

## A very short intro to evolutionary game theory

Game theory developed to study the strategic interaction among rational self regarding players (players seeking to maximize their own payoffs). However, by the early 1970's the theory underwent a transformation and part of it morphed into evolutionary game theory, which allows to increase our understanding of dynamical systems, especially in biology and, more recently, in psychology and the social sciences, with significant ramifications for philosophy. The players are *not* required to be rational at all, but only to have (perhaps hardwired) strategies that are passed on to their progeny. In short, the *notion of player is displaced by that of strategy*, and consequently *the notion of a player's knowledge, complete or incomplete, is dispensed with*. What drives systems is not the rationality of the players but the differential success of the strategies.

As before, we consider only two-player games. A game with strategies  $s_1, \dots, s_n$  for both players is *strategy symmetric* (symmetric, in brief) if:

1. when  $i=j$  the payoffs for the two identical strategies are the same, which means that along the main diagonal (top left to bottom right) the payoffs in each box are the same
2. the payoffs in the remaining boxes on one side of the main diagonal are mirror images of their counterparts on the other side.

For example, *The Prisoners' Dilemma* is a symmetric game. Along the main diagonal, the payoffs are the same in each box that is, (1,1) and (6,-6); moreover, we have (-10, 10) in the top right box and (10, -10) in the bottom left, which are mirror images of each other.

	S	C
S	1;1	10;-10
C	-10;10	-6;-6

A symmetric matrix can be simplified by writing only the payoffs of the row player, as those of the column player can be easily obtained by exploiting the symmetry of the game. So, the previous matrix can be simplified as

	S	C
S	1	10
C	-10	-6

### *Evolutionary Stable Strategies (ESS)*

An important concept of evolutionary game theory is that of *evolutionarily stable strategy* (ESS). To understand it, we need some new notions.

Imagine now that we keep repeating a symmetric game (each round is called a '*stage game*') with *random pairing* in an *infinite* population in which the only relevant consideration is that *successful players get to multiply more rapidly than unsuccessful ones*. (The demand that the population is theoretically infinite excludes random drift). Suppose that all the players (the incumbents) play strategy X, which can be a pure or a mixed strategy. If X is stable in the sense that a mutant playing a different strategy Y

(pure or mixed) cannot successfully invade, then X is an ESS. More precisely, X is an ESS if *either*

1.  $E(X,X) > E(Y,X)$ ,

that is, the payoff for playing X against (another playing) X is greater than that for playing any other strategy Y against X

*or*

2.  $E(X,X) = E(Y,X)$  and  $E(X,Y) > E(Y,Y)$

that is, the payoff of playing X against itself is equal to that of playing Y against X but the payoff of playing Y against Y is less than that of playing X against Y.

Note that *either* (1) or (2) will do.

Obviously, if (1) obtains, the Y invader typically loses against X, and therefore it cannot persist. If (2) obtains, the Y invader does as well against X as X itself, but it loses to X against other Y invaders, and therefore it cannot multiply. In short, Y players cannot successfully invade a population of X players.

It is possible to introduce a strategy that is stronger than an ESS, namely, an unbeatable strategy. Strategy X is *unbeatable* if, given any other strategy Y

$$E(X,X) > E(Y,X) \text{ and } E(X,Y) > E(Y,Y).$$

An unbeatable strategy is the most powerful strategy there is because it strictly dominates any other strategy; however, it is also rare, and therefore of very limited use.

Given a strategy X and any other strategy Y let us call X

*Nash* if  $E(X,X) \geq E(Y,X)$

(X is a best reply to itself)

and

*Strict Nash* if  $E(X,X) > E(Y,X)$

(X is a strict best reply to itself)

Then the following relations obtain, with the arrow indicating entailment:

$$\text{Unbeatable} \rightarrow \text{Strict Nash} \rightarrow \text{ESS} \rightarrow \text{Nash}$$

In sum, an unbeatable strategy is also strict Nash, and so on.

A few final points about ESS should be noted:

- The population has to be infinite.
- The notion of ESS, as we defined it, applies only to repeated symmetric games.
- Every ESS is a strategy in a Nash equilibrium, although the reverse is not true (not all Nash equilibriums are made up of ESS).
- A *strict* Nash equilibrium in which both players follow the same strategy is made up of ESS. So, for example, in *The Prisoners' Dilemma* the strict Nash equilibrium (which is also a dominance equilibrium) is constituted by ESS. Squealing does better against squealing than keeping silent: in a population of squealers keeping silent is a losing strategy, and therefore it cannot invade.

- If  $E(X,X)=E(Y,X)$  and  $E(X,Y)>E(Y,Y)$  obtains, *one* Y invader would do as well as any X, which means that an ESS need not guarantee *the* highest payoff.
- An ESS *can* be defeated since it can have a lower payoff than one of *two or more* simultaneously invading strategies.
- One can relax the requirements for an ESS. For example, X may be stable against Y if Y is pure but not if Y is mixed, in which case X may be said, confusingly, to be an ESS (*of sorts*) in pure strategies.

Often, ESS are associated with mixed strategy equilibriums. For example, *Chicken* (*Snowdrift* is essentially the same game) has two pure strategy Nash equilibriums, neither of which rest on ESS. However, the mixed strategy resulting in a Nash equilibrium is an ESS. (Note that in this context mixed strategies are understood in terms of frequencies of players in a population each playing a pure strategy). A very famous version of ESS is the mixed strategy resulting in Nash equilibrium in *Hawk-Dove*, a biology oriented version of *Chicken*.

We now turn to a more general approach to evolutionary games.

### *Evolutionary Dynamics*

We just saw that in a population in which an ESS has *already* taken over, invasion does not occur successfully. However, under which conditions does a strategy take over in a population? What happens if a game in an infinite population is repeated *indefinitely*? The answer comes from evolutionary dynamics, which studies the behavior of systems evolving under some specific evolutionary rule. The basic idea here is that of the *replicator*, an entity capable of reproducing, that is, of making (relevantly) accurate copies of itself. Examples of replicators are living organisms, genes, strategies in a game, ideas (silly or not), as well as political, moral, religious, or economic customs (silly or not). A *replicator system* is a set of replicators in a given environment together with a given pattern of interactions among them. *An evolutionary dynamics of a replicator system is the process of change of the frequency of the replicators brought about by the fact that replicators which are more successful reproduce more quickly than those which are less successful.* Crucially, this process must take into account the fact that the success, and therefore the reproduction rate, of a replicator *is due in part to its distribution* (proportion) in the population. For example, when playing *Chicken*, although drivers do well against swervers, in a population of drivers a single swerver does better than anybody else. So, it will reproduce more quickly the others. However, at some point or other, there will be enough swervers that the drivers will start to do better again. It would be nice to know whether there is some equilibrium point, and if so what it is.

Since the differential rate of reproduction determines the dynamics of the system, we need to be more precise and specify what we mean by ‘more quickly’. This is determined by the dynamics of the system; the one we are going to study is *replicator dynamics*. There are other models that plausibly apply to evolution, but replicator dynamics is the easiest and the most often used, at least at a first approach. Replicator dynamics makes three crucial assumptions:

- The *population is infinite*. (In practice, this means that the population is sufficiently large, that is, large enough for the level of accuracy we seek).
- There is *no random drift*; in other words, there are no random events interfering with the results of differential fitness, the fact that some individuals are favored in relation to others. This is in effect guaranteed by the previous requirement of infinity. In finite, especially in small, populations, random drift is a significant dynamical force, an issue we shall have to deal with later.
- The interactions among players (strategies) are *random*; that is, the probability of strategy S meeting strategy H is the frequency of H. For example, if 1/3 of the population is H, the probability of an individual playing an H is 1/3 and that of playing an S is 2/3.

In addition, we shall restrict ourselves to studying *repeated games whose stage games are symmetric and have only two players*, so that the math remains easy.

To understand replicator dynamics, we need to introduce a few notions. The first is that of *rate of change*. Experience teaches that things often change at different rates. For example, sometimes accidentally introduces species multiply more quickly in a population than native species: in other words, their rate of growth is greater than that of native species, and this typically results in a decline of the natives. So, if at the moment of introduction the frequency of the non-native species was  $p$  and that of the native species was  $q = 1 - p$ , with  $q \gg p$ , after some time the situation may change and become  $p > q$ . This means that  $p$  has a positive rate of change (it increases) while  $q$  has a negative rate of change (it decreases). Mathematically, we express this by writing

$$D(p) > 0 \text{ and } D(q) < 0,$$

where  $D(p)$  (the derivative of  $p$  with respect to time) means ‘the rate of change of  $p$ ’, and similarly for  $q$ .

So, suppose a population  $P$  increases by 1/3 every second; then if in the beginning  $p = 100$ , then after one second,  $p_1 = 100 + 1/3(100) = 130$ , after 2 seconds,  $p_2 = p_1 + 1/3(p_1) = 130 + 1/3(130)$ , and so on.

The second notion, which we have already met, is that of *expected payoff* of a pure strategy. Suppose a strategy  $s$  is played against strategies  $S_1, \dots, S_n$ , and that  $\Pr(S_i)$  is the probability that  $S_i$  is played. Then,

$$EP(s) = E(s, S_1) \Pr(S_1) + \dots + E(s, S_n) \Pr(S_n).$$

That is, if by  $S_i$  we denote a generic  $S$ , the expected payoff of  $s$  is the sum of the payoffs of  $s$  against each of the  $S_i$  times the probability that  $S_i$  is played.

The third notion is that of *average payoff* of a set of strategies, and to understand this, we need to consider the notion of the *mean*. Suppose that in a group of boxes, 1/3 weigh 30 kilos, 1/2 weigh 20 and 1/6 weigh 60. Then the average weight  $\bar{A}W$  (notice the bar above ‘A’) is:

$$\bar{A}W = 30 \times 1/3 + 40 \times 1/2 + 30 \times 1/6 = 10 + 20 + 5 = 35.$$

In words, *the average weight is the sum of all the weights, each multiplied by its frequency*. (Since 1/3 of the boxes weigh 30 kilos, we multiply 30 by 1/3, and so on).

Similarly, if  $S$  (tag) and  $H$  (are) are the two available strategies, the average payoff is  $\bar{A}EP = EP(S)\Pr(S) + EP(H)\Pr(H)$ .

For example, consider the following *Stag Hunt* matrix, and suppose that  $\Pr(S) = p$ , so that  $\Pr(H) = 1 - p$ .

	S	H
S	3	0
H	2	1

**Table 12**

Then, the EP of S, when played with frequency  $p$  against another S and with frequency  $1-p$  against an H is:

$$EP(S)=3p+0(1-p)=3p.$$

Analogously, the EP of H, when played with frequency  $p$  against another S and with frequency  $1-p$  against another H is

$$EP(H)=2p+1(1-p)=p+1.$$

So, the average expected payoff is  $EP(S)$  times the probability that S is played plus  $EP(H)$  times the probability that H is played:

$$\bar{A}EP=EP(S) \times Pr(S) + EP(H) \times Pr(H)= 3p^2 + (p+1)(1-p)= 2p^2 + 1.$$

In replicator dynamics, if  $Pr(S)=p$ , the dynamical equation (the equation ruling the behavior of the system through time) is:

$$D(p) = [EP(S) - \bar{A}EP]p$$

In other words, *the rate of change of the frequency of a strategy (in this case S), is determined by the difference between the expected payoff of S and the average payoff.*

Consequently, when S's expected payoff is greater than the average payoff, the frequency of S increases, and when it's smaller then the frequency of S decreases. Hence, in our example we have:

$$D(p) = [EP(S) - \bar{A}EP]p = [-2p^2 + 3p - 1]p.$$

Obviously, when  $D(p)=0$  the frequency of S (that is,  $p$ ) does not change. The values of  $p$  for which the frequency of S does not change are called "*fixed points*". So, let us find the fixed points in our example, that is, let us find when

$$[-2p^2 + 3p - 1]p=0.$$

Obviously, one fixed point is  $p=0$ . For the other two, we need to solve

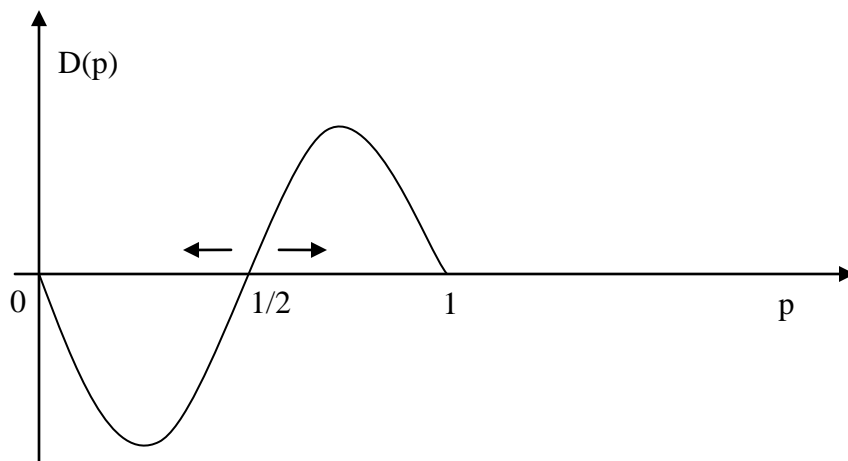
$$-2p^2 + 3p - 1=0,$$

which gives  $p=1$  and  $p=1/2$ . So, when  $p=0$ , or  $p=1$ , or  $p=1/2$ , the frequency of S does not change. But what happens when  $p$  is not equal to any of the three fixed points? Let us

study the plot of

$$D(p)=[-2p^2 + 3p - 1]p.$$

As we can verify by substituting  $1/3$  for  $p$ , when  $0 < p < 1/2$  the rate of growth of  $p$  is negative, and when  $1/2 < p < 1$  the rate of growth of  $p$  is positive (just substitute  $2/3$  for  $p$ , for example). Since for  $p=1/2$  the growth rate of  $p$  is zero, the plot looks (more or less) like this:



If at some time  $p < 1/2$ , as the growth rate is negative  $p$  will eventually become zero, that is, the strategy S will disappear; by contrast, if at some time  $p > 1/2$ , then S will become *fixated*, that is it will remain the only strategy (H will disappear). If  $p = 1/2$ , then exactly half of the population will play S and half H. However, this equilibrium is not stable in the sense that even a minor deviation from it will push one of H or S to extinction and the other to fixation, both of which are stable.

The interval  $(0, 1/2)$  is the *basin of attraction* of which H is the *attractor*, and the interval  $(1/2, 1)$  that of S. The fixed points  $p = 0$  and  $p = 1$  are *asymptotically stable* because each is an attractor of a basin of attraction. If the basin of attraction of an attractor contains the whole interval in which  $p$  is defined, or at least all the interior points, then the attractor is *globally stable*. In our example, no fixed point is globally stable.  $1/2$  is the *interior fixed point* and, as we saw, it is unstable.

#### *Replicator dynamics of a generalized 2 by 2 symmetric game*

A symmetric game with 2 strategies, A and B, can be represented by the following payoff matrix, where the payoff are those of the row strategies:

	A	B
A	a	b
B	c	d

It turns out that *the replicator dynamics does not change if in any column we add or subtract the same quantity from all the boxes*. (For examples, see the exercises). Hence, we can reduce the matrix by subtracting  $c$  from the first column and  $d$  from the second, obtaining

	A	B
A	$a - c$	$b - d$
B	0	0

Let us now determine the dynamics, with  $\Pr(A) = p$ .

$$EP(A) = (a-c)p + (b-d)(1-p).$$

Because of our matrix manipulation  $EP(B) = 0$ , and consequently the average expected payoff is simply

$$\bar{A}EP = p[(a-c)p + (b-d)(1-p)] + 0.$$

Hence,

$$D(p) = p[(a-c)p + (b-d)(1-p) - p^2(a-c) - p(b-d)(1-p)].$$

After a bit of algebra, we get

$$D(p) = p(1-p)[(a-c)p + (b-d)(1-p)],$$

that is,

$$D(p) = p(1-p)[EP(A)].$$

Hence,  $D(p) = 0$  when  $p=0$ , or  $p=1$ , or  $EP(A) = 0$ . Note that solving  $EP(A) = 0$  gives the interior fixed point.

So, to find the interior point and the system's dynamical behavior:

- Reduce the matrix by setting strategy B's payoffs equal to zero and modifying the other payoffs accordingly
- Solve  $EP(A) = 0$
- Determine in which interval  $D(p)$  is positive or negative.

The last step can be done without calculation by noting that here are five cases in a game:

1. A dominates B:  $a \geq c$  and  $b \geq d$ , where *at least one* of the inequalities is strict. It turns out that replicator dynamics wipes out dominated strategies; hence, A will reach fixation.
2. B dominates A:  $c \geq a$  and  $d \geq b$ , where *at least one* of the inequalities is strict. Since A is dominated, B reaches fixation.
3. A is the best response to A and B to B. In other words, your best bet is to mimic the moves of your opponent. Then,  $a > c$  and  $d > b$ , so that in the reduced matrix  $a-c > 0$  and  $b-d < 0$ . The interior point determines an *unstable equilibrium*. The system is *bi-stable*, meaning that one of the two strategies will reach fixation, but which does depends on the initial strategy distribution, that is, the initial value of  $p$ . The strategy that has the larger basin of attraction is *risk dominant*: if the initial distribution is random, on average the risk dominant strategy will reach fixation more often.
4. A is the best response to B and B the best response to A, that is,  $b > d$  and  $c > a$ , so that in the reduced matrix  $a-c < 0$  and  $b-d > 0$ . In other words, the best strategy is to do the opposite of what the other player does. Then the interior fixed point determines a *globally stable equilibrium*: the system will converge to it independently of the original distribution. A and B will coexist in a predetermined fixed ratio. The system is *ergodic*, meaning that the final state is independent of the initial conditions.
5. A and B are neutral:  $a=c$  and  $b=d$ . Then selection is neutral,  $D(p)=0$  at all times, and the original strategy distribution  $p$  will be preserved.

There are some interesting connections between dominance, Nash equilibriums, ESS, and replicator dynamics.

1. Nash equilibriums determine fixed points. However, fixed points such as  $p = 1$  are not associated with a Nash equilibrium.

2. If the fixed point  $p$  is associated with an ESS, then  $p$  is asymptotically stable. The converse need not be true.
3. The fixed point  $p$  is associated with an ESS which uses *every strategy with positive probability* (that is, greater than zero) if and only if  $p$  is globally stable.
4. No strongly dominated strategy survives replicator dynamics.

*The quasi-replicator dynamics of the iterated Prisoners Dilemma*

In replicator dynamics, two players meet randomly, play a one-shot game and then separate, as each randomly meets a player again. As dominated strategies do not survive replicator dynamics, defecting reaches fixation in *The Prisoners Dilemma*. Suppose we play *The Prisoners Dilemma* with

- the evolution equation of replicator dynamics
- *direct reciprocity*, namely the *same* two players repeat the game more than once
- random drift
- the presence of mutations
- occasional strategy execution errors
- ignorance on the side of the players of how many times they are playing each other; all they know is that after each round they have a probability  $p$  of playing again, so that the length of the average play is  $1/(1-p)$  rounds. (This avoids the temptation of using backward induction to defecting all the times).

We may consider a general matrix for cooperation and defection in which only the row payoffs are given:

	C	D
C	R	S
D	T	P

One gets R(eward) for mutual cooperation, P(unishment) for mutual defection, S(ucker) for cooperating against a defector, and T(emptation) for defecting against a cooperator. *The Prisoners' Dilemma* obtains if  $T > R > P > S$ . We could think of the game as follows. The cooperator helps at a cost  $c$  and the receiver of the help gets a benefit  $b$ . Defectors do not help and therefore incur no costs. Then:  $R = b - c$ ;  $S = -c$ ;  $T = b$ ;  $P = 0$ .

To make things more interesting, in addition to ALLC (always cooperate) and ALLD (always defect), let us consider some reactive strategies that act on the basis of what happened in the previous stage.

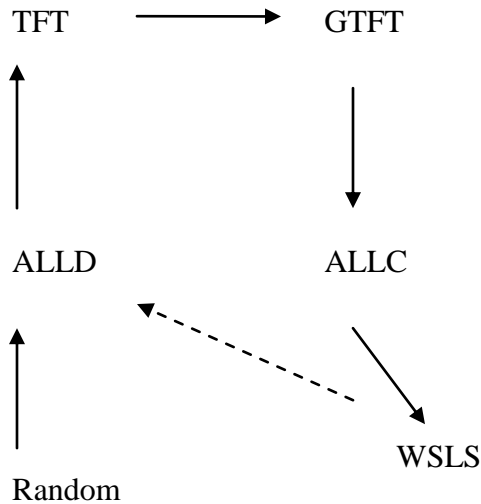
TFT (tit-for-tat) acts as follows: it starts by cooperating and then it considers the opponent's last move; if the opponent cooperated TFT cooperates, and if the opponent defected, it defects.

GTFT (generous tit-for-tat) acts as follows: it's like TFT with one difference: every so many moves (say,  $1/3$  of the times) it cooperates even if in the previous stage the opponent defected.

WSLS (win-stay; lose-shift) acts as follows: WSLS looks at its own payoff in the last stage; if it equal to  $T$  or  $R$  it considers his payoff a success and it repeats the previous

strategy; if not, it shifts strategy. In short, if the previous payoff was one of the two highest, it keeps doing the same thing; if it wasn't, it switches.

Martin Nowak has run programs modeling the following scenario. The matrix has  $R=3, T=5, P=1$ , and  $S=0$ . There is a large number (100 in the run) of randomly chosen and uniformly distributed strategies. There is direct reciprocity; occasionally, the strategies make mistakes, simulating human behavior; new strategies are put into play, simulating mutations, and neutral drift is allowed. What typically happens (M. Nowak, *Evolutionary Dynamics*, ch. 5) can be visualized as follows:



In a random mix of strategies, ALLD does very well, almost taking over. At that point, even a small cluster of TFT, already present or introduced by mutation, will start expanding because it will defect against defectors (ALLD) but cooperate with cooperators (other TFT's mostly). Once TFT becomes abundant, its unforgiving nature makes it succumb to GTFT. The reason is that since mistakes sometimes occur, a TFT playing another TFT might defect instead of cooperating. This will prompt the latter to defect as well in the next stage, thus starting a cycle of cooperation/defection. By contrast, GTFT will at some point try to cooperate again, breaking the cycle and receiving higher payoff. In short, GTFT quickly recovers from mistakes while TFT does not. What happens now depends on how generous GTFT is. If it is sufficiently vindictive, it takes over and becomes stable. However, if it is too generous, once it has taken over it will do no better than an ALLC, which may arise by mutation. If the game is played long enough, ALLC will take over by neutral drift. (In a population of  $N$  individuals with equal fitness, the probability that eventually all the population will be the descendent of a given individual  $A$  is  $1/N$ . Hence, if the game is played long enough, this eventuality will come about). At this point, an ALLD mutation will result in an ALLD explosion. The cycle will start again. However, if when the frequency of ALLC's is high WSLs arises as a mutant, the cycle is broken. When two WSLs  $A$  and  $B$  play each other, if they cooperated in the previous stage, they'll keep cooperating. If  $A$  makes a mistake and defects, here's what happens:

A: CCCDDCCC...

B: CCCCDCCC...

Cooperation, in other words, will resume after two stages.

If A is a WSL and B an ALLC, if they cooperated in the previous stage they'll keep cooperating. However, if A makes a mistake and defects, it will keep defecting against the much too nice B:

A: CCCDDDD...

B: CCCCCC...

In short, WSL exploits ALLC's goodness while cooperating with other WSL's.

When a WSL meets an ALLD, the ALLD is better off, as we have

WSL: CDCD....

ALLD: DDDD...

Note that ALLD averages  $(P+T)/2$  per game. Hence, as long as  $R > (P+T)/2$ , the WSL playing each other will average more than an ALLD playing a WSL. In other words,  $E(\text{WSL}, \text{WSL}) > E(\text{ALLD}, \text{WSL})$ ,

a strict Nash that comes close to delivering an ESS strategy. (It just comes close because the population is finite and random events, random drift for example, are allowed). In other words, one (or just a few) ALLD mutant will not invade. If  $R \leq (P+T)/2$  then a stochastic variant of WSL that cooperates after mutual defection only with probability less than 1 will take over. Occasionally, the system cycles back to ALLD, but the mechanism is unclear.

### *The limits of replicator dynamics*

Replicator dynamics has some features that limit its application.

The dynamics we considered has *no mutation*, in the sense that every replicator produces an identical copy of itself. A side consequence of this is that if a strategy has disappeared, it will never reappear again. (By the way, this is why  $p=1$  and  $p=0$  are *always* fixed points, even when they are not stable). There are ways of dealing with this. For example, one could modify the replicator equation by introducing a term that makes, say, S turn into H with some probability  $q > 0$ , the simplest case of mutation; alternatively, one can use Markov chains. However, as this complicates things we shall not do it. Even so, we can note the following. In our *Stag Hunt* example,  $p=1/2$  is an unstable interior point, which means that random mutations will move the system in either of the two attraction basins with equal probability. However, if we change the payoff matrix to (5,5) when S meets another S, the interior point becomes  $p=1/4$  (check it out!), which means that, given initial uniform distribution, on average random mutations will push systems more often in the basin of attraction with  $p=1$  as the attractor; hence, in a meta-population (a population of populations) on average systems will spend most of their lives in that basin. Of course, if there are  $n$  individuals in the population, there is a probability  $q^n$  that in the transition from one generation to another, *all* the S's (or enough of them) become H, thus bringing H to fixation; however, even for relatively small  $n$ , that probability is likely to be really negligible. For example, if  $q=10\%$  and  $n=17$ , the resulting probability is  $10^{-17}$ , which is really phenomenally low, as  $10^{17}$  is roughly the age of the universe in seconds.

Another limitation of replicator dynamics is that interactions must be random. The problem here is that often individuals interact only with their neighbors, like bacteria in a Petri dish rather than in a constantly stirred solution.

A further feature that limits the application of replicator dynamics is that the population must be *infinite* (in practice, very large); with finite populations, random drift is unavoidable. Consequently, if we are modeling a population that is not very large we need to use different, and more complex, procedures than replicator dynamics.

### *The Dynamics of Finite Populations*

In replicator dynamics, the population must be infinite. Of course, this requirement is unrealistic, but replicator dynamics has the advantage of being straightforward and easy to work with. Hence, as long as the population is large enough it is typically the first modeling approach.

However, often populations are not large enough, and this requires a different approach that involves stochasticity; in other words, realistic finite populations entail jettisoning deterministic evolutionary rules: *in finite populations chance matters*.

### *The Moran Process*

The easiest way to see the role of chance is to consider the *Moran Process* in the case of *neutral drift*, where *selection plays no role*.

Consider a population of  $N$  individuals *reproducing at the very same rate*, which means that selection does not favor one over another: they are *neutral variants*. *At each time step, one individual is randomly chosen for reproduction and one for elimination*. The two individuals may be the same individual  $X$ , in which case  $X$  produces another  $X$  and dies in the same step. (Note that this requirement makes the process of choosing the same as drawing with replacement). It follows that  $N$  remains constant. Suppose now that there are  $i$  individuals of type  $A$  and consequently  $N-i$  individuals of type  $B$ . If we indicate with  $XD$  the fact that  $X$  is chosen for death and with  $XR$  the fact that  $X$  is chosen for reproduction, there are 4 cases:

1.  $AD \ \& \ AR$ , in which case  $\Pr(AD \ \& \ AR) = (i/N)^2$ . Note that the result of this event is that the number of  $A$ 's *remains*  $i$ .
2.  $BD \ \& \ BR$ , in which case  $\Pr(BD \ \& \ BR) = [(N-i)/N]^2$ . Note that the result of this event is that the number of  $A$ 's *remains*  $i$ .
3.  $AR \ \& \ BD$ , in which case  $\Pr(AR \ \& \ BD) = (i/N)[(N-i)/N] = [i(N-i)]/N^2$ . Note that the result of this event is that the number of  $A$ 's *increases* to  $i+1$ .
4.  $AD \ \& \ BR$ , in which case  $\Pr(AD \ \& \ BR) = (i/N)[(N-i)/N] = [i(N-i)]/N^2$ . Note that the result of this event is that the number of  $A$ 's *decreases* to  $i-1$ .

Now let us indicate with  $p_{i,i+1}$  the probability that  $i$  increases to  $i+1$ , and similarly for  $i$  decreasing to  $i-1$ , and  $i$  remaining the same. Then we obtain the following *state transition rules*:

- $p_{i,i+1} = [i(N-i)]/N^2$
- $p_{i,i-1} = [(N-i)(i)]/N^2$
- $p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1} = 1 - 2 [i(N-i)]/N^2$
- $p_{0,0} = p_{N,N} = 1$

(The last is true because when  $i=0$  there are only  $B$ 's and when  $i=N$  there are only  $A$ 's). States  $i=0$  and  $i=N$  are *absorbing states* because when the system reaches one of them it remains there forever; the other states are *transient states*. If we wait long enough, the system will end up with all  $A$ 's or all  $B$ 's. Hence, *although there is no selection, eventually A or B will become fixated*. There are techniques, Markov chains for example,

to determine interesting facts like in how many steps on average the system will get to the fixation of A. However, we shall leave that aside and ask instead a different question we can answer directly: if there are  $i$  A's, what is the probability that A will become fixated? As there is no selection, each individual has the same chance at reproducing and leaving a lineage, namely  $1/N$ ; hence, *that probability is  $i/N$* , as  $i$  is the number of A's.

### *Adding selection to the Moran Process*

Suppose now that we *add selection* to the Moran process as follows. Let A's fitness be  $r$  and B's fitness be 1. Obviously, if  $r > 1$  A is favored by selection; if  $r < 1$  B is favored, and if  $r = 1$  we have neutral drift. We may work the new quantity  $r$  into the previous formulas as follows:

1.  $\Pr(AR) = ri/(ri+N-i)$
2.  $\Pr(BR) = N-i/(ri+N-i)$
3.  $\Pr(AD) = i/N$
4.  $\Pr(BD) = (N-i)/N$

The reason for  $ri$  in the nominator of the first formula,  $\Pr(AR)$ , is obvious: we simulate selection by making the number of A's be higher/lower than it actually is by causing it to be sensitive to  $r$ . The nominator of  $\Pr(BR)$  is given by the fact that B's fitness is 1 by definition. The rationale for the denominator being  $ri+N-i$  rather than merely  $N$  is normalization. Since  $\Pr(AR)+\Pr(BR)=1$ , and the denominators of the two fractions must be identical, the denominators must be equal to the sum of the nominators. Note that when  $r=1$  the formulas revert to those for neutral drift. From (1)-(4) we can obtain the state transition rules, just as before. (What are they?).

It turns out that if A's fitness is  $r$  and the number of A's is  $i$ , A's fixation probability is:  $P = [1 - 1/r^i]/[1 - 1/r^N]$ .

If the population is large and  $r > 1$ ,  $r^N$  will be very large,  $1/r^N$  will be very small and therefore the denominator will become very close to 1. Hence, in a large B population the fixation probability of a single A mutant with fitness  $r > 1$  will be approximately  $\rho_A = 1 - (1/r)$ .

For example, if  $N=100$ ,  $r=1.1$  and  $i=1$ , the numerator becomes .091. In the denominator,  $r^N = 13780$ , so that the denominator becomes  $13779/13780$ , which is very close to 1. Hence,  $\rho_A = .091$  is a good approximation.

### *Spatial Games*

Replicator dynamics assumes *random interactions* among strategies. But this, as we noted, is unrealistic in many contexts. So, in *Stag Hunt* we can then think of groups of S's in an S-structure interacting with H's grouped together in an H structure. Then things can be dramatically different from random interaction situations, as the increase or decrease of S depends *not* on what happens inside the S-structure but on what happens at the *border* between the S's and the H's.

In such contexts, types of evolutionary dynamics different from replicator dynamics are obvious; for example, a simple dynamics could be:

*Every individual looks at its payoffs and at those of its immediate neighbors, and in the next round all individuals simultaneously adopt the strategy that produced the highest payoff.*

The way to make these ideas more precise is to look at spatial games.

Consider a spatial grid in which each individual occupies a position and interacts with all of its neighbors. The payoffs of each interaction are summed and in the next round:

- each player adopts the strategy with the highest payoff in the neighborhood
- all the updatings occur at the same time, which means that generations are not overlapping

	D1	D2	D3	D4	
	D12	C1	C2	D5	
D13	D11	C3	C4	D6	
	D10	D9	D8	D7	

Here we have 4 cooperators from *Stag Hunt* surrounded by 12 defectors. We may imagine this grid as a small part of a larger one that is wrapped around so that there are no boundary effects. A cell's neighborhood is the *von Neumann neighborhood*, constituted by the 4 cells sharing a side with it. For example, C3's neighborhood is constituted by D11, C1, C4, D9. Hence, the fate of C3 depends on its strategy, those of its neighbors D11, C1, C4, D9, and those of its neighbors' neighbors. Let us look at C3's fate. It will obtain a payoff of 6 from cooperating with C1 and C4 and a payoff of 0 from attempting, and failing, to cooperate with D9 and D11. In short, its payoff will be 6. The same is true for the remaining 3 cooperating cells. Consider now D11. It will have a payoff of 3 from its interaction with D13, D12, and D10, and a payoff of 2 from its interaction with C3, for a total of 5. The same is true for the remaining defecting cells. Hence, in the next round the twelve defecting cells will turn into cooperators, and the cooperator square will expand, eventually taking over. Note that cooperation is more successful in this spatial game than under replicator dynamics. This is true of most, but by no means all, interesting spatial games.

A standard way to study an evolutionary game is to consider the conditions for invasion. So, imagine that cooperators have taken over and that one mutates into a defector. Its payoff will be 8, while that of each of its cooperating neighbors will be 9, which means that the defector will vanish in the next round. Two neighboring defectors will have a payoff of 7, while their neighboring cooperators will get 9; hence, the defectors will vanish. With 3 neighboring defectors, the defectors bordering with three cooperators get a payoff of 7, against one of 9 for the cooperators. More defectors will fare even worse. So, a community of cooperators is immune from invasion from defectors.

Imagine now a community of defectors with one mutant cooperator. The cooperator will have a payoff of 0 while each defecting neighbor will have one of 5, with the result that the cooperator will vanish in the next round. Two neighboring cooperators will obtain each a payoff of 3, while each defecting neighbor will get one of 5; consequently, the two cooperators will not survive to the next round. Three neighboring cooperators will evolve into a group of four cooperators with the shape of a latin cross ("+"), with the central cooperator getting 9; this group will hold its own. As we saw, a square of four cooperators will take over. In short, in the spatial version of *Stag Hunt* we considered,

cooperation is much more successful than defection when compared with replicator dynamics.

In addition to von Neumann neighborhoods, one can use *Moore* neighborhoods, in which a cell's neighbors are those touching it, so that the neighbors are all those reachable from the cell by a king move in chess. Grids may become n-dimensional, or, given an appropriate metric, one might define a distance  $r$  from a cell such that only and all the cells within  $r$  are neighbors, with the result that the number of neighbors may vary from cell to cell. Analogously, the transition rules may be changed. For example, a cell might become a cooperator (defector) if the *average* payoff of all the neighborhood cooperators (defectors) is higher than that of the neighborhood defectors (cooperators). Or, the probability of change might be linked to the payoff of the most successful neighbors. Analogously, one can overlay a Moran process, thus obtaining a randomly asynchronous updating: a cell is chosen at random, the relevant payoffs determined and then *only* that cell is updated, thus mimicking overlapping generations. There is, then a great amount of very different dynamics producing very different types of evolutions. Interestingly, games with stochastic (probabilistic) updates often (but not always!) allow for the coexistence of cooperators and defectors (often with a large majority of cooperators) for very long times even in *The Prisoners Dilemma*.