The role of fairness motives and spatial considerations in explaining departures from Nash equilibrium: stationary and evolutionary lessons from 2x2 games

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Abstract. Substantial evidence has accumulated in recent empirical works on the limited ability of the Nash equilibrium to rationalize observed behavior in many classes of games played by experimental subjects. This realization has led to several attempts aimed at finding tractable equilibrium concepts which perform better empirically, often by introducing a reference point to which players compare the available payoff allocations, as in impulse balance equilibrium and in the inequity aversion model. The first part of this paper is concerned with reviewing the recent reference point literature and advancing a new, empirically sound, hybrid concept. In the second part, evolutionary game theoretic models are employed to investigate the role played by fairness motives as well as spatial structure in explaining the evolution of cooperative behavior.

JEL classification: A13; C72; D64

Keywords: Other-regarding preferences; Inequity aversion; Endogenous preferences; Evolutionary stability; Prisoner’s dilemma

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From efficiency to equality: the “distributive” reference point

In recent years experimental economists have accumulated considerable evidence that steadily contradicts the self-interest hypothesis embedded in equilibrium concepts traditionally studied in game theory, such as Nash’s. The evidence suggests that restricting the focus of analysis to the strategic interactions among perfectly rational players (exhibiting equilibrium behavior) can be limiting, and that considerations about fairness and reciprocity should be accounted for. In fact, while models based on the assumption that people are exclusively motivated by their material self-interest perform well for competitive markets with standardized goods, misleading predictions arise when applied to non-competitive environments, for example those characterized by a small number of players (cf. FEHR & SCHMIDT, 2000) or other frictions. For example KAHNEMAN, KNETSCH & THALER (1986) find empirical results indicating that customers are extremely sensitive to the fairness of firms’ short-run pricing decisions, which might explain the fact that some firms do not fully exploit their monopoly power.

One prolific strand of literature on equity issues focuses on relative measures, in the sense that subjects are concerned not only with the absolute amount of money they receive but also about their relative standing compared to others. BOLTON (1991), formalized the relative income hypothesis in the context of an experimental bargaining game between two players. KIRCHSTEIGER (1994) followed a similar approach by postulating envious behavior. Both specify the utility function in such a way that agent $i$ suffers if she gets less than player $j$, but she’s indifferent with respect to $j$’s payoff if she is better off herself. The downside of the latter specifications is that, while consistent with the behavior in bargaining games, they fall short of explaining observed behavior such as voluntary contributions in public good games.

A more general approach has been followed by FEHR & SCHMIDT (1999), who instead of assuming that utility is either monotonically increasing or decreasing in the well being of other player, model fairness as self-centered inequality aversion. Based on this interpretation, subjects resist inequitable outcomes, that is they are willing to give up some payoff in order to move in the direction of more equitable outcomes. More specifically, a player is altruistic towards other players.
if their material payoffs are below an equitable benchmark, but feels envy when the material payoffs of the other players exceed this level. To capture this idea, the authors consider a utility function which is linear in both inequality aversion and in the payoffs. Formally, for the two-player case \((i \neq j)\):

\[
U_i = x_i - \alpha_i \max\{x_j - x_i, 0\} - \beta_i \max\{x_i - x_j, 0\} \quad (1)
\]

Where \(x_i, x_j\) are player 1 and player 2’s payoffs respectively and \(\beta_i, \alpha_i\) are player \(i\)’s inequality parameters satisfying the following conditions: \(\beta_i \leq \alpha_i\) and \(0 \leq \beta_i \leq 1\).

The second term in the equation is the utility loss from disadvantageous inequality, while the third term is the utility loss from advantageous inequality. Due to the above restrictions imposed on the parameters, for a given payoff \(x_i\), player \(i\)’s utility function is maximized at \(x_i = x_j\), and the utility loss from disadvantageous inequality \((x_i < x_j)\) is larger than the utility loss if player \(i\) is better off than player \(j\) \((x_i > x_j)\).

Fehr and Schmidt show that the interaction of the distribution of types with the strategic environment explains why in some situations very unequal outcomes are obtained while in other situations very egalitarian outcomes prevail. In referring to the social aspects introduced by this utility function, one could think of inequality aversion in terms of an interactive framing effect (reference point dependence).

This payoff modification has proved successful in many applications, mainly in combination with the Nash equilibrium concept, and will therefore be employed in this study, although in conjunction with a different equilibrium type, as will be explained in the next section.

**The “psychological” reference point**

The predictive weakness of the Nash equilibrium is effectively pointed out by EREV & ROTH (1998), who study the robustness and predictive power of learning models in experiments involving at least 100 periods of games with a unique equilibrium in mixed strategies. They conclude that “…in some of the games the [Nash] equilibrium prediction does very badly” and that a simple learning model can be used to predict, as well as explain, observed behavior on a broad range of games, without fitting parameters to each game. A similar approach, based ex-post and ex-
ante comparisons of the mean square deviations, will also be employed in this paper to assess to what extent the proposed hybrid model improves the fit of several games.

Based on the observation of the shortcomings of mixed Nash equilibrium in rationalizing observed behavior in many classes of games played by experimental subjects, an alternative tractable equilibrium has been suggested by SELTEN & CHMURA (forthcoming). IBE is based on learning direction theory (SELTEN & BUCHTA, 1999), which is applicable to the repeated choice of the same parameter in learning situations where the decision maker receives feedback not only about the payoff for the choice taken, but also for the payoffs connected to alternative actions. If a higher parameter would have brought a higher payoff, the player receives an upward impulse, while if a lower parameter would have yielded a higher payoff, a downward impulse is received. The decision maker is assumed to have a tendency to move in the direction of the impulse. IBE, a stationary concept which is based on transformed payoff matrices as explained in the next section, applies this mechanism to 2x2 games. The probability of choosing one of two strategies (for example Up) is treated as the parameter, which can be adjusted upward or downward. It is assumed that the second lowest payoff in the matrix is an aspiration level determining what is perceived as profit or loss. In impulse balance equilibrium expected upward and downward impulses are equal for each of both players simultaneously.

The main result of the paper by Selten and Chmura is that, for the games they consider, impulse balance theory has a greater predictive success than the other three stationary concepts they compare it to: Nash equilibrium, sample-7 equilibrium and quantal response equilibrium. While having the desirable feature of being a parameter-free concept as the Nash equilibrium, and of outperforming the latter, the aspiration level framework (to be described) expose the theory to a critique regarding the use of transformed payoffs in place of the original ones for the computation of the equilibrium.

The aspiration level can be thought of as a psychological reference point, as opposed to the social one considered when modeling inequality aversion: the idea behind the present work is that of utilizing IBE but replacing the aspiration level with inequity aversion (social) parameters. The motivation follows from the realization that in non-constant sum games (considered here) subjects’ behavior also reflects considerations of equity. In fact, while finite repetition does little to enlarge the scope for cooperation or retaliation, non-constant sum games offer some cooperation opportunities, and it seems plausible that fairness motives will play an important role in repeated
play of this class of games. A suitable consequence of replacing the aspiration level framework with the inequality aversion one is that the original payoffs can be utilized (and should, in order to avoid mixing social and psychological reference points).

**Experimental setup: IBE**

The table in Appendix A shows the 12 games, 6 constant sum games and 6 non-constant sum games on which Selten and Chmura have run experiments, which have taken place with 12 independent subject groups for each constant sum game and with 6 independent subject groups for each non-constant sum game. Each independent subject group consists of 4 players 1 and 4 players 2 interacting anonymously in fixed roles over 200 periods with random matching. In summary:

Players: $I=\{1,2\}$
Action space: $\{U,D\} \times \{L,R\}$
Probabilities in mixed strategy: $\{P_U, 1-P_U\}$ and $\{Q_L, 1-Q_L\}$
Sample size: (54 sessions) x (16 subjects) = 864
Time periods: $T=200$

In Appendix A, a non-constant sum game next to a constant sum game has the same best reply structure (characterized by the Nash equilibrium choice probabilities $P_U$, $Q_L$) and is derived from the paired constant sum game by adding the same constant to player 1’s payoff in the column for $R$ and 2’s payoff in the row for $U$. Games identified by a smaller number have more extreme parameter values than games identifies by a higher number; for example, Game 1 and its paired non-constant sum Game 7 are near the border of the parameter space ($P_U \approx 0.1$ and $Q_L \approx 0.9$), while Game 6 and its paired non-constant sum Game 12 are near the middle of the parameter space ($P_U \approx 0.5$ and $Q_L=0.6$).

As pointed out, IBE involves a transition from the original game to the transformed game, in which losses with respect to the natural aspiration level get twice the weight as gains above this level. The impulse balance equilibrium depends on the best reply structure of this modified game, which is generally different from that of the original game, resulting therefore in different predictions for the games in a pair.

The present paper utilizes the data on the experiments involving 6 independent subject groups for each of the 6 non-constant sum games (games 7 through 12 in Appendix A). As anticipated above,
this class of games is particularly conceptually suitable to the application of the inequality aversion framework. Further, in completely mixed 2x2 games, mixed equilibrium is the unambiguous game theoretic prediction when they are played as non-cooperative one-shot games. Since non-constant sum games provide incentives for cooperation, such attempts to cooperation may have influenced the observed relative frequencies in Selten’s experiment. Along these lines, it is particularly relevant to see whether inequality aversion payoff modifications can help improve the fit with respect to these frequencies.

The application of inequality aversion parameters to Impulse balance equilibrium provides an opportunity for testing Fehr & Schmidt’s fairness model in conjunction with the IBE, which is itself a simple yet fascinating concept which has proven to be empirically successful in fitting the data in many categories of games and is nevertheless parsimonious due to the straight-forward formulation and parameter-free nature. By including a fairness dimension to it, the hope is to supply favorable empirical evidence and provide further stimulus to expand the types of games empirically tested.

Formally, this involves first modifying the payoff matrices of each game in order to account for the inequality parameters \((\beta, \alpha)\), than creating the impulse matrix based on which the probabilities are computed. In order to clarify the difference between the reference point utilized in Selten and Chmura (the aspiration level) and that utilized in this paper it is useful to start by summarizing the mechanics behind the computation of the IBE.

Let’s consider the normal form game depicted in Figure 1 below,

\[\begin{array}{c|c}
L (Q_L) & R (1-Q_L) \\
\hline
a_L + c_L ; b_U & a_R ; b_U + d_U \\
\uparrow & \downarrow \\
a_L ; b_D + d_D & a_R + c_R ; b_D \\
\hline
\end{array}\]

where \(a_L, a_R, b_U, b_D \geq 0\) and \(c_L, c_R, d_U, d_D > 0\)
$c_L$ and $c_R$ are player 1’s payoffs in favor of $U,D$ while $d_U,d_D$ are player 2’s payoffs in favour of $L,R$ respectively. Note that player 1 can secure the higher one of $a_L,a_R$ by choosing one of his pure strategies, and player 2 can similarly secure the higher one of $b_U,b_D$. Therefore, the authors define the natural aspiration levels for the 2 players are given by:

\[ s_i = \max(a_L,a_R) \text{ for } i=1 \text{ and } s_i = \max(b_U,b_D) \text{ for } i=2 \]

the transformed game (TG) is constructed by leaving player i’s payoff unchanged if it is less or equal to $s_i$ and by reducing the difference of payoffs greater than $s_i$ by the factor $\frac{1}{2}$. Algebraically, calling $x$ the payoffs,

\[
\begin{align*}
if x \leq s_i & \Rightarrow x' = x \\
if x > s_i & \Rightarrow x' = x - \frac{1}{2}(x-s_i)
\end{align*}
\]

If after the play, player i could have obtained a higher payoff with the other strategy, she receives an impulse in the direction of the other strategy, of the size of the foregone payoff in the TG.

**Fig.2: Impulses in T.G. in the direction of unselected strategy**

<table>
<thead>
<tr>
<th>L ($Q_L$)</th>
<th>R (1-$Q_L$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 ; $d_U^*$</td>
<td>$c_R^*$ ; 0</td>
</tr>
<tr>
<td>$c_L^*$ ; 0</td>
<td>0 ; $d_D^*$</td>
</tr>
</tbody>
</table>

The concept of impulse balance equilibrium requires that player 1’s expected impulse from $U$ to $D$ is equal to the expected impulse from $D$ to $U$; likewise, pl.2’s expected impulse from $L$ to $R$ must equal the impulse from $R$ to $L$. Formally,

\[
\begin{align*}
P_UQ_Rc_R^* & = P_DQ_Lc_L^* \\
P_UQ_Ld_U^* & = P_DQ_Rd_D^*
\end{align*}
\]

Which, after some manipulation, can be shown to lead to the following formulae for probabilities:
Experimental setup: equity-driven Impulse Balance Equilibrium

Replacing the aspiration level framework with the inequality aversion one doesn’t require the computation of the TG based on aspiration level framing, as the original payoffs are now modified by including the inequality parameters ($\beta, \alpha$). Formally, recalling that:

$$U_i = x_i - \alpha_i \max\{x_j - x_i, 0\} - \beta_i \max\{x_j - x_i, 0\}$$

Table 1: structure of the 2x2 games accounting for inequality aversion

<table>
<thead>
<tr>
<th>L (QL)</th>
<th>R (1-QL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_L + c_L - \alpha_i \max{b_u - a_L - c_L, 0} - \beta_i \max{b_u - a_L - c_L, 0}$;</td>
<td></td>
</tr>
<tr>
<td>$b_u - \alpha_i \max{a_L + c_L - b_u, 0} - \beta_i \max{a_L + c_L - b_u, 0}$</td>
<td>$a_R - \alpha_i \max{b_u + d_u - a_R, 0} - \beta_i \max{b_u + d_u - a_R, 0}$;</td>
</tr>
<tr>
<td>$b_R + \alpha_i \max{a_R - b_R - d_R, 0} - \beta_i \max{a_R - b_R - d_R, 0}$</td>
<td>$a_R + \alpha_i \max{b_R - a_R - c_R, 0} - \beta_i \max{b_R - a_R - c_R, 0}$;</td>
</tr>
<tr>
<td>$b_d - \alpha_i \max{a_L - b_D - c_R, 0} - \beta_i \max{a_L - b_D - c_R, 0}$</td>
<td>$b_R - \alpha_i \max{a_R + c_R - b_D, 0} - \beta_i \max{a_R + c_R - b_D, 0}$;</td>
</tr>
</tbody>
</table>

Based on these payoffs, the previous section’s computations can be conducted in order to find the impulse balance mixed strategy equilibria corresponding to specific values of $\beta$ and $\alpha$.

Two measures of the relative performance of the I.A.-adjusted Impulse Balance concept: best fit and predictive power

Results in terms of Best fit

The preceding analysis served as an introduction to the more systemic method utilized in the next paragraphs to assess the descriptive and predictive success of the “pure” impulse balance equilibrium in comparison to the proposed Inequality Aversion hybrid.

Following a methodology which has been broadly utilized in the literature to measure the adaptive and predictive success of a point in a Euclidean space, the squared distance of observed and theoretical values is employed (cf. Erev & Roth, 1998 and Selten & Chmura). More precisely, the first part of the analysis consists, for each of the 6 non constant sum games, of a grid search with an MSD criterion on the ($\beta, \alpha$) parameter space to estimate the best fitting parameters, i.e. those that minimize the distance between the model and the data.

Algebraically, the mean over the 6 games in the best fit row will be given by:

$$P_U = \frac{\sqrt{cl^* / cr^*}}{\sqrt{cl^* / cr^* + \sqrt{du^* / dd^*}}} ; Q_L = \frac{1}{1 + \sqrt{cl^* / du^*}}$$
where $MSD_i$ is the mean of game i’s squared distances $(f_{ui} - P_u)^2 + (f_{ii} - Q_i)^2$

The inequality aversion parameters used in the hybrid model must satisfy the constraints $\beta_i \leq \alpha_i$ and $0 \leq \beta_i \leq 1$. The relevant parameter space under investigation is then given, for each $\beta$, by values $\alpha \in [\beta, 0.5]$. Graphically the parameter space can be represented as follows are as follows:

**Figure 3: The correspondence between $\beta$ and $\alpha$**

\[ \forall \beta \in [0,0.35], \alpha \in [\beta, 0.5] \]

In Table 1, a summary of the results of the explanatory power of the two models is presented for each non constant sum game, starting from the transformed or the original payoffs, respectively. The comparisons are made both within game class in column 5 (e.g. within transformed game $i$, $i=7,...,12$), and across game class in the last column (e.g. between original game $i$ and transformed game $i$).

The reason of the two-fold comparison is that not only it is meaningful to assess whether the hybrid model can better approximate the observed frequencies than the I.B. concept, but it is especially important to answer the question: does the hybrid concept applied to the original payoffs of game $i$
outperform the ‘pure’ I.B. applied to the transformed payoffs? In other words, since the inequality aversion concept overlaps to a certain extent to that of having impulses in the direction of the strategy not chosen, applying the inequality aversion adjustment to payoffs that have already been transformed to account for the aspiration level will result in “double counting”. It is therefore more relevant to compare the best fit of hybrid equilibrium on O.G. (see rows highlighted in blue) to that obtained by applying impulse balance equilibrium to T.G.

**Table 2: Ex-post (best fit) descriptive power of hybrid model vs I.B. equilibrium**

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>TG7</td>
<td>[.141; .564]</td>
<td>[.091; 091]</td>
<td>[.104; .634] (0:0)</td>
<td>[.104; .634]</td>
<td>NO</td>
<td>n.a.</td>
</tr>
<tr>
<td>OG7</td>
<td>[.141; .564]</td>
<td>[.091; 091]</td>
<td>[.099; .568] (.054; .055)</td>
<td>[.091; .500]</td>
<td>YES</td>
<td>YES</td>
</tr>
<tr>
<td>OG8</td>
<td>[.250; .864]</td>
<td>[.182; 727]</td>
<td>[.257; .585] (.006; .468)</td>
<td>[.224; .435]</td>
<td>YES</td>
<td>YES</td>
</tr>
<tr>
<td>OG11</td>
<td>[.311; .652]</td>
<td>[.344; 644]</td>
<td>[.357; .652] (.012; .018)</td>
<td>[.354; .646]</td>
<td>YES</td>
<td>YES</td>
</tr>
<tr>
<td>TG12</td>
<td>[.439; .604]</td>
<td>[.496; 575]</td>
<td>[.496; 0.575] (0:0)</td>
<td>[.496; .575]</td>
<td>NO</td>
<td>n.a.</td>
</tr>
<tr>
<td>OG12</td>
<td>[.439; .604]</td>
<td>[.455; 636]</td>
<td>[.439; .604] (.022; .393)</td>
<td>[.408; .547]</td>
<td>YES</td>
<td>YES</td>
</tr>
</tbody>
</table>

Inspection of Table 1 suggests a strong positive answer to the following two relevant questions regarding the ability of the proposed concept to fit the observed frequencies of play: within the same class of payoffs (TG or OG), is the descriptive power of the hybrid concept superior to that of
the IBE? And, perhaps more importantly, is this still true when the two concepts are applied to their natural payoffs, namely the original and the transformed respectively?

The last two columns of Table 1 contain the answers to the two questions, based on a comparison of the mean squared deviations of the predicted probabilities from the observed frequencies under the two methods.

**Results in terms of Predictive power**

The next step in evaluating the performance of the inequality aversion-adjusted impulse balance equilibrium concept is studying its ex ante predictive power. This is done by partitioning the data into subsets, and simulating each experiment using parameters estimated from the other experiments. By generating the MSD statistic repeatedly on the data set leaving one data value out each time, a mean estimate is found making it possible to evaluate the predictive power of the model. In other words, the behavior in each of the 6 non-constant sum games is predicted without using that game’s data, but using the data of the other 5 games to estimate the probabilities of playing up and down. By this cross-prediction technique (known as jackknifing), one can evaluate the stability of the parameter estimates, which shouldn’t be substantially affected by the removal of any one game from the sample. Erev & Roth (1998) based their conclusions on the predictive success and stability of their learning models by means of this procedure, and it has therefore been employed in this work.

Table 2, above, shows summary MSD scores (100*Mean-squared Deviation) organized as follows: each of the first 6 columns represents one non-constant sum game, while the last column gives the average MSD over all games, which is a summary statistic by which the models can be roughly compared. The first three rows present the MSDs of the Nash equilibrium and of the I.B. equilibrium predictions (for $\beta=0=\alpha$) on the transformed and original payoffs respectively. The remaining three rows display MSDs of the I.A.+I.B. model on the original payoffs: in the fourth row, the parameters are separately estimated for each game (12 parameters in total); in the fifth row, the estimated 2 parameters that best fit the data over all 6 games (and over all but Game 7) are employed (the same two $\beta, \alpha$ that minimize the average score over all games are used to compute the MSDs for each game); in the last row the accuracy of the prediction of the hybrid model is showed when behavior in each of the 6 games is predicted based on the 2 parameters that best fit the other 5 games (and excluding Game 7).
Table 3: MSD scores of the IBE and of the proposed equilibrium concept

<table>
<thead>
<tr>
<th>Model</th>
<th>G7</th>
<th>G8</th>
<th>G9</th>
<th>G10</th>
<th>G11</th>
<th>G12</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nash equilibrium, O.G.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 parameters (0;0) All games</td>
<td>6.076</td>
<td>1.225</td>
<td>.354</td>
<td>.708</td>
<td>.422</td>
<td>.064</td>
<td>1.475</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>.555</strong></td>
</tr>
<tr>
<td><strong>I.B. equilibrium, T.G.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 parameters (0;0) All games</td>
<td>.315</td>
<td>.035</td>
<td>.416</td>
<td>.224</td>
<td>.094</td>
<td>.205</td>
<td>.215</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>.195</strong></td>
</tr>
<tr>
<td><strong>I.B. equilibrium, O.G.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 parameters (0;0) All games</td>
<td>.330</td>
<td>1.174</td>
<td>1.825</td>
<td>.878</td>
<td>.497</td>
<td>.209</td>
<td>.819</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>.917</strong></td>
</tr>
<tr>
<td><strong>Hybrid by game, O.G.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12 parameters All games</td>
<td>.090</td>
<td>.003</td>
<td>.031</td>
<td>.033</td>
<td>.056</td>
<td>.000</td>
<td>.035</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td><strong>.025</strong></td>
</tr>
<tr>
<td><strong>Hybrid best fit, O.G.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 parameters All games</td>
<td>.746</td>
<td>.178</td>
<td>.428</td>
<td>.152</td>
<td>.140</td>
<td>.030</td>
<td>.279</td>
</tr>
<tr>
<td></td>
<td>.042</td>
<td>.098</td>
<td>.033</td>
<td>.173</td>
<td>.034</td>
<td></td>
<td><strong>.076</strong></td>
</tr>
<tr>
<td><strong>Hybrid predict, O.G.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 parameters All games</td>
<td>2.220</td>
<td>.238</td>
<td>.585</td>
<td>.186</td>
<td>.141</td>
<td>.031</td>
<td>.567</td>
</tr>
<tr>
<td></td>
<td>.044</td>
<td>.149</td>
<td>.033</td>
<td>.189</td>
<td>.035</td>
<td></td>
<td><strong>.09</strong></td>
</tr>
</tbody>
</table>

Table 3 summarizes further evidence in favor of the newly developed equity-driven impulse balance equilibrium. One can see from the third row that if the parameters of inequality aversion are allowed to be fit separately in each game, the improvements in terms of reduction of MSD are significant, both with respect to the Nash and impulse balance equilibrium.

Moreover, even when restricting the number of parameters to 2 (common to all games, cf. row 5 “best fit”), the mean MSD is still more than five times smaller than Nash’s. If one doesn’t include the extremely high MSD reported in both cases for Game 7 (for reasons discussed below), the gap actually increases, as the hybrid concept’s MSD becomes more than seven times smaller than Nash’s. With respect to the overall MSD mean of the IBE, when considering all games the hybrid has a higher MSD, although the same order of magnitude (.279 and .215 respectively). If one focuses only on games 8-12, again we have a marked superiority of the hybrid model over the IBE, as the MSD of the latter is more than twice that of the new concept.

A similar pattern is appears in the last row of the table, concerning the predictive capability: if Game 7 is excluded, the values are in line with the ones obtained in the fifth row, indicating stability of the parameters who survive the cross-validation test. One comforting consideration
regarding the appropriateness of the exclusion of Game 7 comes from the widespread anomalous high level of its MSD score in all rows of the table, which for both Nash and Hybrid predict is about four times the corresponding mean level obtained over the six games. It is plausible that this evidence is related to the location of Game 7 in the parameter space. It is in fact located at near the border, as previously pointed out, and therefore may be subject to the overvaluation of extreme probabilities by the subjects due to overweighting of small probabilities. An addition to the present work, which is currently in progress, considers incorporating fairness motives in the quantal response equilibrium notion, one that has recently attracted considerable attention thanks to its ability to rationalize behavior observed in experimental games. In addition to providing an interesting case for comparison, it should also allow to shed light on the suspected anomalous nature of Game 7.

**Quantal Response Equilibrium and Inequity Aversion**

The former analysis has also been conducted utilizing the quantal response equilibrium concept (henceforth QRE) in conjunction with preferences that are again allowed to be affected by the counterparty’s fate, via the inequity aversion parameters. Before showing the results, which are given in Table 4 and Table 5 and show an even better overall performance of this concept compared to the one examined in the previous sections, let’s briefly describe the QRE. The concept, introduced by (Mckelvey, Palfrey and Thomas, 1995), models games with noisy players: these probabilistic choice models are based on quantal best responses to the behavior of the other parties, so that deviations from optimal decisions are negatively correlated with the associated costs. That is to say, individuals are more likely to select better choices than worse choices, but do not necessarily succeed in selecting the very best choice. In the exponential form of quantal response equilibrium, considered here, the probabilities are proportional to an exponential with the expected payoff multiplied by the logit precision parameter ($\lambda$) in the exponent: as $\lambda$ increases, the response functions become more responsive to payoff differences. Formally,

$$P_{ij} = \frac{e^{\lambda \pi_{ij}(P_{-i})}}{e^{\lambda \pi_{ij}(P_{-i})} + e^{\lambda \pi_{ik}(P_{-i})}} \tag{2}$$

Where $i,j=1,2$ are the players ($k \neq j$), $P_{ij}$ is the probability of player $i$ choosing strategy $j$ and $\pi_{ij}$ is player $i$’s expected payoff when choosing strategy $j$ given the other player is playing according to the probability distribution $P_{-i}$.
Two measures of the relative performance of the I.A.-adjusted Quantal Response Equilibrium: best fit and predictive power. Results in terms of Best fit

The following is a companion table to Table 2, as it reports the results of comparisons between the new hybrid model and the IBE concept, the former always outperforming the one employing the ‘pure’ IBE on the transformed games. Note that the penultimate column now compares the performance of the two proposed concepts, showing that the one employing QRE outperforms the in five of the six games¹.

Table 4: Ex-post (best fit) descriptive power of QRE with inequity aversion

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>TG7</td>
<td>[.141;.564]</td>
<td>[] (.)</td>
<td>[.104;.634]</td>
<td>n.a.</td>
<td></td>
</tr>
<tr>
<td>OG7</td>
<td>[.141;.564]</td>
<td>[.091;909]</td>
<td><a href=".105;209">.141;.564</a> λ=0.335</td>
<td>[.091;.500] YES</td>
<td>YES</td>
</tr>
<tr>
<td>OG8</td>
<td>[.250;.586]</td>
<td>[.182;727]</td>
<td><a href=".097;386">.250;.586</a> λ=0.335</td>
<td>[.224;435] YES</td>
<td>YES</td>
</tr>
<tr>
<td>TG9</td>
<td>[.254;827]</td>
<td>[] (.)</td>
<td>[.188;764]</td>
<td>n.a.</td>
<td></td>
</tr>
<tr>
<td>OG9</td>
<td>[.254;827]</td>
<td>[.273;909]</td>
<td><a href=".083;316">.254;827</a> λ=0.6</td>
<td>[.162;659] YES</td>
<td>YES</td>
</tr>
<tr>
<td>OG10</td>
<td>[.366;699]</td>
<td>[.364;818]</td>
<td><a href=".250;254">.366;699</a> λ=0.31</td>
<td>[.263;616] YES</td>
<td>YES</td>
</tr>
<tr>
<td>TG11</td>
<td>[.311;652]</td>
<td>[] (.)</td>
<td>[.354;646]</td>
<td>n.a.</td>
<td></td>
</tr>
<tr>
<td>OG11</td>
<td>[.311;652]</td>
<td>[.364;727]</td>
<td><a href=".003;02">.311;652</a> λ=0.91</td>
<td>[.316;552] YES</td>
<td>YES</td>
</tr>
<tr>
<td>TG12</td>
<td>[.439;604]</td>
<td>[] (.)</td>
<td>[.496;575]</td>
<td>n.a.</td>
<td></td>
</tr>
<tr>
<td>OG12</td>
<td>[.439;604]</td>
<td>[.455;636]</td>
<td><a href=".042;137">.439;604</a> λ=0.55</td>
<td>[.408;547] same</td>
<td>YES</td>
</tr>
</tbody>
</table>

¹ in game 12 they achieve a substantially equal equilibrium prediction.
As before, in order to assess the performance of the concepts over multiple games, the parameters are restricted to be the same over all the games, as shown in the penultimate row in Table 5: the QRE+IA concept displays a better fit than the IBE+IA (smaller mean square deviation) in all but game 11, achieving a mean MSD of .147 as opposed to .279 for the latter. As for the predictive power, measured through jackknifing (cross-predicting), when all games are considered the mean MSD is substantially lower for the QRE-based concept incorporating fairness motives, averaging .219 vs. a score of .567 for the IBE-based one.

Two important considerations should be remarked at this point. Firstly, for what concerns the overall fit, even without excluding the potentially problematic game 7, the QRE+IA concept outperforms the traditional impulse balance equilibrium applied to the transformed games (MSD scores are .147 and .215, respectively); this is noteworthy, since it wasn’t the case for the other hybrid concept². Secondly, the above considerations are confirmed by the predictions obtained with

² In fact, the ‘pure’ impulse balance equilibrium obtains dramatically higher MSD scores when the original games are employed in place of the transformed ones, with an almost four-fold increase. The intuition behind this is, loosely speaking, that the IBE is not as parameter-free as it looks: that is, by utilizing transformed payoffs for each game.

---

Table 5: MSD scores of the proposed equilibrium concepts

<table>
<thead>
<tr>
<th>Model</th>
<th>G 7</th>
<th>G 8</th>
<th>G 9</th>
<th>G 10</th>
<th>G 11</th>
<th>G 12</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nash equilibrium, O.G.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.475</td>
</tr>
<tr>
<td>0 parameters (0;0) All games</td>
<td>6.076</td>
<td>1.225</td>
<td>.354</td>
<td>.708</td>
<td>.422</td>
<td>.064</td>
<td></td>
</tr>
<tr>
<td>I.B. equilibrium, O.G.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.819</td>
</tr>
<tr>
<td>0 parameters (0;0) All games</td>
<td>.330</td>
<td>1.174</td>
<td>1.825</td>
<td>.878</td>
<td>.497</td>
<td>.209</td>
<td></td>
</tr>
<tr>
<td>I.B. equilibrium, T.G.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>.215</td>
</tr>
<tr>
<td>0 parameters (0;0) All games</td>
<td>.315</td>
<td>.035</td>
<td>.416</td>
<td>.224</td>
<td>.094</td>
<td>.205</td>
<td></td>
</tr>
<tr>
<td>Hybrid QRE by game, O.G.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>18 parameters</td>
<td>5.5*</td>
<td>2.4*</td>
<td>7.5*</td>
<td>6.4*</td>
<td>7.4*</td>
<td>5.7*</td>
<td>3.3*10^-6</td>
</tr>
<tr>
<td></td>
<td>10^-6</td>
<td>10^-7</td>
<td>10^-6</td>
<td>10^-7</td>
<td>10^-8</td>
<td>10^-6</td>
<td></td>
</tr>
<tr>
<td>Hybrid best fit, O.G.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>parameters (β, α, λ)</td>
<td>.746</td>
<td>.178</td>
<td>.428</td>
<td>.152</td>
<td>.140</td>
<td>.030</td>
<td>.279</td>
</tr>
<tr>
<td>2 par. IBE+IA (157,.160)</td>
<td>.251</td>
<td>.012</td>
<td>.397</td>
<td>.036</td>
<td>.163</td>
<td>.027</td>
<td></td>
</tr>
<tr>
<td>3 par. QRE+IA (147,.243,.43)</td>
<td>.415</td>
<td>.016</td>
<td>.640</td>
<td>.038</td>
<td>.177</td>
<td>.029</td>
<td>.147</td>
</tr>
<tr>
<td>Hybrid predict, O.G.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 par. IBE+IA</td>
<td>2.220</td>
<td>.238</td>
<td>.585</td>
<td>.186</td>
<td>.141</td>
<td>.031</td>
<td>.567</td>
</tr>
<tr>
<td>3 par. QRE+IA</td>
<td>.415</td>
<td>.016</td>
<td>.640</td>
<td>.038</td>
<td>.177</td>
<td>.029</td>
<td>.219</td>
</tr>
</tbody>
</table>
the jackknifing technique: for the QRE+IA specification the mean MSD score based on cross-
predictions is not substantially higher than the one calculated when the parameters that best fit all
games are employed (.219 and .147, respectively). This doesn’t hold for the IBE+IA concept,
whose score roughly doubles from .279 to .567\(^3\).

Based on the above comparisons, the inequity aversion generalization of the quantal response
equilibrium concept appears to emerge as the best performing in terms of goodness of fit among the
considered stationary concepts. Based on this realization and following the behavioral stationary
concept interpretation of mixed equilibrium\(^4\), one may conclude that the proposed other-regarding
generalization of the QRE is the behavioral stationary concept that best models the probability of
choosing one of two strategies in various non constant-sum games spanning a wide parameter
space. More specifically, even when restricting the degrees of freedom of the parametric models
and comparing the goodness of fit utilizing the same parameters \((\beta, \alpha, \lambda \text{ if any})\) for all six games,
the other-regarding QRE outperforms all of the other stationary concepts considered here. The
order, starting with the most successful with the goodness of fit decreasing progressively, is the
following (see the grey highlighted rows in Table 5): QRE+IA, IBE on the transformed games,
IBE+IA and Nash equilibrium.

Of course, the previous comparison is biased against the more parsimonious concepts, in particular
the parameter-free Nash equilibrium and IBE concepts (see footnote 1 regarding the latter). In order
to trade off the predictive parsimony of a theory against its descriptive power, one can employ
Selten’s Measure of Predictive Success (Selten, 1991). This is currently ongoing work.

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\(^3\) Note also that the QRE+IA mean of the MSD when cross-predicting is approximately equal to the mean score for the
‘pure’ IBE on all transformed games, further confirming the stability of the parameters in the other-regarding version
of QRE.

\(^4\) that sees it as the result of evolutionary (or learning) processes in a situation of frequently repeated play with two
populations of randomly matched opponents.
Part II. Evolutionary lessons from the Prisoner’s dilemma

The previous analysis has illustrated the importance of pro-social in explaining departures from the predictions originating from the Nash equilibrium concept. Such predictions, although often diverging from observed behavior, are still to be considered a fundamental benchmark to compare alternative ones with, and indeed perform quite well in competitive contexts. In highly competitive environments, especially in those characterized by a large pool of actors interacting in anonymous and/or single-shot contexts (for instance in financial markets), individual and aggregate behavior is likely to reflect a high degree of focus on the merely materialistic payoff. However, in many real life situations, the drivers of human behavior seem to be far more than the absolute return to an interaction. It has been pointed out by many scholars, that while it may be perfectly acceptable for agents to play the payoff-maximizing strategy and disregard other agents’ payoffs, it is not necessarily the case for environments in which social preferences play an important role, and payoff-maximizing behavior would lead to social stigma and guilt. An often quoted example suggesting that people’s decisions are driven by equity concerns (usually opposing individualistic motives), is that of charity donations, which reflect a tendency towards redistribution of wealth towards the worse-off.

Moreover, experiments have also shown that humans are willing to sacrifice part of their endowments in an effort to reduce disparities between individuals who earn substantially more than the average and those with an income which is substantially below the average. This in a context of random endowment distribution, which does away with punishment originating from behaviors perceived as unjust. That is, most subjects of the experiment invested substantial fractions of their endowment to make the richest less rich and the poorest less poor, even though the opponents just happened to be endowed with those amounts of money, independently of their strategies. Many other studies document departures from the self-interest hypothesis, see for example Gintis et al. (2003) for a review of recent experimental evidence in different classes of games.

In a forthcoming paper, Hoff et al. also show an impressive amount of observed spiteful behavior in a version of the 3-players ultimatum game experiment run in several remote Indian villages (so that the inhabitants of different villages wouldn’t recognize the names of their opponents from different villages. They carefully selected the sample so that individuals would either belong to a

very high caste or a very low one, and the matching technology was devised in such a way that anonymity would be guaranteed, yet players would indirectly extrapolate the caste to which the counterparty belonged. One neat conclusion the authors draw is that high caste individuals exhibit a substantial amount of anti-social behavior, in particular against low-caste subjects, often punishing the cooperating opponent to prove their strengths.

These results suggest that in many situations there is more to human behavior than just selfish behavior as implied by the best reply notion. While own payoff is an important component of one’s strategy, realistic “games of life” are played along other dimensions as well. One such dimension is captured by the Inequity Aversion parameters, which allow for altruistic considerations (α parameter of advantageous IA) as well as more traditional envy considerations by means of the β parameter. In the previous section, we have seen how already powerful stationary concepts such as IBE and QRE can be substantially improved in their ability to fit and predict frequencies of plays for six non-constant sum games spanning a wide parameter space, even when adjusting for the increased number of parameters with Selten’s technique.

In what follows, we will further explore the same question, namely whether social preferences play a tangible role in affecting individuals’ strategies of play, but from a different angle. Firstly, based on the above considerations, we will expand the preference space with respect to the standard IA specification given in (1), by relaxing the constraints on the parameters α and β. Secondly, we will focus on timing and spatial considerations, and in particular on whether cooperative behavior can be evolutionarily robust in relation to the structure of the population and to the level of information agents have on their counterparties. A recurring question that will come out throughout the analysis will be whether altruism has evolved in human beings by means of a process of cultural (or natural) selection. Before proceeding with the details of the modeling specification, a simple analytical result will be shown in order to bridge the previous stationary IA investigation with the current evolutionary approach.

---

6 Individuals were told the family name of the opponent, who would be from a very distant village. This piece of information allows individuals to know what caste does the opponent belong with a high degree of confidence, while preserving anonymity due to the distance between and small size of the villages.

The establishment of cooperation in well-mixed populations: a generalization of IA to other-regarding preferences allowing for pro-social as well as anti-social behavior

Based on the experimental evidence cited above, it seems reasonable to extend the standard inequality aversion model in (1) to more general domains accounting for strong altruism as well as spiteful behavior: in particular, we will consider in turn the implications of dropping the assumptions that Fehr and Schmidt impose on the parameters accounting for inequity aversion in their specification of agent’s utility functions, \( U_i = x_i - \alpha_i \max\{x_j - x_i, 0\} - \beta_i \max\{x_i - x_j, 0\} \).

\[ 0 \leq \beta_i \leq 1 \quad (\text{IA 1}) \]

Let’s first focus on the last term of (1), representing the positive deviations from the reference outcome \((x_j)\). Restricting the parameter space to values of \( \beta \) laying between zero and one means, on one hand \((0 \leq \beta_i)\), ruling out the existence of spiteful individuals who enjoy being better off than the opponent, and on the other hand \((\beta_i \leq 1)\) ruling out the existence of strongly altruistic subjects who care enough about the well being of the other player to incur in a decrease in utility which is greater than the payoff difference \((x_i - x_j)\). Both possibilities are coherent and some degree of similar pro- and anti-social behavior has been observed in the cited literature\(^8\), so excluding them \textit{ex ante} may bias the analysis against well documented behaviors that appear to have survived the evolutionary pressures shaping the evolution of human preferences.

\[ \beta_i \leq \alpha_i \quad (\text{IA 2}) \]

The second assumption that Fehr and Schmidt make on the parameters concerns the presumed loss aversion in social comparisons. When considered in conjunction with the ‘moderate aversion’ to advantageous inequality embodied in (IA 1), it seems in fact plausible to postulate that negative deviations from the reference outcome count more than positive ones (disadvantageous inequity induce higher disutility than advantageous inequity). However, when (IA 1) is dropped and agents are free to exhibit strongly altruistic and spiteful behavior, the assumption that \( \beta \) is at most as big as \( \alpha \) is no longer justified in all domains. To illustrate this point, let’s consider individual \( i \) whose preferences satisfy a slight modification of the above parameter restrictions that maintains the

---

\(^8\) See the references at the end for more literature on the subject.
asymmetric other regarding preferences of the familiar form\(^9\). That is, let the parameters modeling other-regarding (henceforth OR) behavior satisfy the following inequalities:

\[
0 \leq \alpha_i < \beta_i \leq 1 \quad \text{(OR 1)}
\]

Note that the above inequalities violate (IA 2) while satisfying (IA 2), still entailing that an agent responds with a utility loss to both negative and positive deviations from the reference outcome. The difference lies in \(\beta\) no longer being bounded upwards (allowing for strong altruism), and its magnitude (representing the altruistic disutility from advantageous inequality) now being greater than the disutility from disadvantageous inequality. I don’t see any particular reason why this case should be ruled out \(a\ priori\), instead of letting the evolutionary forces decide.

Another example of reasonable preferences that are ruled out in the standard IA model is given by

\[
\alpha_i < 0 < \beta_i \quad \text{(OR 2)}
\]

Loosely speaking, the intuition is that an agent whose preference parameters satisfy the inequalities in (OR 2) simply cares more about the counterparty than about herself\(^10\), a possibility which may well apply to the truly altruistic agents.

Consider a game which sets the harshest conditions for the emergence and survival of cooperation, the Prisoner Dilemma (PD). The following formulation (subset of all PDs) will be employed,

\[
\begin{array}{c|cc}
\text{C} & \text{D} \\
\hline
\text{C} & b-c & -c \\
\text{D} & b & 0 \\
\end{array}
\]

Where \(b\) and \(c\) are, respectively, the benefits and costs to the cooperative effort (e.g. the gains and losses occurring when undertaking contribution to a public good). In a population of size \(N\) and

---

\(^9\) The ‘conditional altruism’ inherent in the inequity aversion framework is preserved so long as \(\alpha\) and \(\beta\) are non-negative, implying that both positive and negative deviations from the opponent’s outcome induce a utility loss.

\(^{10}\) as for a given absolute deviation between the two payoffs, she will incur a bigger utility reduction when being the one with the higher payoff.
consisting of \(i\) cooperators (and \(N-i\) defectors), the payoff to the cooperators and defectors is given, respectively, by:

\[
U_c(b, c, i, N) = \frac{i-1}{N-1} b - c \quad (3)
\]

\[
U_d(b, i, N) = \frac{i}{N-1} b \quad (4)
\]

In terms of the average payoff in the population,

\[
\bar{U}(b, c, i, N) = \frac{i}{N} (b - c) \quad (5)
\]

It is well known that, without any mechanism for the evolution of cooperation, natural selection will favor defectors, since (in a mixed population) they have a higher payoff than cooperators. Interpreting payoffs as fitness, the selection process will eventually drive the frequency of the cooperators (and the average fitness of the population) to zero, implying the extinction of cooperators, and the socially undesirable all-defect 0-outcome reminiscent of the one-shot PD game with self-interested agents.

Now consider modifying the payoff matrix to allow for other-regarding behavior, one gets:

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>(b - c)</td>
<td>(-c - \alpha(b + c))</td>
</tr>
<tr>
<td>D</td>
<td>(b - \beta(b + c))</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 7: row player’s reproductive success in the PD game with OR

Note that there is no ambiguity with respect to the direction of the IA, as off the main diagonal the cooperator is exploited and will have no advantageous inequity aversion (\(\beta=0\)), while the defector free rides the benefit \(b\) without paying the cost \(c\), and will have no disadvantageous inequity aversion (\(\alpha=0\))\(^{11}\). Along the main diagonal, the payoffs aren’t affected by the IA adjustment, as the players get the same materialistic payoff due to the symmetry of the game.

\(^{11}\) See Table 1 for the general payoff matrix under inequity aversion.
Evolutionary escape from the prisoner’s dilemma: theoretical findings

In the PD the only dominant strategy is to Defect, so cooperation in Table 6 will be never achieved, and is by no means evolutionarily stable. If one considers the modified matrix in Table 7, though, one can easily see show that the Cooperate strategy will be ESS provided that the advantageous IA parameter $\beta$ is greater than the ratio of the cost to the sum of the benefit and cost. This follows from the condition for the cooperative strategy to be ESS, which is simply that the sum of a player’s payoffs when cooperating must be greater than the sum of her payoffs when defecting: in the setting described in table (2), this yields precisely the condition

$$\beta > \frac{c}{b + c} \quad (6)$$

Note that (6) doesn’t require a value of $\beta$ greater than 1, i.e. it’s consistent with both the standard IA and the augmented parameter space OR specifications (although allowing for strong altruism reduces the dependency of the result on the small magnitude of the relative cost).

**Proposition 1 (sufficient condition for ESS cooperation)**

So long as the parameter capturing aversion to inequality in one’s own favor is greater than the relative cost of the altruistic act (cooperating), an infinitely large population of cooperators cannot be invaded under deterministic selection dynamics.

By rearranging terms in (6), the condition can be expressed in terms of the benefit-to-cost ratio, as:

$$\frac{b}{c} > \frac{1}{\beta} - 1 \quad (7)$$

This formulation better allows to see the dependency of the evolutionary stability result for cooperation on the magnitude of $\beta$: on one side of the spectrum, we have the complete self-interest case ($\beta = 0$) where no matter how big the rewards to cooperation are, the cooperative strategy will never be ESS; on the opposite side of the spectrum, we have the case of maximal advantageous inequity aversion ($\beta = 1$) where, so long as the benefits are greater than the costs to cooperation,
cooperation will always be an evolutionarily stable strategy and will be immune from defectors invasions.

Such results fits in well with (Nowak, 2006), where rules for the success of cooperation in the standard PD game are derived in terms of the payoffs and of other characteristics which can compensate for the payoff reduction arising from cooperating in a competitive environment (under sole natural selection forces), and establish cooperation. These mechanisms, namely kin selection, direct reciprocity, indirect reciprocity, network reciprocity and group selection, are shown to suffice for the evolution of cooperation whenever the benefit-to-cost ratio exceeds a certain mechanism-specific threshold. Modified payoff matrices qualitatively similar to the one in Table 2 are derived (more on it will follow in the next section) and conditions are given for the cooperative strategy to be ESS (as well as risk dominant\textsuperscript{12}, in what follows RD). For example, in the group selection case, the threshold is \( \frac{b}{c} > \frac{n}{m} + 1 \), and the characteristics added to the basic environment to find an evolutionary escape from the prisoner’s dilemma are the maximum group size \( n \) and the number of groups \( m \). That is to say, the smaller and the more groups there are, the better the chances for cooperation to strive.

Our previous finding also poses conditions for the survival of cooperation, only in terms of how agents’ preferences rather than in terms of the surrounding environmental characteristics, such as groups structure (or genetic relatedness, or probability of encountering the same player in a subsequent round). As we will see from the analysis below, however, inequity averse preferences alone cannot render cooperation a risk dominant strategy, unless one is willing to drop the assumption that \( \beta \) cannot exceed \( \alpha \). This can arise in many meaningful preference specifications that generalize the IA framework to allow for a greater variety of responses to positive and negative deviation from the reference outcome.

\textsuperscript{12} In standard game theory a Nash equilibrium is considered risk dominant if it has the largest basin of attraction, meaning the more uncertainty a player has about the actions of the other player, the more likely the risk dominant strategy will be chosen. Evolutionary models such as Mailath & Rob (1993) and Young (1993) support the idea that the risk dominant equilibrium is favored by evolution, by showing that if the rule to update one’s strategy allows for mutations that asymptotically reach zero over time, the likelihood that the risk dominant equilibrium is reached goes to one (even if it is payoff dominated).
Recent contributions, such as Bolle (2000) and Possajennikov (2000), have drawn the attention on the parameter space concerning the degree of altruism and spite one should allow for when modeling the evolutionary stability of other-regarding preferences. In particular, they have independently criticized and relaxed restrictions that Bester and Guth (1998) had imposed on the parameters. Given the resonance with IA preferences employed here, it is worth briefly introduce some notation from Bester and Guth (BG henceforth). Two agents play a symmetric game and are assumed to maximize a weighted sum of the own payoff and of the counterparty’s payoff, in order to allow for the possibility that individuals have other-regarding preferences that go beyond their material payoffs. Formally,

\[ V_i = U_i(x, y) + \alpha U_j(x, y), \quad i \neq j \quad (8) \]

where \( U_i(x, y) \) is the material payoff to player \( i \), while \( \alpha \) and \( \beta \) are preference parameters (subject to evolutionary selection), which are positive under altruism, zero under own profit maximization and negative under spite. As Bolle and Possajennikov show (respectively in the domains of spiteful and altruistic preferences), the preference restrictions imposed by BG, namely of ruling out spite and what I will call ‘strong altruism’, aren’t theoretically justified and should be relaxed. More specifically, BG assume \( 0 \leq \alpha \leq 1 \) and \( 0 \leq \beta \leq 1 \) and Bolle and Possajennikov separately show that arbitrarily large negative and positive values of the two parameters should be allowed, in order to let the evolutionary pressures ultimately decide whether spite and strong altruism should be ruled out. We will evaluate the importance of these parameter restrictions throughout the remainder of Part II; but first, let’s reconsider the sufficient for cooperation to be ESS:

**Lemma 1**

Even in the absence of structural mechanisms favoring the evolution of cooperation, such as reciprocity (of direct, indirect or network type), non-individual selection (of kin and group kind) or cognitive limits (leading to heuristics such as “imitate the successful behavior” in structured populations), Proposition (1) continues to hold. Therefore, if favorable historical conditions (such as repeated interactions in small groups) have allowed the establishment of cooperation, when other-regarding preferences are allowed and the benefit-to-cost ratio exceeds the \( \frac{1}{\beta} - 1 \) threshold, cooperation cannot be displaced.
Note that the results in Proposition 1 and Lemma 1 follow directly from the general property that a strategy that yields a strict symmetric Nash equilibrium\(^{13}\) is evolutionary stable as well: therefore, when investigating these types of games, in order to assess the evolutionary stability of a strategy, all one needs to show is the existence of the corresponding unique Nash equilibrium.

It should be noted at this point, that although an ESS strategy is resistant against invasion, the relative size of the basin of attraction is what ultimately decides the amount of time spent in the long run in each equilibrium when both are ESS, which is the non-degenerate case we will focus most of the attention on (and depends on the size of \(\beta\) relative to the percentage cost). To argue that, let alone the possibility that historical conditions may have led to the establishment of evolutionarily stable cooperation, cooperators can (under certain conditions) invade a mixed population, we will introduce two more results, followed by some numerical examples aimed at clarifying the propositions.

First, let’s bear in mind that cooperation will be a risk-dominant strategy if there exist values of \(\alpha\) and \(\beta\) for which the sum of a player’s payoffs when cooperating is greater than the sum of her payoffs when defecting. Moreover, cooperation will be advantageous if there exist values of \(\alpha\) and \(\beta\) for which the sum of the payoff to reciprocal cooperation and twice the payoff to cooperating when the opponent defects is greater than the sum of the payoff to defecting when the opponent cooperates and twice the payoff to mutual defection. The last condition plays an important role in determining the fixation probability of cooperation in stochastic game dynamics with finite populations\(^{14}\).

In terms of the payoffs in Table 6, these conditions translate to:

- \(C\) is risk-dominant if \(b - 2c > b\)
- \(C\) is advantageous if \(b - 3c > b\)

Which are obviously never satisfied. Nevertheless, if we again consider subjective utility functions that take also in account the relative standing of one’s payoff with respect to the other player’s, cooperation can be not only risk-dominant, but also advantageous, therefore having a basin of attraction greater than \(\frac{2}{3}\). The following two inequalities, which are obtained simply by applying the

\(^{13}\) For which the agents’ best responses are unique, as is the case for the cooperative strategy in the modified PD game when the threshold is met.

\(^{14}\) See Nowak et al. (2004) for a clear explanation of the implications of being advantageous for a strategy, in terms of the probability that a single mutant originating from it (and its successors) will replace a homogeneous population initially following the other strategy. An advantageous strategy will overtake the ‘hostile’ population with a probability greater than the inverse of its size, therefore fixating with greater probability than the random drift.
conditions for risk-dominance and advantageousness to Table 7, are the basis for the paired propositions aimed at summarizing the findings.

\[(\alpha - \beta) < -2 \frac{c}{b + c} \quad (9)\]

**Proposition 2 (sufficient condition for risk-dominant cooperation)**

So long as the difference between the disadvantageous deviation and the advantageous deviation preference parameters is sufficiently negative (more than twice as negative as the relative cost of the altruistic act), cooperation will risk-dominate defection. Namely, when both strategies are ESS, the basin of attraction of cooperators is greater than \(\frac{1}{2}\).

\[(2\alpha - \beta) < -3 \frac{c}{b + c} \quad (10)\]

**Proposition 3 (sufficient condition for advantageous cooperation)**

So long as the difference between the disadvantageous deviation and the advantageous deviation preference parameters is sufficiently negative (more than three times as negative as the relative cost of the altruistic act), cooperation will be advantageous. Namely, when both strategies are ESS, the basin of attraction of cooperators is greater than \(\frac{1}{3}\).

Note that both conditions (9) and (10) are satisfied so long as \(\alpha \ll \beta\). This amounts to say that whether a cooperator can invade or not a population of defectors boils down to a comparison of the sign and magnitude of the parameters modeling agents’ responses to deviations from the reference outcome. If positive deviations (making more than the other player) are sufficiently more important than negative ones (being worse-off than the opponent), a single cooperator will have a fixation probability that is greater than the inverse of the (finite) population size\(^{15}\). As a last remark on the above propositions, it should be noted that inequalities (6), (9) and (10), corresponding, respectively, to the sufficient conditions for ESS, risk-dominant and advantageous cooperation, are completely characterized in terms of the payoffs of the prisoner’s dilemma game.

\(^{15}\) In the limit of weak selection. Roughly put, this condition means that in a multilevel selection environment, selection between groups (which favors cooperators) is much weaker than selection within groups (which favors defectors). See the section on multilevel selection below.
Evolutionary escape from the prisoner’s dilemma: examples of OR preferences

To better grasp the significance of the other regarding preferences and in order to have a tangible representation of their impact on the achievement and robustness of the mutual cooperation outcome, let’s focus on a numerical version of Table 6; consider the following matrix, given by \( b=5 \) and \( c=1 \):

<table>
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<th></th>
<th>( C )</th>
<th>( D )</th>
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<tbody>
<tr>
<td>( C )</td>
<td>4</td>
<td>-1</td>
</tr>
<tr>
<td>( D )</td>
<td>5</td>
<td>0</td>
</tr>
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</table>

Again, the only dominant strategy is Defect and the Nash equilibrium is \((D,D)\), yielding the inefficient output \((0,0)\). If we introduce the transformed matrix to account for other-regarding preferences, we get:

<table>
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<th></th>
<th>( C )</th>
<th>( D )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( C )</td>
<td>4</td>
<td>(-1 - 6\alpha)</td>
</tr>
<tr>
<td>( D )</td>
<td>(5 - 6\beta)</td>
<td>0</td>
</tr>
</tbody>
</table>

The above specification guarantees that \((C,C)\) is an evolutionarily stable strategy if \( \beta > \frac{1}{6} \). To get an idea of the magnitude of the parameter modeling reactions to positive deviations from the reference outcome, note that in the games investigated in Part 1\(^{16}\), the value of \( \beta \) that best fits all six games is approximately .16 and .15 in the IBE+IA and QRE+IA models respectively, which almost coincides with the \( \frac{1}{6} \) threshold (=.16).

Let’s consider, in turn, different values of \( \alpha \) and \( \beta \) and check what the result will be in terms of the evolutionary fate of cooperation. First, assume agents exhibit identical ‘purely altruistic’ preferences (hereafter PA) with symmetrical reactions to positive and negative departures from the opponent’s outcome given by:

\[ 16 \text{ which were not PD games but rather non-constant sum games spanning a wide parameter space (but including an almost symmetric one, game 12, in terms of the observed frequencies and equilibrium predictions) } \]
An individual with such preferences is a (symmetrical) pure altruist in the sense that she responds to uneven distributions with an (equal magnitude) utility gain or loss when, respectively, her opponent is better-off or worse-off. That is, not only she displays altruistic behavior in the domain of positive deviations from the other player’s outcome (by incurring a utility loss due to the empathy for the other player’s underperformance), but she also responds altruistically in the domain of negative divergences (by experiencing a utility gain associated with the other player outperforming her).

While such a strong form of altruism is admittedly uncommon, it is still insightful to consider the consequences of PA preferences for the evolution of cooperation; moreover, a less demanding case will be subsequently considered.

For the sake of concreteness, consider the following parameter values: \( \alpha = -0.2 \) and \( \beta = +0.2 \) and notice that they satisfy (symmetric PA). Now Table 9 becomes:

**Example 1 - PD subjective payoffs for the row player when \( b = 5, c = 1 \) and PA: \( \alpha = -0.2, \beta = +0.2 > \frac{1}{6} \)**

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<tbody>
<tr>
<td>C</td>
<td>4</td>
<td>0.2</td>
</tr>
<tr>
<td>D</td>
<td>3.8</td>
<td>0</td>
</tr>
</tbody>
</table>

We already know that cooperation is an ESS, since \( \beta \) is larger than the threshold; moreover, defection is not an ESS, as \( 0.2 > 0 \). In fact, one can verify that conditions (9) and (10) are satisfied, implying that cooperation is advantageous for the given parameter values.

Now assume agents still exhibit identical ‘purely altruistic’ preferences, but with asymmetrical reactions to positive and negative departures from the opponent’s outcome\(^\text{17}\), as given by:

\[
\begin{cases}
\alpha < 0 \\
\beta > 0 \\
|\alpha| < |\beta|
\end{cases} \quad \text{(asymmetric PA)}
\]

\(^\text{17}\) To limit the size of the exposition, we will only focus on the \( |\alpha| < |\beta| \) case, although its complementary also lends itself to meaningful interpretations: when, for example, \( \alpha = -0.2 \) and \( \beta = +0.1 \), the resulting game no longer has one symmetric NE, but becomes an anti-coordination game of the Hawk-Dove type, in which it is mutually beneficial for the players to play different strategies, and the two asymmetric Nash equilibria obtain.
An individual with such preferences is an asymmetrical pure altruist in the sense that she responds to uneven distributions with a utility gain or loss of unequal magnitude, depending on whether her opponent is better-off or worse-off. In particular, the above specification implies that the utility gain from the other player’s superior performance is less than the utility loss due to the empathy for the other player’s underperformance. Let $\alpha = -0.1$ and $\beta = +0.2$, leading to:

**Example 2- PD subjective payoffs for the row player when $b = 5, c = 1$ and PA: $\alpha = -0.1, \beta = +0.2 > \frac{1}{6}$**

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<tbody>
<tr>
<td>C</td>
<td>4</td>
<td>-0.4</td>
</tr>
<tr>
<td>D</td>
<td>3.8</td>
<td>0</td>
</tr>
</tbody>
</table>

Now both strategies are ESSs, and we have two symmetric Nash equilibria (unlike in the preceding example where only the mutually cooperative equilibrium was evolutionarily stable). Furthermore, under these OR preference parameters, cooperation is no longer risk-dominant, i.e. defect is the strategy with the largest basin of attraction.

Lastly, consider the case of agents that exhibit identical ‘conditionally altruistic’ preferences, which are given by:

$$
\begin{align*}
\alpha > 0 \\
\beta > 0 \\
\alpha < \beta
\end{align*}
$$

(asymmetric CA)

One such agent reacts with a disutility to both positive and negative deviations from the reference outcome (as in standard IA preferences), displaying asymmetric behavior in the form of envy when being outperformed, and altruistic aversion to advantageous inequality. The last inequality implies that positive deviations from the opponent’s outcome matter more than negative ones. Letting $\alpha = +0.1$ and $\beta = +0.5$, leads to:

**Example 3- PD subjective payoffs for the row player when $b = 5, c = 1$ and CA: $\alpha = +0.1, \beta = +0.5 > \frac{1}{6}$**

<table>
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<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>4</td>
<td>-1.6</td>
</tr>
<tr>
<td>D</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

For this parameterization, we again have the case of two evolutionarily stable strategies and two strict Nash equilibria; what changes with respect to Example 2 is that now cooperation is risk-
dominant, and therefore has a larger basin of attraction. It nevertheless fails to pass the test for advantageousness given by (10), signifying that its basin of attraction (while being larger than that of the defect strategy) is not sufficiently large to guarantee that the lineage originating from a single mutant of the cooperative strategy will prevail over a population of defectors.

Related literature on the evolution of preferences: can altruism survive when preferences are not fully observable?

Of course the sensitivity of the above results on the degree of pro-social behavior (here synthesized by $\beta$) calls for an evolutionary investigation of the latter. To some extent, this has been addressed in the literature (see, for the complete information scenario, Bester and Güth, 1998 and Güth and Napel, 2006), who show that, under certain conditions, the most debated being the transparency of individual preferences resulting from the common knowledge assumption, strategies based on materialistic as well as non-materialistic payoffs such as IA can successfully evolve and stabilize under pairwise random matching in infinitely large populations. The limitations of the perfect observability of preferences have recently been explored by Ok and Vega-Redondo (2001) and Dekel et al. (2007), and some alternatives have come forward in order to allow for imperfect inference of preferences. Both papers agree on the conclusion that, in the complete lack of information on other players’ preferences, Nash materialistic-only solutions will be restored. However, in both cases important qualifications must be made.\(^{18}\)

In Ok, Vega-Redondo, the stress is posited on the conditions affecting the degree of knowledge about the opponents’ preferences, which in their model are context-dependent, since the population and group sizes determine the level of “effective uncertainty” faced by the agents, so that when preference unobservability doesn’t induce sizeable uncertainty (e.g. the size of the population is small), incomplete information is not enough to ensure the stability of individualistic preferences. In other words, with little *de facto* uncertainty, although unobservable, individualistic agents need not prosper at the expense of the altruists.

\(^{18}\) One debatable characteristic that both papers share is the assumption that the aggregate play in the population corresponds to a Bayesian-Nash equilibrium: this requires an incredible amount of computational ability on the part of rational agents, especially when one’s opponents are allowed to be a multiplicity (as in Ok and Vega-Redondo). In fact, in a Bayesian game, a strategy for a player is a complete plan of actions that covers every contingency that might arise for every type that player might be. A strategy must not only specify the actions of the player given the type that he is, but must specify the actions that he would take if he were of another type.
In Dekel et al., the graduated levels of preference observability are explicitly considered (rather than emerging indirectly as a result of the informational content of the number of subgroups in the population) and are treated as exogenous in order to analyze the consequences for stability of various degrees of observability. Namely, the parameter \( p \) captures the amount of knowledge that an agent has on her opponent (the probability of observing her preferences) independently of what the opponent observes, as is the case, say for a poker game with private information on the cards and different bluffing abilities\(^{19}\). While the general conclusions they draw support Nash equilibrium in the context of the evolution of preferences when \( p=0 \) (the case of complete lack of information on the opponent), these conclusions don’t readily carry over to the cases of intermediate observability and, of course, to the opposite degenerate case of complete (payoff and preference) information, where the stability of altruism is recovered and the efficient payoff achieved. An important remark with respect the scope of the present analysis, concerns the authors’ findings regarding PD games, that “inefficient strict equilibria (i.e. Defect-Defect) may fail to be stable with any arbitrarily small degree of observability (despite being stable with no observability)”. In fact, they show that the only other stable distribution obtains for \( p=1 \), and is characterized by a monomorphic population\(^{20} \) where all individuals are ‘unexploitable’ conditional cooperators, who will only cooperate if the opponent cooperates with probability one. Such a preference turns out to be evolutionarily stable as, loosely speaking, those who possess it are exempt from the typical exploitation from defectors or from cooperators who will cooperate on fewer occasions, this last situation being ruled out by the degenerate value of \( p=1 \).

To summarize, the lesson to be drawn from the recent literature on the evolution of preferences is that, unlike in the traditional biological and evolutionary game theoretic models, in which genetically programmed behavior is the mold on which evolution operates, when it comes to the evolution of human preferences in complex adaptive systems, it seems unlikely that an inherited behavioral package guides agents in all the decisions to be made throughout life. It may instead well be the case that preferences are context-dependent and a different answer might apply depending on the specifics of the interactions that are considered. That is to say, certain environments will favor altruistic behavior, while others will favor individualism. In particular, factors that augment the observability of types, such as the presence of relatively large subgroups in Ok and Vega-Redondo (implying a small effective matching uncertainty) or the ability to detect the opponent’s intentions

\(^{19}\) Note that this specification doesn’t suit well in situations where opponents’ reciprocal information is highly correlated. For example, to further expand the gaming analogy, in community card poker games such as Texas hold’em, one player’s information on an opponent is not independent of the opponent’s knowledge.

\(^{20}\) A monomorphic population is one where all individuals have identical preferences
in Dekel et al. (which, for example, is likely to be greater in societies where agents frequently engage in face-to-face interactions), can suffice to immunize altruism against egoistic mutants.

Hence, in contexts where preferences are, to some degree at least, observable, the match between evolution of preferences and standard evolutionary models is likely to dissolve, leaving room for successful pro-social behavior.

To sum up, even from the three stylized cases considered above, one can already draw meaningful lessons about other-regarding behavior in the prisoner’s dilemma. Namely, the above examples shed light on the importance of the context in determining whether cooperation will spread and whether it will be stable once it has established itself in a large population. The answer to the latter question is yes (given the choice of \( \beta \)), but, when it comes to the former, we get mixed results. The most favorable one for altruism obtains in Example 1, where cooperation is not only risk-dominant, but also advantageous (and Defect is not an ESS). Such a neat conclusion supporting the evolutionary success of cooperation is not achieved in Example 2, in which both strategies are ESS, but Defect has a larger basin of attraction. Finally, Example 3 gives us an opportunity to observe a mixed bag result: again both strategies are ESS and two symmetric pure Nash equilibria arise, as was the case for the previous example. In comparison to the latter, however, cooperation now has the larger basin of attraction (but not sufficiently large to be advantageous).

**Spatial considerations in the prisoner’s dilemma**

One alternative way to model the (experimentally observed) tendency to cooperation is, as mentioned above, to allow for spatial considerations such as those arising when imposing structure on the population, i.e. via group formation and splitting. Before turning to these considerations, we’ll extend the preceding analysis by investigating the evolutionary implications of other-regarding preferences that are slightly more complicated than the above linear IA ones. Recall the linear IA specification

\[
U_i(\alpha_i, \beta_i, x_i, x_j) = x_i - \alpha_i \max\{x_j - x_i, 0\} - \beta_i \max\{x_i - x_j, 0\}, \quad i \neq j; \beta_i \leq \alpha_i; \quad 0 \leq \beta_i \leq 1.
\]

In the non-linear specifications agents’ preferences again contain terms representing two-sided inequality aversion, in order to represent the taste for equitable material payoffs. More specifically, to be consistent with the indirect evolutionary analysis performed by [Guth, Napel] and in order to make comparisons with their results, let’s consider two alternative quadratic IA preferences, for
both of which an agent always suffers from unequal material payoffs no matter who is
disadvantaged:

\[ U_i(y_i, x_i, x_j) = x_i - y_i \sqrt{|x_i - x_j|} \quad \text{(DMD)} \]

\[ U_i(y_i, x_i, x_j) = x_i - \frac{y_i}{4} |x_i - x_j|^2 \quad \text{(IMD)} \]

Note that the gamma specification, in terms of the standard IA parameters (\( \alpha \) and \( \beta \)), imposes the
following constraint: \( \alpha_i = \beta_i = \gamma_i \geq 0 \)
In other words, individual \( i \) has a non-negative aversion of the same magnitude with respect to
disadvantageous as well advantageous inequality. While this assumption may seem strong, it has
been utilized in the cited literature, and, it is backed to some extent from the analysis performed in
SECION A on the 6 non-constant sum games. In fact, the results for the best overall fitting
parameters in the two hybrid games are as follows:
IBE+IA: \( \alpha = .160 \quad \beta = .157 \)
QRE+IA \( \alpha = .243 \quad \beta = .147 \)
Suggesting a strong relevance of the advantageous inequity aversion sentiments, especially when
modeling the equilibrium decisions with the IB concept, for which the value of \( \alpha \) is remarkably
close to the value of \( \beta \).
For the sake of concreteness, let’s assume also \( \gamma_i = \gamma_j \) and let’s repeat the evolutionary stability
analysis for the new utility functions, by resorting to the modified payoff matrices:

**Table 10: subjective PD payoffs for row player, accounting for non-linear inequity aversion with decreasing marginal damage (DMD)**

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<tbody>
<tr>
<td>C</td>
<td>( b - c )</td>
<td>(-c - \gamma \sqrt{b + c} )</td>
</tr>
<tr>
<td>D</td>
<td>( b - \gamma \sqrt{b + c} )</td>
<td>0</td>
</tr>
</tbody>
</table>

**Table 11: subjective PD payoffs for row player, accounting for non-linear inequity aversion with increasing marginal damage (IMD)**

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<tbody>
<tr>
<td>C</td>
<td>( b - c )</td>
<td>(-c - \frac{\gamma}{4} (b + c)^2 )</td>
</tr>
<tr>
<td>D</td>
<td>( b - \frac{\gamma}{4} (b + c)^2 )</td>
<td>0</td>
</tr>
</tbody>
</table>
Using the same conditions for ESS and risk dominance, we can check whether the non-linear specification can rationalize cooperation in the PD game. As before, cooperation will be ESS under conditions that can be interpreted in terms of the magnitude of the preference parameter relative to the game payoffs. Namely, the following two are the sufficient conditions for cooperation to be evolutionarily stable, under decreasing marginal damage IA and increasing marginal damage IA respectively:

\[ \gamma > \frac{c}{\sqrt{b+c}} \quad (11) \]

\[ \gamma > \frac{4c}{(b+c)^2} \quad (12) \]

Cooperators, however, will never be risk-dominant (for positive cost of the altruistic action), as there is no value of \( \gamma \) for which the sum of a player’s payoffs when cooperating is greater than the sum of her payoffs when defecting. This is due to the symmetrical structure of the utility loss, which, unlike in the IA and its OR generalization considered above, is assumed by utilizing one parameter only (\( \gamma \)). Such assumption rules out the \( \beta \gg \alpha \) possibility which is the driver behind conditions (9) and (10), which can only be satisfied when negative deviations from the reference outcome have a different impact than positive ones (as frequently observed in the empirical literature).

**Structured populations**

To shed light on the determinants of altruistic behavior, we introduce structure in the population. Several authors have discussed the implications of allowing for population clusters to play a role in determining the evolution of norms. For example, Boyd and Richerson (2002), BR in what follows, utilize a replicator dynamics model of imitation taking place in isolated population to show that “group beneficial norms can spread rapidly under plausible conditions”.

More specifically, by utilizing replicator equations on a structured population, they model the situation where most encounters take place with group members, but “payoffs are determined by the composition of the local group, but cultural traits can diffuse among groups…partially isolated groups can be stabilized at different equilibria with different average payoffs.” Consequently, behaviors can rapidly spread from high payoff groups to neighboring low payoff ones, provided the
rate at which imitation among individuals take place is sufficiently high. This feature is the driver of the faster time-scale of the norm spread achieved in BR, which sets apart their model from those based on group extinction (or splitting, Nowak).

This approach overcomes some limitations inherent in the majority of the pre-existing literature, identified by the authors with respect to the broad category of group selection considered.

For the within-group models of equilibrium selection in the spirit of [Kandori et al., 1993], which focus on the within-group effects of random processes on the frequencies of play of different strategies, they highlight a shortcoming which holds for finite but large populations. That is, if mutation rates are small, as is generally assumed in the literature, the stable equilibrium that survives the evolutionary process will be the one with the largest basin of attraction, and not (necessarily) the group beneficial trait.

For the between groups models, characterized by competition between groups on alternative stable equilibrium, the time required to transition from one equilibrium to another (possibly more beneficial) is on a time-scale of a millennium, making these models well suited to explain historical transitions to group beneficial behavior, but not diffusion of a number of social institutions from one society to another, which may well take place on much shorter time-scales.

The crucial assumption behind BR is that successful strategies are imitated by neighboring groups, even if these strategies will lower imitators’ payoffs in their own group (where different social norms are implemented). This assumption is the mechanism that drives the diffusion of the group beneficial trait, as it provides the basis for the escape from the “segregation” outcome, namely that imitation only takes place within isolated groups.

**Multilevel selection: historical justifications for the evolution of cooperation**

If we are satisfied with this historical account of the establishment of altruistic behavior via group selection, we are guaranteed that cooperation will not be wiped out by the insurgenge of defecting free-riders even in the absence of group selection today, as long as the gains and losses implicit in the environment (b,c) and the other-regarding preferences (β) satisfy (6). This is important, as in a modern society interactions among agents have shifted towards the anonymous single-shot type (for instance due to the customary use of the internet as a mediator for transactions between anonymous partners parties in an increasingly global arena). One might argue that in a world characterized by impersonal interactions, the conditions that allowed altruistic groups to prevail are no longer in
place, and consequently groups of cooperators will not be able to sustain themselves due to the increased cost of credibly signaling one’s adherence to the cooperative norm.

Following Nowak (2006), one can classify the mechanisms by which cooperation can evolve according to five broad categories: kin selection (the inclination of related individuals to engage in cooperative behavior), direct reciprocity (the “I will scratch your back if you scratch mine” attitude towards reciprocating), indirect reciprocity (I will scratch your back because someone else scratched mine), network reciprocity (spatial structure is assumed to allow for unevenly mixed populations where some individuals interact more frequently than others) and multilevel selection (where the population is divided into groups whose members are allowed to enact different strategies depending on whether they are matched with own-group members or with members of other groups).

In the present work we will adopt the latter mechanism to study the evolution of cooperation, and we will focus on a rather simple formulation of multilevel (or group) selection, which is suitable to analytical investigation and nevertheless captures the basic idea that selection acts not only at the individual level (via frequency-dependent selection), but also affects differentially different groups at the higher spatial level (via constant selection arising from group splitting occurring when groups reach the maximum size due to the addition of offsprings). That is, it seems reasonable to presume that different groups will spread at different rates; in the simplest form of multilevel selection, assume that cooperator groups (only cooperating among each other by paying a cost $c$ for each other member of the group to receive a benefit $b$) and defector groups (never cooperating with anyone and therefore incurring neither costs nor benefits) can develop and also be subject to selection pressures leading to a higher rate of splitting for successful groups. This is modeled by matching every group birth with the extinction of a randomly selected group. Arguably they will evolve at different paces, and it may well be that a group of cooperators fares better than a group of defectors.

For the sake of concreteness, we will continue to focus on the prisoner’s dilemma, because of its resistance to the cooperative equilibrium. In this environment, the population updating of strategies takes place asynchronously, meaning that at any period a single individual is selected for reproduction. These payoffs describe the commonly assumed non-dynamical interactions taking place at the group level, namely that groups split at rates that are proportional to the average fitness of individuals in that group. When a group splits (with probability $p$), a randomly selected group is taken out in order to maintain the population constant. For small $p$, the fixation probability of a
single cooperator in the entire population is given by the fixation probability of a single cooperator in a group times the fixation probability of that group.

Utilizing the findings from Nowak (2006) and Langer et al. (2008), and recalling the PD formulation in table (1), one can shift attention to a payoff matrix which accounts for both levels of selection (individual and at the group level). First note that, since cooperator groups have a constant payoff $b - c$, while defector groups have a constant payoff 0, one can think of the between-group selection in terms of a payoff matrix as well, as if the groups were playing the following game:

**Table 12: between group selection**

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>$b - c$</td>
<td>$b - c$</td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Let $m$ and $n$ be the maximum group size and the maximum number of groups respectively. Nowak shows that the payoffs corresponding to the overall dynamics (stemming from the frequency-dependent selection at the individual level and from the constant selection at the group level), can be aggregated by simply adding the two matrices multiplied by their respective population sizes. This yields a unified payoff matrix whose payoffs summarize all the relevant information,

**Table 13: combined matrix accounting for within and between selection**

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>$(b - c)(n + m)$</td>
<td>$bm - c(m + n)$</td>
</tr>
<tr>
<td>D</td>
<td>$bn$</td>
<td>0</td>
</tr>
</tbody>
</table>

The rationale behind this way of aggregating payoffs is as follows: for fixation of a new strategy in a homogeneous population using the other strategy, first the game dynamics within one group (of size $n$) have to be won and then the game dynamics between $m$ groups have to be won. For weak selection and large $m$ and $n$, the overall fixation probability is the same as the fixation probability in the single game using the combined matrix in table (13) and population size, $mn$. The stochastic process on two levels can be studied by a standard replicator equation using the combined matrix (and is work currently in progress).
References


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*PNAS* vol.105, no.7


Appendix A: Games utilized in Selten & Chmura; in this paper only games 7 to 12 (non-constant sum games) are investigated.

<table>
<thead>
<tr>
<th>Constant Sum Games</th>
<th>Non-Constant Sum Games</th>
</tr>
</thead>
<tbody>
<tr>
<td>Game 1</td>
<td>Game 7</td>
</tr>
<tr>
<td><img src="#" alt="Game 1 Matrix" /></td>
<td><img src="#" alt="Game 7 Matrix" /></td>
</tr>
<tr>
<td>Game 2</td>
<td>Game 8</td>
</tr>
<tr>
<td><img src="#" alt="Game 2 Matrix" /></td>
<td><img src="#" alt="Game 8 Matrix" /></td>
</tr>
<tr>
<td>Game 3</td>
<td>Game 9</td>
</tr>
<tr>
<td><img src="#" alt="Game 3 Matrix" /></td>
<td><img src="#" alt="Game 9 Matrix" /></td>
</tr>
<tr>
<td>Game 4</td>
<td>Game 10</td>
</tr>
<tr>
<td><img src="#" alt="Game 4 Matrix" /></td>
<td><img src="#" alt="Game 10 Matrix" /></td>
</tr>
<tr>
<td>Game 5</td>
<td>Game 11</td>
</tr>
<tr>
<td><img src="#" alt="Game 5 Matrix" /></td>
<td><img src="#" alt="Game 11 Matrix" /></td>
</tr>
<tr>
<td>Game 6</td>
<td>Game 12</td>
</tr>
<tr>
<td><img src="#" alt="Game 6 Matrix" /></td>
<td><img src="#" alt="Game 12 Matrix" /></td>
</tr>
</tbody>
</table>

L: left  R: right
U: up    D: down

Player 1’s payoff is shown in the upper left corner.
Player 2’s payoff is shown in the lower right corner.