

Evolutionary consequences of behavioral diversity - Supporting Information

Alexander J. Stewart^{*1}, Todd L. Parsons² and Joshua B. Plotkin^{*3}

¹ Department of Genetics, Environment and Evolution, University College London, London, UK

² Laboratoire de Probabilités et Modèles Aléatoires, CNRS UMR 7599, Université Pierre et Marie Curie, Paris 75005, France.

³ Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA

* E-mail: alex.stewart@ucl.ac.uk, jplotkin@sas.upenn.edu

In this supplement we construct an analytical framework for determining the outcome of infinitely iterated games played between two players using arbitrary memory-1 strategies in an arbitrary, finite action space. The organization of the supplement is as follows: In section 1 we generalize the results of Press & Dyson 2012 [1], which were constructed for memory-1 strategies in iterated two-player games under a two-choice action space, to the case of an arbitrary (but finite) action space. We show that, just as in the two-choice case, a player with memory-1 can unilaterally choose her strategy in such a way as to constrain the payoffs received by both players and, in particular, she can enforce a linear relationship via a zero-determinant (ZD) strategy. We also show that the result of Press & Dyson 2012 [1] on memory capacity – that a memory-1 strategy that is robust against all other memory-1 strategies is also robust against all memory- m strategies – holds in the case of arbitrary action spaces as well. In section 2 we construct a coordinate system for arbitrary memory-1 strategies, which allows us to determine whether a resident strategy in an evolving population of players is robust to invasion by a mutant. These results are a generalization of [2, 3] to arbitrary (finite) action spaces, and to games with discounting rate δ . In section 3 we apply these results to the case of a multi-choice public goods game played in an evolving population, and we determine the conditions under which a two-choice strategy with access only to investment levels C_1 and $C_2 > C_1$ can resist invasion by *any* mutant with access to an arbitrary investment level C . Finally in section 4 we consider the case of a game with a non-transitive payoff structure,

such as the rock-paper-scissors game, and determine to what extent access to memory in a repeated game can guard against loss of behavioral diversity in an evolving population.

1 Infinitely Iterated Multi-choice Games

In this section, we generalize the results of [1] to a game with an arbitrary number d of pure strategies, which we refer to as different “choices”. We show that, in a game between two players, each using a d -choice memory-1 strategy, either player can unilaterally choose her strategy in such a way as to constrain the payoffs received by both players, in precisely analogy to the results of [1] for the case $d = 2$. This provides a formula for the construction of zero-determinant (ZD) strategies, which enforce a linear relationship between both players average payoffs.

We start by repeating Press & Dyson’s argument for relating the longterm payoffs for each player in the repeated game to a determinant. The essential fact for their argument is that 1 is a simple (left) eigenvalue for an $n \times n$ Markov transition matrix \mathbf{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 \mathbf{M}^T and \mathbf{M} are equal: $\det(\lambda\mathbf{I} - \mathbf{M}^T) = \det(\lambda\mathbf{I} - \mathbf{M})$).

Now, 1 is always a left eigenvalue of any transition matrix – because the rows must sum to 1, the vector $\mathbb{1}$ with all entries equal to 1 is a right eigenvector for the eigenvalue 1. The only constraint to generalizing the result of [1] to more than two choices is that 1 must continue to be a simple eigenvalue *i.e.* up-to-scalar multiples, the (left) eigenvector \mathbf{v} such that $\mathbf{v}^T \mathbf{M} = \mathbf{v}^T$ must be unique (for the sake of concreteness, we will normalize \mathbf{v} so that its entries sum to 1). This is a consequence of the Perron-Frobenius Theorem, which says that if \mathbf{M} is a non-negative (*i.e.* all entries are non-negative), irreducible matrix, then the spectral radius of the matrix (here equal to 1) is a simple eigenvalue. We recall a matrix \mathbf{A} is *reducible* if there exists a permutation matrix \mathbf{P} such that \mathbf{PAP}^T is block upper triangular, and is *irreducible* otherwise. A more revealing equivalent expression for irreducibility is that there exists k such that $(A^k)_{ij} > 0$ for all i, j , *i.e.* the Markov chain has a positive probability of getting from state i to state j in finite time. A two-player game is not necessarily irreducible, *e.g.* the game in which one of the players always plays the same 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, in which that player always makes the same choice). As this example highlights, since all entries of \mathbf{M} are non-negative, it can only be reducible if at least one entry is 0, which given their product form, means that for one possible outcome of the previous round, at least one of the players will never make one of the choices available to them. Thus at least one of the players' strategies lies in the (lower-dimensional) boundary of the set of available strategies. In particular, in the presence of white noise, the probability of lying in this set of strategies is zero. Such noise occurs naturally if we assume that players execute their play with some error rate (see also [3]).

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

$$\text{Adj}(\mathbf{M}')^T \mathbf{M}' = \det(\mathbf{M}') \mathbf{I} = \mathbf{0},$$

from which we conclude that every column of $\text{Adj}(\mathbf{M}')$ 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 \mathbf{A} , the classical adjoint of \mathbf{A} , $\text{Adj}(\mathbf{A})$ is the matrix with entries equal to the cofactors of \mathbf{A} :

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

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

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

Now, in [1], the authors observe that if \mathbf{f} is any column vector in \mathbb{R}^n and $(\mathbf{A}|\mathbf{f})$ is the matrix

obtained by replacing the n^{th} column of \mathbf{A} with \mathbf{f} , then

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

(*n.b.* $(\mathbf{A}|\mathbf{f})(i|n)$ is obtained by deleting the n^{th} column of $(\mathbf{A}|\mathbf{f})$, and thus is equal to $\mathbf{A}(i|n)$, whereas $(\mathbf{A}|\mathbf{f})_{in} = f_i$ by construction). Now, the rightmost expression is the dot product of the n^{th} column of $\text{Adj}(\mathbf{A})$ with \mathbf{f} . Now, as we have already observed, the n^{th} column of $\text{Adj}(\mathbf{M}')$ is $\alpha \mathbf{v}$, for some non-zero α , so

$$\det((\mathbf{M}'|\mathbf{f})) = \alpha \mathbf{v} \cdot \mathbf{f}$$

for arbitrary \mathbf{f} . In particular, recalling that all entries of \mathbf{v} sum to 1, we have

$$\det((\mathbf{M}'|\mathbb{1})) = \alpha \mathbf{v} \cdot \mathbb{1} = \alpha$$

and thus

$$\frac{\det((\mathbf{M}'|\mathbf{f}))}{\det((\mathbf{M}'|\mathbb{1}))} = \mathbf{v} \cdot \mathbf{f}. \quad (1)$$

Next, recall that $\det(\mathbf{A})$ is an alternating multilinear function of the columns of \mathbf{A} , so for arbitrary m , vectors $\mathbf{f}_1, \dots, \mathbf{f}_m \in \mathbb{R}^n$, and scalars $\alpha_1, \dots, \alpha_m$

$$\det \left(\left(\mathbf{A} \left| \sum_{k=1}^m \alpha_k \mathbf{f}_k \right. \right) \right) = \sum_{k=1}^m \alpha_k \det((\mathbf{A}|\mathbf{f}_k)),$$

and thus,

$$\frac{\det((\mathbf{M}'|\sum_{k=1}^m \alpha_k \mathbf{f}_k))}{\det((\mathbf{M}'|\mathbb{1}))} = \sum_{k=1}^m \alpha_k (\mathbf{v} \cdot \mathbf{f}_k).$$

Press & Dyson then observe that player 1's payoff is $S_{12} := \mathbf{v} \cdot \mathbf{R}_1$ and player 2's payoff is $S_{21} := \mathbf{v} \cdot \mathbf{R}_2$, where \mathbf{R}_i is the vector of payoffs received by player i and \mathbf{v} is the vector giving the equilibrium rate of different plays in an infinitely iterated game. If there are 2 players, then

$$\frac{\det((\mathbf{M}'|\alpha_1 \mathbf{R}_1 + \alpha_2 \mathbf{R}_2 + \alpha_3 \mathbb{1}))}{\det((\mathbf{M}'|\mathbb{1}))} = \alpha_1 S_{12} + \alpha_2 S_{21} + \alpha_3.$$

Now, to enforce 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 [1] to $d > 2$ actions, 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 recall that for any matrix \mathbf{A} , $\det(\mathbf{A})$ 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 $(\mathbf{M}'|\mathbf{f})$ to a matrix $(\tilde{\mathbf{M}}'|\mathbf{f})$ with one column that only depends on player i 's strategy, say \mathbf{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

$$\alpha_1 \mathbf{R}_1 + \alpha_2 \mathbf{R}_2 + \alpha_3 \mathbb{1}.$$

In what follows, we show that in the case of d choices, which we label $1, \dots, d$, the transition matrix \mathbf{M} is such that for an arbitrary vector $\mathbf{f} \in \mathbb{R}^n$ (here, $n = d^2$) $(\mathbf{M}'|\mathbf{f})$ has $d - 1$ columns that are completely determined by player 1 and $d - 1$ 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 $d(j - 1) + k^{\text{th}}$ 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_{kj}^i ($i = 1, \dots, d$, $j = 1, \dots, d$, $k = 1, \dots, d$) 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 , so for all pairs j, k we have

$$\sum_{i=1}^d p_{jk}^i = 1 \quad \text{and} \quad \sum_{i=1}^d q_{jk}^i = 1.$$

With this notation, the transition matrix \mathbf{M} has entries

$$m_{jk,il} = p_{jk}^i q_{kj}^l,$$

which, for $d = 3$ gives us

$$\mathbf{M} = \begin{bmatrix} p_{11}^1 q_{11}^1 & p_{11}^1 q_{11}^2 & p_{11}^1 (1 - q_{11}^1 - q_{11}^2) & \cdots \\ p_{12}^1 q_{21}^1 & p_{12}^1 q_{21}^2 & p_{12}^1 (1 - q_{21}^1 - q_{21}^2) & \cdots \\ p_{13}^1 q_{31}^1 & p_{13}^1 q_{31}^2 & p_{13}^1 (1 - q_{31}^1 - q_{31}^2) & \cdots \\ p_{21}^1 q_{12}^1 & p_{21}^1 q_{12}^2 & p_{21}^1 (1 - q_{12}^1 - q_{12}^2) & \cdots \\ \vdots & \vdots & \vdots & \\ p_{33}^1 q_{33}^1 & p_{33}^1 q_{33}^2 & p_{33}^1 (1 - q_{33}^1 - q_{33}^2) & \cdots \end{bmatrix}$$

Next, \mathbf{M}' has entry $m'_{i,j} = m_{i,j} - \epsilon_{i,j}$, where $\epsilon_{i,j}$ is 1 if $i = j$ and 0 otherwise. Again, for $d = 3$, this gives

$$\mathbf{M}' = \begin{bmatrix} p_{11}^1 q_{11}^1 - 1 & p_{11}^1 q_{11}^2 & p_{11}^1 (1 - q_{11}^1 - q_{11}^2) & \cdots \\ p_{12}^1 q_{21}^1 & p_{12}^1 q_{21}^2 - 1 & p_{12}^1 (1 - q_{21}^1 - q_{21}^2) & \cdots \\ p_{13}^1 q_{31}^1 & p_{13}^1 q_{31}^2 & p_{13}^1 (1 - q_{31}^1 - q_{31}^2) - 1 & \cdots \\ p_{21}^1 q_{12}^1 & p_{21}^1 q_{12}^2 & p_{21}^1 (1 - q_{12}^1 - q_{12}^2) & \cdots \\ \vdots & \vdots & \vdots & \\ p_{33}^1 q_{33}^1 & p_{33}^1 q_{33}^2 & p_{33}^1 (1 - q_{33}^1 - q_{33}^2) & \cdots \end{bmatrix}$$

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

$$p_{jk}^1 q_{kj}^1, \dots, p_{jk}^1 q_{kj}^d, p_{jk}^2 q_{kj}^1, \dots, p_{jk}^j q_{kj}^k - 1, \dots, p_{jk}^d q_{kj}^1, \dots, p_{jk}^d q_{kj}^{d-1}, f_{jk},$$

and continuing to illustrate this with $d = 3$, we have

$$(\mathbf{M}'|\mathbf{f}) = \begin{bmatrix} p_{11}^1 q_{11}^1 - 1 & p_{11}^1 q_{11}^2 & p_{11}^1(1 - q_{11}^1 - q_{11}^2) & \cdots, f_{11} \\ p_{12}^1 q_{21}^1 & p_{12}^1 q_{21}^2 - 1 & p_{12}^1(1 - q_{21}^1 - q_{21}^2) & \cdots, f_{12} \\ p_{13}^1 q_{31}^1 & p_{13}^1 q_{31}^2 & p_{13}^1(1 - q_{31}^1 - q_{31}^2) - 1 & \cdots, f_{13} \\ p_{21}^1 q_{12}^1 & p_{21}^1 q_{12}^2 & p_{21}^1(1 - q_{12}^1 - q_{12}^2) & \cdots, f_{21} \\ \vdots & \vdots & \vdots & \\ p_{33}^1 q_{33}^1 & p_{33}^1 q_{33}^2 & p_{33}^1(1 - q_{33}^1 - q_{33}^2) & \cdots, f_{33} \end{bmatrix}$$

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

$$\sum_{l=1}^d p_{jk}^1 q_{kj}^l - \epsilon_{kj,1l} = \begin{cases} p_{jk}^1 - 1 & \text{if } j = 1 \\ p_{jk}^1 & \text{otherwise} \end{cases}$$

Similarly for the second d entries, and so on. Thus, if for each $a = 1, \dots, d-1$, we replace the ad^{th} column by the sum of columns $(a-1)d, (a-1)d+1, \dots, (a-1)d+d-1$, a transformation that leaves $\det((\mathbf{M}'|\mathbf{f}))$ unchanged, the resulting matrix has a ad^{th} column with jk^{th} entry

$$\begin{cases} p_{jk}^a - 1 & \text{if } j = a \\ p_{jk}^a & \text{otherwise} \end{cases}$$

i.e. the ad^{th} column depends only on player 1, and player 1 controls $d-1$ columns. Proceeding similarly, we see that player 2 also controls exactly $d-1$ columns.

To see this concretely, for $d = 3$, if we replace the third column of $(\mathbf{M}'|\mathbf{f})$ by the third column

plus the first and the second (which preserves the determinant), we get

$$(\tilde{\mathbf{M}}|\mathbf{f}) = \begin{bmatrix} p_{11}^1 q_{11}^1 - 1 & p_{11}^1 q_{11}^2 & p_{11}^1 - 1 & \cdots & f_{11} \\ p_{12}^1 q_{21}^1 & p_{12}^1 q_{21}^2 - 1 & p_{12}^1 - 1 & \cdots & f_{12} \\ p_{13}^1 q_{31}^1 & p_{13}^1 q_{31}^2 & p_{13}^1 - 1 & \cdots & f_{13} \\ p_{21}^1 q_{12}^1 & p_{21}^1 q_{12}^2 & p_{21}^1 & \cdots & f_{21} \\ \vdots & \vdots & \vdots & & \\ p_{33}^1 q_{33}^1 & p_{33}^1 q_{33}^2 & p_{33}^1 & \cdots & f_{33} \end{bmatrix} \quad (2)$$

Thus, player 1 controls the third column of $(\tilde{\mathbf{M}}|\mathbf{f})$ 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.

1.1 Memory in multi-choice games

In this section we repeat the argument of Appendix A of [1], which 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. Thus, in an evolving population, if player 1 can resist invasion against all invaders with memory m_1 she can also resist invasion against all invaders of memory $m_2 > m_1$, and in particular strategies with memory-1 that are robust against all other memory-1 strategies are also robust against all longer-memory strategies.

This argument 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. $S_1(n)$ and $S_2(n)$ are non-anticipating random variables, so that $S_1(n+1)$ and $S_2(n+1)$ are independent conditional on the prior history of play \mathcal{H}_n .

That player i has memory m_i is the statement that

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

where \mathbb{E} denotes the expectation with respect to the joint probability distribution for the pair of random variables $S_1(n), S_2(n)$ (here we are marginalizing over the second player). We note that this is an identity, depending only on the memory of the players, and is independent of the further specifics of the underlying joint probability distribution.

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

$$\begin{aligned} \mathbb{P}\left(\tilde{S}_2(n) = s \mid (S_1(n-1), S_2(n-1)), \dots, (S_1(n-m_1), S_2(n-m_1))\right) \\ = \mathbb{E}\left[\mathbb{P}(S_2(n) = s \mid (S_1(n-1), S_2(n-1)), \dots, (S_1(n-m_2), S_2(n-m_2)))\right], \end{aligned}$$

where the expectation is over the outcomes of the plays $(S_1(n-m_1), S_2(n-m_1)), \dots, (S_1(n-m_2), S_2(n-m_2))$ *i.e.* we are defining a new probability distribution by marginalising over all history longer than the shorter memory of player 1. Then \tilde{S}_2 is a memory m_1 strategy and it is shown in [1] 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 definition of equilibrium in an evolving population depends only on the expected payoff, this tells us that we may equally well determine whether the strategy of player 1 is an equilibrium by considering the payoff off the modified strategy \tilde{S}_2 playing against the shorter memory player 1.

2 Coordinate system for memory-1 strategies in multi-choice games

In this section we construct a coordinate system for memory-1 strategies under a d -choice action space. The advantage of the coordinate system we construct is that it allows us to write the longterm average payoffs received by the two players in a simple relationship, which can in turn be used to determine whether a particular resident strategy in an evolving population can resist invasion, and thus be “evolutionary robust” [2,3]. We present our results for repeated games with

discounting factor δ , which can be understood as meaning either that the game is repeated after each round with probability δ , or that the game is assuredly repeated but the payoff received in each round is reduced by a factor δ [4,5]. Regardless of the interpretation of δ the results are the same. We first define the coordinate system, and we then use it to determine a simple relationship between two players' expected scores. Finally we explicitly write down the relationship between the new coordinate system and the more standard coordinate system in which strategies are expressed as probabilities p_{jk}^i (probability of playing action i given that the focal player played j and her opponent played k in the preceding round).

Consider a d -choice, two-player game with strategy $(\mathbf{p}^1, \mathbf{p}^2, \dots, \mathbf{p}^d)$ where each \mathbf{p}^i 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. In addition we must also specify the play in the first round, which we denote p_i^0 , i.e. the probability that a player makes choice i at time 0. Each vector \mathbf{p}^i is composed of d^2 coordinates p_{jk}^i . These coordinates specify a point in "strategy space" i . Each action i thus has its own "strategy space", however, by definition, any realizable strategy must satisfy $\sum_i p_{jk}^i = 1, \forall j, k \in \mathcal{D}$, where \mathcal{D} is the set of possible choices in the game. Each strategy space is thus composed of d^2 basis vectors \mathbf{e}_{jk}^i , with each direction corresponding to a different outcome jk of the preceding round. We wish to construct an alternate coordinate system for this strategy space. In order to do so we must choose a new set of d^2 vectors that form a basis \mathbb{R}^{d^2} . We make our choice as follows: in directions that correspond to both players behaving the same way in the previous round (i.e. $j = k$) we retain the old coordinates. In directions that correspond to players making different choices in the preceding round, we choose a new pair of orthogonal vectors in directions $\mathbf{e}_{jk}^i + \mathbf{e}_{kj}^i$ and $\mathbf{e}_{jk}^i - \mathbf{e}_{kj}^i$. This provides us with an alternate basis for each strategy space i . Under this new coordinate system a strategy vector \mathbf{p}^i for playing choice i is written as

$$\mathbf{p}^i = \sum_k \mathbf{e}_{ik}^i - \sum_j \left[\Lambda_{jj}^+ \mathbf{e}_{jj}^i + \sum_{k>j} \Lambda_{jk}^+ (\mathbf{e}_{jk}^i + \mathbf{e}_{kj}^i) + \Lambda_{jk}^- (\mathbf{e}_{jk}^i - \mathbf{e}_{kj}^i) \right]. \quad (3)$$

Writing a strategy in this way, Eqs. 1 and 2 tell us that the following equality must hold

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

where v_{ij} is the equilibrium rate of the play ij , with the focal player's move is listed first. It is Eq.3 that we will use to derive our relationship between two player's average payoffs.

2.1 The average payoff received by the two players

In this section we derive a relationship between the average payoffs received by two players X and Y , given that player X uses strategy \mathbf{p}^i when choosing to play action i , which we write in terms of the alternate coordinate system defined in the preceding section. Similarly, we assume that player Y uses strategy \mathbf{q}^i when choosing to play action i . Let the expected payoff to a focal player X and her opponent Y be S_{xy} and S_{yx} respectively (we adopt the convention that, when referring to an evolving population, we use player labels X and Y rather than 1 and 2 as in the previous section). Furthermore let the probability that the play jk occurs in round t of the repeated game be v_{jk}^t .

In an iterated game the probability of play ij in round $t + 1$ is given by

$$v_{ij}^{t+1} = \sum_k \sum_l v_{kl}^t p_{kl}^i q_{lk}^j$$

where p_{kl}^i is the probability that the focal play plays i given that she played k and her opponent played l in the preceding round and q_{lk}^j is the equivalent quantity for her opponent. We must also specify an initial condition, which is the probability the each pair of plays jk in the first round, v_{jk}^0 . This probability is given by simply $v_{jk}^0 = p_j^0 q_k^0$ where p_j^0 is the probability that the focal player makes choice j in the first round and q_k^0 is the probability that her opponent makes choice k . Using our assumed coordinate transform for \mathbf{p} , Eq. 3, we recover

$$v_{ij}^{t+1} = - \sum_k \left(\Lambda_{kk}^+ v_{kk}^t q_{kk}^j + \sum_{l>k} \Lambda_{kl}^+ (v_{kl}^t q_{lk}^j + v_{lk}^t q_{kl}^j) + \Lambda_{kl}^- (v_{kl}^t q_{lk}^j - v_{lk}^t q_{kl}^j) \right) + \sum_l v_{il}^t q_{li}^j$$

We can now sum over j , the choice made by player Y, to give

$$\sum_j (v_{ij}^{t+1} - v_{ij}^t) = - \sum_k \left(\Lambda_{kk}^+ v_{kk}^t + \sum_{l>k} \Lambda_{kl}^+ (v_{kl}^t + v_{lk}^t) + \Lambda_{kl}^- (v_{kl}^t - v_{lk}^t) \right).$$

If we now sum over t , from the first round up to round τ we get

$$\sum_j (v_{ij}^\tau - v_{ij}^0) = - \sum_{t=0}^{\tau} \sum_k \left(\Lambda_{kk}^+ v_{kk}^t + \sum_{l>k} \Lambda_{kl}^+ (v_{kl}^t + v_{lk}^t) + \Lambda_{kl}^- (v_{kl}^t - v_{lk}^t) \right) \quad (4)$$

Here we note that

$$\sum_j v_{ij}^0 = p_i^0$$

where p_i^0 is the probability of using i as the initial play for player X . Equation 4 now allows us to calculate the expected payoffs to both players as a function of their strategy. Assuming a rate of discounting δ , and summing over all rounds from $t = 0$ to infinity, we can now write

$$\sum_j \sum_{t=0}^{\infty} \delta^t (1 - \delta) v_{ij}^t - p_i^0 = -\delta \sum_{t=0}^{\infty} \delta^t \sum_k \left(\Lambda_{kk}^+ v_{kk}^t + \sum_{l>k} \Lambda_{kl}^+ (v_{kl}^t + v_{lk}^t) + \Lambda_{kl}^- (v_{kl}^t - v_{lk}^t) \right) \quad (5)$$

Now note that, with discounting, the sum of the two players scores are given by

$$S_{xy} + S_{yx} = (1 - \delta) \sum_{i=1}^d \sum_t \delta^t \left(2R_{ii} v_{ii}^t + \sum_{j=i+1}^d (R_{ij} + R_{ji}) (v_{ij}^t + v_{ji}^t) \right)$$

and the difference between the two player's scores by

$$S_{xy} - S_{yx} = (1 - \delta) \sum_{i=1}^d \sum_{j=i}^d \sum_{t=1}^{\infty} \delta^t (R_{ij} - R_{ji})(v_{ij}^t - v_{ji}^t)$$

This suggests the following strategy for choice i :

$$\begin{aligned} \Lambda_{ii}^+ &= (\phi - \chi)R_{ii} - (\phi - \chi)\kappa + \lambda_{ii}^i - \frac{1 - \delta}{\delta} \\ \Lambda_{ii}^- &= 0 \\ \Lambda_{ij}^+ &= \frac{\phi - \chi}{2}(R_{ij} + R_{ji}) - (\phi - \chi)\kappa + (\lambda_{ij}^i + \lambda_{ji}^i)/2 - \frac{1 - \delta}{2\delta} \\ \Lambda_{ij}^- &= -\frac{\phi + \chi}{2}(R_{ij} - R_{ji}) + (\lambda_{ij}^i - \lambda_{ji}^i)/2 - \frac{1 - \delta}{2\delta} \\ \Lambda_{kl}^+ &= \frac{\phi - \chi}{2}(R_{kl} + R_{lk}) - (\phi - \chi)\kappa + (\lambda_{kl}^i + \lambda_{lk}^i)/2 \\ \Lambda_{kl}^- &= -\frac{\phi + \chi}{2}(R_{kl} - R_{lk}) + (\lambda_{kl}^i - \lambda_{lk}^i)/2 \end{aligned} \tag{6}$$

for all terms $j, k \neq i$. Replacing this in Eq. 5 now leaves us with

$$\phi^i S_{yx} - \chi^i S_{xy} - (\phi^i - \chi^i)\kappa^i + \sum_{k=1}^d \sum_{l=1}^d \lambda_{kl}^i \sum_t (1 - \delta)\delta^t v_{kl}^t - \frac{1 - \delta}{\delta} p_i^0 = 0 \tag{7}$$

Of course there are $d - 1$ such equations for each choice i (rather than d equations, due to the constraint that the probability of playing any possible action must sum to 1), and any linear combination of these $d - 1$ equation must also hold. Notice that we now have three extraneous Λ parameters. In general it is convenient to choose $\lambda_{11} = \lambda_{dd} = 0$ and $\lambda_{1d} = \lambda_{d1}$, however other, more convenient choices might be made depending on the payoff structure of the game being considered. Equation 7 gives us the discrete version of the relationship in McAvoy & Hauert [5], generalized to the full space of memory-1 strategies. For notational convenience we now write

$$\sum_t^{\infty} (1 - \delta) \delta^t v_{kl}^t = v_{kl}$$

which is the equilibrium rate of the play kl in a game with discounting. This gives us the following equalities

$$\phi^i S_{yx} - \chi^i S_{xy} - (\phi^i - \chi^i) \kappa^i + \sum_{k=1}^d \sum_{l=1}^d \lambda_{kl}^i v_{kl} - \frac{1 - \delta}{\delta} p_i^0 = 0 \quad (8)$$

for the relationship between the equilibrium payoffs given the strategy of player X , where we recall that p_i^0 denotes the probability that the focal player makes choice i in the first round of play. Notice that, with the introduction of discounting, Eq. 8 depends on the probability of X playing i in the first round.

In our simplified notation we can also write

$$S_{xy} + S_{yx} = \sum_{i=1}^d \left(2R_{ii} v_{ii}^t + \sum_{j=i+1}^d (R_{ij} + R_{ji})(v_{ij} + v_{ji}) \right) \quad (9)$$

and

$$S_{xy} - S_{yx} = \sum_{i=1}^d \sum_{j=i}^d (R_{ij} - R_{ji})(v_{ij} - v_{ji}) \quad (10)$$

For the sum and the difference of the two player's payoffs, which will be useful in the next section.

We now use this coordinate system and the equality Eq. 8 that it allows us to derive in order 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.

3 Robust strategies in multi-choice public goods games

In this section we determine the conditions for a two-choice strategy to be able to resist invasion by any rare mutant in an evolving population of N individuals playing pairwise public goods games. Under a multi-choice public goods game, a pair of players who choose to invest C_j and C_k respectively in a given round of play generate a total benefit B_{jk} such that the player who invested C_j receives payoff

$$R_{jk} = B_{jk}/2 - C_j$$

We focus on strategies that use only two investment levels, C_1 and $C_2 > C_1$. We determine whether a strategy which, when resident in a population, stabilizes investment at either C_1 or C_2 , can resist invasion by players with access to arbitrary investment levels. We then investigate particular cases of two choice strategies that react to investment levels other than C_1 and C_2 according to a threshold rule.

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 investing at level C_2 :

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

where $p_{jk}^1 = 1 - p_{jk}^2$. The resulting relationship between players' scores is given by

$$\phi S_{yx} - \chi S_{xy} - (\phi - \chi)\kappa + \lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) = \frac{1 - \delta}{\delta} p_2^0 \quad (11)$$

We can observe immediately that the first four terms of Eq. 11 correspond 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

$$S_{xy} + S_{yx} = (B_{11} - 2C_1)v_{11} + (B_{22} - 2C_2)v_{22} + (B_{12} - C_1 - C_2)(v_{12} + v_{21}) + \sum_{j=3}^d (B_{1j} - C_1 - C_j)v_{1j} + (B_{2j} - C_2 - C_j)v_{2j} \quad (12)$$

and

$$S_{xy} - S_{yx} = (C_2 - C_1)(v_{12} - v_{21}) + \sum_{j=3}^d (C_j - C_1)v_{1j} + (C_j - C_2)v_{2j} \quad (13)$$

In the next section we will use Eqs. 11-13 to derive conditions for evolutionary robustness of the resident strategy.

3.1 Robustness of strategies that stabilize investment at level C_2

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_2 when resident in a population, i.e. a strategy such that $p_{22}^2 = 1$ which in turn implies that $\kappa = B_{22}/2 - C_2 - \frac{1}{\phi-\chi} \frac{1-\delta}{\delta}$. Notice that in order to ensure investment is stabilized at C_2 in the presence of discounting, the strategy must have $p_0^2 = 1$, i.e. players must always invest C_2 in the first round. Such a strategy always invests C_2 in the first round and always invests C_2 if both players invested C_2 in the preceding round. In general, when resident in a population, such a strategy ensures all players invest C_2 at equilibrium.

From Eqs. 12 and 13 we can set upper and lower bounds on players scores such that

$$\begin{aligned} S_{xy} + S_{yx} &\leq (B_{22} - 2C_2) + (B_{21} + C_2 - C_1 - B_{22})(v_{12} + v_{12}) \\ &+ \sum_{j=3}^d (B_{2j} + C_2 - C_j - B_{22})v_{2j} + (B_{1j} - C_1 - C_j - B_{22} + 2C_2)v_{1j} \end{aligned} \quad (14)$$

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

$$\begin{aligned} S_{xy} + S_{yx} &\geq (B_{11} - 2C_1) + (B_{21} - C_2 + C_1 - B_{11})(v_{12} + v_{12}) \\ &+ \sum_{j=3}^d (B_{2j} - C_2 - C_j - B_{11} + 2C_1)v_{2j} + (B_{1j} + C_1 - C_j - B_{11})v_{1j} \end{aligned} \quad (15)$$

which becomes an equality when $v_{22} = 0$, and

$$S_{xy} - S_{yx} \geq -(C_2 - C_1)(v_{12} + v_{21}) + \sum_{j=3}^d (C_j - C_1)v_{1j} + (C_j - C_2)v_{2j} \quad (16)$$

which becomes an equality when an opponent never invests C_1 and

$$S_{xy} - S_{yx} \leq (C_2 - C_1)(v_{12} + v_{21}) + \sum_{j=3}^d (C_j - C_1)v_{1j} + (C_j - C_2)v_{2j} \quad (17)$$

which becomes an equality when an opponent never invests C_2 .

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

$$S_{yx} > \frac{N-2}{N-1}(B_{22}/2 - C_2) + \frac{1}{N-1}S_{xy}. \quad (18)$$

This condition means that selection favors the rare mutant over the resident strategy. Our goal is to identify strategies that resist invasion by all possible mutants, which we call evolutionary robust strategies. The condition above is related to the ESS_N condition for a resident strategy to be stable against invasion *and replacement* by a mutant in a finite population [6]. However, since we are concerned only with strong selection we focus on the invasion condition alone. Furthermore, we discuss our results in terms of the evolutionary robustness of strategies, (i.e. those that cannot be selectively invaded) because, in the large space of memory-1 strategies, no strategy is strictly stable because all strategies can be replaced neutrally by drift. The best that can be achieved is robustness, i.e. the ability to resist selective invasion [3]. Combining the expression above with Eq. 11 we obtain.

$$\left(\chi - \phi \frac{1}{N-1}\right) (S_{xy} - (B_{22}/2 - C_2)) > \lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) \quad (19)$$

Combining this with Eq. 14 and Eq. 16 we derive two conditions that together are necessary and sufficient for evolutionary robustness. Firstly, if $(N - 1)\chi > \phi$ we have

$$\begin{aligned} & \frac{N}{N-1} \left(\lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) \right) > \\ & \left(\chi - \phi \frac{1}{N-1} \right) \left[(B_{21} + C_2 - C_1 - B_{22})(v_{12} + v_{21}) \right. \\ & \left. + \sum_{j=3}^d (B_{2j} + C_2 - C_j - B_{22})v_{2j} + (B_{1j} - C_1 - C_j - B_{22} + 2C_2)v_{1j} \right] \end{aligned} \quad (20)$$

which means that in order to ensure robustness we must have

$$\frac{N}{N-1} (\lambda_{ij}) > - \left(\chi - \phi \frac{1}{N-1} \right) (B_{22} - 2C_2 - B_{ij} + C_i + C_j) \quad (21)$$

We also retrieve a second inequality when $(N - 1)\chi < \phi$:

$$\begin{aligned} & \frac{N-2}{N-1} \lambda_{12}(v_{12} + v_{21}) + \frac{N-2}{N-1} \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) \\ & > - \left(\chi - \phi \frac{1}{N-1} \right) \left[(C_2 - C_1)(v_{12} + v_{21}) - \sum_{j=3}^d (C_j - C_2)v_{2j} + (C_j - C_1)v_{1j} \right] \end{aligned} \quad (22)$$

which means that in order to ensure robustness we must also have

$$\frac{N-2}{N-1} \lambda_{ij} > \left(\chi - \phi \frac{1}{N-1} \right) (C_j - C_i), \quad \forall j > 2 \quad (23)$$

This second condition is always hardest to satisfy when C_j is minimized.

The first condition depends on how benefits change with investment. If we assume $B_{ij} = r(C_i + C_j)^\alpha$ we get

$$\frac{N}{N-1} \lambda_{ij} > \left(\chi - \phi \frac{1}{N-1} \right) (r(2C_2)^\alpha - 2C_2 - r(C_i + C_j)^\alpha + (C_i + C_j))$$

which is hardest to satisfy when the right hand side is maximized. When this occurs depends in general on the choice of α , but if $\alpha = 1$ this condition is also hardest to satisfy when $C_j = 0$. We can convert Eq. 20-23 back to the original coordinate system, i.e write conditions for robustness in terms of the probability p_{jk}^i of playing choice i given the outcome of the preceding round. This yields the following set of two-choice strategies that are evolutionary robust against all possible mutants and stabilize investment level at C_2 when resident in a population:

$$\begin{aligned} \mathcal{C}_2^d = & \left\{ (p_{11}, p_{12}, \dots, p_{1d}, p_{21}, p_{22}, \dots, p_{2d}) \mid p_{22} = 1, \right. \\ & p_{2j} < 1 - \frac{N-2}{N} (1 + p_{12} - p_{21}) \frac{C_2 - C_j}{C_2 - C_1} \left[\frac{N-1}{N-2} - \frac{r}{2} \right], \\ & p_{1j} + \frac{1-\delta}{\delta} < \frac{N-2}{N} (1 + p_{12} - p_{21}) \left[\frac{r}{2} - \left(\frac{N-1}{N-2} - \frac{r}{2} \right) \frac{C_2 - C_j}{C_2 - C_1} + \frac{1}{N-2} \right], \\ & p_{2j} < 1 - \frac{p_{11}}{r-1} \frac{C_2 - C_j}{C_2 - C_1} \left[\frac{N-1}{N-2} - \frac{r}{2} \right] \\ & \left. p_{1j} + \frac{1-\delta}{\delta} < \frac{p_{11}}{r-1} \left[\frac{r}{2} - \left(\frac{N-1}{N-2} - \frac{r}{2} \right) \frac{C_2 - C_j}{C_2 - C_1} + \frac{1}{N-2} \right] \right\}, \end{aligned} \tag{24}$$

Finally, in order for a robust strategy to exist it must be both viable and belong to the set described by Eq. 24. The relevant values of r (i.e. those that produce a social dilemma in the public goods game) are those in the range $1 \leq r \leq 2$. Thus p_{2j} can always be chosen to be both viable and robust. However p_{1j} can only be chosen to be both viable and robust in all cases if

$$\frac{1-\delta}{\delta} < 2\frac{N-2}{N} \left[\frac{r}{2} - \left(\frac{N-1}{N-2} - \frac{r}{2} \right) \frac{C_2 - C_j}{C_2 - C_1} + \frac{1}{N-2} \right]$$

and

$$\frac{1-\delta}{\delta} < \frac{1}{r-1} \left[\frac{r}{2} - \left(\frac{N-1}{N-2} - \frac{r}{2} \right) \frac{C_2 - C_j}{C_2 - C_1} + \frac{1}{N-2} \right]$$

are satisfied. The first condition is only the more stringent in general for values $N < 4$, thus we calculate conditions for strategies to be viable under the second condition. This gives

$$\frac{(r-1)(2\delta-1)}{\delta \frac{r}{2} + \delta \frac{1}{N-2} - (1-\delta)(r-1)} > \frac{C_1}{C_2} \quad (25)$$

as the condition which must be satisfied in large population ($N > 4$) in order for a robust two-choice strategy to exist, i.e. in order for the set \mathcal{C}_2^d to be non-empty.

3.2 Robustness of strategies that stabilize investment at level C_1

In this section we repeat the results of the preceding section for strategies that stabilize investment at level C_1 , i.e. those which have $p_{11} = 0$, which implies $\kappa = B_{11} - C_1$ and $p_2^0 = 0$. In order for a rare mutant Y to invade a population with a resident X we must have

$$S_{yx} > \frac{N-2}{N-1} (B_{11}/2 - C_1) + \frac{1}{N-1} S_{xy} \quad (26)$$

Combining this with Eq. 11 we then get

$$\left(\chi - \phi \frac{1}{N-1} \right) (S_{xy} - (B_{11}/2 - C_1)) > \lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) \quad (27)$$

Combining this with Eq. 15 and Eq. 17 we then get two conditions for evolutionary robustness, firstly, when $(N - 1)\chi < \phi$ we find

$$\begin{aligned} & \frac{N-2}{N-1} \left(\lambda_{12}(v_{12} + v_{21}) + \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) \right) > \\ & \left(\chi - \phi \frac{1}{N-1} \right) \left[(B_{21} + C_1 - C_2 - B_{11})(v_{12} + v_{12}) \right. \\ & \left. + \sum_{j=3}^d (B_{2j} - C_2 - C_j - B_{11} + 2C_1)v_{2j} + (B_{1j} + C_1 - C_j - B_{11})v_{1j} \right] \end{aligned} \quad (28)$$

which means that in order to ensure robustness we must have

$$\frac{N-2}{N-1} (\lambda_{ij}) > \left(\chi - \phi \frac{1}{N-1} \right) (B_{11} - 2C_1 - B_{ij} + C_i + C_j) \quad (29)$$

We also retrieve a second inequality when $(N - 1)\chi > \phi$:

$$\begin{aligned} & \frac{N}{N-1} \lambda_{12}(v_{12} + v_{21}) + \frac{N}{N-1} \sum_{j=3}^d (\lambda_{1j}v_{1j} + \lambda_{2j}v_{2j}) \\ & > \left(\chi - \phi \frac{1}{N-1} \right) \left[(C_2 - C_1)(v_{12} + v_{21}) + \sum_{j=3}^d (C_j - C_2)v_{2j} + (C_j - C_1)v_{1j} \right] \end{aligned} \quad (30)$$

which means that in order to ensure robustness we must also have

$$\frac{N}{N-1} \lambda_{ij} > \left(\chi - \phi \frac{1}{N-1} \right) (C_j - C_i), \quad \forall j > 2 \quad (31)$$

Assuming a linear public goods game, the first in equality is hardest to satisfy when $C_j = 0$.

However the second in equality is hardest to satisfy when C_j is maximized. This latter result is important because it illustrates the instability of extortionate strategies in larger populations. Extortion strategies have $\lambda_{ij} = 0$ and $\chi > 0$. Our results show that two-choice extortion strategies are never universally robust, and are vulnerable to invaders who contribute more than them to the public good.

3.3 Two-choice strategies with thresholds

In this section we consider the robustness of two choice strategies that stabilize investment at C_2 when resident in a population, but are constrained in their ability to “perceive” an invader who invests at a level $C \neq \{C_1, C_2\}$. Such a case is highly relevant because it is natural to assume that a player who is limited in her ability to access a large action space may also be limited in her ability to perceive actions that she cannot access. The most natural case of limited perception is to assume that the focal, two-choice player, reacts to all of her opponents plays as though they are investments at either level C_1 or C_2 . Thus her strategy consists of only four probabilities, $\{p_{11}, p_{12}, p_{21}, p_{22}\}$ as well as a probability of investing C_2 in the first round, p_2^0 . We assume that this player uses a threshold in her perception of her opponent’s investment, whereby an opponent’s investment of $C < C_T$ results in her treating his play as an investment of C_1 and otherwise she treats it as an investment of C_2 . Clearly $C_1 \leq C_T \leq C_2$ is the most realistic case.

Returning to the case of a resident strategy that stabilizes investment at level C_2 we see from Eq. 24 that, for values of $C_T < C_2$ the strategy cannot be robust (since these conditions imply that $p_{22} < 1$ whereas a strategies that stabilize investment at C_2 have $p_{22} = 1$ by definition). However if we select a threshold $C_T = C_2$ we retrieve the following conditions for robustness (for $\delta = 1$):

$$\begin{aligned}
p_{12} \frac{C_2}{C_2 - C_1} \left[\frac{N-1}{N-2} - \frac{r}{2} \right] &< (1 - p_{21}) \left[\frac{N}{N-2} - \frac{C_2}{C_2 - C_1} \frac{N-1}{N-2} + \frac{r}{2} \frac{C_2}{C_2 - C_1} \right], \\
p_{11} &< \frac{N-2}{N} (1 + p_{12} - p_{21}) \left[\frac{r}{2} - \left(\frac{N-1}{N-2} - \frac{r}{2} \right) \frac{C_2}{C_2 - C_1} + \frac{1}{N-2} \right], \\
1 - p_{21} &> \frac{p_{11}}{r-1} \frac{C_2}{C_2 - C_1} \left[\frac{N-1}{N-2} - \frac{r}{2} \right] \\
\frac{C_1}{C_2} &< \frac{(r-1)}{\frac{r}{2} + \frac{1}{N-2}}
\end{aligned} \tag{32}$$

All of these can be satisfied for some choice of $\{p_{11}, p_{12}, p_{21}\}$ provided the final condition is satisfied. However this is precisely the condition for universal robustness given in section 1, in the case $\delta = 1$. We have also verified this condition via simulation (Fig. S1). Note that in order to derive these conditions only Eq. 25 is required, and the same procedure can be repeated to determine whether any ‘‘perception scheme’’ of interest can produce a universally robust strategy.

4 Games with non-transitive payoff structures

In this final section we consider the rock-paper-scissors game, which is a three-choice, non-transitive game. We write down the coordinate transform for the three-choice non-transitive game and we show that in general no ZD strategies can exist. We also determine the conditions for a mixed strategy (one that makes use of all three choices) to be invaded by a pure strategy, which uses only a single type of play. In this way we assess the ability of a population to maintain behavioral diversity.

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 without discounting ($\delta = 1$), a strategy is written as

$$\begin{aligned}
p_{11}^1 &= 1 - (\phi^1 - \chi^1) (B/2 - C_1 - \kappa^1) \\
p_{12}^1 &= 1 - (\phi^1(B - C_2) + \chi^1 C_1 - (\phi^1 - \chi^1)\kappa^1) \\
p_{13}^1 &= 1 + (\phi^1 C_3 + \chi^1(B - C_1) + (\phi^1 - \chi^1)\kappa^1) \\
p_{21}^1 &= \lambda_{21}^1 + (\phi^1 C_2 + \chi^1(B - C_1) + (\phi^1 - \chi^1)\kappa^1) \\
p_{22}^1 &= \lambda_{22}^1 - (\phi^1 - \chi^1) (B/2 - C_2 - \kappa^1) \\
p_{23}^1 &= \lambda_{23}^1 - (\phi^1(B - C_3) + \chi^1 C_2 - (\phi^1 - \chi^1)\kappa^1) \\
p_{31}^1 &= \lambda_{31}^1 - (\phi^1(B - C_1) + \chi^1 C_3 - (\phi^1 - \chi^1)\kappa^1) \\
p_{32}^1 &= \lambda_{32}^1 + (\phi^1 C_2 + \chi^1(B - C_3) + (\phi^1 - \chi^1)\kappa^1) \\
p_{33}^1 &= \lambda_{33}^1 - (\phi^1 - \chi^1) (B/2 - C_3 - \kappa^1)
\end{aligned}$$

and

$$\begin{aligned}
p_{11}^2 &= \lambda_{11}^2 - (\phi^2 - \chi^2) (B/2 - C_1 - \kappa^2) \\
p_{12}^2 &= \lambda_{12}^2 - (\phi^2(B - C_2) + \chi^2 C_1 - (\phi^2 - \chi^2)\kappa^2) \\
p_{13}^2 &= \lambda_{13}^2 + (\phi^2 C_3 + \chi^2(B - C_1) + (\phi^2 - \chi^2)\kappa^2) \\
p_{21}^2 &= 1 + (\phi^2 C_2 + \chi^2(B - C_1) + (\phi^2 - \chi^2)\kappa^2) \\
p_{22}^2 &= 1 - (\phi^2 - \chi^2) (B/2 - C_2 - \kappa^2) \\
p_{23}^2 &= 1 - (\phi^2(B - C_3) + \chi^2 C_2 - (\phi^2 - \chi^2)\kappa^2) \\
p_{31}^2 &= \lambda_{31}^2 - (\phi^2(B - C_1) + \chi^2 C_3 - (\phi^2 - \chi^2)\kappa^2) \\
p_{32}^2 &= \lambda_{32}^2 + (\phi^2 C_2 + \chi^2(B - C_3) + (\phi^2 - \chi^2)\kappa^2) \\
p_{33}^2 &= \lambda_{33}^2 - (\phi^2 - \chi^2) (B/2 - C_3 - \kappa^2)
\end{aligned}$$

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

$$\begin{aligned}
p_o^o &= 1 - (\phi - \chi)(B/2 - C - \kappa) \\
p_-^- &= 1 - (\phi(B - C) + \chi C - (\phi - \chi)\kappa) \\
p_+^+ &= 1 + (\phi C + \chi(B - C) + (\phi - \chi)\kappa) \\
p_+^o &= \lambda_+^o + (\phi C + \chi(B - C) + (\phi - \chi)\kappa) \\
p_o^- &= \lambda_o^- - (\phi - \chi)(B/2 - C - \kappa) \\
p_-^+ &= \lambda_-^+ - (\phi(B - C) + \chi C - (\phi - \chi)\kappa) \\
p_-^o &= \lambda_-^o - (\phi(B - C) + \chi C - (\phi - \chi)\kappa) \\
p_+^- &= \lambda_+^- + (\phi C + \chi(B - C) + (\phi - \chi)\kappa) \\
p_o^+ &= \lambda_o^+ - (\phi - \chi)(B/2 - C - \kappa)
\end{aligned}$$

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 $p_o^+ + p_o^- + p_o^o = 1$ etc so that the following must hold:

$$\begin{aligned}
\lambda_o^- + \lambda_o^+ &= 3(\phi - \chi)(B/2 - C - \kappa) \\
\lambda_+^o + \lambda_+^- &= -3(\phi C + \chi(B - C) + (\phi - \chi)\kappa) \\
\lambda_-^+ + \lambda_-^o &= 3(\phi(B - C) + \chi C - (\phi - \chi)\kappa)
\end{aligned} \tag{33}$$

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

$$\begin{aligned}
\phi S_{yx} - \chi S_{xy} - (\phi - \chi)\kappa + \lambda_+^o v_{21} + \lambda_-^o v_{31} &= 0 \\
\phi S_{yx} - \chi S_{xy} - (\phi - \chi)\kappa + \lambda_o^+ v_{11} + \lambda_-^+ v_{31} &= 0 \\
\phi S_{yx} - \chi S_{xy} - (\phi - \chi)\kappa + \lambda_o^- v_{11} + \lambda_+^- v_{21} &= 0
\end{aligned}
\tag{34}$$

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:

$$S_{xy} + S_{yx} = B - 2C \tag{35}$$

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. 33-35 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:

$$p_o^-(1 - p_-^- - p_+^-) > p_o^+(1 - p_+^+ - p_-^+) \tag{36}$$

5 Supplementary figures

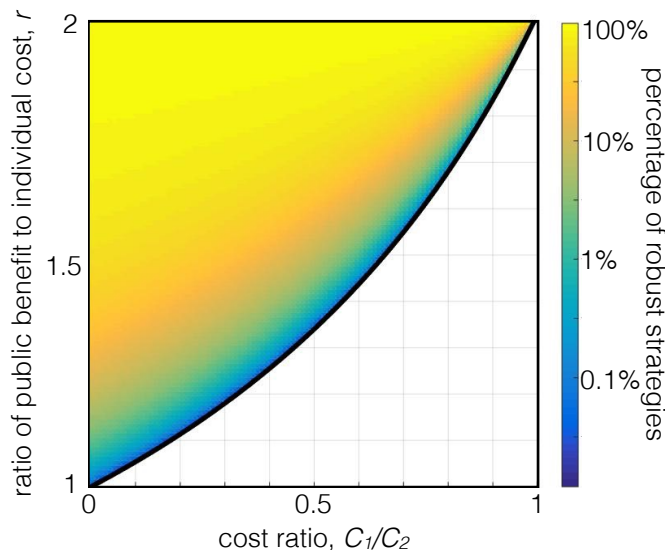


Figure 1: The volume of universally robust two-choice strategies for the linear public goods game, with a threshold perception model. We consider two-choice strategies that can invest either C_1 or $C_2 > C_1$ and that stabilize investment at C_2 when resident in a population. We compete these strategies against opponents with access to arbitrary investment levels, but we assumed that the resident two-choice strategy reacts to all opponents as though they have invested either C_1 or C_2 , treating investments $C \geq C_2$ as an investment of C_2 and treating everything else as an investment of C_1 . We drew 10^6 random resident strategies for each value of the benefit scaling factor r and investment reduction C_1 (keeping $C_2 = 1$ fixed). We competed each strategy against 10^6 invaders who use three investment levels $C_1^* = 0$, $C_1 < C_2^* < C_2$ and $C_3^* > C_2$, where we draw $C_2^* \in [C_1, C_2]$ and $C_3^* \in [C_2, 10C_2]$ uniformly for each invader. From this we calculated the volume of robust two-choice strategies, i.e. the probability that a random two-choice strategy of this type can resist all simulated invaders. The white region indicates parameters for which no strategy was found to be robust, in good agreement with the analytical prediction (black line, Eq. 3). Simulations were conducted with population size $N = 100$ with selection strength $\sigma = 10$.

References

- [1] Press WH, Dyson FJ (2012) Iterated prisoner’s dilemma contains strategies that dominate any evolutionary opponent. *Proc Natl Acad Sci U S A* 109:10409–13.
- [2] Akin E (2012) Stable cooperative solutions for the iterated prisoner’s dilemma. *arXiv:1211.0969*.

- [3] Stewart AJ, Plotkin JB (2014) Collapse of cooperation in evolving games. *Proc Natl Acad Sci U S A* 111:17558–63.
- [4] Hilbe C, Traulsen A, Sigmund K (2015) Partners or rivals? strategies for the iterated prisoner’s dilemma. *Games Econ Behav* 92:41–52.
- [5] McAvoy A, Hauert C (2016) Autocratic strategies for iterated games with arbitrary action spaces. *PNAS* Early Edition.
- [6] Nowak MA (2006) *Evolutionary dynamics: exploring the equations of life* (Belknap Press of Harvard University Press, Cambridge, Mass.).