Evolution
Mutation
Selection
Sequence space
Fitness landscapes
Evolutionary game dynamics
Cooperation
Fairness
Evolution: major events

?  Origin of life
3500  Bacteria
1500  Eukaryotic cells
600  Multicellular organisms
1  Human language
(million years ago)
Evolution needs populations of reproducing individuals.

Evolutionary change occurs by mutation and selection.
Mutation

Genome:

...ACTATACGGCCGGCATTACCTTATTATGG...

Replication

...ACTATACGC*GGGCATTACCTTATTATATGG...
Selection
Selection

Fitness of B = 1.1

Fitness of A = 1
Selection

B out-competes A
Genomes live in sequence space

...ACTATA\textcolor{red}{C}GCGCGGTC\textcolor{red}{A}TTACCTTATTATGG...

Length, \( L \)

Arrange all sequences such that nearest neighbors differ by one point mutation. You will need \( L \) dimensions.
Genomes live in sequence space

...ACTATACGCGGCCGTCATTACCTATTATATG... 

Length, L

- a small virus  L = 10000
- a bacterium  L = 4 million
- humans  L = 3.5 billion
- newts  L = 19 billion
Genomes live in sequence space

...ACTATACGCGGCATTACCTTATTATATGG...

Length, L

- a small virus: \( L = 10000 \)
- a bacterium: \( L = 4 \text{ million} \)
- humans: \( L = 3.5 \text{ billion} \)
- newts: \( L = 19 \text{ billion} \)

\[ 4^{10000} \approx 10^{6000} \]

There are only \( 10^{80} \) protons in the universe.
Populations of genomes explore fitness landscapes

Each genome has a reproductive rate (=fitness)

Evolutionary dynamics are given by the quasispecies equation:

$$\Delta x_i = \sum_j x_j f_j Q_{ji} - \bar{f} x_i$$
Error threshold

Mutation rate (per base) < \( \frac{1}{\text{Genome length}} \)

necessary for adaptation
(=finding peaks in fitness landscape)
A special case: the **fitness landscape** is constant
In general, the **fitness landscape** changes as the population moves across sequence space.
In general, the **fitness landscape** changes as the population moves across sequence space = evolutionary game theory
Constant selection

Fitness of type A = 1

Fitness of type B = 1.1
Evolutionary game theory

Fitness depends on the relative abundance of different types.

Fitness of type A = 1
Fitness of type B = 1.1

Fitness of type A = 1
Fitness of type B = 0.9
Evolutionarily stable strategy

If every individual of a population adopts the evolutionarily stable strategy, then no mutant can invade.

Nash equilibrium
Replicator dynamics

Successful strategies spread by natural selection. Payoff = fitness.

\[ \mathbf{x}_i = x_i \left[ f_i(x) - \bar{f}(x) \right] \quad i = 1, \ldots, n \]
Successful strategies spread by natural selection. Payoff = fitness.

\[ \mathcal{A}_i = x_i [f_i(x) - \bar{f}(x)] \quad i = 1, \ldots, n \]

\[ \bar{f}(x) = \sum_i x_i f_i(x) \]
Successful strategies spread by natural selection. Payoff = fitness.

\[ \dot{x}_i = x_i [f_i(x) - \bar{f}(x)] \quad i = 1, \ldots, n \]

\[ \bar{f}(x) = \sum_i x_i f_i(x) \quad f_i(x) = \sum_j a_{ij} x_j \]
Replicator dynamics

Successful strategies spread by natural selection. Payoff = fitness.

\[ \mathbf{\Delta} = x_i [ f_i(x) - \bar{f}(x) ] \quad i = 1, \ldots, n \]

\[ \bar{f}(x) = \sum_i x_i f_i(x) \]

\[ f_i(x) = \sum_j a_{ij} x_j \]

= Lotka Volterra equation of ecology
Social insects

• Workers do not reproduce, but raise the offspring of another individual, the queen.
• How can evolution design such altruistic behavior?
Natural selection is based on competition. How can natural selection lead to cooperation?
Cooperation between relatives

Hamilton’s rule

\[ r > \frac{c}{b} \]

- \( r \) … coefficient of relatedness
- \( c \) … cost of cooperation
- \( b \) … benefit of cooperation
Cooperation between relatives

‘I will jump into the river to save 2 brothers or 8 cousins’

J.B.S Haldane
How to get cooperation between non-relatives?
<table>
<thead>
<tr>
<th></th>
<th>Cooperate: C</th>
<th>Defect: D</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C - C</strong></td>
<td>3 : 3</td>
<td><strong>C - D</strong></td>
</tr>
<tr>
<td><strong>D - C</strong></td>
<td>5 : 0</td>
<td><strong>D - D</strong></td>
</tr>
</tbody>
</table>
Rational players choose defection

\[
\text{D - D } 1 : 1
\]

but cooperation would have been better for both:

\[
\text{C - C } 3 : 3
\]

Cooperation is ‘irrational’.
Natural selection chooses defection

D wins against C
3 possibilities for the evolution of cooperation

- Direct reciprocity
- Indirect reciprocity
- Spatial reciprocity
Direct reciprocity

I help you,
but I expect we will meet again.
Then you can help me.
Repeated Prisoner’s Dilemma

Player 1 : C D C D C C C C C C ....
Player 2 : D C D D C C C C C C ....
Repeated Prisoner’s Dilemma

Player 1: C D C D C C C C ... 
Player 2: D C D D C C C C ... 

What is a good strategy for the repeated Prisoner’s Dilemma?

Robert Axelrod
Tit-for-tat

- If you cooperate, then I will cooperate.
- If you defect, then I will defect.

Anatol Rapaport
Errors destroy cooperation

Tit-for-tat: CCCCCCDCDCDCDDDDDDDDDD....

Tit-for-tat: CCCCCDCDCDCD

Tit-for-tat: CCCCCDCDCDCD

Tit-for-tat: CCCCCDCDCDCDDDDDDDD....
Let natural selection design a strategy

Random
Let natural selection design a strategy

Always defect

Random
Let natural selection design a strategy

- Tit-for-tat
- Always defect
- Random
Let natural selection design a strategy

- Tit-for-tat
- Generous Tit-for-tat
- Always defect
- Random
Generous Tit-for-tat

• If you cooperate, then I will cooperate.
• If you defect, then I will cooperate with probability 1/3.

*Never forget a good move.*
*Sometimes forgive a bad move.*
Let natural selection design a strategy

- Tit-for-tat
- Generous Tit-for-tat
- Always defect
- Random
Let natural selection design a strategy

Tit-for-tat

Always defect

Random

Generous Tit-for-tat

Always cooperate
Let natural selection design a strategy

Tit-for-tat \(\rightarrow\) Generous Tit-for-tat

Always defect \(\rightarrow\) Always cooperate

War and peace
Let natural selection design a strategy

- Tit-for-tat
- Generous Tit-for-tat
- Always defect
- Always cooperate
- Win-stay, lose-shift
Win-stay, lose-shift

Win-stay:
C (3) .... C  D (5) .... D
C
C

Lose-shift:
C (0) .... D  D (1) .... C  (probabilistic)
D
D

Fudenberg & Maskin
Experimental observations

Manfred Milinski
Direct reciprocity

‘I help you, you help me.’
Indirect reciprocity

‘I help you, somebody else helps me.’
## Indirect reciprocity

<table>
<thead>
<tr>
<th></th>
<th>donor</th>
<th>recipient</th>
<th>donor’s reputation</th>
</tr>
</thead>
<tbody>
<tr>
<td>cooperate</td>
<td>-c</td>
<td>+b</td>
<td>+1</td>
</tr>
<tr>
<td>defect</td>
<td>0</td>
<td>0</td>
<td>-1</td>
</tr>
</tbody>
</table>
Natural selection chooses strategies that base their decision to cooperate on the reputation of the recipient: ‘help those who have helped others’

*Give and you shall receive.*
A rule for indirect reciprocity

$q > \frac{c}{b}$

$q \ldots$ probability to know someone’s reputation
$c \ldots$ cost of cooperation
$b \ldots$ benefit of cooperation
A universal constant of nature

- 0.7380294688… is the maximum fraction of people who can be bad in the beginning such that everyone will be good in the end
Spatial reciprocity

Cooperators
Defectors
Spatial reciprocity

Von Neumann invented both game theory and cellular automata.
Fairness
Ultimatum Game

Proposer makes an offer.

$1,000,000
Ultimatum Game

Proposer makes an offer.

$1,000,000

Responder says yes or no.
Ultimatum Game

Proposer makes an offer.

Responder says yes or no.

$100
What does game theory suggest?

- A ‘rational’ responder should prefer $1 to $0.
- Therefore, a ‘rational’ proposer should offer $1 and keep almost the whole sum.
What do the experiments show?

- People are not ‘rational’.
- Most proposers offer 30-50%.
- Most responders reject offers below 30%.
Evolutionary ultimatum

Strategies $S(p,q)$

$p$...offer when proposer

$q$...minimum acceptance level when responder
Evolutionary ultimatum

Strategies \( S(p,q) \)

\( p \) … offer when proposer

\( q \) … minimum acceptance level when responder
Evolutionary ultimatum

Strategies $S(p,q)$

$p$...offer when proposer

$q$...minimum acceptance level when responder

The rational strategy $S(0,0)$
Strategies $S(p,q)$
$p$...offer when proposer
$q$...minimum acceptance level when responder

The rational strategy $S(0,0)$
The fair strategy $S(1/2,1/2)$
Evolutionary dynamics

The rational strategy $S(0,0)$
Natural selection chooses

- ... low offers, low demands.
- It costs to reject offers, therefore low acceptance levels are favored.
- If acceptance levels decline, then offers will decline too.
How can we explain the evolution of fairness?
Reputation

- Suppose there is a chance that it will become known what offer a person has accepted.

- Accepting low offers increases the probability of receiving reduced offers in the future.

- Rejecting low offers is costly, but buys the reputation of being someone who demands a fair share.
Evolutionary dynamics

The fair strategy $S(1/2,1/2)$
The most fascinating game that evolution plays...

... is human language.
Program for **Evolutionary dynamics**

- Games in finite populations
- Evolutionary graph theory
- Evolution of language
- Learning
- Somatic evolution of cancer
- Evolution of infectious agents
- Phenotypic error-thresholds
- Evolution of multi-cellularity

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