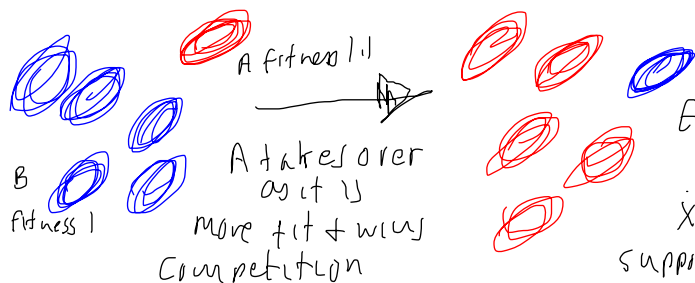


# Evolutionary Games

Game Theory was invented by Oskar Morgenstern & John von Neuman & mathematically characterized by John Nash (Nobel Prize). William Hamilton & Robert Trivers applied it to biology & John Maynard Smith to evolution.



Here fitness is a somewhat abstract concept, which we will formalize later.

Example 1.

$$\dot{x} = x(1-x) \quad x \rightarrow 1 \quad \text{now introduce } y$$

$$\dot{x} = x(1-x-ay) \quad \dot{y} = y(1-y-bx)$$

suppose  $a > 1$ ,  $b < 1$ , small amount of  $y$  takes over.

more general idea. Let  $\vec{x} = (x_A, x_B)$ , & let  $f_A(\vec{x})$  be fitness of A,  $f_B(\vec{x})$ , fitness of B. Suppose  $x_A, x_B$  are fraction of pop that is A, B resp.

Let  $\phi = x_A f_A + x_B f_B$  be the average fitness. Then we write:

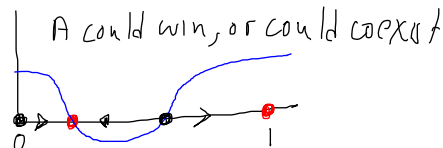
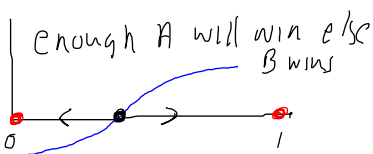
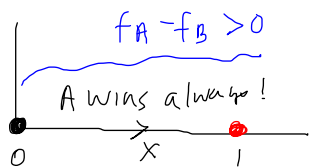
$$\dot{x}_A = x_A (f_A(\vec{x}) - \phi), \quad \dot{x}_B = x_B (f_B(\vec{x}) - \phi). \quad \text{Since } x_A + x_B = 1, \text{ check:}$$

$$\dot{x}_A + \dot{x}_B = x_A f_A + x_B f_B - \phi (x_A + x_B) = \phi (1 - (x_A + x_B)) \Rightarrow \dot{x}_A + \dot{x}_B = 0$$

$$\text{Let } x_A = x, x_B = 1-x, \text{ so } f_A(\vec{x}) = f_A(x), f_B(\vec{x}) = f_B(x) \Rightarrow$$

$$\dot{x} = x(f_A(x) - (x f_A + (1-x) f_B)) = x(f_A(1-x) - (1-x) f_B) = x(1-x)(f_A(x) - f_B(x))$$

So:  $x=0, x=1, f_A(x)=f_B(x)$  are all the fixed points



Clearly:  $x=0$  stable iff  $f_A(0) - f_B(0) < 0$ ,  $x=1$  stable iff  $f_A(1) > f_B(1)$ , interior point

$x^*$  is stable, iff  $f_A'(x^*) - f_B'(x^*) < 0$

## Games + Payoff Matrices

A game with two strategies, A, B is described by a payoff matrix:

$$\begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{matrix}$$

A + B are NOT the players, but the strategies

If each player plays strategy A, then both get "a"

If both play "B", they get "d"

If one plays A + the other plays B, the one playing A, gets "b"

the one playing B gets "c"

In evolutionary game theory the fitness is determined by the expected

payoff. So, a player that takes strategy A, can expect

$$f_A = a x_A + b x_B \quad (\text{where } x_A, x_B \text{ are fraction playing A, B})$$

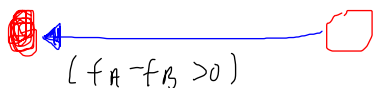
$$f_B = c x_A + d x_B. \quad \text{These are a linear fitness model.}$$

$$x = x_A, \quad 1-x = x_B, \quad \dot{x} = x f_A + (1-x) f_B$$

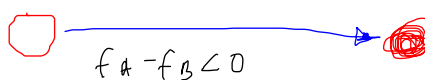
$$\dot{x} = x(1-x)[f_A - f_B] = x(1-x)[(a-b-c+d)x + b-d] = x(1-x)[(a-c)x + (b-d)(1-x)]$$

$$x^* = \frac{b-d}{c-a+b-d} = \frac{d-b}{a-b-c+d}$$

A dominates B  $a > c, b > d$



B dominates A,  $c > a, d > b$



A, B bistable,  $a > c, d > b$



coexistence,  $a < c, d < b$



$a = c, b = d$  Neutral (inf # equ)



A is stable when  $a > c$ , B is stable when  $d > b$

(If you play A against A, it is always better than playing B against A)

## Nash Equilibrium

A Nash Equilibrium is a strategy such that if any player deviates, he will not increase his payoff. (decrease  $\rightarrow$  strict)

$$\begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{matrix}$$
 You can think of a strategy as a vector  $\vec{x}$  of prob, say  $(1,0) \equiv \text{pure } A$

(1) A is a strict Nash Equil if  $a > c$  } These are "local", just like stability of equilib

(2) A is a NE if  $a \geq c$

(3) B is a SNE if  $d > b$  (Recall that A will be a stable equil of the above eqn if  $a > c$ , sim B ( $d > b$ ))

(4) B is a NE if  $d \geq b$

$$\begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix} \end{matrix}$$
 B is a strict Nash Equilibrium, but note it is not the best global strategy - both playing A is better

However, if you play A + I switch to B, I do much better (I get 5, you get 0!) This is an example of the prisoners dilemma where

it pays to "cheat"

$$\begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} 3 & 1 \\ 5 & 0 \end{pmatrix} \end{matrix}$$
 If both play A, one can improve by switching to B  
 If both play B, then again one can improve by switching to A

So neither is Nash Equilibrium

$$\begin{matrix} & \begin{matrix} A & B \end{matrix} \\ \begin{matrix} A \\ B \end{matrix} & \begin{pmatrix} 5 & 0 \\ 3 & 1 \end{pmatrix} \end{matrix}$$
 Here cannot improve if both play A, nor can you improve if both play B. A, B are Nash equilibria

### Evolutionarily Stable Strategy (ESS) (John Maynard Smith)

Suppose a lot of A players + a single mutant B player arises. Will A be able to hold off invasion of B? Let  $\epsilon$  be freq of B +  $1-\epsilon$  = freq of A

$$a(1-\epsilon) + b\epsilon > c(1-\epsilon) + d\epsilon \Rightarrow a > c \text{ or } a = c + b > d. \text{ A is ESS.}$$

$$\begin{matrix} f_A \\ f_B \end{matrix}$$

More than 2 strategies

Let  $E(S_i, S_j)$  be payoff for strategy  $S_i$  against strategy  $S_j$

(i)  $S_k$  is a strict Nash equilibrium if

$$E(S_k, S_k) > E(S_i, S_k) \quad \forall i \neq k$$

(ii) Nash Eq if  $E(S_k, S_k) \geq E(S_i, S_k) \quad \forall i$

(iii) ESS if  $E(S_k, S_k) > E(S_i, S_k) \quad \forall i$

$$\text{or } E(S_k, S_k) = E(S_i, S_k) \wedge E(S_k, S_i) > E(S_i, S_i) \quad \forall i \neq k$$

ESS  $\Rightarrow$  selection will oppose any potential invader

same true for strict N.E. but not for a N.E. If  $E(S_k, S_k) = E(S_j, S_k)$

and  $E(S_k, S_i) < E(S_j, S_j)$  Then  $S_k$  is still a N.E. but selection will favor  $S_j$  invading  $S_k$ .

(iv) "Weak ESS"  $E(S_k, S_k) > E(S_i, S_k) \quad \forall i \neq k$  or

$$E(S_k, S_k) = E(S_i, S_k) \wedge E(S_k, S_i) \geq E(S_i, S_i) \quad \text{Strict NE} \Rightarrow \text{ESS} \Rightarrow \text{weak ESS}$$

$$\text{"Unbeatable strategy"} \quad E(S_k, S_k) > E(S_i, S_k) \wedge E(S_k, S_i) > E(S_i, S_i) \quad \forall i \neq k \quad \Rightarrow \text{NE}$$

dominates all other strategies

General Replicator dynamics

For  $n$  strategies, there is an  $n \times n$  matrix,  $A = [a_{ij}]$  which is the payoff

Let  $x_i$  be the frequency of strategy  $i$ . The fitness is  $f_i = \sum_{j=1}^n a_{ij} x_j = [Ax]_i$

The mean fitness is  $\sum_{i=1}^n x_i f_i = X \cdot Ax = \bar{f}$ , so we write:

$$\dot{x}_i = x_i (f_i - \bar{f}) \quad \text{or} \quad \dot{x}_i = x_i ([Ax]_i - \bar{X} \cdot Ax)$$

we will show this is equivalent to an  $(n-1)$  dim LV system. Note it is a cubic ODE not quadratic as is LV. For  $n=2$ , we see this reduces to

a one-d ODE. There is an interior fixed point iff

$$\frac{d-b}{a-b-cd} > 0 \quad \begin{pmatrix} a & b \\ c & d \end{pmatrix} \rightarrow \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \rightarrow \frac{a_{22} - a_{12}}{a_{11} - a_{21} - a_{12} + a_{22}} > 0 \Leftrightarrow (a_{11} - a_{21})(a_{22} - a_{12}) < 0 \quad (\text{prove this!!})$$

Formal definitions:

We say a point  $\hat{x} \in S_n$  ( $x_i \geq 0 \mid \sum x_i = 1$ ) is a Nash equilibrium if  $x \cdot A \hat{x} \leq \hat{x} \cdot A \hat{x}$  for all  $x \in S_n$  + an Evolutionarily Stable State (ESS) if  $\hat{x} \cdot A x > x \cdot A x$  for all  $x \neq \hat{x}$  in a nbhd of  $\hat{x}$

### ASIDE Game Theory

Suppose there are  $N$  pure strategies,  $R_1$  to  $R_N$  + allow players to use mixed strategies as well, playing the pure strategies with probability  $p_1, \dots, p_n$ . A strategy,  $\vec{p} \in S_N$ . Corners of simplex are the pure strategies and the interior is a completely mixed strategy. Let's suppose only two players with  $u_{ij}$  being the payoff for a player using pure  $R_i$  against pure  $R_j$ .  $U = (u_{ij})$  is the payoff matrix. An  $R_i$  strategist obtains expected payoff  $(U \vec{q})_i = \sum u_{ij} q_j$  against  $\vec{q}$  strategist + a  $\vec{p}$  vs  $\vec{q}$  is then  $p \cdot U q = \sum_{ij} p_i u_{ij} q_j$ . Let  $\beta(q)$  be the set of "best replies" to  $q$ . That is, the value of  $p$  such that  $p \cdot U q$  obtains maximum value. Thus we now see that a Nash Equilibrium is a strategy that is the best reply to itself.

### END ASIDE

Before continuing with example games, I will show a relationship between replicator dynamics + LV. In one of your exercises, you prove that you can add a constant  $c_j$  to each column  $j$  without changing the dynamics, so, eg. the last row of  $a_{ij}$  can be made zero with no loss of generality!

Theorem There exists a differentiable, invertible map  $f$  from  $\hat{S}_n = \{x \in S_n \mid x_n > 0\}$  onto  $\mathbb{R}_+^{n-1}$  mapping the orbits of  $\dot{x}_i = x_i((Ax)_i - x \cdot Ax)$  onto the orbits of the LV

$$\dot{y}_i = y_i \left( r_i + \sum_{j=1}^{n-1} a'_{ij} y_j \right), i=1, \dots, n-1$$

where  $r_i = a_{in} - a_{nn}$ ,  $a'_{ij} = a_{ij} - a_{nj}$

Proof: Let  $y_n = 1$  + consider the transformation  $y \rightarrow x$  given by  $x_i = \frac{y_i}{\sum_{j=1}^n y_j}$   $i=1, \dots, n$

which maps  $\{y \in \mathbb{R}_+^n : y_n = 1\}$  onto  $\hat{S}_n$ . The inverse  $x \rightarrow y$  is

$$y_i = \frac{y_i}{y_n} = \frac{x_i}{x_n}, \quad j=1, \dots, n$$

consider  $\dot{x}_i = x_i((Ax)_i - x \cdot Ax)$   $\xrightarrow{\phi}$

With no loss in generality, we subtract the last row of  $A$  from every other row of  $A$ , so that the last row of  $A$  is now zero (see exercise)

$$\dot{y}_i = \left( \frac{\dot{x}_i}{x_n} \right) = \frac{\dot{x}_i x_n - x_i \dot{x}_n}{x_n^2} = \frac{x_i x_n ((Ax)_i - \phi) - x_n x_i ((Ax)_n - \phi)}{x_n^2} = \left( \frac{x_i}{x_n} \right) [(Ax)_i - (Ax)_n]$$

but  $(Ax)_n = 0 \Rightarrow$

$$\dot{y}_i = y_i \left( \sum_{j=1}^n a_{ij} x_j \right) = y_i \left( \sum_{j=1}^n a_{ij} y_j \right) x_n.$$

Since  $x_n > 0$ , we can rescale time (see ODE 1) to get rid of  $x_n$  without changing the phase portrait. Finally, recall that  $y_n = 1$  so that

$$\dot{y}_j = y_j \left( a_{jn} + \sum_{i=1}^{n-1} a_{ij} y_i \right). \quad \square$$

So - 3 strategies Replicator has no limit cycles!!