Primer on Evolutionary Game Theory

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1 Evolutionary Game Theory

1.1 Why Study Evolutionary Game Theory

To model an evolutionary process we need to ascribe a fitness to each individual in a population. The fitness should correspond to expected number of offspring, according to certain heritable features of the individual in question. Characteristics of individuals may come in certain discrete classes, or in continuous form, but in either instance if a character is associated with a greater than average fitness it should increase in frequency in the population, until it reaches fixation. However, this leads to a contradiction with observations of the natural world. There is often large variation in phenotype within single populations, which is of a greater level than can be accounted for by the stochastic aspects of the selection process (e.g. mutation, crossover, non-deterministic development etc.). What kind of processes can account for such variation? One potential answer is a phenomenon known as frequency dependent selection. Frequency dependent selection refers to the case in which it is no longer possible to ascribe a fitness to a certain phenotype in isolation, but only with respect to the frequency of other phenotypes in the population. This is particularly apparent when the phenotype in question is a social behaviour or 'strategy'. Maynard Smith and Price [5] were particularly interested in one such example with which they spawned the field of evolutionary game theory. They were interested in the fighting behaviour of stags. Naturalists had observed that the fights between males of the species very rarely ended in all out conflict, but instead were often theatrical displays involving ritualised conflict. At first they considered two possible social strategies which they named Hawk and Dove. Hawks fight, to the death if necessary, whereas Doves back down upon being shown aggression. The territory that the individuals fight over has some worth to each individual in terms of access to resources or mates, but serious injury results in a large penalty (in terms of fitness). Clearly this fits the description of frequency dependent selection in that it is no longer possible to ascribe fitness to a certain strategy without taking into account the strategies of other individuals. A hawk in a population of doves is very fit, but a dove in a population of Hawks is likewise of high fitness. This type of situation is a more challenging scenario for the evolutionary theorist as the frequency dependence introduces extra mathematical and conceptual difficulties, but, as Maynard Smith and Price showed, frequency dependent selection (of a certain form) can very neatly be represented in terms of game theory.

Game theory itself was born not in biology but in economics. Game theory is the study of strategic interactions in which rational players have preferences over outcomes, and outcomes depend not only on the focal individual's behaviour, but on the behaviour of other players in the game. John Nash showed that the outcome of a game between rational players would be a so called Nash equilibrium. A Nash equilibrium is an outcome in which no player can become better off if they unilaterally change their strategy (There are many texts on game theory, but a good one is Binmore [1]). Furthermore, Nash was able to show that all games have at least one Nash equilibrium. However, the concept of Nash equilibria has a number of potential weaknesses. Firstly, and most glaringly, the concept relies on the notion of rationality, which, taken literally is absurd. No living thing can be truly rational, with infinite computational power and complete information. Secondly, there may exist many Nash Equilibria, and deciding which one should be considered the outcome of the game has occupied the efforts of many economists and game theorists with no clear resolution.

Evolutionary game theory takes an entirely different approach. It assumes no intelligence on behalf of the individuals in a population. Instead each individual plays a certain strategy blindly and interacts with other members of the population, acquiring payoff (in the form of Darwinian fitness). Those that do well in the game are disproportionately represented in the next generation. The outcome of this process, iterated over many generations, is the semblance of rationality. That is that those individuals who happened to approximate rationality purely accidently tend to be favoured by natural selection.

Evolutionary game theory is then the study of the dynamic evolution of strategic behaviours. Whilst evolutionary game theory was born out of conventional game theory it is not axiomatically equivalent to it, and is a mathematical discipline in its own right. Whilst there are many analogous concepts between the two interpretations, and a certain amount of gestalt switching between the two interpretations is often beneficial, the evolutionary framework introduces many of its own concepts and results.

1.2 Evolutionarily Stable Strategies

The concept of the evolutionarily stable strategy (henceforth ESS) in many ways plays the role the Nash Equilibrium does in conventional game theory. The ESS tries to capture the notion of un-invadeability in natural selection. That is that a population which all play the ESS cannot be invaded by a mutant strategy present in small quantities. Consider a strategy X which represents a certain social behaviour, which could include probabilistic or conditional behaviour. The payoff that X receives against another strategy Y is given by $U(X, Y)$. Clearly if there exists a strategy Y that receives a higher payoff against X than X does against itself then X cannot be an ESS because it can be invaded by Y. Therefore one can write down a necessary condition for X to be an ESS:

$$U(X, Y) \leq U(X, X)\ \forall Y \tag{1}$$

In the special case where Y is an equally good response to X as X is to itself it may be possible that X is still an ESS. This would happen if X were a better response to Y than Y is to itself. That is if the equality holds in equation (1) then the following must be true for X to be an ESS: $U(X, Y) > U(Y, Y)$, for all y. One can thus consider very roughly the concept of an ESS as a strategy which is its own best response, bearing in mind the previous caveat.

1.3 Replicator Dynamics

The ESS concept is not a satisfactory formulation of evolutionary game theory for the simple reason that it gives no account of the dynamics of selection, but rests purely on the notion of stability. A familiarity with non-linear systems implies that periodic or chaotic motion are both conceivable possibilities for the dynamics of evolution. Furthermore, there may exists more than one ESS which leads to a problem analogous to the equilibrium selection problem in game theory. It is therefore desirable to have a complete dynamic description of the action of selection, which describes the time evolution of the state of the population. This is the role played by the replicator equation [11].

The replicator equation assumes that there are n social strategies indexed via i. The state of the system at time t is given by the vector $\underline{x}(t)$, where x_i represents the density of strategy i. The replicator equation assumes that the rate of change of a given strategy i is proportional to its current density and its payoff with respect to the average payoff of the population. The replicator equation therefore assumes that types breed true and that fitness is an inherently relative concept. Both assumptions may be problematic in certain circumstances, but often the outcome of evolution does not depend too sensitively upon these assumptions. Let π_i be the payoff to player i and let $\bar{\pi}$ be the average payoff in the population. The replicator equation is given by:

$$\dot{x}_i = x_i(\pi_i - \bar{\pi}) \tag{2}$$

It remains to demonstrate how payoffs are calculated. Payoff information can be represented very succinctly via a payoff matrix M, where M_{ij} represents the payoff that player i receives against player j. It is usually assumed that players interact pairwise and at random so that payoff can be written as:

$$\pi_i = \sum_j M_{ij} x_j \tag{3}$$

Average payoff is defined as:

$$\bar{\pi} = \sum_i \pi_i x_i \tag{4}$$

In matrix form the replicator equation has an elegant representation:

$$\dot{\underline{x}} = \underline{x}\,(M.\underline{x} - \underline{x}.M.\underline{x}) \tag{5}$$

One final assumption is often made which states that the total size of the population is constant, i.e.:

$$\sum_i x_i = 1 \tag{6}$$

This reduces the effective dimensionality of the replicator equation by 1. So that for n strategies the dynamics take place on the simplex S_N. (A simplex is a coordinate space in which any of the dimensions can be specified via the others, so that S_2 is a line, S_3 a triangle and S_4 a pyramid).

At this point it is useful to note a few simple but important features of the replicator equation. Firstly, note that the replicator equation conserves the total size of the population, which by convention is set to one. Secondly, note that if a strategy is extinct at time t, then it remains extinct for all time. This is because the replicator equation does not include the possibility of mutation. Thirdly, if a strategy has an average payoff it will neither increase nor decrease in frequency.

The replicator equation invites yet another notion of stability which is distinct from both the Nash equilibrium and the ESS concepts. These are simply the stable fixed points of the replicator equation for which $\dot{x} = 0$, and for which small perturbations return towards the fixed point. (This can be verified by showing that the eigenvalues of the Jacobian at the fixed point are all negative real.) Nash equilibria are necessarily ESSs, which are necessarily stable fixed points of the replicator equation. But the converse of each of these statements is not true. Therefore, to say that a state is a stable fixed point of the replicator equation is the strongest statement to make, this shall be the concept which I have in mind when I speak about stability.

1.4 Invariance of the replicator dynamics

A concept which is frequently of interest to mathematician and physicists is invariance. An invariance is a transformation which leaves all concepts of interest unchanged. Specifically here I am interested in transformations of payoffs which do not alter the replicator dynamics. For dynamics given by the replicator equation (5) and a payoff matrix M the affine transformation $M \to \gamma M + \lambda$ (where γ is a positive constant and λ is any constant) leaves the replicator dynamics unchanged, provided one rescales time by a factor γ. For a proof see Weibull [12].

The invariance under affine transformation result is potentially useful in that it allows one to reduce the dimensionality of the problem by two. A general two strategy game may have four parameters (the entries in the payoff matrix), but an affine transformation will reduce this to only 2 parameters, greatly reducing the effort of the analysis.

Another invariance result is that so called *local payoff transformations* leave the replicator equation unchanged. That is adding a constant to every column of the payoff matrix (but the constant may be different for every column). For a proof also see Weibull ([12]).

This is an even more powerful result, in that an n strategy game has n redundant degrees of freedom. However, this result has a drawback which the affine transformation does not suffer from which I will explain in section 1.7.

1.5 Two-Player, Two-Strategy Symmetric Games

It is possible to systematically categorise the location and stability of all fixed points in two-player two-strategy symmetric games (a symmetric game is one in which neither player has an a prior special role and does not imply that the payoff matrix itself is symmetric). This can be done by transforming a two player game into standard form and solving for all values of the given parameters. It is highly desirable to have standard form in that, upon investigating any game of the same dimension, all that need be done is to transform the game into standard form and read off the result.

Any two player symmetric game can be represented via a two-by-two matrix which has four arbitrary parameters:

$$M = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

I call the first strategy A and the second B. The only assumption that I make is: $a > d$. If d were greater than a one could simply re-label to reverse this relationship. The special case of $a = d$ would need to be analysed separately.

However, the fact that the replicator equation is invariant under affine transformations means that two of these parameters are not real degrees of freedom and can be eliminated by the transformation $M \to \frac{1}{a-d}(M-d)$. Let $S = \frac{b-d}{a-d}$

and $T = \frac{c-d}{a-d}$ such that the transformed payoff matrix can be written as:

$$M \to \begin{pmatrix} \frac{a-d}{a-d} & \frac{b-d}{a-d} \\ \frac{c-d}{a-d} & \frac{d-d}{a-d} \end{pmatrix} = \begin{pmatrix} 1 & S \\ T & 0 \end{pmatrix}$$

The replicator equation (from (5)) for this game is:

$$\dot{x} = x(1-x)(S(1-x) + x(1-T))$$

where x is the density of strategy A (and therefore $1-x$ is the density of strategy B).

Fixed points exisit at $x = 0$ and $x = 1$. There is also a mixed state which is fixed at the point $x = \frac{S}{S+T-1}$. This lies in the interval $(0, 1)$ only if $(S < 0 \wedge T < 1) \vee (S > 0 \wedge T > 1)$ (here $\wedge$ means and and $\vee$ means or). Stability can be inferred from the sign of

$$\frac{d\dot{x}}{dx} = S\left(3x^2 - 4x + 1\right) + x(3x-2)(T-1)$$

(stable fixed points have negative curvature, and unstable positive).

Working this through one arrives at the categorisation of all two-player two-strategy games in terms of four qualitatively different behaviours:

1. $T > 1 \wedge S > 0$: The Snowdrift Game: $x = 0$ and $x = 1$ are both unstable. The single stable fixed point is mixed and is given by:

$$x^* = \frac{S}{(S+T-1)} \tag{7}$$

2. $T > 1 \wedge S < 0$: The Prisoner's Dilemma: The mixed fixed point lies outside of the interval $(0, 1)$, $x = 1$ is unstable. The single stable fixed point is $x^* = 0$.

3. $T < 1 \wedge S < 0$: The Stag-Hunt Game: $x = 0$ and $x = 1$ are both stable, the interior fixe point exists but is unstable. The basins of attraction of each fixed point lies at either side of the unstable fixed point.

4. $T < 1 \wedge S > 0$: The Harmony Game: $x = 0$ is unstable, the interior fixed point is outside the permitted range. Only $x^* = 1$ is stable.

Figure 1 illustrates the results of such an analysis.

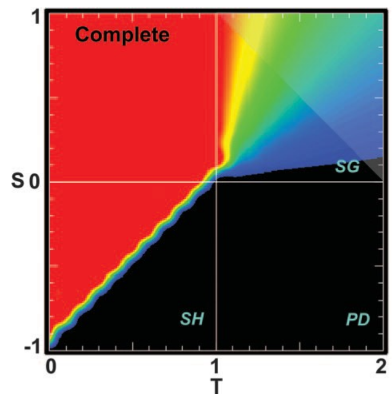

Figure 1: ST space, colour represents equilibrium level of cooperation reached from initial conditions of $x = 0.5$. (From Santos et. al. [9]).

1.6 Mixed Strategies

The source of much confusion in evolutionary game theory is the distinction between a stable state and a stable strategy. In a game with a polymorphic equilibrium such as the snowdrift game there are two possible interpretations of the equilibrium, one is that the population is composed of pure strategies with the specified frequencies, and the other is that the population consists of individuals who themselves play each strategy with the given frequencies, this would be a so called mixed strategy. In two strategy games the distinction is not important. Any population composition in which the average probability of playing strategy A is equal to (7) is stable. However, no such result exists for higher dimensional games. Furthermore, the result also rests on the assumption that the interactions within a population are random.

Here I will briefly show how one can set up replicator dynamics for two strategy games in which individuals can play either strategy, A or B, with a genetically determined probability. In the case of two pure strategies a mixed strategy can be represented via a single real number representing the probability of playing A. An individual with mixed strategy p meeting one with mixed strategy q receives an expected payoff given by:

$$U(p,q) = pqM_{11} + p(1-q)M_{12} + (1-p)qM_{21} + (1-p)(1-q)M_{22}$$

The state of the population is a continuous function between 0 and 1 $x(p)$ such that $\int_a^b x(p)dp$ represents the density of individuals playing a strategy between a and b. The fixed population size assumption is asserted via: $\int_0^1 x(p)dp = 1$. Payoff to strategy i is then

$$\pi(p) = \int_0^1 U(p,q)x(q)dq$$

Average payoff is simply:

$$\bar{\pi} = \int_0^1 \pi(q)x(q)dq$$

One can apply the replicator equation using these payoff functions with the interpretation of the relevant quantities as continuous, rather than discrete, variables.

1.7 Social Efficiency

Another important concept in evolutionary game theory is social efficiency. The notion of social efficiency attempts to formalise the idea of a 'desirable' state, or alternatively the notion of 'the greater good' [12]. A socially efficient state (hence forth SES) is a state which is (at least locally) optimal, in the sense that it maximises average payoff for the population. Formally:

$$\begin{aligned} x_{\text{SES}} &= \text{arg max}\,\{\bar{\pi}\} \\ &= \text{arg max}\,\{\underline{x}.M.\underline{x}\} \end{aligned}$$

If x is an SES given the payoff matrix M then it is also an SES of the payoff matrix which is an affine transformation of the original payoff matrix. However, the same is not true of local payoff transformations. In general the SESs will be altered by local payoff transformations.

Even though all individuals try to maximise their payoff there is no guarantee that selection will lead to a socially efficient state, as is the case in the prisoner's dilemma. Although Fisher's fundamental theorem is often interpreted in saying that selection will maximise average payoff, this is only true if (among other assumptions) the environment is constant. In the case of frequency dependent selection the other individuals are the environment, so that selection effectively is not only causing adaptation, but is also changing the environment and thus average fitness may not increase. However, there is a certain class of games for which individual selection is guaranteed to lead to an SES, these are the partnership games. A partnership game is a game for which the payoffs of any interaction fall equally between the two players. That is that $M_{ij} = M_{ji}$. (This should be intuitive, but see [3] for a proof).

The concept of social efficiency should not be confused with Pareto efficiency, which is an entirely different concept from classical game theory. The outcome of a game is Pareto inefficient if there are alternative outcomes which make somebody better off without making anyone worse off. The idea of a socially efficient state is a stronger one which says that this state is the one which maximises average welfare, and it may be necessary to make one individual worse off to achieve it.

1.8 Cost Benefit Games

An illuminating class of games to study are the so called cost benefit games, or donor recipient games. In such a game there are an arbitrary number of strategies N. Strategy i incurs a cost c_i to itself. Upon meeting another individual it donates a benefit b_i to that individual. We can therefore write the elements of the payoff matrix as:

$$M_{ij} = b_j - c_i \tag{8}$$

the N player game is specified via $2N$ parameters (two lists of size N), so that this representation is a special subset of all games (i.e. there exist games which cannot be represented as a cost benefit game). A special feature of these games is that the costs from switching from strategy i to strategy j are independent of the state of the population. If we were to hypothetically change the strategy of player two in a pairwise interaction the resulting change of payoff would be independent of the strategy of player one. Mathematically this is expressed as:

$$M_{ik} - M_{il} = M_{jk} - M_{jl} \; \forall i, j, k, l \tag{9}$$

clearly the matrix in equation (8) satisfies this relation. Equation (9) stands as a general definition of a cost benefit game.

There is an elegant application of the invariance of local payoff transformation result which can be applied here. Recall that the result states that the replicator dynamics are unaltered upon the addition (or by extension subtraction) of a constant to each column of the payoff matrix. Let the constant be $-b_j$ (b_j is constant going down the columns) so that:

$$M_{ij} \to -c_i$$

this shows that in effect individuals are trying to minimise their costs, and are entirely indifferent to the benefits that they bestow to others. They are neither cooperative nor spiteful. Only the state with the minimum cost is a stable fixed point. The socially efficient state is the pure state which maximises $b_i - c_i$. Later we will see that assortment can reduce the selfish nature of individuals.

1.9 Assortment in game theory

Very frequently in nature the interactions between agents are not of a random nature. Specifically it is often the case that like individuals tend to interact more frequently than would be the case for random interactions. This phenomenon is known as assortment. Assortment can occur whenever there is limited dispersal, group structure or the ability of individuals to recognise one another. The replicator equation in its most basic form (2) does not assume anything about the pattern of interactions, but the way in which payoffs are calculated does assume such random interactions. By extension the vector form of the replicator equation (equation (5)) assumes random interactions and is invalid whenever there is population structure. This section sketches a procedure for generalising this assumption.

Let P_{ij} be the conditional probability that a focal agent meets another agent of type j, given that it is of type i. The payoff of an agent of type i is given by:

$$\pi_i = \sum_j P_{ij} M_{ij} \tag{10}$$

for a well mixed population $P_{ij} = x_j$. That is a focal agent, i, will meet an agent of type j in direct proportion to js frequency in the population, regardless of what type i is.

Assortment is modelled as follows: an individual meets another player which has the same strategy as itself with probability α and with probability $1-\alpha$ it meets a random member of the population. Thus we can write P as:

$$P_{ij} = \begin{cases} \alpha + (1-\alpha)\, x_j & i = j \\ (1-\alpha)\, x_j & i \neq j \end{cases} \tag{11}$$

which sums to one as probabilities must.

The matrix δ_{ij} is equal to one if $i = j$ and equal to zero otherwise. The above result can be neatly characterised using the δ matrix, as follows:

$$P_{ij} = (1-\alpha)x_j + \delta_{ij}\alpha \tag{12}$$

1.10 Assortment in cost benefit games

To understand the effects of assortment on cost benefit games note that in effect selection creates individuals that act as if they were trying to maximise their payoff. In the well mixed case the payoff of individual i is given by:

$$\begin{aligned} \pi_i &= \sum_j x_j\,(b_j - c_i) \\ &= \underline{x}.\underline{b} - c_i \end{aligned}$$

Maximisation is unaffected by the addition of constant terms so that one can safely ignore the constant $\underline{x}.\underline{b}$, and conclude that (at least approximately) individuals act as if to minimise their costs (maximise $-c$), as we saw in the previous section.

However, in an assorted population the payoff is given by:

$$\pi_i = \sum_j \left((1-\alpha)x_j + \delta_{ij}\alpha\right)(b_j - c_i)$$

I make use of the relation: $\sum_j \delta_{ij} x_j = x_i$. It follows that:

$$\pi_i = (1-\alpha)\,\underline{b}.\underline{x} + \alpha b_i - c_i \tag{13}$$

Again I can subtract the constant term and arrive see that individuals should be maximising:

$$\pi_i = \alpha b_i - c_i \tag{14}$$

This is exactly the neighbour modulated fitness of individual i [10].

This leads immediately to an interesting result. For any cost-benefit game there exists an $\alpha < 1$ such that this α is sufficient to make the socially efficient state stable. In other words assortment can solve any dilemma with payoff matrix in the form (9).

1.11 Possible Extensions

The purpose of this section is to illustrate some of the extensions to the replicator framework which have been proposed, some of which are recent developments. I won't in any way give a full account of these fields; my aim is instead to merely note their existence and point out a few relevant references in each case.

1.11.1 Non-Symmetric games

The theory of non-symmetric games has a long history and in fact goes almost to the very beginning of evolutionary game theory [4]. A non-symmetric game is one in which a certain player plays a special role. In the case of two player game it might be that player one has strategies available to it which player two does not. For instance this might relate to an animal which is defending a territory competing with an animal which is invading the territory, or a game in which the two roles are male and female. In which case the payoff structure needs to be specified via two matrices (which is why these games are sometime called bi-matrix games). Let L_{ij} be the payoff player one receives on playing strategy i against a player two who plays a strategy j. Conversely the matrix M plays the equivalent role for player two. In general these matrices need not be square as the number of strategies available to player one might be different to the number available to player two. Payoffs are calculated in a similar manner to before, but the payoff of a strategy is in general the sum of payoffs acquired by being in role one and in role two, weighted by the sum of the probability of assuming each role. In general a genotype would need to specify strategies for each role.

A special case of this formalism is when the two roles refer to two different species. A replicator equation can be written down for this situation. This can lead to different dynamics owing to the fact that a member of species A can never competitively exclude a member of species B [12].

1.11.2 N-player games

One of the restrictive assumptions that Maynard Smith's framework makes, and which has been followed by much subsequent work, is that the interactions between individuals are all pairwise. The theory of N-player games [**?**, 2] relaxes this assumption and assume that players meet, usually at random, in groups of N where $N \geq 2$. In this instance we need to specify the payoff to each player. The payoff matrix is now an N dimensional object. If $N = 3$ then M_{ijk} is the payoff which i receives upon finding itself in a group with a j and a k. If, in this instance, the payoff is not a simple mean of the payoff it would receive from playing j and playing k each pairwise then the game has a non-trivial N-player structure. The general form of the replicator equation holds but the manner in which payoffs are calculated is different. In general payoff calculations should have the form of (in the $N = 3$ case) $\sum_{j,k} P_{ijk} M_{ijk}$, where P_{ijk} is the probability that i finds itself in a group with a j and a k. If group formation is random this probability can be calculated via some standard results in probability theory (to do with the theory of multi-nomal sampling).

1.11.3 Finite Populations and Variable Population Size

The replicator equation assumes both that populations are infinite, and that the total population size is conserved. Recent attempts have been made to relax these assumptions. The theory of finite populations [6, 7] relies heavily on stochastic differential equations, which is quite an advanced topic from theoretical physics. One important result from this field is that, even if the fixed point of the replicator equation is an attractor, finite population effects may lead to periodic motion. In many cases, however, the infinite population assumption does not lead to a quantitative change in dynamics.

Novak et. al. [8] have recently written down a version of the replicator equation for variable population size and have begun the investigation of such systems. They show that fixed points of each equation are the same, but that stability of the fixed points may differ in each case.

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