe strategies for multi-choice games and their effects on long-term payoffs. In the context of public goods games, we have shown that simple strategies that use only two levels of investment can nonetheless stabilize cooperative behavior against arbitrarily diverse mutant invaders, provided the simple strategy has sufficient opportunity to punish defectors. More generally, a greater diversity of investment options can either facilitate or hinder the evolution of cooperation, depending on the ratio of public benefit produced to an individual’s investment cost. We have applied the same analytical framework to study more complicated multi-choice iterated games with non-transitive payoffs, such as the rock-paper-scissors game. In this case, behaviorally diverse strategies that employ multiple actions are often evolutionary robust, even in a well-mixed population, and they can likewise invade populations that lack diverse behaviors. Overall, the view emerges that
Figure 4: Can behavioral diversity be maintained under non-transitive payoff structures? We considered a rock-paper-scissors type game in which players could employ up to three different behaviors, at a cost $C_1$, $C_2$ and $C_3$, in an attempt to obtain a fixed benefit $B$. The payoff structure was non-transitive so that action 1 dominates action 2, action 2 dominates action 3, and action 3 dominates action 1. We determined whether a memory-1 strategy that employs all three behaviors can resist invasion by a player who uses a single action exclusively (either 1, 2, or 3). (a) With fixed benefit $B = 2$ and cost $C_3 = 1$ we systematically varied costs $C_1$ and $C_2$, and we calculated the percentage of memory-1 strategies that could successfully maintain behavioral diversity. Behavioral diversity can indeed be maintained for a wide range of costs. The highest level of robust diverse strategies occurs in the symmetric case, when $C_1 = C_2 = C_3$. But diverse behaviors are across a broad range of parameters including, surprisingly, when both $C_1 > B$ and $C_2 > B$. This is seen more clearly in (b) which shows the percentage of robust strategies as a function of $C_1$ with $C_2 = C_3$.

Simple behavioral interactions are sometimes surprisingly robust against diverse alternatives, and yet, in many circumstances, diverse behavior serves the mutual benefit of a population and is a likely outcome of evolution.

Our results on the impact of multiple behavioral choices should be compared to those of McAvoy & Hauert [31], who studied ZD strategies in the two-player donation game, with an arbitrary action space. Those authors established that ZD strategies exist even in this general setting. They focused especially on extortion strategies, whereby one player unilaterally sets the ratio of scores against her opponent. McAvoy & Hauert found, remarkably, that extortion strategies exist with support on only two actions, even against an opponent who can choose from an uncountable number of actions. Our results form a intriguing contrast to those of McAvoy & Hauert. Instead of studying ZD strategies and extortion in the classical context of two players, we have studied all memory-1 strategies and the prospects for robust cooperation in a population of $N > 2$ players. We find that behaviorally depauperate strategies that rely on only two actions can nonetheless sustain cooperation in a population facing diverse invaders; and yet diversity can either hinder or facilitate cooperation, depending upon the ratios of public benefit to individual cost.

We have analyzed the entire space of memory-1 strategies for iterated multi-choice games. The purview of our analysis can be put in context by comparison to the yet wider space of long-memory strategies, on the one hand, and the smaller space of ZD strategies, on the other hand. As discussed here and elsewhere, strategies that are evolutionary robust against the full space of memory-1 strategies are also robust against all longer-memory strategies [2][33] (also see Supporting Information), making this a natural strategy space to consider from an evolutionary perspective. Nonetheless, memory can have an important impact on the relative success of different types of robust strategies, by making them more or less evolvable [3], or by allowing qualitatively different types of decision-making via tagging or kin recognition [54]. Conversely, it is important to consider the full space of memory-1 strategies in the context of multi-choice games.
because, as we have shown, such games may contain no ZD strategies at all, as in the case of iterated rock-papers-scissors.

It is perhaps unsurprising that games with non-transitive payoffs do not in general admit the opportunity for one player to exert unilateral control over the game’s outcome via ZD strategies – after all, a player cannot successfully extort an opponent whose behavior is so diverse that it cannot be pinned down. Yet our analysis also offers a novel perspective on the problem of diversity maintenance in evolving populations. One-shot rock-paper-scissors games have long been studied in the context of evolutionary ecology as a system that cannot easily maintain diversity without spatial structure or other exogenous population heterogeneity [44–50]. Here, by contrast, we have shown that behaviorally diverse strategies in the iterated game can easily emerge and resist invasion by behaviorally depauperate mutants, an observation which is relevant to behavioral interactions within a single population and also to interactions between species.

Overall we have seen that, as players gain access to more behavioral choices, either due to environmental shifts or evolutionary innovation, the dynamics of social evolution can be profoundly altered. This view is reflected by empirical studies, which have found that greater behavioral choice, via factors such as the ability to communicate or signal to others, has a significant impact on the level of cooperation in a group [8–11]. Moving forward, we must connect the insights drawn from complex behavioral and evolutionary models of the type described here to empirical studies, where we can now seek quantitative predictions for the dynamics of group behavior in real populations.

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Supporting Information

In this supplement we first generalize the results of Press & Dyson 2012 and Stewart & Plotkin 2014 [1] to the case of an infinitely iterated, d-choice, two-player game. We then apply those results to study evolutionary robustness of cooperation in a public goods game and maintenance of behavioral diversity in a rock-paper-scissors game.

Infinitely Iterated Multi-choice Games

In this supplement, we generalize the results of [2] to a game with an arbitrary number of choices. We start by repeating Press & Dyson’s argument for relating the payoffs for each player to a determinant.

The essential fact for their argument is that 1 is a simple (left) eigenvalue of any transition matrix $M$. Recall that, for square matrices, the left and right eigenvalues are the same and have equal multiplicities (this is easily seen by observing that the characteristic equations for $M^T$ and $M$ are equal: $\det(\lambda I - M^T) = \det(\lambda I - M)$).

Now, 1 is always a left eigenvalue of any transition matrix - because the rows must sum to 1, the vector $\mathbf{1}$ with all entries equal to 1 is a right eigenvector for the eigenvalue 1. The only constraint to generalizing the result of [2] to more than two choices is that 1 must continue to be a simple eigenvalue. We start by repeating Press & Dyson’s argument for relating the payoffs for each player to a determinant.

We consider the case in which player one always plays the choice they played in the previous round, and the eigenvector $\mathbf{v}$ need not be unique (in the aforementioned example, there are as many distinct eigenvectors as there are choices). Nonetheless, reducible strategies are a lower dimensional subspace of all strategies, and are thus non-generic.

Now, suppose that $\mathbf{v}$ is the unique left eigenvector of $M$ corresponding to the eigenvalue 1 and set $M' := M - I$. Then $\mathbf{v}$ is the unique vector such that $\mathbf{v}^T M' = \mathbf{0}$, so 0 is an eigenvalue of $M'$. Thus, $\det(M') = 0$, and Cramer’s rule tells us that

$$\text{Adj}(M') M' = \det(M') I = 0,$$

from which we conclude that every row of $\text{Adj}(M')$ is a left eigenvector for the eigenvalue 0, and thus must be a scalar multiple of $\mathbf{v}$.

Recall that, given an $n \times n$ matrix $A$, the classical adjoint of $A$, $\text{Adj}(A)$ is the matrix with entries equal to the cofactors of $A$:

$$\text{Adj}(A)_{ij} = (-1)^{i+j} \det(A(i|j)),$$

where $A(i|j)$ is the $(n-1) \times (n-1)$ matrix obtained by deleting the $i$th row and $j$th column of $A$. We also recall Laplace’s cofactor expansion for the determinant: for any choice of row $i$ or column $j$, we have

$$\det(A) = \sum_{j=1}^{n} (-1)^{i+j} \det(A(i|j)) a_{ij} = \sum_{i=1}^{n} (-1)^{i+j} \det(A(i|j)) a_{ij}.$$

Now, in [2], the authors observe that if $f$ is any column vector in $\mathbb{R}^n$ and $(A|f)$ is the matrix obtained by replacing the $n$th column of $A$ with $f$, then

$$\det((A|f)) = \sum_{i=1}^{n} (-1)^{i+n} \det((A|f)(i|n))(A|f)_{in} = \sum_{i=1}^{n} (-1)^{i+n} \det(A(i|d)) f_i = \sum_{i=1}^{n} \text{Adj}(A)_{in} f_i.$$

15
(n.b. $A(i|n)$) is obtained by deleting the $n^{th}$ column of $(A|f)$, and thus is equal to $A(i|n)$, whereas $(A|f)_{in} = f_i$ by construction), and that this latter is the dot product of the $n^{th}$ column of Adj$(A)$ with $f$. Now, as we have already observed, the $n^{th}$ column of Adj$(M')$ is $\alpha v$, for some non-zero $\alpha$, so
\[
\det((M'|f)) = \alpha v \cdot f
\]
for arbitrary $f$. In particular, recalling that all entries of $v$ sum to 1, we have
\[
\det((M'|1)) = \alpha v \cdot 1 = \alpha
\]
and thus
\[
\frac{\det((M'|f))}{\det((M'|1))} = v \cdot f.
\]
(6)

Next, recall that det$(A)$ is an alternating multilinear function of the columns of $A$, so for arbitrary $m$, vectors $f_1, \ldots, f_m \in \mathbb{R}^n$, and scalars $\alpha_1, \ldots, \alpha_m$
\[
\det \left( \left( A \mid \sum_{k=1}^{m} \alpha_k f_k \right) \right) = \sum_{k=1}^{m} \alpha_k \det((A|f_k)),
\]
and thus,
\[
\frac{\det((M'|\sum_{k=1}^{m} \alpha_k f_k))}{\det((M'|1))} = \sum_{k=1}^{m} \alpha_k (v \cdot f_k).
\]
Press & Dyson then observe that player $i$’s payoff is $S_i := v \cdot R_i$, where $R_i$ is the vector of payoffs received by player $i$ and $v$ is the vector giving the equilibrium rate of different plays in an infinitely iterated game. If there are 2 players, then
\[
\frac{\det((M'|\alpha_1 R_1 + \alpha_2 R_2 + \alpha_3 1))}{\det((M'|1))} = \alpha_1 S_{12} + \alpha_2 S_{21} + \alpha_3.
\]
Now, to get the enforced relation
\[
\alpha_1 S_{12} + \alpha_2 S_{21} + \alpha_3 = 0,
\]
Press & Dyson use the alternating property of the determinant, namely that if any two columns are equal (or more generally, if there exists a subset of columns such that some linear combination of those columns is equal to one of the remaining columns) then the determinant is 0.

Thus, to generalize the result of [2], we need only verify that each of the two players can independently force the equality of at least two columns.

The first step in doing this to recalling that for any matrix $A$, det$(A)$ is left unchanged by replacing any row or column by itself plus a linear combination of the other rows or columns, respectively. Thus, if by such operations, we can transform $(M'|f)$ to a matrix $(M'|f)$ with one column that only depends on player $i$’s strategy, say $p$, then player $i$ can enforce the linear relation (and, since $i$ is arbitrary, so can any other player) by setting a column that they control equal to
\[
\alpha_1 R_1 + \alpha_2 R_2 + \alpha_3 1.
\]
In what follows, we show that in the case of $d$ choices, which we label $0, \ldots, d-1$, the transition matrix $M$ is such that for an arbitrary vector $f \in \mathbb{R}^n$ (here, $n = d^2$) $(M'|f)$ has $d$ columns that are completely determined by player 1 and $d$ columns that are controlled by player 2.

We order the possible outcomes of play by the $d$-ary ordering. That is to say, we denote the event where player 1 plays choice $j$ and player 2 strategy $k$ by $jk$, and order these events such that $jk$ is the
\((d - 1)j + k^{th}\) possible outcome. Throughout this section, we will use \(d = 3\) as an example to clarify the discussion; in this case, we have possible plays

\[11, 12, 13, 21, 22, 23, 31, 32, 33\]

Let \(p_{jk}^i\) and \(q_{jk}^i\) \((i = 1, \ldots, d; j, k = 1, \ldots, d)\) denote the probabilities that player 1 and player 2 respectively use choice \(i\) given that in the previous round player 1 used choice \(j\) and player 2 used choice \(k\)

\[
\sum_{j=1}^{k} \sum_{k=1}^{k} p_{jk}^i = 1 \quad \text{and} \quad \sum_{j=1}^{k} \sum_{k=1}^{k} q_{jk}^i = 1.
\]

With this notation, the transition matrix \(M\) has entries

\[m_{i,jk} = p_{jk}^i q_{jk}^i,
\]

which, for \(d = 3\) gives us

\[
M = \begin{bmatrix}
p_{11}^1 q_{11}^1 & p_{11}^1 q_{11}^2 & p_{11}^1 (1 - q_{11}^1 - q_{11}^2) & \cdots \\
p_{12}^1 q_{21}^1 & p_{12}^1 q_{21}^2 & p_{12}^1 (1 - q_{21}^1 - q_{21}^2) & \cdots \\
p_{13}^1 q_{31}^1 & p_{13}^1 q_{31}^2 & p_{13}^1 (1 - q_{31}^1 - q_{31}^2) & \cdots \\
p_{21}^1 q_{12}^1 & p_{21}^1 q_{12}^2 & p_{21}^1 (1 - q_{12}^1 - q_{12}^2) & \cdots \\
p_{22}^1 q_{22}^1 & p_{22}^1 q_{22}^2 & p_{22}^1 (1 - q_{22}^1 - q_{22}^2) & \cdots \\
p_{23}^1 q_{32}^1 & p_{23}^1 q_{32}^2 & p_{23}^1 (1 - q_{32}^1 - q_{32}^2) & \cdots \\
p_{31}^1 q_{13}^1 & p_{31}^1 q_{13}^2 & p_{31}^1 (1 - q_{13}^1 - q_{13}^2) & \cdots \\
p_{32}^1 q_{23}^1 & p_{32}^1 q_{23}^2 & p_{32}^1 (1 - q_{23}^1 - q_{23}^2) & \cdots \\
p_{33}^1 q_{33}^1 & p_{33}^1 q_{33}^2 & p_{33}^1 (1 - q_{33}^1 - q_{33}^2) & \cdots 
\end{bmatrix}
\]

Next, \(M'\) has entry \(m'_{i,j} = m_{i,j} - \delta_{i,j}\), where \(\delta_{i,j}\) is Kronecker’s delta function. Again, for \(d = 3\), this gives

\[
M' = \begin{bmatrix}
p_{11}^1 q_{11}^1 - 1 & p_{11}^1 q_{11}^2 & p_{11}^1 (1 - q_{11}^1 - q_{11}^2) & \cdots \\
p_{12}^1 q_{21}^1 - 1 & p_{12}^1 q_{21}^2 & p_{12}^1 (1 - q_{21}^1 - q_{21}^2) & \cdots \\
p_{13}^1 q_{31}^1 - 1 & p_{13}^1 q_{31}^2 & p_{13}^1 (1 - q_{31}^1 - q_{31}^2) & \cdots \\
p_{21}^1 q_{12}^1 & p_{21}^1 q_{12}^2 & p_{21}^1 (1 - q_{12}^1 - q_{12}^2) & \cdots \\
p_{22}^1 q_{22}^1 & p_{22}^1 q_{22}^2 & p_{22}^1 (1 - q_{22}^1 - q_{22}^2) & \cdots \\
p_{23}^1 q_{32}^1 & p_{23}^1 q_{32}^2 & p_{23}^1 (1 - q_{32}^1 - q_{32}^2) & \cdots \\
p_{31}^1 q_{13}^1 & p_{31}^1 q_{13}^2 & p_{31}^1 (1 - q_{13}^1 - q_{13}^2) & \cdots \\
p_{32}^1 q_{23}^1 & p_{32}^1 q_{23}^2 & p_{32}^1 (1 - q_{23}^1 - q_{23}^2) & \cdots \\
p_{33}^1 q_{33}^1 & p_{33}^1 q_{33}^2 & p_{33}^1 (1 - q_{33}^1 - q_{33}^2) & \cdots 
\end{bmatrix}
\]

Finally, the row corresponding to the plays \(jk\) of \((M'|f)\) has entries

\[p_{jk}^{d_1} q_{kj}^{d_1}, \ldots, p_{jk}^{d_k} q_{kj}^{d_k}, p_{jk}^{d_{k-1}} q_{kj}^{d_{k-1}}, \ldots, p_{jk}^{d_1} q_{kj}^{d_1} - 1, \ldots, p_{jk}^{d_k} q_{kj}^{d_k}, \ldots, p_{jk}^{d_{d-1}} q_{kj}^{d_{d-1}}, f_{jk},
\]

and continuing to illustrate this with \(d = 3\), we have

\[
(M'|f) = \begin{bmatrix}
p_{11}^1 q_{11}^1 - 1 & p_{11}^1 q_{11}^2 & p_{11}^1 (1 - q_{11}^1 - q_{11}^2) & \cdots, f_{11} \\
p_{12}^1 q_{21}^1 - 1 & p_{12}^1 q_{21}^2 & p_{12}^1 (1 - q_{21}^1 - q_{21}^2) & \cdots, f_{12} \\
p_{13}^1 q_{31}^1 - 1 & p_{13}^1 q_{31}^2 & p_{13}^1 (1 - q_{31}^1 - q_{31}^2) & \cdots, f_{13} \\
p_{21}^1 q_{12}^1 & p_{21}^1 q_{12}^2 & p_{21}^1 (1 - q_{12}^1 - q_{12}^2) & \cdots, f_{21} \\
p_{22}^1 q_{22}^1 & p_{22}^1 q_{22}^2 & p_{22}^1 (1 - q_{22}^1 - q_{22}^2) & \cdots, f_{22} \\
p_{23}^1 q_{32}^1 & p_{23}^1 q_{32}^2 & p_{23}^1 (1 - q_{32}^1 - q_{32}^2) & \cdots, f_{23} \\
p_{31}^1 q_{13}^1 & p_{31}^1 q_{13}^2 & p_{31}^1 (1 - q_{13}^1 - q_{13}^2) & \cdots, f_{31} \\
p_{32}^1 q_{23}^1 & p_{32}^1 q_{23}^2 & p_{32}^1 (1 - q_{23}^1 - q_{23}^2) & \cdots, f_{32} \\
p_{33}^1 q_{33}^1 & p_{33}^1 q_{33}^2 & p_{33}^1 (1 - q_{33}^1 - q_{33}^2) & \cdots, f_{33}
\end{bmatrix}
\]

Thus, the sum of the first \(d\) entries of the \(jk^{th}\) row of \((M'|f)\) is

\[p_{jk}^{d_1} q_{kj}^{d_1} + \cdots + p_{jk}^{d_k} q_{kj}^{d_k} = \begin{cases} p_{jk}^{d_1} - 1 & \text{if } j = 1 \\ p_{jk}^{d_k} & \text{otherwise} \end{cases}
\]
Similarly for the second \(d\) entries, and so on. Thus, if for each \(a = 0, \ldots, d-1\), we replace the \(ad\)th column by the sum of columns \(ad, ad + 1, \ldots, ad + d - 1\), a transformation that leaves \(\det((M'[f]))\) unchanged, the resulting matrix has a \(ad\)th column with \(jk\)th entry

\[
p_{jk}^{a+1} = \begin{cases} 
1 & \text{if } j = a + 1 \\
0 & \text{otherwise}
\end{cases}
\]

i.e. the \(ad\)th column depends only on player 1, and player 1 controls \(d\) columns, one for each available choice. Proceeding similarly, we see that player 2 also controls exactly \(d\) columns.

To see this concretely, for \(d = 3\), if we replace the third column of \((M'[f])\) by the third column plus the first and the second (which preserves the determinant), we get

\[
(M'[f]) = \begin{bmatrix}
p_{11}^{1}q_{11}^{1} - 1 & p_{11}^{1}q_{11}^{2} & p_{11}^{1}q_{11}^{3} & p_{12}^{1} - 1 & p_{12}^{1}q_{12}^{2} & p_{12}^{1}q_{12}^{3} & p_{13}^{1} - 1 & p_{13}^{1}q_{13}^{2} & p_{13}^{1}q_{13}^{3} \\
p_{12}^{1}q_{21}^{1} & p_{12}^{1}q_{21}^{2} - 1 & p_{12}^{1}q_{21}^{3} & p_{13}^{1} - 1 & p_{13}^{1}q_{21}^{2} & p_{13}^{1}q_{21}^{3} & p_{14}^{1} - 1 & p_{14}^{1}q_{21}^{2} & p_{14}^{1}q_{21}^{3} \\
p_{13}^{1}q_{31}^{1} & p_{13}^{1}q_{31}^{2} & p_{13}^{1}q_{31}^{3} & p_{14}^{1} - 1 & p_{14}^{1}q_{31}^{2} & p_{14}^{1}q_{31}^{3} & p_{15}^{1} - 1 & p_{15}^{1}q_{31}^{2} & p_{15}^{1}q_{31}^{3} \\
p_{21}^{1}q_{21}^{1} & p_{21}^{1}q_{21}^{2} & p_{21}^{1}q_{21}^{3} & p_{22}^{1} - 1 & p_{22}^{1}q_{22}^{2} & p_{22}^{1}q_{22}^{3} & p_{23}^{1} - 1 & p_{23}^{1}q_{22}^{2} & p_{23}^{1}q_{22}^{3} \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
p_{33}^{1}q_{33}^{1} & p_{33}^{1}q_{33}^{2} & p_{33}^{1}q_{33}^{3} & p_{33}^{1} & p_{33}^{1}q_{33}^{2} & p_{33}^{1}q_{33}^{3} & p_{33}^{1} & p_{33}^{1}q_{33}^{2} & p_{33}^{1}q_{33}^{3}
\end{bmatrix}
\]

Thus, player 1 controls the third column of \((M'[f])\) with their probabilities of playing choice 1. Similarly replacing column 6 with the sum of columns 4, 5, and 6, we get a new column 6 with entries

\[
p_{11}^{2}, p_{12}^{2}, p_{13}^{2}, p_{21}^{2} - 1, p_{22}^{2} - 1, p_{23}^{2} - 1, p_{31}^{2}, p_{32}^{2}, p_{33}^{2}
\]

to conclude that player 1 controls 2 columns.

**Memory in multi-choice games**

Appendix A of [2] tells us that if player 1 has memory \(m_1\) and player 2 has memory \(m_2 > m_1\), then for any strategy played by player 2, there is a memory \(m_1\) strategy that will yield the same expected payoff, which should be qualified by clarifying that the expected payoff refers to expectation with respect to all possible histories (as opposed to, say, expectation conditional on a given history of play). Let \(\mathcal{H}_n\) denote the history of plays up until the \(n\)th round, and let \(S_1(n), S_2(n)\) denote the strategy played by player 1 and 2 respectively in the \(n\)th round; then player \(i\) has memory \(m_i\) is the statement that

\[
\mathbb{E}[S_i(n) = s|\mathcal{H}_n] = \mathbb{E}[S_i(n) = s|(S_1(n-1), S_2(n-1)), \ldots, (S_1(n-m_i), S_2(n-m_i))]
\]

Now, let \(\tilde{S}_2\) be a random variable such that

\[
\mathbb{P}\left(\tilde{S}_2(n) = s|(S_1(n-1), S_2(n-1)), \ldots, (S_1(n-m_1), S_2(n-m_1))\right) = \mathbb{E}\left[\mathbb{P}(S_2(n) = s|(S_1(n-1), S_2(n-1)), \ldots, (S_1(n-m_2), S_2(n-m_2)))\right],
\]

where the expectation is over the outcomes of the plays \((S_1(n-m_1), S_2(n-m_1)), \ldots, (S_1(n-m_2), S_2(n-m_2))\). Then \(\tilde{S}_2\) is a memory \(m_1\) strategy and it is shown in [2] that player 1 has the same payoff playing against the new player \(\tilde{S}_2\) as against the original opponent playing \(S_2\). Since the Nash equilibrium depends only on the expected payoff, this tells us that we may equally well determine the Nash equilibrium by playing against the shorter memory player.
Coordinate system for memory-1 strategies in multi-choice games

Just as in the case of two-choice games, we can use Eqs. 1 and 2 to construct a coordinate system for the space of memory-1 strategies. Consider a \(d\)-choice, two-player game with strategy \((p_1^1, \ldots, p_d^d)\) where each \(p_i^j\) is a vector of \(d^2\) probabilities, each corresponding to the probability that a player makes choice \(i\) in the next round given the outcome of the preceding round. By definition we must have \(\sum_j p_j^i = 1, \forall j \in D\) where \(D\) is the set of possible choices in the game. In order to construct an alternate coordinate system we must choose \(d^2\) vectors that form a basis \(\mathbb{R}^{d^2}\). To do this we choose \(d(d+1)/2\) vectors that have entry 1 at the \(i\)th and \(j\)th position for all pairs \(i, j\) and entry zero otherwise. We also choose \(d(d-1)/2\) vectors that have entry 1 at the \(i\)th and entry \(-1\) at the \(j\)th for all pairs \(i, j\), where we adopt the convention that the first entry is positive. The new coordinate system is the \(\{\Lambda_{11}^+, \ldots, \Lambda_{1d}^+, \ldots, \Lambda_{dd}^+, \ldots, \Lambda_{d1}^-, \ldots, \Lambda_{dd}^-\}\) and we have in the case \(d = 3\)

\[
\begin{bmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 1 & 0 \\
0 & 1 & 0 & 0 & 0 & -1 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 1 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & -1 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & -1 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0
\end{bmatrix}
\]

which is a basis \(\mathbb{R}^{9}\) as required. From Eqs. 1 and 2 we then end up with

\[
\sum_{i=1}^{d} \left( \Lambda_{ii}^+ v_{ii} + \sum_{j=i+1}^{d} \Lambda_{ij}^+ (v_{ij} + v_{ji}) + \Lambda_{ij}^- (v_{ij} - v_{ji}) \right) = 0
\]

(9)

where \(v_{ij}\) is the equilibrium rate of the play \(ij\), with the focal player’s move is listed first. Now let the expected payoff to a focal player \(X\) and her opponent \(Y\) to be \(S_{xy}\) and \(S_{yx}\) respectively. By definition these satisfy:

\[
S_{xy} + S_{yx} = \sum_{i=1}^{d} \left( 2R_{ii} v_{ii} + \sum_{j=i+1}^{d} (R_{ij} + R_{ji})(v_{ij} + v_{ji}) \right)
\]

(10)

and

\[
S_{xy} - S_{yx} = \sum_{i=1}^{d} \sum_{j=i}^{d} (R_{ij} - R_{ji})(v_{ij} - v_{ji})
\]

(11)

where \(R_{ij}\) is the payoff to the focal player in a given round in which she played \(i\) and her opponent \(j\). Note also that

\[
\sum_{i=1}^{d} \sum_{j=1}^{k} v_{ij} = 1
\]

(12)

be definition. If we now set

\[
\Lambda_{ij}^+ = \frac{\phi - \chi}{2} (R_{ij} + R_{ji}) - (\phi - \chi) \kappa + \lambda_{ij}^+
\]

(13)
\[ \Lambda_{ij}^+ = -\frac{\phi + \chi}{2}(R_{ij} - R_{ji}) + \lambda_{ij}^- \] (14)

and define
\[ \lambda_{ij} = \lambda_{ij}^+ + \lambda_{ij}^- \]

and
\[ \lambda_{ji} = \lambda_{ij}^+ - \lambda_{ij}^- \]

for all \( j > i \), we can combine Eqs.4-9 to recover the following relationship:
\[ \phi S_{yx} - \chi S_{xy} - (\phi - \chi)\kappa + \sum_{i=1}^{d} \sum_{j=1}^{d} \lambda_{ij} v_{ij} = 0 \] (15)

Notice that we now have three extraneous parameters. In general a convenient choice is \( \lambda_{11} = \lambda_{dd} = 0 \) and \( \lambda_{1d} = \lambda_{d1} \), however more convenient choices can be made depending on the payoff structure of the game being considered. Under this coordinate system, for a game with \( d = 3 \) we end up with

\[
\begin{align*}
\pi_{11} &= 1 - (\phi R_{11} - \chi R_{11} - (\phi - \chi)\kappa) \\
\pi_{12} &= 1 - (\phi R_{21} - \chi R_{12} - (\phi - \chi)\kappa + \lambda_{12}) \\
\pi_{13} &= 1 - (\phi R_{31} - \chi R_{13} - (\phi - \chi)\kappa + \lambda_{31}) \\
\pi_{21} &= - (\phi R_{12} - \chi R_{21} - (\phi - \chi)\kappa + \lambda_{21}) \\
\pi_{22} &= - (\phi R_{22} - \chi R_{22} - (\phi - \chi)\kappa + \lambda_{22}) \\
\pi_{23} &= - (\phi R_{32} - \chi R_{23} - (\phi - \chi)\kappa + \lambda_{23}) \\
\pi_{31} &= - (\phi R_{13} - \chi R_{31} - (\phi - \chi)\kappa + \lambda_{31}) \\
\pi_{32} &= - (\phi R_{23} - \chi R_{32} - (\phi - \chi)\kappa + \lambda_{32}) \\
\pi_{33} &= - (\phi R_{33} - \chi R_{33} - (\phi - \chi)\kappa) \\
\end{align*}
\]

where we have used the superscript 1 to indicate that this is the probability of choosing to play 1. Clearly the same argument holds for choices 2 and 3, with the caveat that \( \sum_{i}^{d} p_{ij} = 1, \forall j \in D \).

We now use this coordinate system to analyse two multi-choice cases of particular interest: two-choice strategies playing against multi-choice invaders in a public goods game, and multi-choice strategies playing against single choice invaders in a rock-paper scissors game.

**Robust strategies in multi-choice public goods games**

We now turn our attention to a multi-choice public goods game, in which a pair of players who invest \( C_j \) and \( C_k \) respectively in a given round of play generate a total benefit \( B_{jk} \) such that

\[ R_{jk} = B_{jk}/2 - C_j \]
We are interested in whether a two-choice strategy can be evolutionary robust against an invader who can vary his investment level in an arbitrary way. Thus we assume a focal strategy that can invest either \(C_1\) or \(C_2\). We assume \(\lambda_{11} = \lambda_{22} = 0\) and \(\lambda_{12} = \lambda_{21}\). When faced with an opponent who plays with \(d\) investment levels, the two-choice player may in general have \(2d\) probabilities for cooperation

\[
\begin{align*}
p_{11}^1 &= 1 - ((\phi - \chi)(B_{11}/2 - \kappa) - \phi C_1 + \chi C_1) \\
p_{12}^1 &= 1 - ((\phi - \chi)(B_{12}/2 - \kappa) - \phi C_2 + \chi C_1 + \lambda_{12}) \\
p_{13}^1 &= 1 - ((\phi - \chi)(B_{13}/2 - \kappa) - \phi C_3 + \chi C_1 + \lambda_{13}) \\
&\vdots \\
p_{1d}^1 &= 1 - ((\phi - \chi)(B_{1d}/2 - \kappa) - \phi C_d + \chi C_1 + \lambda_{1d}) \\
p_{21}^1 &= - ((\phi - \chi)(B_{12}/2 - \kappa) - \phi C_1 + \chi C_2 + \lambda_{12}) \\
p_{22}^1 &= - ((\phi - \chi)(B_{22}/2 - \kappa) - \phi C_2 + \chi C_2) \\
p_{23}^1 &= - ((\phi - \chi)(B_{23}/2 - \kappa) - \phi C_3 + \chi C_2 + \lambda_{23}) \\
&\vdots \\
p_{2d}^1 &= - ((\phi - \chi)(B_{2d}/2 - \kappa) - \phi C_d + \chi C_2 + \lambda_{2d})
\end{align*}
\]

where \(p_{jk}^2 = 1 - p_{jk}^1\). The resulting relationship between players’ scores is given by

\[
\phi S_{yx} - \chi S_{xy} - (\phi - \chi)\kappa + \lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^{d} (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) = 0 \quad (16)
\]

We can observe immediately that the first four terms of Eq. 11 corresponds to the type of two-choice games that have been studied extensively elsewhere.

Looking at the sum and difference between players’ scores in this game we find

\[
S_{xy} + S_{yx} = (B_{11} - 2C_1)v_{11} + (B_{22} - 2C_2)v_{22} + (B_{12} - C_1 - C_2)(v_{12} + v_{12}) + \sum_{j=3}^{d} (B_{1j} - C_1 - C_j)v_{1j} + (B_{2j} - C_2 - C_j)v_{2j} \quad (17)
\]

and

\[
S_{xy} - S_{yx} = (C_2 - C_1)(v_{12} - v_{21}) + \sum_{j=3}^{d} (C_j - C_1)v_{1j} + (C_j - C_2)v_{2j} \quad (18)
\]

Now let us focus on a resident, two-choice strategy who can invest either \(C_1\) or \(C_2\) where \(C_1 > C_2\), and which stabilizes cooperation investment at \(C_1\) when resident in a population, i.e such that \(\kappa = B_{11}/2 - C_1\). We have bounds on players scores of

\[
S_{xy} + S_{yx} \leq (B_{11} - 2C_1) + (B_{12} + C_1 - C_2 - B_{11})(v_{12} + v_{12}) + \sum_{j=3}^{d} (B_{1j} + C_1 - C_j - B_{11})v_{1j} + (B_{2j} - C_2 - C_j - B_{11} + 2C_1)v_{2j} \quad (19)
\]
which becomes an equality when $v_{22} = 0$, and

$$S_{xy} + S_{yx} \geq (B_{22} - 2C_2) + (B_{12} - C_1 + C_2 - B_{22})(v_{12} + v_{12})$$

$$+ \sum_{j=3}^d (B_{1j} - C_1 - C_j - B_{22} + 2C_2)v_{1j} + (B_{2j} + C_2 - C_j - B_{22})v_{2j} \quad (20)$$

which becomes an equality when $v_{11} = 0$, and

$$S_{xy} - S_{yx} \geq -(C_1 - C_2)(v_{12} + v_{21}) + \sum_{j=3}^d (C_j - C_1)v_{1j} + (C_j - C_2)v_{2j} \quad (21)$$

which becomes an equality when an opponent never invests $C_2$ and

$$S_{xy} - S_{yx} \leq (C_1 - C_2)(v_{12} + v_{21}) + \sum_{j=3}^d (C_j - C_1)v_{1j} + (C_j - C_2)v_{2j} \quad (22)$$

which becomes an equality when an opponent never invests $C_1$.

In order for a rare mutant $Y$ to invade a population with a resident $X$ we must have

$$S_{yz} > \frac{N - 2}{N - 1}(B_{11}/2 - C_1) + \frac{1}{N - 1}S_{xy} \quad (23)$$

Combining this with Eq. 11 we then get

$$\left(\chi - \phi \frac{1}{N - 1}\right)(S_{xy} - (B_{11}/2 - C_1)) > \lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) \quad (24)$$

Combining this with Eq 14. and Eq. 16 we then get two conditions for evolutionary robustness, firstly

$$\frac{N}{N - 1} \left(\lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j})\right) >$$

$$\left(\chi - \phi \frac{1}{N - 1}\right) \left[(B_{12} + C_1 - C_2 - B_{11})(v_{12} + v_{12})ight.$$  

$$+ \sum_{j=3}^d (B_{1j} + C_1 - C_j - B_{11})v_{1j} + (B_{2j} + C_2 - C_j - B_{11} + 2C_1)v_{2j}\right] \quad (25)$$

which means that we must have

$$\frac{N}{N - 1} \lambda_{ij} > -\left(\chi - \phi \frac{1}{N - 1}\right)(B_{11} - 2C_1 - B_{ij} + C_i + C_j) \quad (26)$$

We also get
\[
\frac{N-2}{N-1} \lambda_{12} (v_{12} + v_{21}) + \frac{N-2}{N-1} \sum_{j=3}^{d} (\lambda_{1j} v_{1j} + \lambda_{2j} v_{2j})
\]

\[
> - \left( \chi - \phi \frac{1}{N-1} \right) \left[ (C_1 - C_2)(v_{12} + v_{21}) - \sum_{j=3}^{d} (C_j - C_1)v_{1j} + (C_j - C_2)v_{2j} \right] \quad (27)
\]

which means we must have

\[
\frac{N-2}{N-1} \lambda_{ij} > \left( \chi - \phi \frac{1}{N-1} \right) (C_j - C_i), \quad \forall j > 2
\]

This second equation is always hardest to satisfy when \( C_j \) is minimized. For the former condition, we assume \( B_{ij} = r(C_i + C_j)^\alpha \) to get

\[
\frac{N}{N-1} \lambda_{ij} > \left( \chi - \phi \frac{1}{N-1} \right) (r(2C_1)^\alpha - 2C_1 - r(C_i + C_j)^\alpha + (C_i + C_j))
\]

which is hardest to satisfy when the right hand side is maximized. When this occurs depends in general on the choice of \( \alpha \), but if \( \alpha = 1 \) this condition is also hardest to satisfy when \( C_j = 0 \). Thus we have:

\[
\begin{align*}
\frac{N}{N-1} \lambda_{10} &> - \left( \chi - \phi \frac{1}{N-1} \right) (r-1)C_1 \\
\frac{N}{N-1} \lambda_{20} &> - \left( \chi - \phi \frac{1}{N-1} \right) ((r-1)(2C_1 - C_2)) \\
\frac{N-2}{N-1} \lambda_{10} &> \left( \chi - \phi \frac{1}{N-1} \right) C_1 \\
\frac{N-2}{N-1} \lambda_{20} &> \left( \chi - \phi \frac{1}{N-1} \right) C_2
\end{align*}
\]

as our conditions for a two-choice strategy to be robust. We can also convert Eq. 20-23 back to the original coordinate system to give the following robustness conditions

\[
C_s^d = \left\{ (p_{11}, p_{12}, \ldots, p_{1d}, p_{21}, p_{22}, \ldots, p_{2d}) \middle| p_{11} = 1, \right. \\
\left. p_{1j} < 1 - \frac{N-2}{N} \left( 1 - p_{12} + p_{21} \right) \frac{1 - c^*}{1 - c} \left[ \frac{N-1}{N-2} - \frac{r}{2} \right], \right. \\
\left. p_{2j} < \frac{N-2}{N} \left( 1 - p_{12} + p_{21} \right) \left[ \frac{r}{2} - \left( \frac{N-1}{N-2} - \frac{r}{2} \right) \frac{1 - c^*}{1 - c} + \frac{1}{N-2} \right], \right. \\
\left. p_{1j} < 1 - \frac{p_{22}}{r-1} \frac{1 - c^*}{1 - c} \left[ \frac{N-1}{N-2} - \frac{r}{2} \right], \right. \\
\left. p_{2j} < \frac{p_{22}}{r-1} \left[ \frac{r}{2} - \left( \frac{N-1}{N-2} - \frac{r}{2} \right) \frac{1 - c^*}{1 - c} + \frac{1}{N-2} \right] \right\},
\]
which is Eq. 3 of the main text. Finally in order for a strategy to be robust it must be viable, in addition to satisfying Eq. 25, which leaves us with the condition

$$\frac{r - 1}{\frac{1}{2} + \frac{1}{N-2}} > \frac{C_2}{C_1}$$

which must be satisfied in order for a robust two-choice strategy to exist.

**Games with non-transitive payoff structures**

We now consider the rock-paper-scissors game, which is a three-choice, non-transitive game. We assume a payoff structure $R_{13} = B - C_1$, $R_{21} = B - C_2$, $R_{32} = B - C_3$, $R_{31} = -C_3$, $R_{12} = -C_1$ and $R_{23} = -C_2$ which gives a non-transitive relationship between the choices 1=rock, 2=paper and 3=scissors. We assume that when two players make the same choice they receive equal payoff: $R_{11} = B/2 - C_1$, $R_{22} = B/2 - C_1$ and $R_{33} = B/2 - C_1$. In the alternate coordinate system a strategy is written as

$$
p_{11}^1 = 1 - (\phi^1 - \chi^1) \left( B/2 - C_1 - \kappa^1 \right)
$$

$$
p_{12}^1 = 1 - (\phi^1(B - C_2) + \chi^1C_1 - (\phi^1 - \chi^1)\kappa^1)
$$

$$
p_{13}^1 = 1 + (\phi^1C_3 + \chi^1(B - C_1) + (\phi^1 - \chi^1)\kappa^1)
$$

$$
p_{21}^1 = \lambda_{21}^1 + (\phi^1C_2 + \chi^1(B - C_1) + (\phi^1 - \chi^1)\kappa^1)
$$

$$
p_{22}^1 = \lambda_{22}^1 - (\phi^1 - \chi^1) \left( B/2 - C_2 - \kappa^1 \right)
$$

$$
p_{23}^1 = \lambda_{23}^1 - (\phi^1(B - C_3) + \chi^1C_2 - (\phi^1 - \chi^1)\kappa^1)
$$

$$
p_{31}^1 = \lambda_{31}^1 - (\phi^1(B - C_1) + \chi^1C_3 - (\phi^1 - \chi^1)\kappa^1)
$$

$$
p_{32}^1 = \lambda_{32}^1 + (\phi^1C_2 + \chi^1(B - C_3) + (\phi^1 - \chi^1)\kappa^1)
$$

$$
p_{33}^1 = \lambda_{33}^1 - (\phi^1 - \chi^1) \left( B/2 - C_3 - \kappa^1 \right)
$$

and

$$
p_{11}^2 = \lambda_{11}^2 - (\phi^2 - \chi^2) \left( B/2 - C_1 - \kappa^2 \right)
$$

$$
p_{12}^2 = \lambda_{12}^2 - (\phi^2(B - C_2) + \chi^2C_1 - (\phi^2 - \chi^2)\kappa^2)
$$

$$
p_{13}^2 = \lambda_{13}^2 + (\phi^2C_3 + \chi^2(B - C_1) + (\phi^2 - \chi^2)\kappa^2)
$$

$$
p_{21}^2 = 1 + (\phi^2C_2 + \chi^2(B - C_1) + (\phi^2 - \chi^2)\kappa^2)
$$

$$
p_{22}^2 = 1 - (\phi^2 - \chi^2) \left( B/2 - C_2 - \kappa^2 \right)
$$

$$
p_{23}^2 = 1 - (\phi^2(B - C_3) + \chi^2C_2 - (\phi^2 - \chi^2)\kappa^2)
$$

$$
p_{31}^2 = \lambda_{31}^2 - (\phi^2(B - C_1) + \chi^2C_3 - (\phi^2 - \chi^2)\kappa^2)
$$

$$
p_{32}^2 = \lambda_{32}^2 + (\phi^2C_2 + \chi^2(B - C_3) + (\phi^2 - \chi^2)\kappa^2)
$$

$$
p_{33}^2 = \lambda_{33}^2 - (\phi^2 - \chi^2) \left( B/2 - C_3 - \kappa^2 \right)
$$

where we set $\lambda = 0$ for the case where a player uses the same move as she played in the preceding round. If we consider the symmetrical case $C_1 = C_2 = C_3$ we can set
\[ p_0^- = 1 - (\phi - \chi) (B/2 - C - \kappa) \]
\[ p_0^+ = 1 + (\phi C + \chi (B - C) + (\phi - \chi) \kappa) \]
\[ p_+^- = \lambda_+^0 + (\phi C + \chi (B - C) + (\phi - \chi) \kappa) \]
\[ p_+^0 = \lambda_+^- - (\phi - \chi) (B/2 - C - \kappa) \]
\[ p_+^- = \lambda_+^- - (\phi (B - C) + \chi C - (\phi - \chi) \kappa) \]
\[ p_+^0 = \lambda_+^0 - (\phi - \chi) (B/2 - C - \kappa) \]

where subscript indicates the outcome of the preceding round – win (+), lose (-) or draw (o) and the superscript refers to the choice to switch to the move that would have resulted in that outcome in the preceding round. Note also that by definition \( p_0^- + p_0^0 + p_0^+ = 1 \) etc so that the following must hold:

\[
\begin{align*}
\lambda_0^- + \lambda_0^+ &= 3(\phi - \chi) (B/2 - C - \kappa) \\
\lambda_0^+ + \lambda_0^- &= -3 (\phi C + \chi (B - C) + (\phi - \chi) \kappa) \\
\lambda_0^- + \lambda_0^+ &= 3 (\phi (B - C) + \chi C - (\phi - \chi) \kappa)
\end{align*}
\]

(32)

Against an opponent who only plays rock=1, the following relationships between players scores must hold

\[
\begin{align*}
\phi S_{yx} - \chi S_{xy} - (\phi - \chi) \kappa + \lambda_0^- v_{21} + \lambda_0^+ v_{31} &= 0 \\
\phi S_{yx} - \chi S_{xy} - (\phi - \chi) \kappa + \lambda_0^+ v_{11} + \lambda_0^- v_{31} &= 0 \\
\phi S_{yx} - \chi S_{xy} - (\phi - \chi) \kappa + \lambda_0^- v_{11} + \lambda_0^+ v_{21} &= 0
\end{align*}
\]

(33)

with equivalent equalities for invaders who only play paper or scissors, which we can ignore due to the assumed symmetry of the problem.

Finally, note that in the totally symmetrical game the sum of both players longterm average payoffs is constant:

\[ S_{xy} + S_{yx} = B - 2C \]

(34)

and in order for a mutant to successfully invade therefore requires

\[ S_{yx} > \frac{N - 2}{N - 1} (B/2 - C) + \frac{1}{N - 1} S_{xy} \]

which in turn implies

\[ B/2 - C > S_{xy} \]
Combining Eqs. 27-29 we can now solve for $v$ and arrive at the following inequality as the condition for a strategy to maintain behavioral diversity in the symmetrical rock-paper-scissors game:

$$p_o^-(1 - p^- - p_+^-) > p_o^+(1 - p_+^- - p^-)$$

(35)

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