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Game theory

Evolutionary game theory different from economic game theory

Evolutionary game theory has significant attention from both biologists and mathematicians

Formally, a game consists of

- a set of players
- a set of strategies for each player, S_i
- a payoff function $E_i(s)$ which gives the pay off to player I for each play $s \in S_1 \times S_2 \times \ldots \times S_n$
- a description of information available when choosing the strategy (one player plays first or simultaneous plays, memory or not of past encounters, etc)

Canonical evolutionary game

- 2 players
- strategy sets S discrete and finite
- $S_i=S_j$
- $E_1(I,J)=E_2(I,J)$
  Above 2 mean game is symmetrical
- memoryless
- asexual population
- fixed size population
- reproductive success monotonically increasing with payoff

An example

- Hawk/Dove - assume two players encounter each other and they have a choice of fighting (hawk) or retreating (dove).
- There is a benefit (V) to winning some reward and a cost (C) to losing. The matrix is:

$$\begin{bmatrix} & H & D \\ H & \frac{V-C}{2} & V \\ D & 0 & \frac{V}{2} \end{bmatrix}$$

- If V>C then assume everybody else is playing hawk, your best choice is to play hawk as well, However, assume everybody else is playing dove, your best choice is to play hawk. Therefore Hawk is an evolutionarily stable strategy.
- If V<C then it is not so clear. Let's use V=4, C=8 as an example: $\begin{bmatrix} -2 & 4 \\ 0 & 2 \end{bmatrix}$

If everybody is playing Hawk, I can come along and play dove and do better. If everybody is playing dove, I can come along and play hawk and do better. This suggest that there is an interior equilibrium where sometimes the population plays hawk, and sometimes plays dove. If the newcomer is to be indifferent to playing hawk or dove, the payoffs should be the same, so use I=pH+(1-p)D such that the payoff is equal - i.e. -2p+(1-p)4=0p+(1-p)2 or 4p=2 or p=0.5 - ie I= $\begin{bmatrix} 0.5 \\ 0.5 \end{bmatrix}$

Notation & matrix formulation of canonical game

- Assume the strategies available are number 1, …, n and the players are A&B
- A strategy then consists of a probability vector (vector whose elements are positive and sum to one). Each entry represents the probability of playing that specific strategy on a given turn
- Normally these strategy vectors are denoted I or J
- I1 denotes a pure strategy of playing only strategy #1 all the time. If I has more than one element that is non-zero it is called a mixed strategy.
- s(I) is the support of I - i.e. all the strategies in 1…n which are non-zero in I
- If the strategy sets are discrete and finite and there are two players, the payoffs can be written in a bimatrix form:

  Error!
- If E_A (I,J)= -E_B(I,J) it is called a zero-sum game - evolutionary games are not zero sum
- If E_A(I,J)=E_B(I,J) it is called a symmetric game and the A or B subscript is dropped
- In either case, the bimatrix can be written as a true matrix (recover other half by putting a negative sign in or taking the transpose)
- Then $E_A(I,J)=I^TAJ$ and the payoff for zero-sum is $E_B(I,J)=I^T(-A)J$ and a symmetric game is $E_B(I,J)=I^TA^TJ$
- Often times when using two strategies J&K, we write I=pJ+(1-p)K as a shorthand for using J p% of the time and K the remainder. J & K may be pure or mixed strategies
- The payoff is "linear" under this - ie E(I,pJ+(1-p)K)=pE(I,J)+(1-p)E(I,J)
- Adding a constant to the whole matrix doesn't change the game
- Adding a constant to a column doesn't change the structure of the game

Formalizing stability

Maynard Smith - an ESS is "a strategy such that, if all members of the population adopt it, then no mutant strategy could invade the population under the influence of natural selection"

How to formalize this

- **Equilibrium** - an economic game theory hold-over. I is an equilibrium when for every i,j $\in$ s(I), E(i,I)=E(j,I) - this means that at least among the supported strategies, no strategy can do better than I, but it says nothing about strategies not supported
- **Nash equilibrium** - if E(J,I) $\leq$ E(I,I) for all J then I is a Nash equilibrium. If it is strictly less then it is a strong nash equilibrium, otherwise a weak equilibrium. Note need a pair if it is not symmetric. Also a carryover from economic game theory
- **Attractor** - if we can define differential or difference equations about how the population evolves, then attractors would be stable
- **ESS (Evolutionarily stable strategy**) - defined by Maynard Smith and Price in 1973:
  - a derivation is:

    let there be an invasion of a population all playing I by a population ε big playing J

    $w_I=w_0+E(I)=w_0+(1-\varepsilon)E(I,I)+\varepsilon E(I,J)$

    $w_J=w_0+E(J)=w_0+(1-\varepsilon)E(I,J)+\varepsilon E(J,J)$

    if $w_i>w_j$ as lim as $\varepsilon \to 0$ then must have ESS conditions i and ii below so I is an ESS if:

i) $E(J,I) \leq E(I,I)\ \forall\ J$

ii) for each J either

iia) $E(J,I)<E(I,I)$

iib) $E(J,I)>E(J,J)$

- i is an equilibrium criteria, ii is a stability criteria
- ii says either J must be strictly worse against I than I OR J does worse against itself than I does

- **ES State** - similar to ESS but the J's tested are only the pure strategies
- **Other** - can also be more general than ESS - e.g. allow invasion by two mutants simultaneously

How do these relate?

- strict Nash equilibria $\Rightarrow$ ESS
- ESS $\Rightarrow$ weak Nash equilibria
- ES State $\subset$ ESS
- ESS $\Rightarrow$ equilibrium (Bishop & Canning 1978)
  although weak Nash $\Rightarrow$ equilibria is in game theory
- ESS $\Leftrightarrow$ ES State for 2×2
- ES State but not ESS for n>2: e.g. $\begin{bmatrix} 1 & 1 & 1 \\ 1 & 0 & 10 \\ 1 & 10 & 0 \end{bmatrix}$ 1 is stable vs pure strategy 2 or 3, but not mixed with 2 and 3
- ESS is an attractor under either continuous or discrete dynamics
- attractor $\not\subset$ ESS (some attractors exist that are not ESS's)

Some examples

(borrowed from Bulmer and other sources)

$$\begin{bmatrix} 2 & 3 \\ 1 & 4 \end{bmatrix}$$

Has

- 3 Nash equilibria $\begin{bmatrix} 1 \\ 0 \end{bmatrix}, \begin{bmatrix} 0.5 \\ 0.5 \end{bmatrix}, \begin{bmatrix} 0 \\ 1 \end{bmatrix}$ 2 of which are strict, one mixed
- three equilibria (the 2nd is most interesting because it actually is a mixed strategy)
- the two strict Nash equilibria are therefore also ESS and therefore also ES States

$$\begin{bmatrix} 0 & 5 & -4 \\ -7 & 0 & 8 \\ -1 & 2 & 0 \end{bmatrix}$$

Has

- 3 Nash equilibria $\begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix}, \begin{bmatrix} 0.8 \\ 0 \\ 0.2 \end{bmatrix}, \begin{bmatrix} 0.33 \\ 0.33 \\ 0.33 \end{bmatrix}$
- 2 ES States (1st and 3rd) - 2nd is not because value of I2 vs. itself is worse than vs. the others
- 1 ESS (1st) - 2nd is not as above, 3rd is vulnerable to a $\begin{bmatrix} 0 \\ 0.5 \\ 0.5 \end{bmatrix}$ strategist

Some notes and theorems

- There may be more than 1 ESS (e.g. Hawk/Dove with C>V)
- There is always an ESS if n=2 (see next section)
- There may be no ESS if n>2, e.g. rock-scissors-paper $\begin{bmatrix} \varepsilon & 1 & -1 \\ -1 & \varepsilon & 1 \\ 1 & -1 & \varepsilon \end{bmatrix}$ (the pure strategies are clearly not ESS's, pick a mixed strategy of any 2 and it will look like $\begin{bmatrix} \frac{1}{1-\varepsilon} \\ \frac{-\varepsilon}{1-\varepsilon} \end{bmatrix}$ i.e. tending to pick the pure strategy containing the -1 and the ε in the column making it easy to beat by picking the remaining strategy with a payoff of 1.
- If a diagonal element strictly dominates its column, the pure strategy of that column is an ESS.
- Likewise if a diagonal element weakly dominates its column, and all members of its column that are equal to the diagonal are greater than the diagonal element in its row, then the pure strategy of that column is an ESS
- Nested ESS's may not occur - i.e. if I,J ESS's then it is impossible to have $s(I) \subset s(J)$

Classifying 2x2 games

Assume we have $\begin{bmatrix} a & b \\ c & d \end{bmatrix}$ then we have four cases:

- **Case I: a>c, d<b:** I1 is the only ESS. I2 is not because E(I2,I1)>E(I2,I2), no mixed because it contains I1 which is
- **Case II: a<c, d>b**: I2 is the only ESS. As above.
- **Case III: a>c, d>b:** I1, I2 are both ESS's. Mixed can not be because that would be nested.
- **Case IV: a<c, d<b:** Mixed is the only ESS. Using Bishop & Canning as a necessary condition get: $pa+(1-p)b=pc+(1-p)d$ which gives $p=\frac{d-b}{(a-c)+(d-b)}$. This mixed strategy can be proved to be an ESS.

Note that we have proved that a 2x2 always has at least one ESS.

Dynamics & genetic constraints

Dynamics Background

The assumed milieu is an asexual population where each member has reproductive success related positively to its payoff in the game. What if we actually take a population, start it at any initial condition - i.e. strategy, and watch evolution. Will it converge on the ESS?

First we must interpret what a mixed strategy means to a population. If each individual plays all the supported strategies in a mixed strategy I according to the probabilities in I, this is called a **monomorphic** population. If each individual only plays one pure strategy supported by I, but the proportions of the subpopulations playing the various pure strategies is given by I, this is called a **polymorphic** population. The dynamics look different under these two scenarios.

Note that normally we expect a monomorphic interpretation to hold up to an ESS and a polymorphic population only to hold up to an ES State. However, we can also imagine the other two scenarios as well.

The dynamics equations given below are for a polymorphic population. To analyze a monomorphic population one uses an analysis of the trajectory of the average population behavior (Taylor and Jonker 1978)?. Also note that these dynamics are also all for asexual populations.

Dynamics equations

Similar to the frequency dependent models of population genetics

let $W_i=W_0+\Sigma\, p_jE(i,j)$ and $\overline{\mathbf{W}} = \Sigma\, p_iW_i$

$$\mathbf{p_{i,t+1}} = \frac{\mathbf{W_i}}{\overline{\mathbf{W}}}\mathbf{p_{i,t}}$$

or $\Delta \mathbf{p_i} = \frac{\mathbf{W_i} - \overline{\mathbf{W}}}{\overline{\mathbf{W}}}\mathbf{p_i}$ for a discrete dynamic

or $\frac{\mathbf{dp_i}}{\mathbf{dt}} = \frac{\mathbf{W_i} - \overline{\mathbf{W}}}{\overline{\mathbf{W}}}\mathbf{p_i}$ for a continuous dynamic

- Others have used a mean population approach or a Lyupanov function approach

Dynamic Results

Confirmation of ESS and ES State definitions

- if it is an ESS, then it is a stable attractor to 1 mixed or pure invader under continuous or discrete dynamics
- if the dynamics are continuous and it is an ESS (vs mixed invasions), then it is stable as an ES State vs pure invasions
- if it is an ES state but not an ESS, then it may be unstable vs. mixed invasions (just as ES States are not always ESS's)
- cyclic dynamics are possible when n>2 (although not about an ESS) -e.g. the rock/scissors/paper game

New

- mixed ESS's in games with n>2 are not necessarily stable to invasions by more than one mutant simultaneously (pincer effect)
- conversely, some attractors are not an ESS
- if the dynamics are discrete, then the ES State is neither necessary nor sufficient for stability

Perturbations from canonical game

Asymmetric

- either because strategy sets not the same (e.g. male and female) or the payoffs aren't the same (e.g. territory defender vs. territory invader, big vs small)
- Selton has shown that in an asymmetric game any ESS must be pure, not mixed (although mixed ES States are still possible) (proved in Bulmer p 173)
- Cyclic dynamics are possible
- Can be solved by expanding to a symmetric game with roles. Example Hawk/Dove and Defender/Invader go to 4 strategies (Hawk always, Dove always, Bourgeois=Hawk if Defender, Dove if invader; and Idiot=Hawk if invader, Dove if defender)

    if I/J is play I if player A, J if player B then $E(I/J, K/L) = \frac{1}{2} E_A(I,L) + \frac{1}{2} E_B(K,J)$
- Get payoff matrix (in order H/D/B/I) with value V to owner and value v to invader

$$\begin{bmatrix} \frac{V+v-2C}{4} & \frac{V+v}{2} & \frac{2V+v-C}{4} & \frac{V+2v-C}{4} \\ 0 & \frac{V+v}{4} & \frac{V}{4} & \frac{v}{4} \\ \frac{V-C}{4} & \frac{2V+v}{4} & \frac{V}{2} & \frac{V+v-C}{4} \\ \frac{v-C}{4} & \frac{V+2v}{4} & \frac{V+v-c}{4} & \frac{v}{2} \end{bmatrix}$$

- when V=16, v=8, C=20 B & X are are both ESS although X is hardly biologically realistic
- if V goes up to 20 only B is an ESS
- Note that starting with a mixed H/D population B can invade but X cannot

N-Player

- also called playing the field - e.g. plant with 6 neighbors in hexagonal grid
- E(I,J) now interpreted as benefit of individual playing I vs a population playing J
- usually notated W(I,J)
- W not necessarily symmetric or linear
- ESS needs modified definition
  iib) $W(J, \varepsilon J + (1-\varepsilon) I) < W(I,I)$
  equivalent to old iib iff linearity holds

Continuous payoffs

- S no longer assumed discrete but continuous over some interval [a,b] or often $[a,\infty)$
- also have W(u,v) which is benefit of individual playing point u vs population playing point v
- ESS condition is now equated to being a maximum
  interior maximum ($\frac{\partial w}{\partial u}\big|_{u=v^*}=0$ and $\frac{\partial^2}{\partial u^2}w\big|_{u=v^*}<0$)
  boundary maximum (on boundary and 1st derivative gives moving up towards boundary)
- sometimes require global maximum
- sometimes require stable vs. a perturbation in the population strategy v^* (say due to drift)
  $$\left[\frac{\partial^2 w}{\partial u^2}+\frac{\partial^2}{\partial u\,\partial v}\right]_{u=v=v^*}<0 \qquad \text{(proved in Bulmer p 174)}$$

is called continuously stable

- note that a mixed strategy can be formulated as a continuous game
- The war of attrition and vigilance against predator games are classic examples of this

Opponents related

- Sometimes beneficial to lose a la Hamilton's rule
- ESS criterion for I to be an ESS is $E(I,I) \geq r\,E(J,J) + (1-r)\,E(J,I)$ where r=% of encounters that are identical by descent

Memory aka iterated games

- One key assumption is no memory of individual preferences. An alternative way to phrase this is there are no repeated contests against the same individual
- If this assumption changes, then very different results can occur
- The classic example is the prisoner's dilemma
- Two suspects jointly committed a major crime (sentence 8 years) and a minor crime (2 years). The DA can prove the minor, but no the major and offers a deal, anybody who confesses on the other will not be prosecuted on the minor crime. The payoff (tattle, silence) is:

$$\begin{bmatrix} & T & S \\ T & 8 & 10 \\ S & 0 & 2 \end{bmatrix}$$

- In a traditional ESS to both tattle as being silent is subject to invasion by a mutant who tattles, but not vice a versa. Note that this means the altruistic choice which is beneficial to both is not an ESS
- or more generally $\begin{bmatrix} & D & C \\ D & 0 & b \\ C & -c & b-c \end{bmatrix}$ where b is the benefit from a cooperating (i.e. C) opponent and c is the cost of cooperating (b>c) (D=defect) Note: use b=2, c=0 and add 10 which doesn't change it to get the example above
- However, if this game is played repeatedly, then a new strategy called tit-for-tat is possible (Be silent the first time then do whatever your opponent did last time)
- the payoff matrix then is (Axelrod and Hamilton 1981, Axelrod and Dion 1988) $\begin{bmatrix} & AD & TFT \\ AD & 0 & b \\ TFT & -c & \frac{b-c}{1-p} \end{bmatrix}$ where AD=always defect, TFT=tit-for-tat and p=probability of meeting again- note $E(TFT,TFT)=(b-c)+p(b-c)+p^2(b-c)+\ldots=\frac{b-c}{1-p}$
- AD is always an ESS, TFT is an ESS iff pb>c (cf. w/ Hamilton's rb>c) but even here hard to see how to evolve to cooperation if start at AD
- What if AC (always cooperate) evolves first for relatives? The payoff is

$$\begin{bmatrix} & AD & TFT & AC \\ AD & 0 & b & \frac{b}{1-p} \\ TFT & -c & \frac{b-c}{1-p} & \frac{b-c}{1-p} \\ AC & \frac{-c}{1-p} & \frac{b-c}{1-p} & \frac{b-c}{1-p} \end{bmatrix}$$

- now TFT is no longer an ESS (a pure TFT population is invasion proof against an AD when pb>c as before, but if an AC invades it can grow by drift as it is fitness equal to TFT when only the two are present, then AD can invade because it is superior to AC).
- another more recent strategy than TFT is Pavlov which says repeat what you did last time if you benefit, and do the opposite if you were unsuccessful. This appears to be the current "champion" strategy (Nowak and Sigmund 1993)

Stochastic payoffs

- random fluctuations in the payoff matrix A have been studied

Diploid sexual population

- Doesn't substantially change the dynamics (Maynard-Smith 1983, Treisman 1981, Hines 1980, Hines and Bishop 1983, see review in Hines 1987)
- Treisman showed this for both additive and dominance models

Multispecies

- definitely asymmetric (even if strategy sets same, no longer reasonable to assume payoffs are, often strategy sets are now different as well - e.g. predator vs. prey)

- so have $W_1(u,v)$ and $W_2(w,x)$ where the W's may or may not be structurally different
- so the field that species 1 encounters depends not just on v, but also on x and the number of species 1 and 2 - i.e. abundances now matter
- ESS definition:
  I an ESS within its own species 1 when J fixed
  J an ESS within its own species 2 when I fixed
  the populations are stable

Coevolution

- This starts to raise questions about the population size being fixed though and whether this is really stable
- A fully dynamic approach would appear to make more sense
- It has the benefits of combining ecology and evolutionary processes
- It is an effective model of coevolution
- Need a clear definition of fitness
  - per capita net growth rate (=per capita reproductive rate over replacement)

    $W(u,N)=\frac{1}{N}\frac{dN}{dt}$ in ecology equations

    =r for exponential growth

    =r(1-N/K) for logistic growth
- Dynamics
  ecology/population: $\Delta N = N_t \cdot W$
  quantitative evolution: $\Delta W = k\,\frac{\partial W}{\partial u}$
  can iterate over time
- Statics
  ecological equilibrium $W(N^*,u^*)=0$ (i.e. $\Delta N=0$)
  evolutionary equilibrium $W(N^*,u^*)$ is a local/global maximum

  i.e. $\frac{\partial W}{\partial u} = 0$, $\frac{\partial^2 W}{\partial u^2} = 0$ at N*, u* (i.e. $\Delta W(N^*,u^*)=0$)

- History
  Roughgarden (1976, 1979, 1983)
    W(u,v,N,M)
    builds many tools based on circuit analysis
    computer not required
    no intraspecific frequency dependence, makes wrong in asymmetric competition
  Brown & Vincent (1987, 1988)
    W(u,N,M,***u,p,v,q***)
    applies to asexual lines rather than species
    based on game theory
  Slatkin (1980)
    W(u,N,M,**p(·),q(·)**)
    based on quantitative genetics
    computationally very demanding
  Taper & Case (1992) comparison (plus others)
    Roughgarden = to Brown & Vincent if no intraspecific frequency dependence
      but Roughgarden wrong if there is
    V&B method is limiting case of Slatkin as σ^2 goes to 0

Proofs

Bishop Canning

If I is an ESS and $i,j \in s(I) \Rightarrow E(i,I)=E(j,I)=E(I,I)$

Let I be a mixed ESS. Take $i \in s(I)$.
I an ESS $\Rightarrow E(I,I) \geq E(i,I)$ so $E(i,I) \ngtr E(I,I)$
Now show $E(i,I) \nless E(I,I)$ and thus $E(i,I)=E(I,I)$
Break I into I_i and $I_{\sim i}$ where I_i is the pure strategy i and $I_{\sim i}$ is I without i renormalized.
Let p be the probability of playing i in I.
So $I=pI_i+(1-p)I_{\sim i}$ Therefore
$E(I,I)=E(pI_i+(1-p)I_{\sim i},I)=pE(I_i,I)+(1-p)E(I_{\sim i},I) <$ (by assumption) $p\,E(I,I)+(1-p)E(I_{\sim i},I)$
$\therefore\ (1-p)E(I,I)<(1-p)E(I_{\sim i},I) \Rightarrow E(I,I)<E(I_{\sim i},I)$ which is impossible if I is an ESS
$\Rightarrow \Leftarrow$
QED

No nested ESS

If I,J are ESS's $\Rightarrow s(I) \not\subset S(J)$

Assume $s(I) \subset s(J)$
Take $i \in I$. So also $i \in J$. So $E(i,J)=E(J,J)$ by Bishop Canning

Now by linearity $I=\sum_{i \in s(I)} p_i I_i$

so $E(I,J)=\sum_{i \in s(I)} p_i E(i,J)$ = (by Bishop Canning above) $\sum_{i \in s(I)} p_i E(J,J) = E(J,J) \sum_{i \in s(I)} p_i = E(J,J) \bullet 1 = E(J,J)$

so we have shown under nesting $E(I,J)=E(J,J)$ but J an ESS implies $E(J,J)>E(I,J)$ or (if $E(J,J)=E(I,J)$ then $E(I,J)>E(I,I)$ i.e. $E(I,J)$ is either > or < $E(I,I)$ but not =
$\Rightarrow \Leftarrow$
QED

There exists a ESS for 2x2 - aka the mixed equilibrium is ESS if a<c, d<b

See 2x2 classification above. It remains to prove that the p given is an ESS.
Let I be the strategy $\begin{bmatrix} p \\ (1-p) \end{bmatrix}$. Let J be any strategy $q \bullet 1 + (1-q) \bullet 2$
Now by Bishop Canning $E(1,I)=E(I,I)=E(2,I)$
So by linearity $E(J,I)=qE(1,I)+(1-q)E(2,I)=qE(I,I)+(1-q)E(I,I)=E(I,I)$
So meets i) of ESS and will meet iib) of ESS if $E(I,J)>E(J,J)$ or equivalently $E(I,J)-E(J,J)>0$
Now $E(I,J)-E(J,J)=E(I,J)-E(I,I)+E(I,I)-E(J,J)=IAJ-IAI+JAI-JAJ$ (where A=payoff matrix)
$=(I-J)AJ-(I-J)AI=(I-J)A(J-I)=-(J-I)A(J-I)$
but $J \neq I$ so $J-I>0$ and A negative definite so $-(J-I)A(J-I)>0$ so $E(I,J)-E(J,J)>0$
A negative definite since $|A_1|=a>0$ and $|A_2| = ad-bc<0$ (since $a<c$, $d<b$)
QED

Dynamics equation

Define

$N = \Sigma N_i$

$p_i = N_i / N$

$w_i = \frac{1}{N_i}\frac{dN_i}{dt}$

$\overline{w} = \Sigma p_i w_i$

Now

$$\overline{w} = \Sigma \frac{N_i}{N}\frac{1}{N_i}\frac{dN_i}{dt} = \frac{1}{N}\Sigma\frac{dN_i}{dt} = \frac{1}{N}\frac{dN}{dt}$$

$$\frac{dp_i}{dt} = \frac{1}{N}\frac{dN_i}{dt} + N_i\frac{d}{dt}\left(\frac{1}{N}\right) = \frac{1}{N}\frac{dN_i}{dt} - \frac{N_i}{N^2}\frac{dN}{dt} = \frac{1}{N}\frac{dN_i}{dt} - \frac{N_i}{N}\frac{1}{N}\frac{dN}{dt} = \frac{N_i}{N}\left(\frac{1}{N_i}\frac{dN_i}{dt} - \frac{1}{N}\frac{dN}{dt}\right)$$

$$= p_i(w_i - \overline{w})$$

divide by $\overline{w}$ to get a fixed population size?