

# Complexity in social dynamics : from the micro to the macro

## Lecture 4

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# 1 Evolution and game theory

## Outline

1. Evolutionary models.
2. Fitness landscapes.
3. Game theory.
4. Iterated games. Prisoner dilemma.
5. Finite populations.

## Evolutionary dynamics

- The word “evolution” is traditionally related to biological systems.
- Actually, it was introduced in the economic/social context (Darwin was inspired by Malthus).
- Evolutionary theories changed in the '70s when game theory was introduced (e.g., Maynard-Smith). Game theory (von Neumann, Nash) was born in politics and economics. Iterated games (Axelrod) were a subject of sociology.
- Now, evolutionary theory (memes) are coming back to psychology. And actually, brains are shaped by evolution.
- Evolutionary computation (e.g., genetic algorithms) are common tools for optimization problems.

## Evolution

- Evolution is composed by three ingredients: reproduction, selection and mutations (or recombination).
- We can think to a finite population of  $N$  individuals. Each one has a *genetic information* (genotype  $g$ ) that determines its actions (phenotype  $f$ ).
- Selection may act on survival probability or on reproduction efficiency. It is a function of the phenotype and depends on the composition of the whole population.
- Individuals that survive or reproduce better tend to replace others with its copies.
- However, during reproduction or lifetime, mutations can appear. “Sexual” reproduction moreover can mix genotypes.
- It is possible to have evolution without selection (neutral evolution).

## Selection (fitness)

- Let us assume that the the probability of survival  $A$  depends on the phenotype  $A(f)$ .
- In general, it depends also on the distribution of other phenotypes in the network of contacts (hares do not like to stay near to lynxes, the latter have opposite opinions).
- The probability of passing (and spreading) the genotype to the following generation depends also on available space, which may be considered a global coupling.

## Red Queen

- Fitness is a relative concept: [0.2cm] *Well, in our country,* said Alice, still panting a little, *you'd generally get to somewhere else – if you run very fast for a long time, as we've been doing.*[0.2cm] *A slow sort of country!* said the **Red Queen**. *Now, here, you see, it takes all the running you can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that!* [0.2cm] One's performances  $A(g)$  have always to be compared with the average ones  $\langle A \rangle$ .

## Implementation

Fixed size population, nonoverlapping generations, stirred (mean field).

- An individual is represented as a string of  $L$  bits  $g_1, \dots, g_L$ .
- The environment  $E$  is an array of  $N$  individuals.
- For each generation, one has to fill up another environment  $E'$ .
  - Choose an individual  $i$  at random.
  - Compute  $A = A(E(i), E)$  (may depend on the other phenotypes).
  - With probability **proportional** to  $A$  it is copied to  $E'$ , with mutations.
  - Repeat until  $E'$  is full.
  - Replace  $E$  with  $E'$ .
- $A$  may be an arbitrary positive quantity, the survival probability is computed as  $A/\langle A \rangle$ .

## Fitness (or adaptive) Landscape

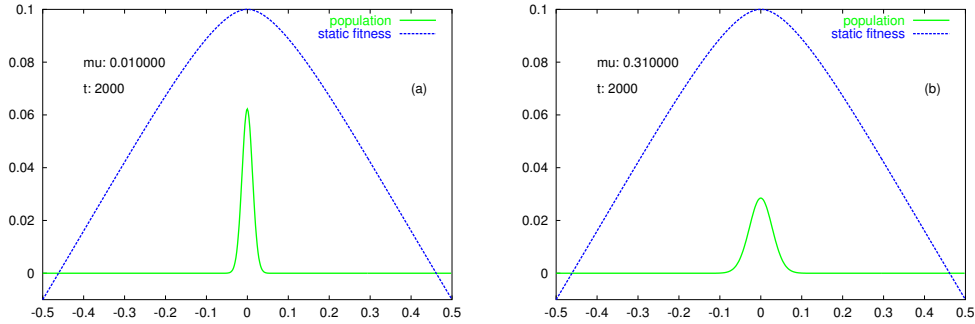
- If the fitness  $A = A(g)$  does not depend on the distribution of phenotypes, one can visualize  $A$  as a surface.
- Mutations corresponds to small or large jumps in the genotypic space ( $g$ ).
- The selection acts either on the probability of survival, or on the efficiency in reproduction.
- If selection is (inversely) proportional to fitness, evolution is like a search for the global maximum of  $A$ .
- There is a strong correspondence between genotype and configurations, fitness and energy, mutations and temperature.

## Evolution on a fitness landscape

- For vanishing mutations the average fitness  $\langle A \rangle$  is a nondecreasing function of time (Fisher theorem),
- And the asymptotic population distribution is a delta peak at the global maximum of the fitness (master sequence).
- For finite mutations, the master sequence is surrounded by a cloud of mutants with lower fitness (quasispecies).
- Broader peaks may “win” over sharper and slightly higher ones.
- Coexistence is fragile. Anyhow, coexisting strains have the same average fitness (Gause principle).
- The portions of the genome subjected to higher selective pressure are less mutable than “neutral” ones.

## Quasispecies.

- In “equilibrium”, infinite population, static fitness landscape, no mutations: just one strain (Fisher theorem).
- Mutations widen the distribution (quasispecies) and lower its average fitness



## Infinite population

In the case of infinite population, one can use the probability distribution  $p(g) = \lim_{N \rightarrow \infty} \frac{\sum_i [g_i = g]}{N}$ . The evolution equation is, for discrete time intervals

$$p(g, t + 1) = \frac{A(g)}{\langle A \rangle} p(g, t) + \text{mutations}$$

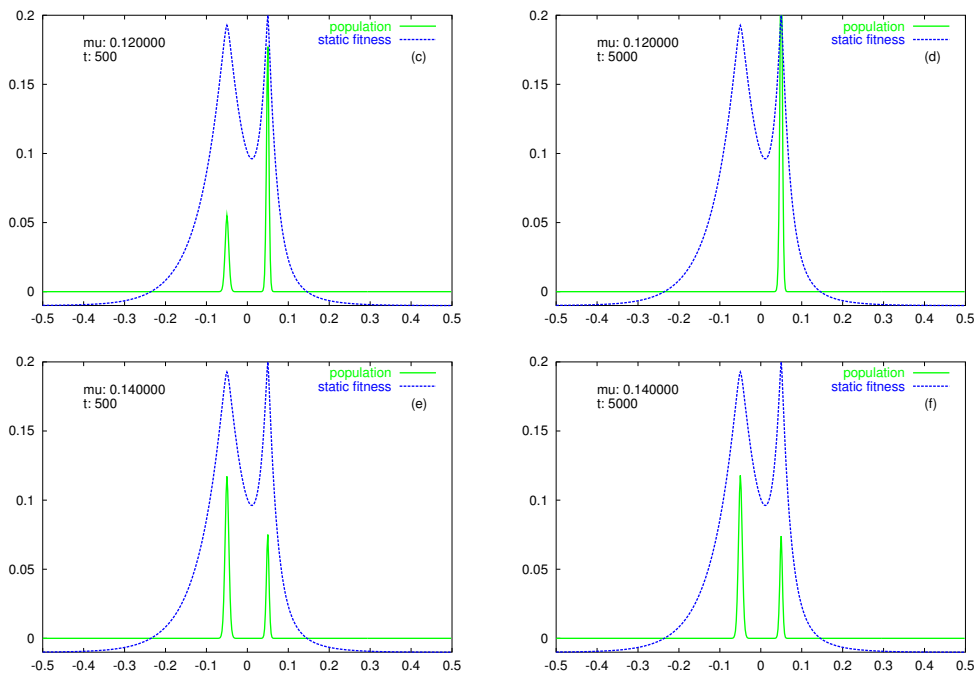
or, for continuous time

$$\frac{\partial p(g, t)}{\partial t} = (A(g) - \langle A \rangle) p(g, t) + \text{mutations}$$

Evolution is a kind of pattern formation in genotypic space.

## Coexistence.

- Coexistence is possible, but it is very sensitive to the mutation rate



## Genetic algorithms

- In order to maximize a function of a discrete (Boolean) parameters, identify the parameters with a genetic code, and the function with the fitness.
- Let a population evolve under selection and competition.
- If the only source of variability is mutation, it is essentially a Monte-Carlo sampling. By lowering the mutation rate (simulated annealing) one recovers the global maximum.
- One can also add recombination (sex) by exchanging pieces of genomes. It works on “separable” problems (but remember that sex was not invented to speed-up evolution, but rather to escape parasites and plagues).

## Competition

The fitness actually depends also on the population distribution.

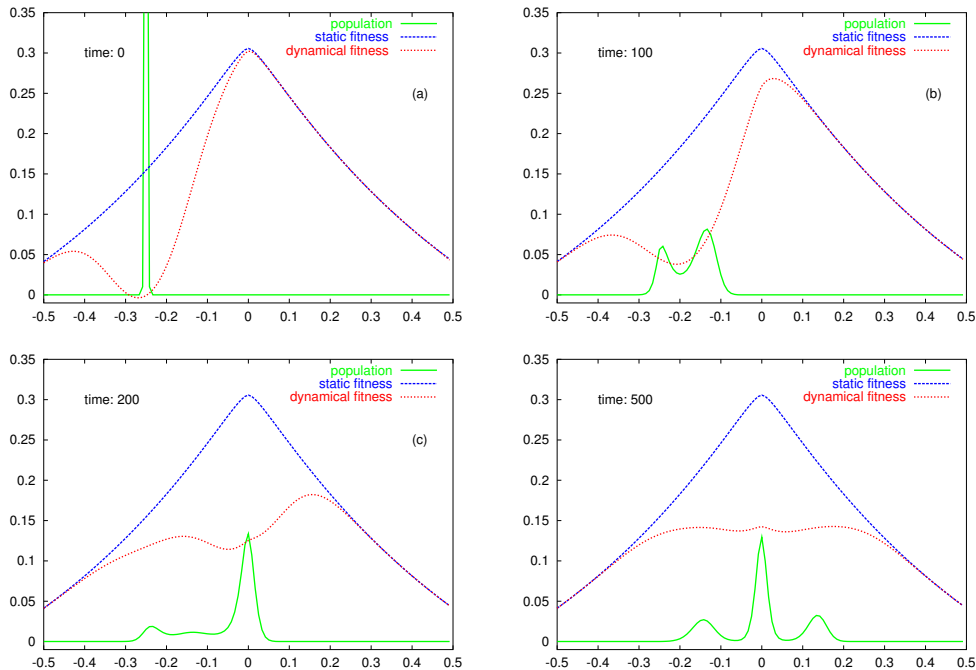
$$\frac{\partial p(g)}{\partial t} = \frac{A(g, \mathbf{p})}{\langle A \rangle} p(g) + \text{mutations},$$

$$A(g, \mathbf{p}) = \exp \left( H_0(g) + \sum_{g' \simeq g} H_1^{(i)}(g, g') p(g') + \sum_{g' \neq g} H_1^{(e)}(g, g') p(g') \right).$$

- One can include simple competition terms: intraspecies ( $H_1^{(i)}$ ) and interspecies ( $H_1^{(e)}$ ) contributions.
- Intraspecies competition broadens the distribution, favouring dispersion.
- Interspecies competition stabilizes coexistence.
- Predation induces competition between predators and between preys.

## Competition.

- Short-range competition stabilizes coexistence



## Games

- Game theory has changed the way we look at evolution.
- We can think to a population of agents (automata), that interact (play the game).
- A strategy can be seen as a “rule” for an automata, either deterministic (pure rules) or stochastic (mixed rules).
- The ingredients to the strategy are present and past states.
- The selection of the best strategy depends on the payoff (evolutionary stable strategies).
- Individuals whose strategies give higher payoff reproduce (and mutate).

### Example: evolution of cooperation

- Interspecies interaction can be divided into predation (or parassitism), cooperation and competition.
- Predation may lead to interspecies competition (your enemy is my friend).
- Cooperation is strongly related to competition: there is no “natural” cooperation (genes are selfish).
- Nevertheless, cooperation is common: genes, social insect, multicellular organisms, slime molds, even humans...
- So, what are the evolutionary basis of cooperation?

### Payoff

Suppose that there are only two states (card 0 and 1 or cooperate (C) and defect (D)). Players play cards at the same moment. The generic payoff table (for one of participant) is:

payoff	C	D
C	$\alpha$	$\beta$
D	$\delta$	$\gamma$

### Strategy

- A strategy can be given by a “hard” rule, that states what to play next. Given a certain memory of deals, a strategy is thus an automaton rule.
- Another possibility is to give probabilities (stochastic rule or mixed strategy).
- For memory equal to 1, a mixed strategy is just given by a probability  $p$  of playing C, and  $1 - p$  of playing D.

### Equilibrium

- Nash equilibrium: no person can increase his payoff by changing his strategy alone.
- There may be no Nash equilibrium for pure strategies, but there is always an equilibrium for mixed strategies (Nash theorem).
- In a large population, an evolutionary stable strategy (ESS) is a strategy that cannot be invaded by a single mutant.
- An “unstable” strategy may become ESS and even invade other strategies in repeated games.

## Prisoner dilemma

For instance, in the single game, with the payoff matrix

payoff	C	D
C	3	0
D	5	1

the Nash equilibrium corresponds to both payers playing  $D$  (non collaborating), even though collaboration gives higher payoff. In repeated games, it may be worth collaborating.

## Evolutionary games

- In evolutionary games, the payoff is related to fitness. One may think for instance that in a population two players are picked at random, and play one or more deals (the number of deals or the probability of ending the game is an important parameter).
- By playing, individuals accumulate payoffs (may be negative).
- After some tournament, couples of individuals ( $i$  and  $j$ ) are chosen, one of them dies and the other duplicates with mutations.
- The probability  $A(i)$  of surviving (fitness) is related to payoff ( $E(i)$  and  $E(j)$ ) and to the “temperature”  $T$

$$A(i) = \frac{1}{1 + \exp\left(\frac{E(j) - E(i)}{T}\right)}$$

## Mean field analysis

payoff	C	D
C	$\alpha$	$\beta$
D	$\delta$	$\gamma$

Let us denote with  $p$  the fraction of population “playing”  $C$  (and  $1 - p$  those playing  $D$ ). If the payoff is related to fitness

$$p' = \frac{\alpha p^2 + \beta p(1 - p)}{\alpha p^2 + \beta p(1 - p) + \delta p(1 - p) + \gamma(1 - p)^2}$$

neglecting fluctuation, the asymptotic state is given by the fixed points of the previous equations.

## Evolution on finite populations

A society of cooperators has an higher fitness than a society of defectors, but is in general susceptible to invasions or mutation by defectors. Possible scenarios are:

- (D) If the only stable point is  $p^* = 0$ , defectors always dominates.
- (ESS) If there are two stable points,  $p^* = 0$  and  $p^* = 1$ , but the latter has only a tiny basin, then cooperators are evolutive stable strategie (ESS): a single mutant cannot invade, but multiple ones can, helped by fluctuations.  $\alpha > \beta$ .
- (RD) If the basin of  $p^* = 1$  extends up to  $p_0 = 1/2$ , it is favoured by fluctuations.  $\alpha + \gamma > \beta + \delta$
- (AD) The basin extends up to  $p_0 = 2/3$  can be shown to be related to stability respect to fixation of a single mutant (Kimura theory).  $\alpha + 2\gamma > \beta + 2\delta$
- (C) Finally, if the basin extends up to  $p_0 \simeq 1$ , cooperators always dominate (except for  $p_0 = 1$ ).

## Standard payoff

payoff	C	D
C	$b - c$	$-c$
D	$b$	$0$

Benefits (may be long term like parental cares) have to be greater than costs. However, defectors always wins.

### Kin selection

Haldane one said: “I will jump inot the river to save two brothers or eight cousins”. If you cooperate with a relative that shares a fraction  $r$  of your genes, then your payoff (well, that of your genes) is augmented by a fraction  $r$  of the payoff of your opponent.

payoff	C	D
C	$(b - c)(1 + r)$	$br - c$
D	$b - rc$	0

For  $\frac{c}{b} < r$ , cooperation is ESS,RD,AD. Kin selection says that cooperation among relatives (cells in multicellular organisms, social insects) derives by selfishness of genes.

### Direct reciprocity

For a “one shot” game the best strategy is to defect. But Axelrod discovered by computer experiments that for repeated games between two opponents it is best to cooperate and to forgive: tit for tat or similar strategies. In this case the parameter is the probability  $w$  of another encounter (or the expected number  $1/w$  of rounds).

payoff	C	D
C	$(b - c)/(1 - w)$	$-c$
D	$b$	0

- ESS for  $c/b < w$
- RD for  $c/b < w/(2 - w)$
- AD for  $c/b < w/(3 - 2w)$

### Reputation (indirect reciprocity)

For humans, reputation is a valuable quantity. It is defined as the average cooperation-to defection record. It may be known with a probability  $q$ . If you know that the opponent is a defector, defect, otherwise cooperate.

payoff	C	D
C	$(b - c)$	$-c(1 - q)$
D	$b(1 - q)$	0

- ESS for  $c/b < q$
- RD for  $c/b < q/(2 - q)$
- AD for  $c/b < q/(3 - 2q)$

### Network reciprocity

Human societies are structurate networks. For a given connectivity  $k$  of a node, a cooperator pays a cost  $c$  and each of the neighbors receive a benefit  $b$ .

payoff	C	D
C	$(b - c)$	$H - c$
D	$b(1 - H)$	0

with  $H = \frac{(b-c)k-2c}{(k+1)(k-2)}$ . ESS, RD, AD for  $c/b < 1/k$

### Group selection

Group selection is based on the higher payoff of cooperation, but one has to find a mechanism for stabilizing it against defectors. The idea is that the society automatically splits into  $m$  groups of size  $n$ . Cooperators help only inside groups, and successful groups split more often.

payoff	C	D
C	$(b - c)(n + m)$	$bm - c(m + n)$
Theoretical and D	$bn$	0

ESS, RD, AD for  $c/b < m/(m + n)$ .