

Evolutionary biology

Introduction

Definition of evolution:

Evolution means biological change over time. Phenotypes vary in a population and whose frequencies change over time and are encoded by heritable genotypes.

Darwinian evolution:

Species change over time due to microevolution (change in allele frequencies), lineages split and diverge, resulting in speciation. New-life forms derive from older forms (macroevolution) and all life forms derive from a common ancestor. Descent with modification together with survival of the fittest leads to adaption of a population over time.

Observance of evolution:

- Microevolution
- Indirect observation via macroevolution: Law of succession, general pattern of correspondence between fossil and living forms
- Speciation: evidence of single species (called Ringarten) splitting into two (are already too different when they meet again and thus cannot reproduce anymore)
- Bacterial adaption to antibiotic stress
- Adaption of species of a higher trophic level due to migrated species of a lower trophic level
- Rudimentary traits and vestigial structures: f. ex. all birds have wings, but not all birds can fly or the coccyx (Steissbein), appendix (may be safe house for good bacteria) or goose bumps of humans
- Transitional forms: Archaeopteryx shares trait with dinosaurs (reptilian traits) and today's birds (avian traits)
- Homologies: the same organ in different animals under every variety of form and function
- Molecular biology: based on RNA-coding genes can common ancestry be shown
- Artificial selection

Natural selection – The process underlying adaptive evolution

Natural selection is the process of selecting individuals with favourable traits according to the current environment. It acts on individuals, but its consequences occur in populations. Natural selection cannot optimise all traits at once, it only leads to adaption, not to perfection. It is non-random, but not progressive either and always one step behind the present.

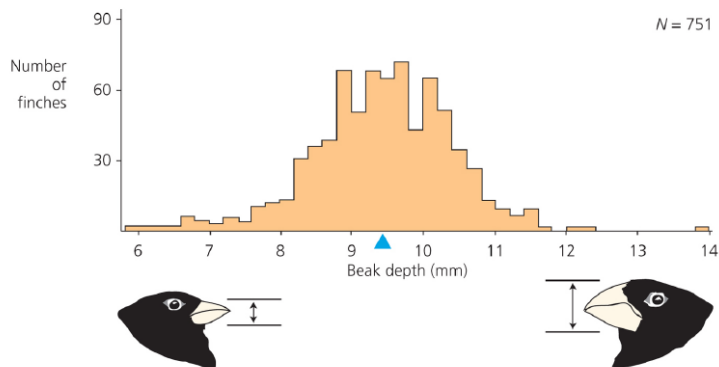
Darwin studied domestic selection and concluded, that there must be a similar process in nature only slower. He noted that the reproductive capacities of organisms always exceed their potentials and thus formulated the following postulates, which held the given data:

Darwin's four postulates:

1. All populations contain variable individuals
2. Variations among individuals are heritable
3. Some individuals are more successful at surviving and breeding
4. Individuals with the most favourable variation given the environment are more successful at surviving and reproducing.

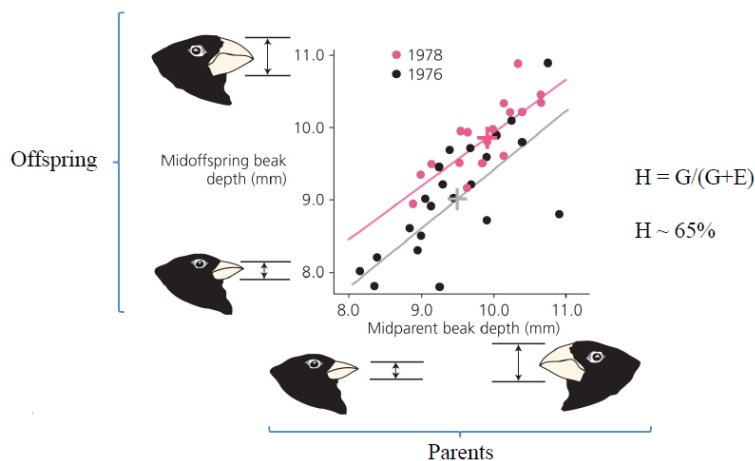
On the Galapagos islands he studied different finches, all endemic species. To test the first postulate, he looked at the beak depth of the finches, which gave result to a Gaussian bell curve.

Postulate 1: Is the Finch population variable?

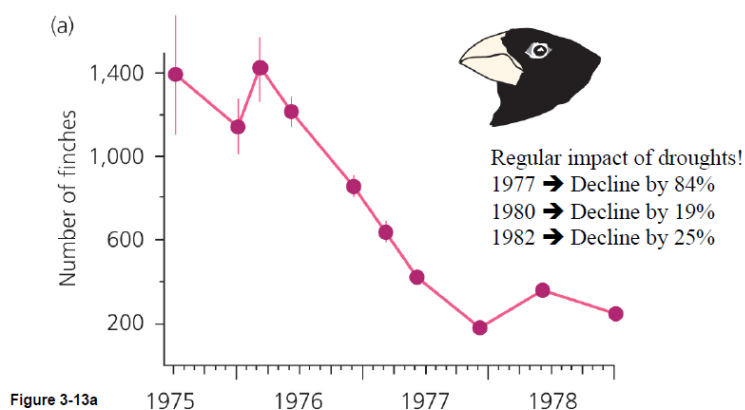


To test the second postulate, he looked at the heritability of beak depths. Heritability is ... Factors, which bias heritability measures, are misidentified paternity or maternity, food abundance and quality and maternal effects concerning the egg quality.

Postulate 2: Is (some) of the variation among individuals heritable?

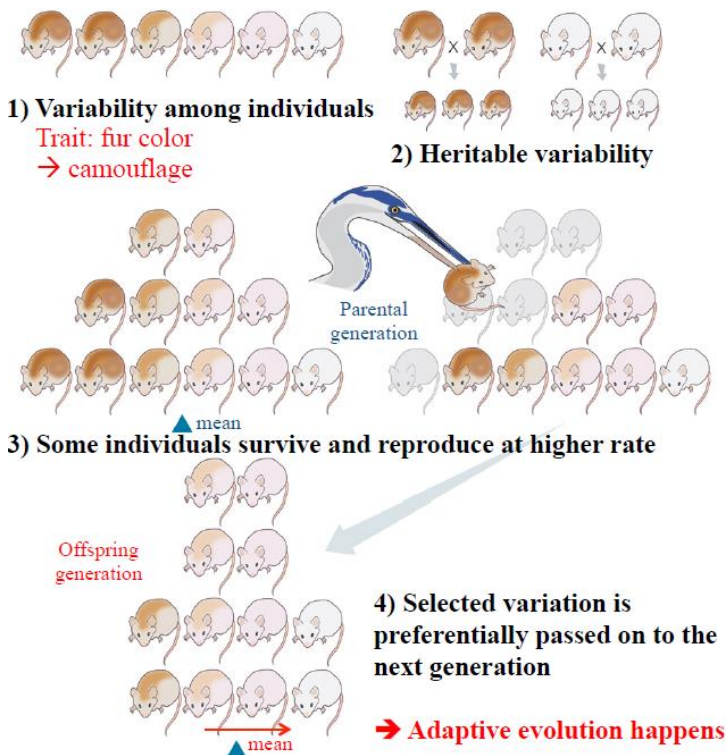
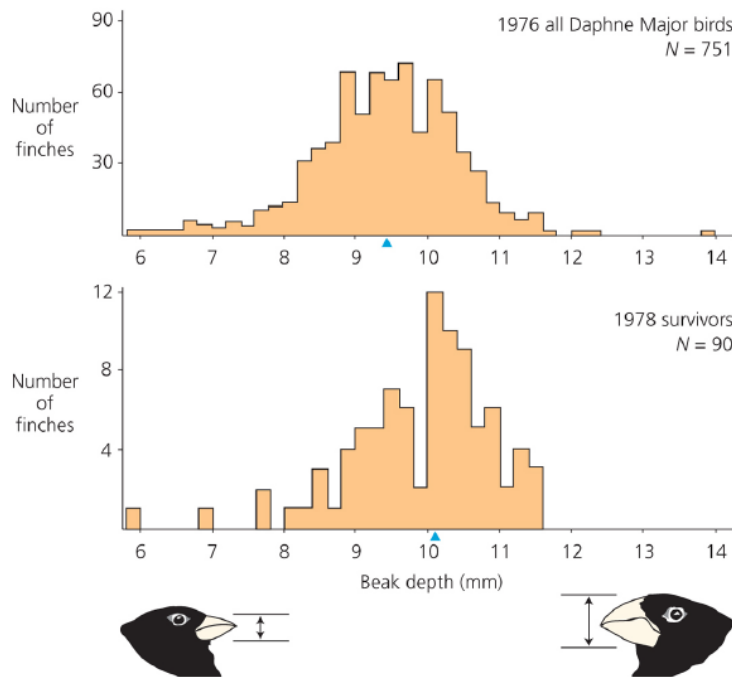


To test the third postulate, he wanted to find out, if there are differences among individuals in survival and reproduction. He noted, that after a major drought less finches survived.



Darwin noted, that finches with bigger beaks survived, because after the drought the seeds had thicker coats, thus he tested postulate number four.

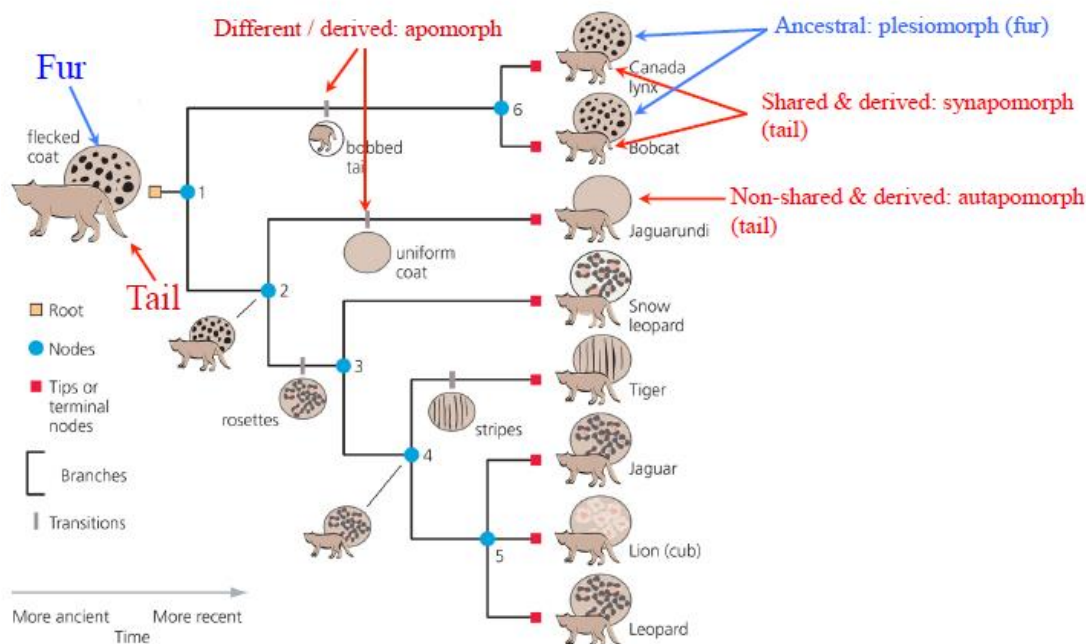
Postulate 4: Is **survival** non-random?



Lamarckian evolution:

Lamarck was the first to develop a coherent theory of evolution. Inheritance of acquired characters (LAC) can be used in epigenetics. Certain genes can be switched on or off for example by methyl groups. After a famine, up to two generations had epigenetic changes. Lamarckian evolution is more short-termed and does not influence the genes themselves but the chromosomal packaging.

Phylogenetics



Terminology

Basal group: Group which is closest related to the common ancestor (root)

Plesiomorph: a trait is the same in the root

Apomorphy: A novel evolutionary trait that is unique to a particular species and all its descendants and which can be used as a defining character for a species or group in phylogenetic terms

Synapomorphy: Shared, derived (different), homologous traits, used to determine phylogenetic trees

Autapomorphy: non-shared, but derived traits, cannot be used to determine phylogenetic trees

Homoplasy: traits shared by several species but not by their common ancestor (convergence)

Polytomy: not enough data to distinguish these groups

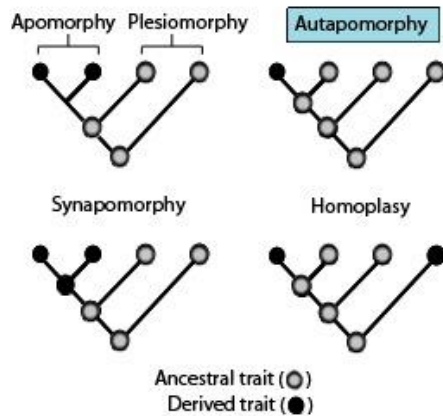
Monophyletic group: a group with a common ancestor and all descendants (clade)

Paraphyletic group: a group with a common ancestor, but without all descendants

Cladistics: search of monophyletic groups

Phylogeny: represents the evolutionary history of species. It visualises the timing and pattern of diversification events.

The parsimony principle: The phylogenetic tree with the least evolutionary steps is usually preferred. If there are several parsimonious trees, the bootstrapping procedure which generates bootstrap replicate (statistically randomised bases). Calculations with maximum likelihood and molecular clocks (lice example)



Used data:

- Skeletal features and other morphological traits
- DNA sequence (each nucleotide is viewed as an independent character)

Co-option & Mutation

Deduction and Induction

Deduction: inferences from general to particular. Given the truth of an assumption, a valid deduction guarantees the truth of the conclusion.

Induction: infers generalisation based on individual instances that support its conclusion without guaranteeing its truth.

Aristotle's four causes (only two are relevant for this course)

- **Efficient cause:** cause-effect relation
- **Final cause:** the purpose for which a thing exists, or an action is done.

Co-option

Co-option or exaptation is the process by which a structure or system with an original function adds or changes to a new function.

Myxococcus xanthus

Myxococcus xanthus are very social bacteria, that have two different modes of moving: one is individual movement (A for Adventurous motility by rotating the focal adhesion points), the other requires cell-cell interactions and is called S for social motility (type IV pili at cell poles). Thus, they can digest other bacteria, yeast and fungi. They show a social multicellular development and monitor their cell density by quorum sensing. Their social interaction gives rise to "cheaters", which are more fit in a community but go extinct alone.

Sources of phenotypic variation

- Genetic variation
- Environmental variation
- Genotype x environment variation: genetic differences cause distinct individuals to respond
- environmental variation differently

Mutations

Base-pair matching during synthesis is very accurate, because of mismatch repair. "Mutation Accumulation Lines" are used to look at mutations.

Calculating Mutation Rates from “Mutation Accumulation Lines”

Maintain 25 replicate lineages.

Grow for 500 generations.

Sequence one chromosome (say chromosome X, 130,000,000 base-pairs long) from ancestor and one from individual taken from each replicate lineage.

You find a total of 35,000 mutations among the 25 terminal individuals (average of 1400 in each).

What is the average mutation rate per base-pair per generation?

Total # of mutations/(# of bps x # of generations x # of lineages) =
 $35,000 / (130,000,000 \text{ bps} \times 500 \text{ gen.} \times 25 \text{ lineages}) =$
 2.1×10^{-8} mutations per bp per generation.

If there are 130,000 genes on the chromosome, what is the average mutation rate per gene per generation?

2.1×10^{-5} mutations per gene per generation.

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New genes

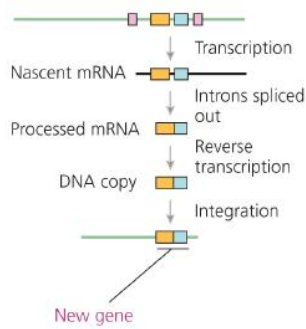
(b) **Retro-transposition:** results in genes without intron or regulatory regions in eukaryotes (reverse transcriptase needed, that transcribe RNA into DNA, resulting in a non-functional gene, if there is no promoter, but it can be functional if it is transcribed along with other genes).

(a) **Unequal crossing-over during meiosis:** results in new copies with introns and regulatory regions.

Over time new gene copies can either be lost, deactivated or retained as pseudogene or it can diverge to serve a different function. **Paralogs** are intra-specific homologs. **Orthologs** are inter-specific homologs.

(c) **Instant genome expansion:** a mutation causes the production of diploid gametes and self-fertilisation in the next generation occurs ($2n + 2n = 4n$), meaning a massive new input of genetic material that can evolve. This is common in plants, especially in self-fertilisers, but only in very few animals e.g. in salmon.

(b) Duplication by retroposition



(a) Duplication by unequal crossing over

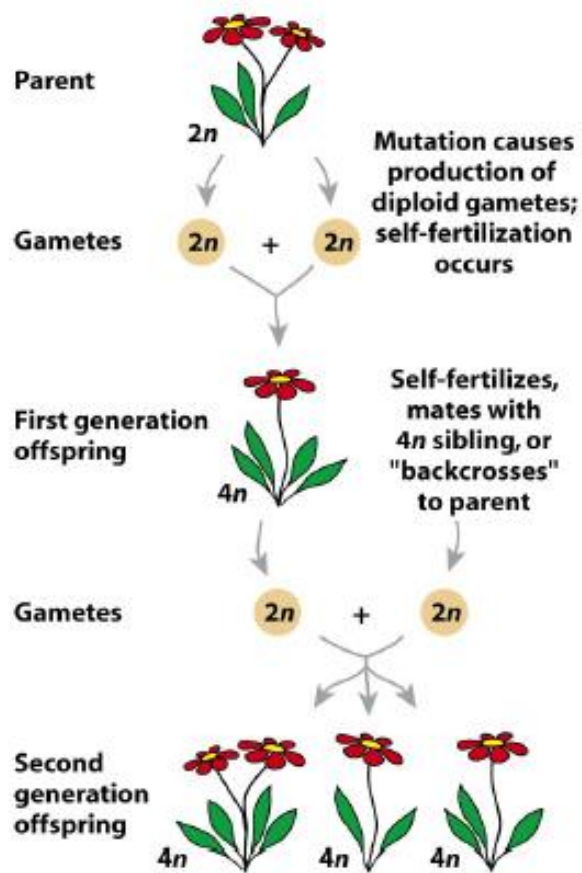
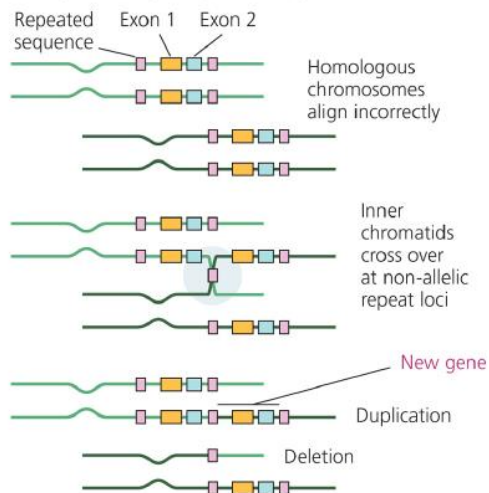


Table 5.2 Types of mutation with significant evolutionary impact: A summary

Name	Description	Mechanism	Significance
Point mutation	Base pair substitutions in DNA sequences	Chance errors during DNA synthesis or during repair of damaged DNA	Creates new alleles
Chromosome inversion	Flipping of a chromosome segment, so order of genes along the chromosome changes	Breaks in DNA caused by radiation or other insults	Alleles inside the inversion are likely to be transmitted together, as a unit
Gene duplication	Duplication of a short stretch of DNA, creating an extra copy of the sequence	Unequal crossing-over during meiosis or retrotransposition	Redundant new genes may acquire new functions, by mutation
Genome duplication	Addition of a complete set of chromosomes	Errors in meiosis or (in plants) mitosis	May create new species; massive gene duplication

Populations genetic

Seeks to document and explain changes in allele, genotype and phenotype frequencies. This offers a quantifiable definition of evolution in a population. It integrates Darwin's theory of evolution by natural selection with Mendelian genetics and seeks to quantify evolutionary change over time.

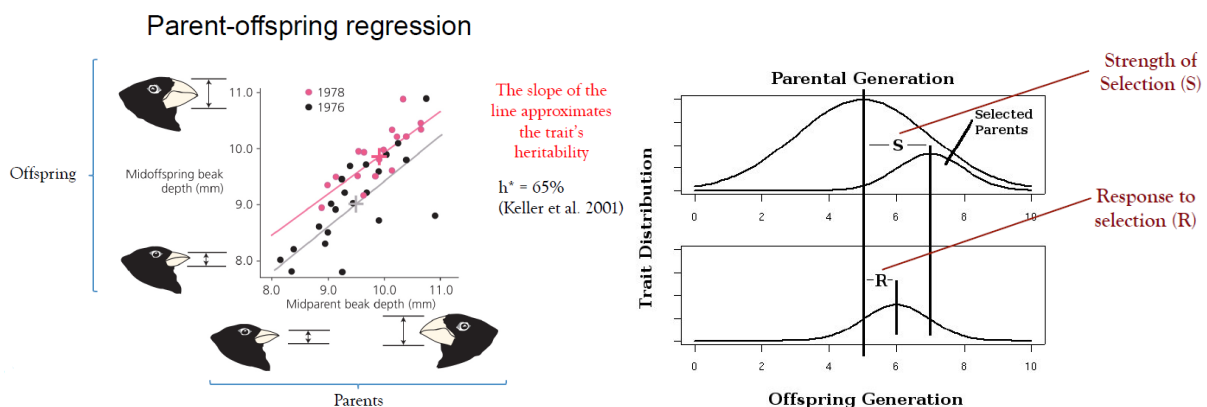
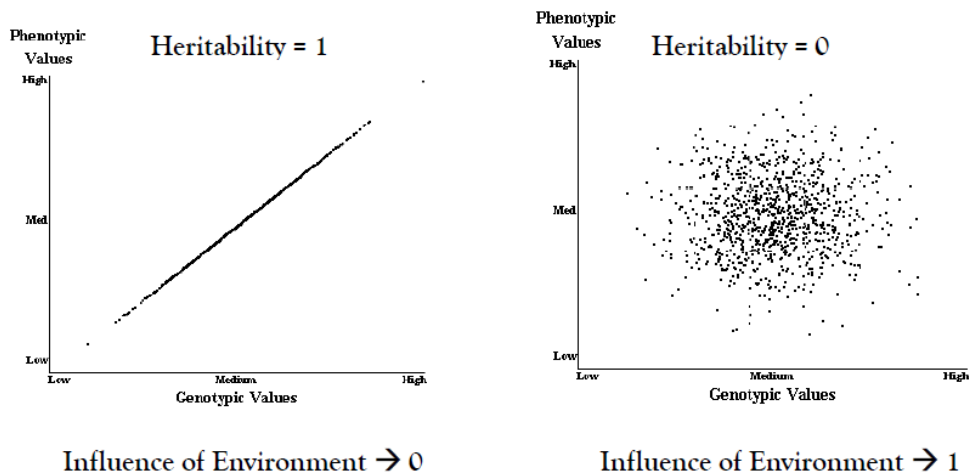
Heritability:

Variance of genotype divided by variance of phenotype.

$$h^2 = \frac{\sigma_G^2}{\sigma_P^2}$$

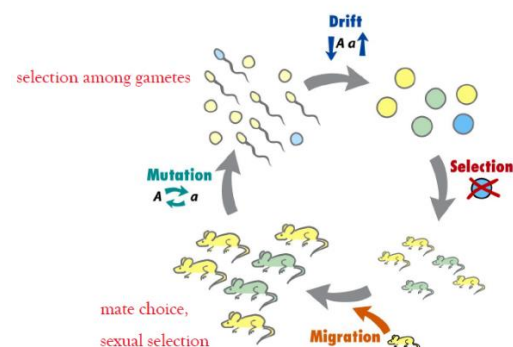
Other: Heritability H is the response to selection R (mean of offspring generation – mean of parental generation) divided by the strength of selection S (mean of selected individuals from parental generation – mean of parental generation).

$$H = \frac{R}{S}$$



The forces causing evolution in real populations:

- Mutation
- Selection among gametes
- Genetic drift
- Selection
- Migration of genes
- Mate choice, sexual selection



The Hardy-Weinberg-Principle:

The ideal population does not evolve. This requires an infinite population size, random mating among individuals, no selection, mutation, migration or genetic drift. The HWP is a null model against which one tests if a population is evolving or not. The laws of mendelian genetics are obeyed. Allele frequencies remain stable at any rate between 0 and 1.

Calculating genotype and allele frequencies in a Punnett square:

	AA	Aa	aa	N (no. of individuals)	N (no. of alleles)
f(genotype)	36/100 (f(AA))	48/100 (f(Aa))	16/100 (f(aa))	100	200
f(A) allele freq. p	(36+36+48)/200 = 0.6				
f(a) allele freq. q	(48+16+16)/200 = 0.4				
f(A)+f(a)	1 (must always add up to 1)				

HWE equation: $p^2 + 2pq + q^2 = 1$

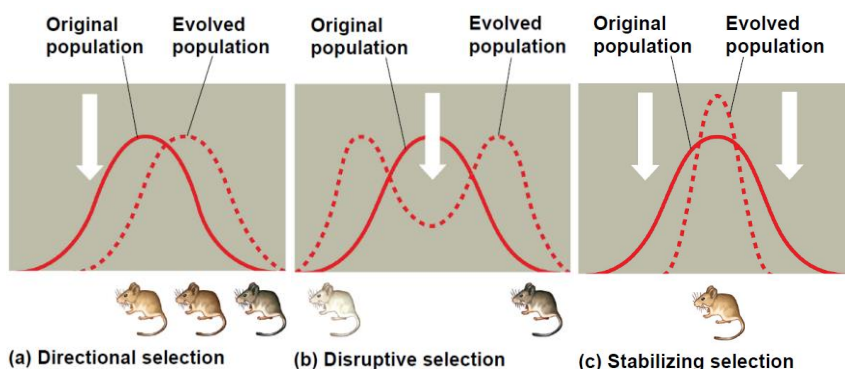
General: $\sum_i^n (p_i)^2$

Violations of the HWE:

- Allele frequencies change over time
- Genotype frequencies (p^2 , $2pq$, q^2) do not meet numbers of observed genotype (f(AA), f(Aa), f(aa))

Selective forces:

- **Directional selection:** mean changes, but variance remains, favours one extreme phenotypes
- **Disruptive selection (bimodal):** mean remains, variance increases, favours all extreme phenotypes
- **Stabilising selection:** mean remains, variance decreases, acts against extreme phenotypes
- Frequency-dependent selection: the fitness of a phenotype depends on its frequency in the population. **Positive FDS** is when the phenotype increases if it becomes most common in the population, favours the most common phenotype. **Negative FDS** when the phenotype declines if it becomes most common in the population, acts against the more common phenotype.



Selection coefficient s: Fitness w (relative reproductive success) is inversely correlated to the selection coefficient s . The larger s , the faster allele frequencies change.

$$w = 1 - s$$

Average fitness of the population: $w = p^2 \cdot w(AA) + 2pq \cdot w(Aa) + q^2 \cdot w(aa)$

Genotype frequencies after selection: $f'(AA) = p^2 \cdot \frac{w(AA)}{w}$

$$f'(Aa) = 2pq \cdot \frac{w(Aa)}{w}$$

$$f'(aa) = q^2 \cdot \frac{w(aa)}{w}$$

Allele frequencies among gametes after selection and random mating:

$$f'(A) = p' = f'(AA) + \frac{1}{2} \cdot f'(Aa)$$

$$f'(a) = q' = f'(aa) + \frac{1}{2} \cdot f'(Aa)$$

$$\Delta p = p' - p \quad \Delta q = q' - q$$

Population genetics II

Fitness w:

$$w(+/+) = 1$$

$$w(+/-) = 1$$

$$w(-/-) = 0$$

Generation	(+/+)	(+/-)	(-/-)	f(+)	f(-)	W _{pop}
0	0	1000	0	0.5	0.5	
1 (HWE)	250	500	250	0.5	0.5	1
1 (selection)	250	500	0	0.66	0.33	0.75
2 (selection)	436	436	0	0.75	0.25	0.87

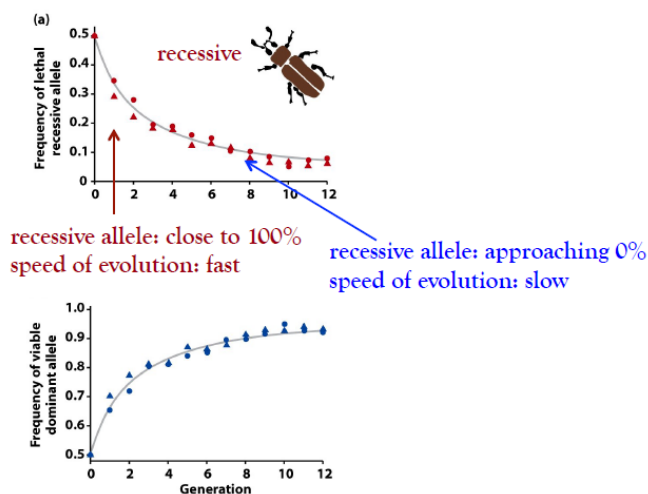
Punnett Quadrat for HWE:

	+	-
+	p ²	pxq
-	qxp	q ²

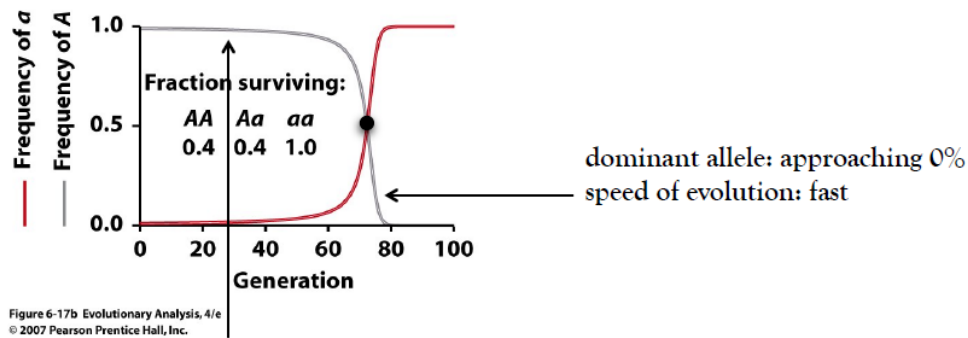
Genotype frequency: $p^2 = 0.66 \times 0.66 \times 1000$

Selection

Selection against recessive alleles is less efficient over time.

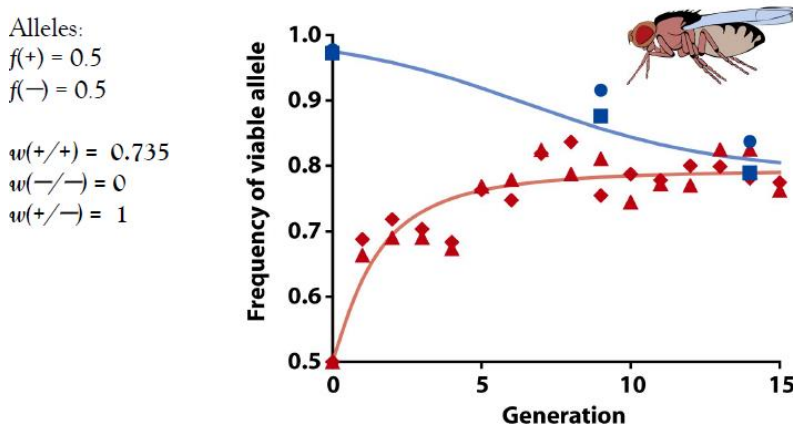


Selection for a recessive allele and against a dominant allele ($s = 0.6$)



dominant allele: close to 100%
speed of evolution: slow

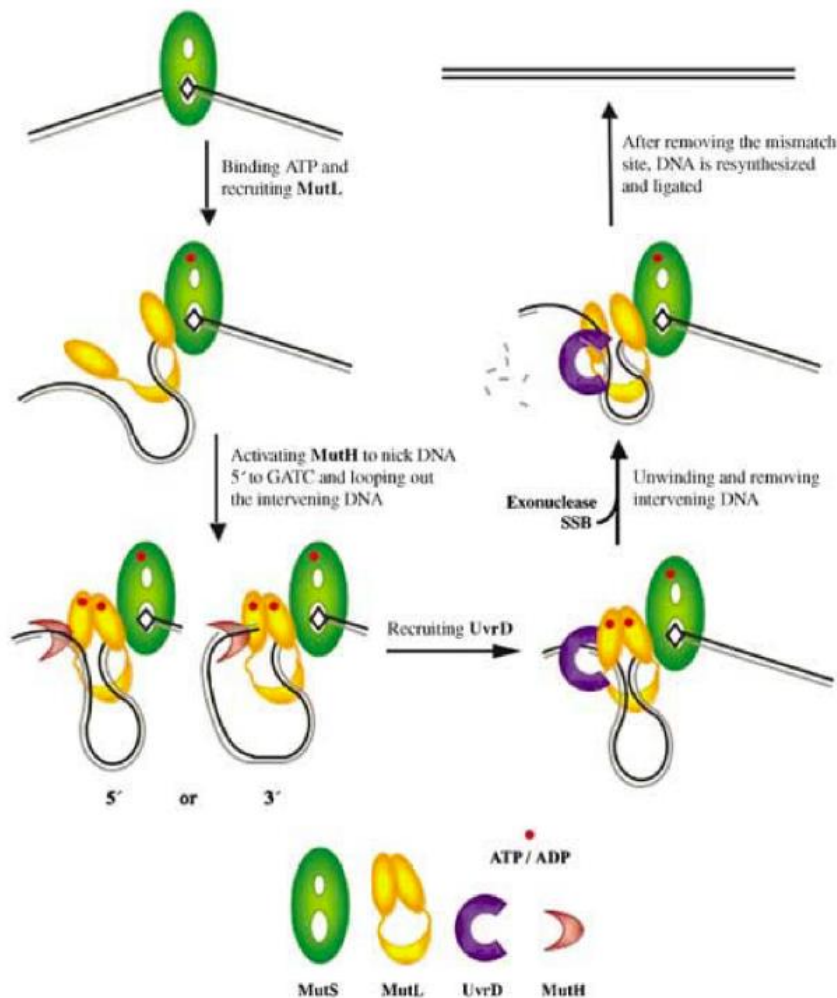
Overdominance: the phenomenon of heterozygote superiority, that leads to a stable equilibrium (does not matter which frequencies are taken to begin with).



Underdominance: the phenomenon for heterozygote inferiority, that leads to an unstable equilibrium (matters with which allele frequencies are taken to begin with).

Mutation:

Mutation is the ultimate source of genetic variation and leads to substantial change in the long-term. Mutation rate changes can speed up evolutionary rates. The combination of mutations and selection leads to an increase of fitness. Positive mutations are rare, but selected for increase. More common are neutral mutations, whose fate is determined by genetic drift or hitchhiking. Most common are negative mutations, which are selected against and their level in the population is determined by mutation-selection balance. Mismatch repair is an important mechanism in preventing mutations. The old strand is marked by methylation.



Mutation rate estimation: $\mu = \frac{\text{Mutations}}{\text{Time} \cdot \text{genetic target}}$

Induced mutagenesis is a SOS response to stress and interrupted DNA replication. It leads to a transient increase of mutability, by a more error prone polymerase, increased DNA uptake/recombination and activating of sleeping prophages in genome.

In the beginning, beneficial mutations are fixed, that is why the fitness is augmenting strongly, later it increases at a lower rate but steady. The number of mutations over time is approximately linear. There are so called hypermutator, organisms which gain higher fitness faster. When a fitness peak is reached, a balance will form between the rate new deleterious mutations occur and the rate they are selected against. A high selection coefficient means few or no offspring.

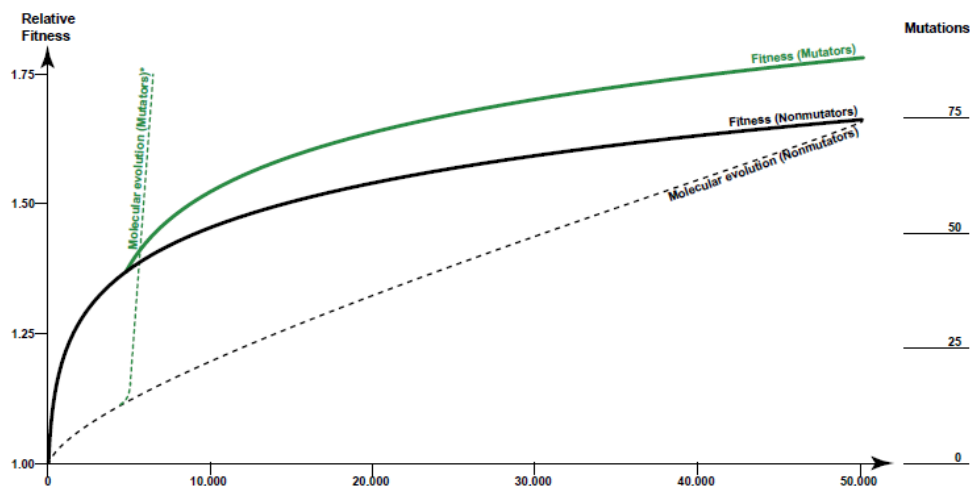
Mutation - Selection Balance for recessive deleterious alleles

$$\hat{q} = \sqrt{\frac{\mu}{s}}$$

\hat{q} = equilibrium frequency of mutant allele

μ = rate of mutation to mutant allele

s = coefficient of selection against mutant allele



Sex & Adaption

The purpose of sex

Sexual versus asexual reproduction does not influence the number of offspring per mother, the mother's survival, the offspring's survival or fitness. Male care of offspring can increase female fitness, but this is done very rarely. In the short term asexual females outcompete sexual females in the total number of offspring. It dilutes genes by half in offspring and recombination happens.

Sex allows selection to purge unfavourable multi-locus allele combinations that might drift to fixation in the absence of sex (creation of linkage disequilibrium by drift). It allows the creation of new favourable multi-locus allele combinations that can be promoted by selection (creation of disequilibrium by selection). In a constant environment, asexual reproduction is favoured, but in a changing environment sexual reproduction generates variation resulting in adaption.

Adaption

Adaptations are traits that enhance fitness. To test if a trait is an adaptation, it is removed. Testing adaption hypotheses by performing an experiment in which the study groups differ by only one controlled variable. Correlation does not imply causation.

Multi-level selection

Mitochondria can be turned into parasites by deleting genes necessary for respiration. Parasitic mitochondria replicate faster than respiring mitochondria *within* yeast cells. Yeast cells with only respiring mitochondria grow faster than yeast cells with only parasitic, non-respiring mitochondria. In a population of few yeasts the number of fermenting mitochondria exceed those which respire aerobically, in populations with high numbers, there are almost no fermenting parasitic mitochondria within yeast cells.

Sexual selection

Selection on relative mating success that affects overall reproductive success, strongest when mating opportunities limit reproductive success. There is an **asymmetric parental investment** (females normally invest more in offspring, even if there is no post-birth parental care). This is due to different reproduction limits of sexes: Female's reproduction is limited by the number of eggs produced or pregnancies carried, whilst male reproduction is only limited by the number of mating opportunities. The sex that invests more in offspring (usually females) is limited by resources and time, not potential mates and should lead to greater choosiness about mates. The sex that invests less in

offspring (usually males) is limited by number of mates, not resources and time and should lead to greater intra-sex competition for mates.

Intra-sex sexual selection: competition among males by physical combat, sperm competition (release of more sperm when other males are around, scooping out other males' sperm, guard mates, long copulation, transfer pheromones to make females unattractive to other males), infanticide and being sneaky (e.g. ahead prepared ejaculation in iguanas lessens the risk of interruption by other males in foreign territory).

Inter-sex sexual selection: female choosiness. Females care about differences among males, especially when what is favoured by sexual selection is not favoured by non-sexual natural selection. Reasons are:

- **The good genes hypothesis:** genes of favoured males are so good that the bad trait in terms of selection favoured by females plays no role in survival.
- **Males bearing gifts:** females expecting good food for sex, the bigger the gift the more likely the respective male is chosen and the longer the copulation.
- **Male exploitation of female sensory bias:** e.g. male water mites deposit sperm on plants and mimic the movement of prey such that females are attracted and catch the sperm instead of the prey. Males building shelter to attract females.
- **Female preference can be reinforced by "sexy sons":** attractive males are favoured by sexual selection, thus females bearing attractive sons are favoured by natural selection, because they are more likely to have offspring. This generates a reinforcing loop, working with any trait.

Sexual selection on females occurs when having more mates rather than few increases fitness.

Sociality and Cooperation

Benefits of living in groups are the many-eyes effect, predator swamping (the likelihood of being eaten decreases the larger the group), defence against parasites, communal defence and group hunting. There are also stress buffer benefits in reduced heat loss by piling up on to one another, moisture retention in grouping bacteria, protection from toxins and pH extremes (biofilms). There is reduced cost of transport as well in air, water and under water.

Microbial social behaviour:

Trait	Proposed/known benefits
Fruiting body construction	dispersion, protection from predators, stress, 'wolf-pack' feeding
Viral gene expression during co-infection	increased host exploitation efficiency
Rhizobial nitrogen fixation	access to plant nutrients
Siderophore production	enhanced growth under iron limitation
Biofilm formation	niche exploitation, protection from host defences or environmental stresses, pathogenesis
Interference competition	resource sequestration
Extracellular metabolism	increased local concentration of extracellular enzymes
Quorum sensing	delay of costly gene expression until density-dependent benefits can be realized

Siderophores: small, high-affinity iron-chelating compounds secreted by microorganisms such as bacteria and fungi. Siderophores are amongst the strongest soluble Fe^{3+} binding agents known.

Disadvantages of group living are competition with other group members and disease transmission. If group living benefits the individual reproduction, spontaneous group formation will be favoured. Once established, selection will affect the behaviour of individuals in a group.

Possible interaction behaviours:

Do not interact or interact neutrally

Perform social acts that do not significantly help or harm anyone.

Be “selfish”

Perform acts that benefit yourself but harm others.

Be “spiteful”

Perform acts that harm both yourself and others.

Cooperate (mutually beneficial cooperation)

Perform acts that benefit both yourself and others.

Be altruistic (altruistic cooperation)

Perform acts that benefit others at a cost to yourself.

Altruism: cooperative behaviour becomes altruistic whenever cheaters show up.

Economic altruism: invest resources which do not reduce the reproductive fitness.

Reproductive altruism: invest resources that diminish reproductive fitness.

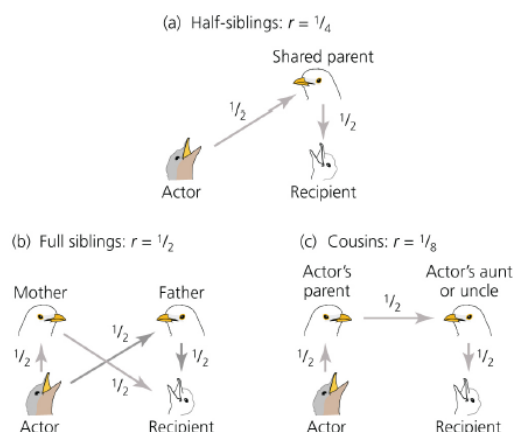
Kin selection: Selection can favour traits that result in decreased fitness of an actor if they increase the fitness of close relatives. Relatives are more likely to share alleles that promote cooperation altruism than are non-relatives. Cooperation towards kin increases the likelihood of spreading similar genes. Selection for alleles shared by close relatives that might cause individuals to behave in a manner that is detrimental to their own individual fitness but beneficial for the spread of the alleles under selection.

Hamilton's rule: $rB - C > 0$

r = coefficient of relatedness: probability that the homologous alleles in two individuals are identical by descent

B = fitness benefit of altruism to recipient

C = fitness cost of altruism to actor



Altruism is more likely to spread when the benefits to the recipient are large, the cost to the actor is low, and the actor and recipient are close relatives. Inclusive fitness is the sum of direct fitness (directly beneficial) and indirect fitness (benefits a relative).

Eusociality: cooperative brood care and non-reproducing castes (e.g. bees).

Reciprocal altruism: altruistic behaviour later returned by the recipients by repeated reciprocation over time. Requires: $b(\text{recipient}) > c(\text{actor})$ and that non-reciprocating individuals are punished. This is favoured by stable group associations that allow repeated interactions among the same individuals, many within-lifetime interaction opportunities, good memories and that altruists interact in symmetrical situations. The above conditions in turn are favoured by small groups of an intelligent and long-lived species in which individuals rarely change groups, are highly inter-dependent across different selective conditions important for fitness, and are good at detecting cheaters. Reciprocity may also contribute to the maintenance of altruism among non-kin in species that meet particular requirements, such as the amount of time spent together. Reciprocal altruism is hard to study in species due to confounders such as interacting kin-selection.

Speciation

Speciation is a three-step process:

1. Geographical isolation
2. Genetic divergence
3. Fostering species boundaries in secondary contact

A species can be defined as the smallest evolutionarily independent unit and a nearly complete lack of gene flow.

Species concepts

The morphospecies concept MSC: The central criterion is morphological similarities. This concept is easy and intuitive and works both for extinct and asexual species. Disadvantages are that some phenotypes are difficult to define (e.g. cryptic species: newly formed species), and convergence can be misleading. Additionally, the concept is hard to standardise.

The biological species concept BSC: The central criterion is reproductive isolation, mostly due to allopatric speciation (speciation from spatially separated populations). This is usually the common mechanism of speciation among sexual and it can be rigorously tested using population genetics. Disadvantages are that it is hard to set absolute limits to gene flow (porous gene pools) and it is not applicable to asexuals, extinct species and hybridising organisms. **Reticulate evolution:** formerly independent species combine due to recombination to one species. This occurs mostly in asexual species, bacteria or in plants. **Hybridisation:** two organisms produce offspring while being distinct species.

The phylogenetic species concept PSC: The central criterion is monophyly, meaning to identify the smallest monophyletic group. This concept is broadly applicable, based on genetic divergence in general and gene flow across species is important. It is very labour intensive, costly and abstract. Phylogeny works best at evolutionary time-scales.

The ecological species concept ESC: the central criterion is the ecological niches (where does the species live and how does it live). Applicable also for new species and relevant for rapid speciation events. It is well-suited to explain sympatric speciation (no spatial separation of a habitat inhabited by two different species). It is difficult to define species in the absence of ecological information and because they are often morphological identical.

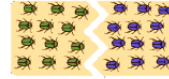
Researchers mostly apply multiple species concepts to study speciation. E.g. monophyletic groups are brought together and studied if they can produce fertile offspring.

Modes of speciation

Allopatric

(allo = other, patric = place)

new species from: geographically isolated populations



Peripatric

(peri = near, patric = place)

new species from: a small population isolated at the edge of a larger population



Parapatric

(para = beside, patric = place)

new species from: a continuously distributed population



Sympatric

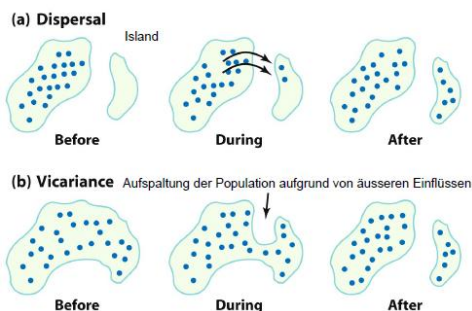
(sym = same, patric = place)

new species from: within the range of the ancestral population



Dispersal: migrating species. Dispersal may lead to allopatric speciation.

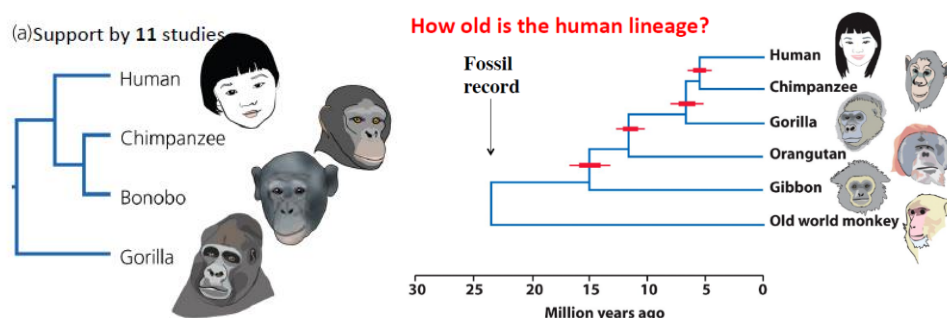
Vicariance: the geographical separation of a population, typically by a physical barrier (e.g. formation of an island) such as a mountain range or river, resulting in a pair of closely related species. May lead to allopatric speciation.



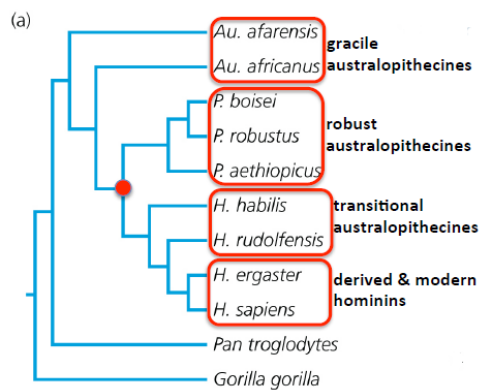
Human evolution

In comparative morphology humans are part of the African great ape clade including old world monkeys, gibbons, orangutans, gorillas, common chimpanzees, bonobos and humans. Apes differ from monkeys by a loss of tail, bigger brains, higher flexibility in hips, ankles, wrist, thumb and different shoulder/arm structure.

Incomplete lineage sorting has led to conflicting gene trees, because gene trees and species trees can differ. Solutions to this problem are the usage of more genes or to use genes that reflect the species tree.

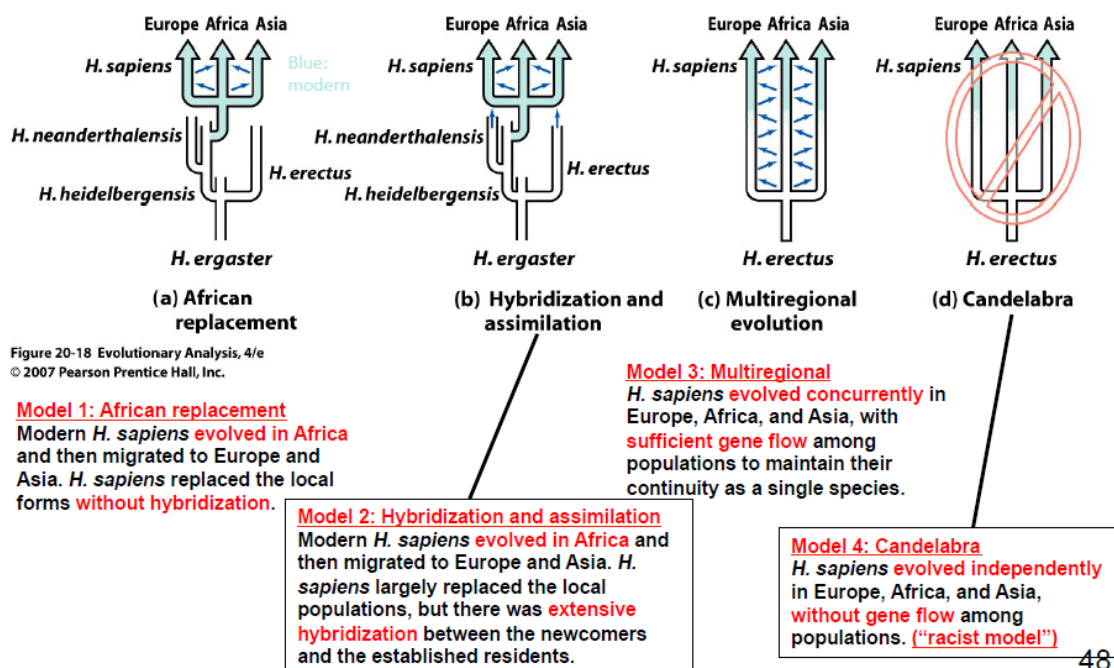


Evolutionary radiation of human lineage



All earlier hominids were found in Africa. Later fossils which were classified as homo sapiens were found in Israel and Europe, thus suggesting a migration event. Concerning the origin of modern humans, sequencing results suggest a combination of the first and second model (**leaky replacement hypothesis**) of the following chart:

Models of the origin of modern humans



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Life history

Trade off: biological constraint limiting possible combination of traits. Natural selection favours the combination that maximises lifetime reproductive success.

Senescence: late-life decline in fertility and survival. Bacteria also age by accumulation of mutations and by pole aging: When cells divide through fission there are two new end poles generated by the fission site. Each daughter cell receives an old end from the mother cell, thus the cell poles define age in microbes. It was found that cells with older poles divide more slowly than those with new poles. There are three major hypotheses concerning aging in organisms:

Biological constraints: Organisms have reached the limit of what is possible. There is evidence against this hypothesis because artificial selection and beneficial mutations (e.g. increased telomerase activity) can increase the life-span of organisms.

Mutation accumulation: selection is weak against deleterious alleles that arise late in life. Such alleles accumulate in populations due to mutation-selection balance or genetic drift. Evidence undermines that inbreeding depression increases with age, meaning that selection acts weaker against senescence alleles.

Antagonistic pleiotropy: Pleiotropy means that a mutation has multiple effects. Mutations that increase reproduction early in life sometimes hasten senescence.

History of biology

Aristotle: emphasised on **empirical ideas** and had a huge impact on western science by founding the fields of logic, biology and psychology. Although he did not make any inductive experiment but made deductive conclusions. He invented the **scala natura**: eleven degrees of natural perfection culminating in humans.

Socrates conducted dialectic inquiry.

Plato emphasised on spiritual ideas and Essentialism: organisms have a fundamental essence.

Hippocrates emphasised the importance of taking careful notes.

Scientific revolution of the 16th/17th centuries in Europe: Some pre-cursors were pre-university scholarly institutions e.g. monasteries which developed into cathedral schools and universities. Also, the western encyclopaedic tradition, philosophical appreciation of natural causation and regularity, the byzantine preservation and Islamic spread of Greek literature, 12th Century Greco-Arabic translations, rigorous, public scientific methods, formal integration of questions, observation, experimentation, induction and deduction, dynamic international University system and the establishment of natural philosophy as core of university curriculum all lead to the scientific revolution and the revision or rejection of many Aristotelian ideas. Important figures of the scientific revolution: Copernicus, Kepler, Galileo, Descartes, Francis Bacon, Newton, Vesalius.

Andreas Vesalius: foundations of anatomy, observed differences between species.

William Harvey: tried to find mechanistic rules in biology and founded modern embryology.

Nicholas Steno: helped found stratigraphy in geology (layers in rocks), law of superposition: horizontal rock layers represent a time sequence, fossils are snapshots of life in the past, principles of original horizontality and lateral continuity.

Carolus Linnaeus (Carl de Linné): DRASKOFGA, established universal naming conventions and classified humans with other primates. He defined three kingdoms (Animal, Plants, Minerals) and the binary nomenclature.

Comte de Buffon: spontaneous generation of life, common ancestry of human and apes, suggested species change, variety in different regions.

Erasmus Darwin: competition and selection case changes within species, observation of domestic animals.

Jean Baptiste Lamarck: inheritance of acquired characters, first theory proposing a mechanism for evolutionary change.

Thomas Malthus: exponential versus linear growth (he concluded that populations grow exponentially but food supply accumulates only linear), applied population-level thinking to humans.

William Paley: Natural theology, influenced Darwin's mode of argument.

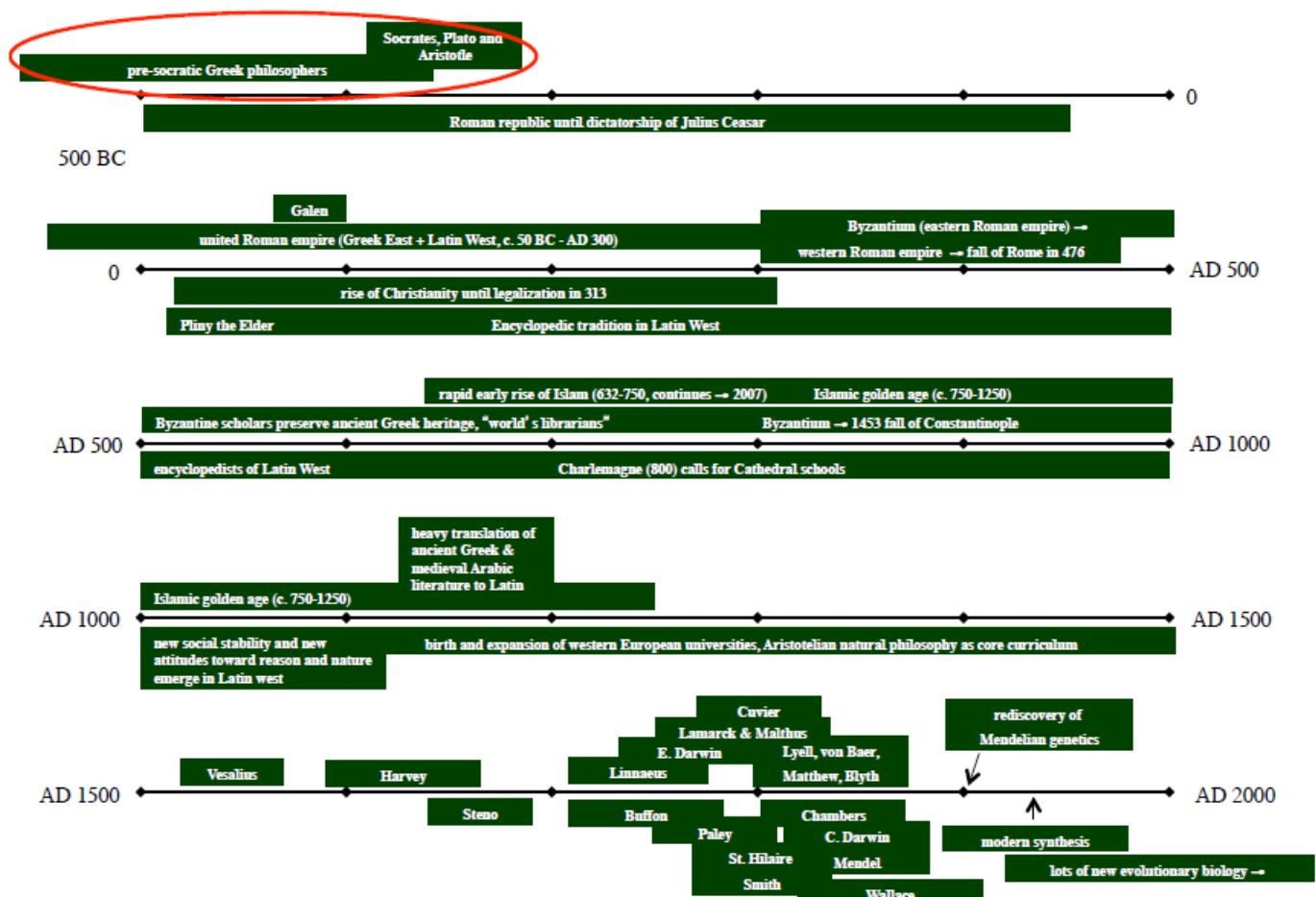
Georges Cuvier: Comparative anatomy, catastrophic events lead to extinction of species (catastrophism), demonstrated that many species are extinct.

Etienne Geoffrey St. Hilaire: transmutation: species can evolve into new species over time, defined the principle of homology, had ideas about evolution and natural selection.

William Smith: relative dating of rocks using fossils.

Charles Lyell: Uniformitarianism, gradual long-term processes shaped earth similar to geological processes.

Charles Darwin: The origin of species, descent with modification.



History of science/biology overview