Genes, populations and evolution

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Course for the interdisciplinary program
"Behavior, Economics, and Evolution" (BEE)
of the University of Lausanne

Short timeline of history

- circa 13.8 billion years (ya): matter and energy appear. Beginning of physics. Atoms and molecules appear. Beginning of chemistry.
- circa 4.5 billion ya: formation of planet Earth.
- circa 3.7 billion ya: emergence of self-replicating molecules. Beginning of biology.
- circa 2.5 million ya: emergence of the genus *Homo* in Africa. Beginning of technology.
- circa 100-70 thousand ya: Language becomes fully operational and bargaining becomes possible. Beginning of economics.

Broad goals of the course

- Introduction to the quantitative theory of evolution: provides an ultimate reason for morphological, physiological, and behavioral traits.
- Because economics deals with interacting behavior, it makes sense to have some knowledge of how behaviors evolve and what are their genetic underpinnings.
- Foundation for the biology BEE courses of semester 4.2

Practicals

- 14 times 2 hours of course + 2 hours of exercise (Friday afternoon, 12h30-14h00, room 5033).
- Lecture notes are posted each week along the lecture slides on Moodle. The password (enrolment key) is Darwin.
- Oral exam, 15 minutes. (details will be given in due course).

Two parts to the course

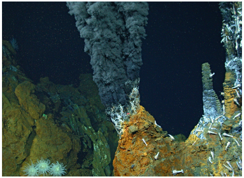
- Today: stylized facts about life on earth and evolution, genetics, and overview and motivation of the course for economists.

- Rest of the semester: formalization and modeling of evolution. Mainly simple mathematical models motivated by concrete real life examples pertaining to humans and other species.

- Overall requirements: basic algebra, probability, and calculus, while most high-school genetics will be recalled during the course.

The creation

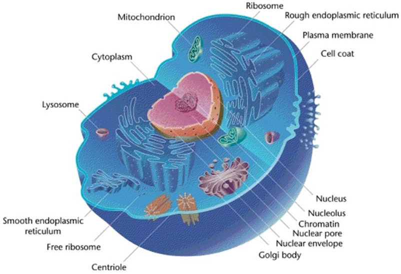
Life on Earth presumably finds its origins at the bottom of the ocean, in a phase transition that took place in hydrothermal vents (fissures in earths surface with hot water).

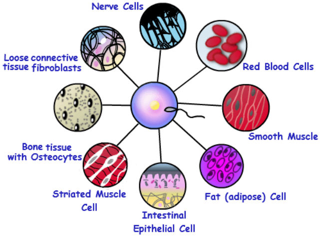


- Regardless of the exact nature of life's origin, we know that this led to the emergence of self-replicating molecules, which transformed over millions of years into the first reproducing organisms.
- About 10 to 50 million plant and animal species live on earth today. There are also billions or trillions of bacteria types and untold numbers of fungi, algae, and archae.

The basic functional biological unit is the cell

Every living organism, from bacteria to plants to animals, is made of cells, whose number is about 3×10^{13} (about 30 trillions) in an adult human.

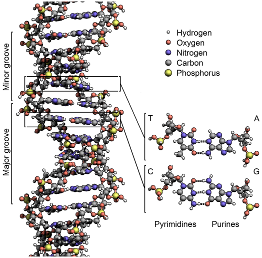




Cells are of different types (e.g., skin cells, muscle cells, neurons, blood cells, stem cells, and others), and they all have an outer membrane containing the many biomolecules making up the cell.

Cells contain the hereditary information carrier DNA

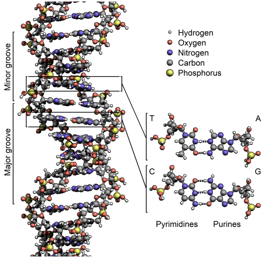
- Cells of higher organisms (such as plants and animals) also contain a nucleus, a spherical body centrally located that contains the material *deoxyribonucleic acid* (DNA).
- DNA carries the hereditary information used in the growth, development, and reproduction of living organisms, and thus the synthesis of organisms.
- DNA is an organism's executive code.



Cells contain the hereditary information carrier DNA

- DNA is a long complex molecule who's key ingredients are four nucleobases (or bases for short): adenine (A), guanine (G), thymine (T), and cytosine (C).

- These nucleotides are linked to each other in a sequence and arranged in a double helix. The pairing being always A-T and G-C. Therefore the information carried by DNA is in the sequence along a single helix, say a sequence like:

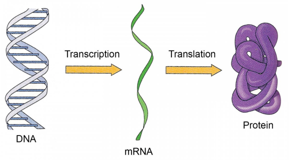


ATGCACGTATAGGATTTTAG

Cells contain the hereditary information carrier DNA

- Genes are specific regions of DNA where three nucleotides in a row code for an amino acid and a sequence of amino acid codes for a protein (genes are on average 2000 nucleotide long)[1].

- A protein (contains one or several folded chains of amino acids) is the main biomolecule performing the functions within the cell, including metabolic reactions, DNA replication, etc.



[1] Not all of the DNA (roughly about 6.4×10^9 bases long in humans) encodes biological information and DNA is usually decomposed into regions of interest. A *gene* is roughly the region of DNA that codes for an amino acid chain and thus a simple protein (there are 20000 human protein-coding genes).

The central dogma of biology

We thus have a two step process:

1. DNA is translated by the cell machinery into proteins.
2. Proteins themselves subtend the main biological functions of the organism.

This yields the following arrow of causation in all organisms

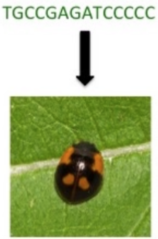
$$\text{DNA} \quad \longrightarrow \quad \text{proteins} \quad \longrightarrow \quad \text{organismic features}$$

This says that DNA influence organismic features, but not the other way round.[2]

[2] There are exceptions to this rule but they are beyond the scope of this course.

The central dogma of biology simplified

- The phenotype of an individual comprises any molecular, physiological, morphological, or behavioral trait.
- The genotype of an individual is the set of all its genes and thus consists of the DNA sequences affecting phenotype.



We can thus look at the arrow of causation in this simplified way without considering explicitly molecular biology

$$\text{genotype} \quad \longrightarrow \quad \text{phenotype(s)}$$

Gene and environmental interactions

A more accurate representation of an individual's phenotype is

$$\text{genotype} \times \text{environment} \quad \longrightarrow \quad \text{phenotype(s)}$$

This mutliplication cross $\times$ here means that the genotype interacts with the enviroment to produce an individual's phenotype, an important point to which we will return later in this course.

The fact that the phenotype is also influenced by the environment leads to the nature-nurture question.

The nature-nurture question

The three laws of behavior genetics (Turkheimer, 2001):

1. All human behavioral traits (phenotypes) are heritable.
2. The effect on behavior of being raised in the same family is smaller than the effect of genes.
3. A substantial portion of complex human traits is not accounted for by the effect of genes or families.

This implies that all phenotypes are influenced by the genotype and it is useful to study the concept of heritability to understand what this really means, which will be carried out in the course and turns out to be tightly related to concepts studied in econometrics.

The two hallmarks of living systems

In addition to the distinctive arrow of causation in biological organisms, going from gene(s) to phenotype, living systems are also characterized by two additional hallmarks.

1. Diversity. Organisms come in a tremendous diversity of forms.
2. Functional organization (agency). All organisms display purposefulness in form and goal-directedness in behavior.

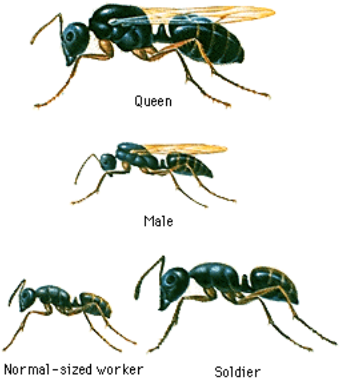
The diversity of life

About 10 to 50 million of animal and plant species live on earth today and they are everywhere (at leat a trillion of microbe types).

Maybe about 10 billion species lived on earth.

The diversity of morphologies

Organisms within the same species express very different morphologies.



The diversity of physiologies

Organisms express very different physiological states during their lifespan.

The diversity of behavior (and cultures)

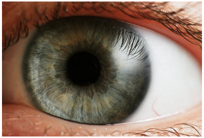
Organisms express very different behaviors.

Purposefulness (or agency) of organisms

From physiological structures within individuals to behavioral interactions between them, organisms have the appearance of design.

wings are built to fly

eyes are built to see



carapaces are built to protect

jaws are built to tear appart

The central question

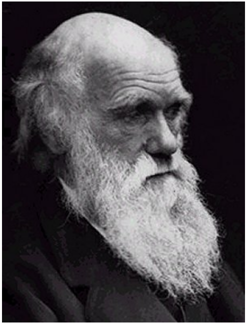
- Can we provide a scientific coherent explanation and rationalization of the two hallmarks of living systems (diversity and design)?

- This question is studied by the field of evolutionary biology, and the broad answer is YES. The arguments that will be developed in detail in this course relies on two facts about living systems, first discussed by Charles Darwin.

The course will focus more on the aspect of purposefulness and agency of organisms rather than explaining the maintenance of diversity.

Charles Darwin: common descent and evolution

Two crucial facts.



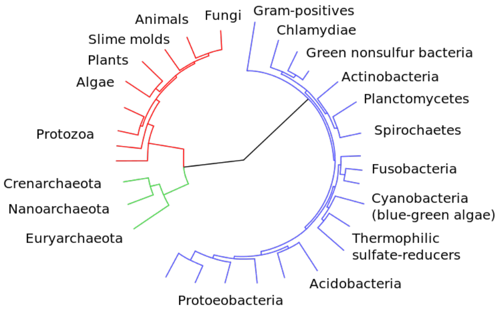
1. All existing organisms are modified descendants of one or a few ancestors that arose on Earth in the distant past.
2. Organisms evolve. Evolution is broadly defined as the change in phenotypes or traits over time.

The Darwinian revolution forced people to face the fact that humans are part of nature.

(On the origin of species, 1859)

The tree of life

As we now know the common ancestor originated about 3.9 billion years ago and gave rise to three domains of life: bacteria, archea, and eukaryotes (includes plants and animals).



Reconstruction based on comparing genetic material as all organisms have the same genetic code.

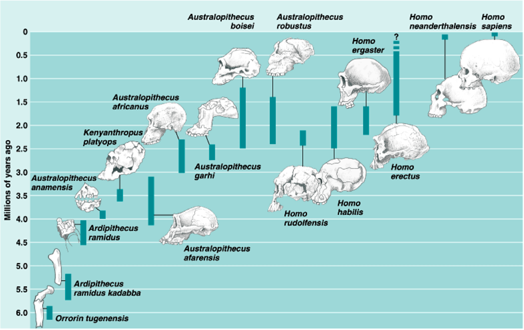
The evidence for evolutionary change

1. The fossil record.
2. Artificial evolution.
3. Experimental evolution.
4. Evolution within us.

(The Evidence of Evolution, A. Rogers, 2011)

Fossils: human lineage

- Human lineage split off from its common ancestor with the big apes about 6 millions years ago.
- Many intermediate steps and patterns of relationship have been documented.



Sequence of fossils documenting increase in brain size

Artificial evolution

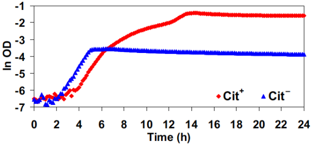
Anything we eat we had evolve!

1957 (panel a) and 2001 (panel b) broiler (chicken for roasting) carcasses taken at different ages. From left to right: 43, 57, 71, and 85 days old.

Change in trait values in a population can be dramatically fast!

Experimental evolution

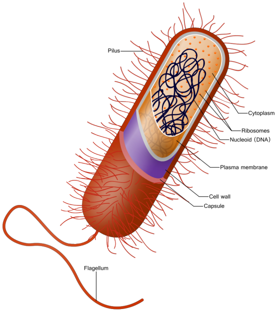
- The *Esherishia coli* long-term experiment is an experimental evolution led by Richard Lenski that started in 1988. This bacteria evolved towards being able to use a new resource (citrate) after 31500 generations, and caused an increase in population size and diversity.



(Zachary et al., 2008)

Evolution within us

- Bacteria become resistant to antibiotics (e.g, tuberculosis).
- Cancerous cells differentiate and can also become resistant to chemotherapy.



Understanding host and disease or pathogen coevolution is fundamental for many health issues in humans.

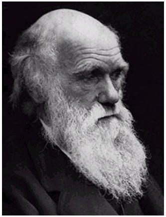
Evolution there is but what is the mechanism?

- That organisms evolve and have common ancestry is nowadays as factual as the Earth is round.
- The real question, however, is how does evolution occur?

Answering this question should help answering the question of where organisms' agency comes from.

Natural selection: a mechanism of evolution

Darwin argued that the main driver of organic evolution is natural selection. This results from three conditions:



1. Living organisms reproduce.
2. Living organisms vary in their reproductive and survival abilities.
3. Living organisms display heredity: like begets like.

If variation in trait value is inherited from one time step to the next and affects reproduction, then natural selection occurs.

Natural selection explains the appearance of design

Natural selection not only predicts evolutionary change, it explains why individual are adapted to their environment and display the appearance of design.

- Binocular vision solves the puzzle of catching camouflaged preys as it allows to perceive depth.
- It solves a reproductive puzzle.

This is the idea of the "survival of the fittest".

Darwin: a reason for everything?

Darwin argued that if we want to understand the purpose of a trait (the ultimate cause), we need to understand what reproductive and survival puzzle is solved by expressing it.

- Why are there boys and girls?
- Why do we live in groups?
- Why are we in conflict with parents and siblings?
- Why do we age?
- Why do we have consciousness?
- Why do we trees have autumn colours?

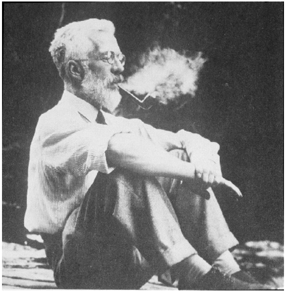
Concrete example: sex ratio

- Since males compete for females, the resource allocation of a female to producing sons and daughters should be 1/2.
- This can be understood as an outcome of natural selection.

Evolutionary theory predicts well the evolutionary stable sex-ratio (the long term phenotypic equilibrium in a population).

Evolution is not natural selection

- Natural selection is a driver of evolution, it is what we call an evolutionary force.
- There are other evolutionary forces.



R. A. Fisher, one of the founder of modern statistics and quantitative evolutionary biology.

(The Genetical Theory of Natural Selection, Fisher, 1930)

Mutation: appearance of diversity is an evolutionary force

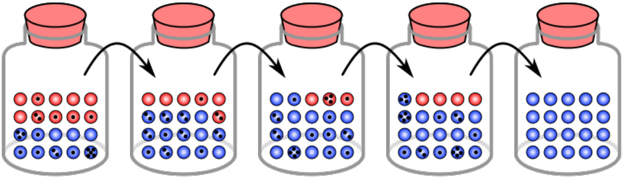
DNA is not fully stable and there can be spontaneous changes.

- Mutations are random changes in the genetic material.
- Without mutations there would be no change.
- Evolution thus depends on both chance and necessity.

Albino girl from Papua New Guinea, resulting from a mutation in an enzyme synthesizing melanin

Random genetic drift: a stochastic evolutionary force

Owing to finite population size, populations are subject to sampling drift since by chance not everybody reproduces.



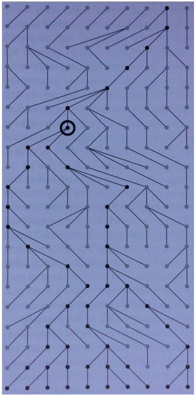
Repeated sampling

Genetic drift leads to the loss of diversity.

Random genetic drift: loss of diversity and study of ancestry

Genetic drift leads to the survival of the "luckiest".

- The genetic code is redundant and synonymous mutations evolve by random drift.
- Evidence that genome complexity (genome size) has evolved by random drift.



The three evolutionary forces

Organic evolution depends on three evolutionary forces:

1. Natural selection.
2. Mutation.
3. Random drift.

- We will study all these forces and their interplay. But we will develop most intensively natural selection because this is the force that explains adaptation.
- Once we understand these forces we can investigate the evolution of relevant traits behaviors (life history evolution, evolution of resource consumption and competition).

All of life is social

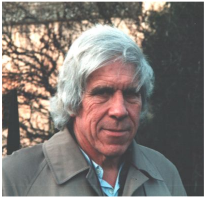
Interactions between individuals occur at essentially all levels of life.

Evolution needs to be investigated in an interactive, ecological and game theoretic context. Modern evolutionary biology is to a large extend the study of cooperation and conflict at all scales.

The genetical theory of social behavior

- Some social behaviors are puzzling to explain in a classical Darwinian framework such as altruism and sexual reproduction.

- This can be understood by realizing that phenotypes solve reproductive puzzles at the level of the gene.

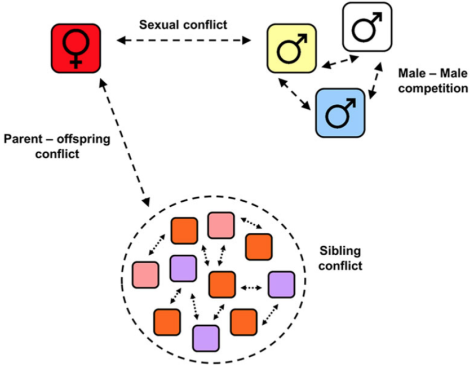


W. D. Hamilton

The Hamiltonian revolution forced people to face the fact that adaptation are “good” not for the individual but for the gene so deep inside ourselves there is no individual unity.

This leads to many predictions about the evolution of behavior in social interactions, in particular to conflict between individuals.

The web of family interactions and potential conflicts: sexual selection and kin selection



We will investigate how natural selection shapes interactions (cooperation and conflict) among family members (male-female interactions, parent-offspring conflict, and sibling rivalry, and genomic impriting).

Evolution is a complicated process

- Multidimensional and multifactorial.
- Different forces involved occur at different time-scales.
- Extremely interactive ("game theoretic" like).
- Difficult to appreciate the subtleties and implications without studying it.

So why should economists study this? There are several reasons.

(1) Charles Darwin, microeconomist

Natural selection is a model of a competitive process.

- Success depends on how well an individual fares relative to others.
- Absolute strength or smartness does not matter. What matters is how well you do relative to others.
- Adam Smith's invisible hand (and modern general equilibrium theory) is a model of a competitive process where absolute success matters.

The invisible hand model is thus a special case of natural selection. Understanding the consequence of relative success can be helpful to economics.

(2) Charles Darwin, political economist

An economy (or an organization or a society) is a humanly devised system of interaction.

- The economic (or societal) rules are the result of an evolutionary process (cultural).
- The economy is the outcome of a gene-culture coevolutionary process.
- Economics is rather silent on the origin of economics.

Understanding how social systems evolve in organisms can be useful to economics for at least three reasons.

(3) Charles Darwin, behavioral economist

What are humans goals and motivations?

- Human motivations reside in the brain.
- The mechanistic causes of behavior and the functioning of the brain are difficult to ascertain without knowing what behavior is supposed to achieve.
- Different hypothesis, e.g., modularity of mind, domain general rationality, computational theory of mind, "selfishness", "prosociality".

The Darwinian framework is the method to understand how the brain has evolved to steer behavior. It allows to formulate consistent hypothesis and separate proximate from ultimate causes of behavior.

Summary: use of evolutionary biology for economists

- Understanding of the main forces driving change in nature.
- Self-understanding and clarification of nature-nurture issue.
- Micro-foundations for behavioral economics.
- Emphasize the role of both chance and necessity.

However, there are no concrete tools or concepts that apply to say management. This is a pure science class.

Genes, populations and evolution: main ingredients

In the remainder of this course we will study:

- Population dynamics as this subtend any evolutionary process.
- The three evolutionary forces: selection, mutation, and drift.
- Long term adaptive dynamics and evolution of interactions within the family (cooperation and conflict).
- Heritability and multifactorial trait determination ("nature-nurture" question).

Overall requirements: basic algebra, probability, and calculus, while most high-school genetics will be recalled during the course.

You will have self-consistent lecture notes but some books may nevertheless be useful:

- "The Selfish Gene", by R. Dawkins.
- "Climbing Mount Improbable", by R. Dawkins.
- "Population Genetics: a Concise Guide", by J. Gillespie.
- "Evolution", by N. Barton, D. Briggs, D. Godstein, and N. Patel.