ETH
Eidgenössische Technische Hochschule Zürich
Swiss Federal Institute of Technology Zurich

D-BSSE
Department of Biosystems
Science and Engineering

What is evolution?

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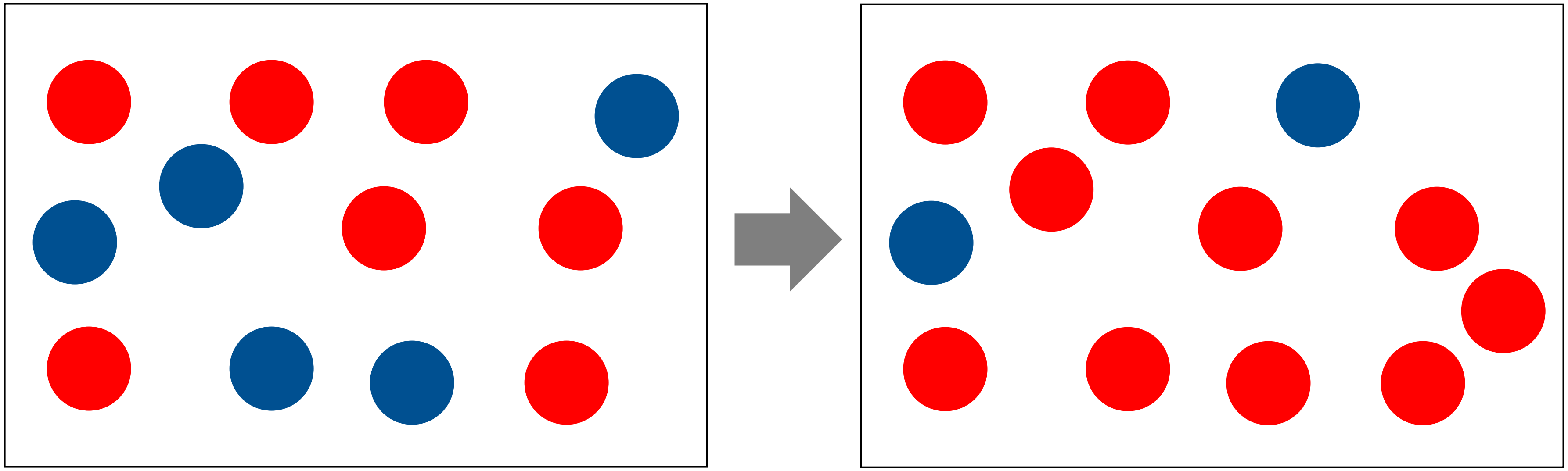
Evolution



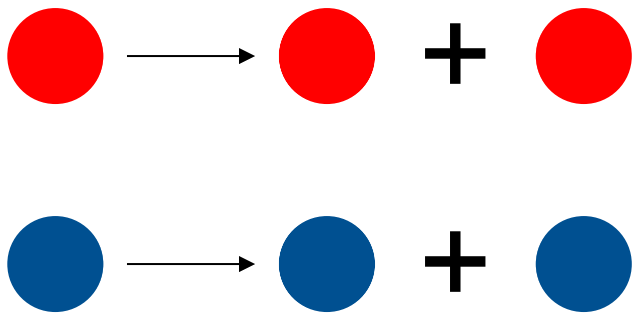
What evolution is

- In a population of individuals of different types, evolution is the change in the frequency of types from one generation to the next.
- Biological evolution is the change in allele frequencies within a gene pool.

- Only populations can evolve.
- Evolution generates inheritable traits.
- Evolution is driven by replication, mutation, and selection.

Reproduction

- Evolution requires a population of reproducing individuals.



Exponential growth ("Malthusian law")

- Consider dividing cells in discrete generations t and let x_t be the number of cells in generation t.
- The difference equation $x_{t+1} = 2x_t$ has the solution $x_t = x_0 2^t$, where x_0 is the initial number of cells.

- Now, consider continuous time t and let x(t) be the continuous number (fraction) of cells at time t.
- Assume that the generation time T is exponentially distributed with average 1/r, i.e., $\text{Prob}(T \leq \tau) = 1 - e^{-r\tau}$.
- The differential equation $x' = dx/dt = rx$ has the solution $x(t) = x_0 e^{rt}$, where r is the rate of cell division.

Cell death

- Suppose that cells have an average life span of 1/d.
- The differential equation becomes $x' = (r - d)\, x$.
- The quantity $R_0 = r/d$ is called the *basic reproductive ratio*. It denotes the expected number of offspring from a single individual.
- If $R_0 > 1$, then the population expands indefinitely.
- If $R_0 < 1$, then the population goes extinct.
- If $R_0 = 1$, then the population size remains constant, but the equilibrium $x^* = x_0$ is not stable.

Logistic growth

- Suppose that the population has a *carrying capacity*, K.
- The logistic equation x' = rx(1 – x/K) has the solution

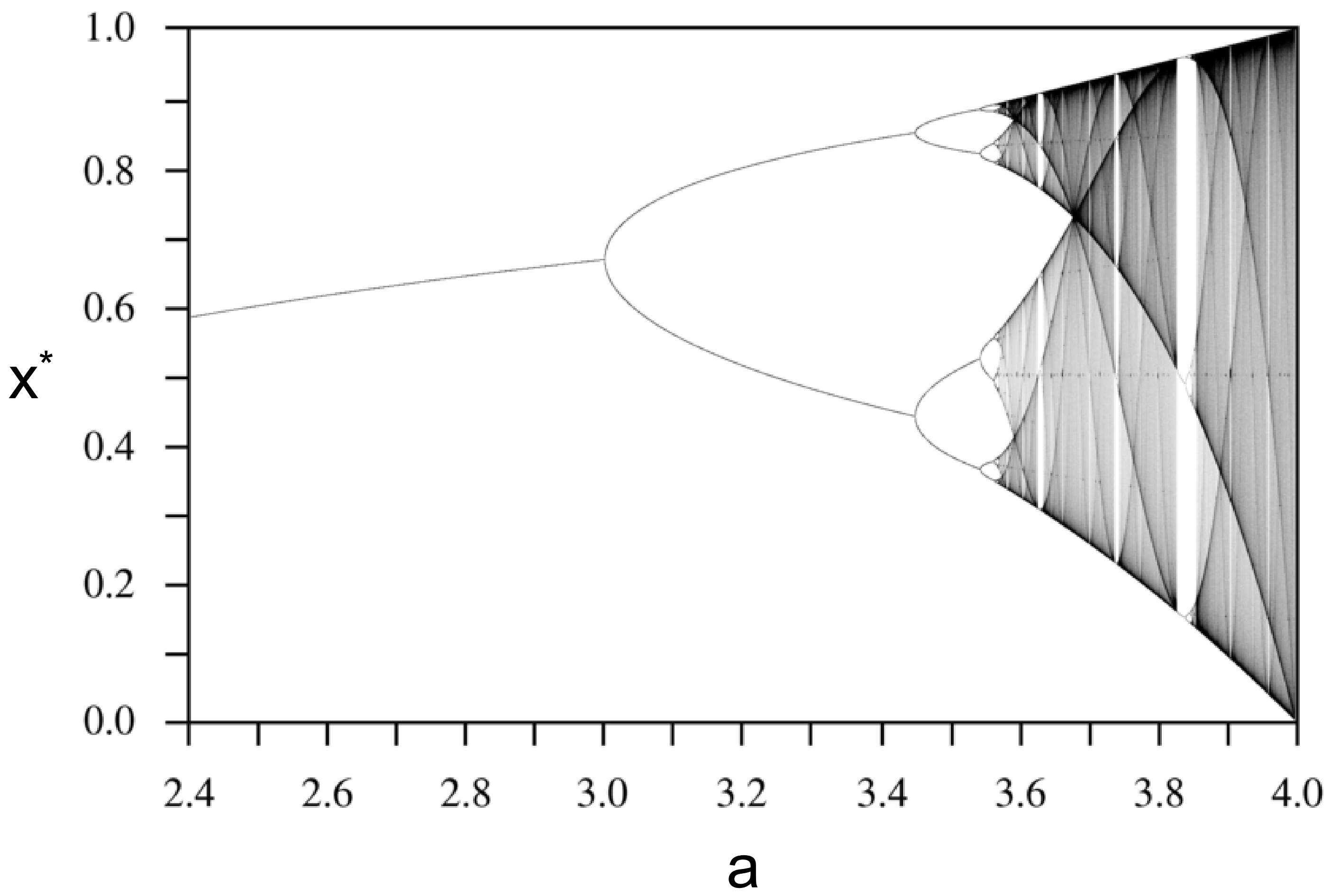
$$x(t) = \frac{Kx_0e^{rt}}{K + x_0(e^{rt} - 1)}$$

- We have $x^* = \lim_{t\to\infty} x(t) = K$

The logistic difference equation

- Most famous example of a "simple mathematical model with very complicated dynamics" (Robert M. May, *Nature* 261, 1976).
- After rescaling, assume K = 1. Then $x_{t+1} = ax_t(1 - x_t)$ is the logistic difference equation.
- The growth rate, a, corresponds to r in the logistic differential equation.
- The limit behavior of the system as $t \to \infty$ depends on the parameter a.
- For a = 4, the equation produces a *deterministic chaos*.

Bifurcation diagram of the logistic map



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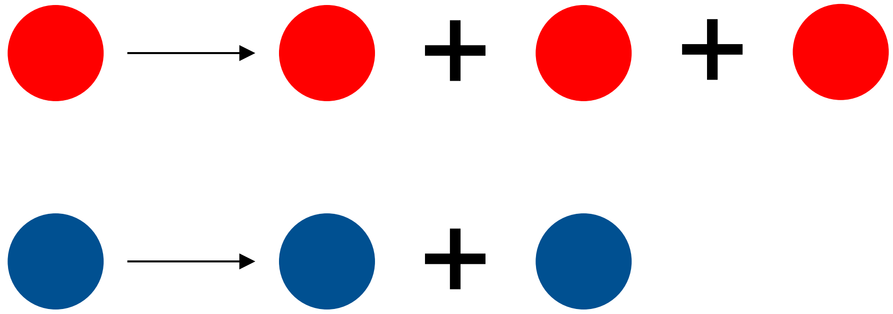
Selection

- Selection is the result of different growth rates associated with different types of individuals.



Two independent exponentially growing types

- Consider two types of individuals,
  - type A with growth rate a and abundance x(t),
  - type B with growth rate b and abundance y(t),

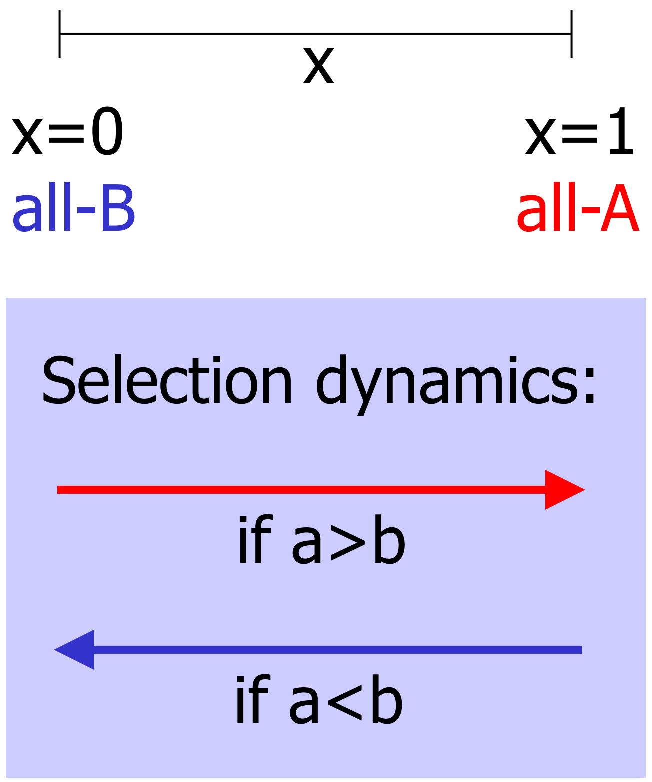
  growing according to $x' = ax$ and $y' = by$.
- Neither type can go extinct, if the *fitness* values $a, b > 0$.
- For their ratio, $\rho(t) = x(t)/y(t)$, we have
  $\rho' = (x'y - xy')/y^2 = (a - b)\rho$ and thus $\rho(t) = \rho_0 e^{(a - b)t}$.
- If $a > b$, then $\rho \to \infty$. Selection favors A over B.
- If $a < b$, then $\rho \to 0$. Selection favors B over A.
- If $a = b$, then $\rho(t) = \rho_0$.

Two competing types

- Let x and y be relative abundances (fractions, frequencies), and $x(t) + y(t) = 1$ for all $t \geq 0$.
- This constraint arises, for example, if the population has a carrying capacity. Thus, a relationship between type A and type B individuals is introduced.
- The dynamics are described by the equations
  $$x' = x(a - \phi),$$
  $$y' = y(b - \phi),$$
  where $\phi = ax + by$ is the average fitness of the population.
- The terms involving ϕ ensure that $x + y = 1$.
- The system is equivalent to $x' = x(1 - x)(a - b)$.

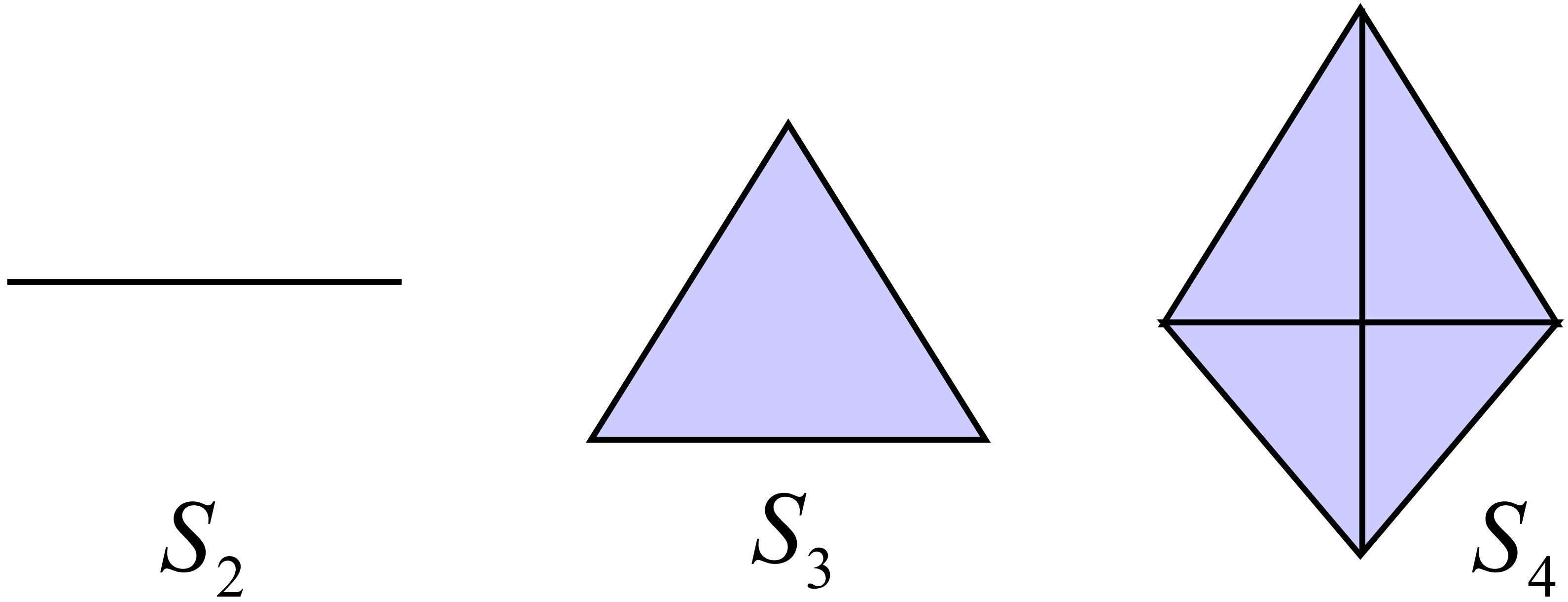
Selection dynamics: survival of the fitter

- The equation $x' = x(1 - x)(a - b)$ has two equilibria.

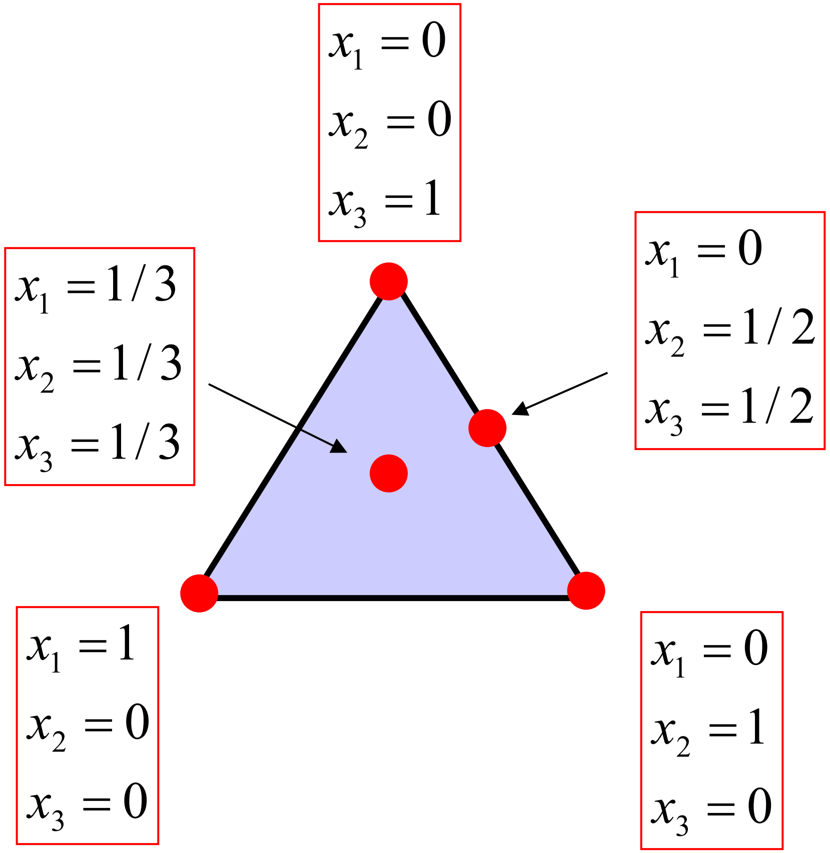


Probability simplex

$$S_n = \left\{ (x_1, \ldots, x_n) \mid x_i \geq 0, \ \sum_{i=1}^{n} x_i = 1 \right\}$$



Each point in S_n is a discrete probability distribution, or a population.



Survival of the fittest

- Consider n types with fitness values f_i, frequencies $x_i(t)$, and $x_1(t) + \ldots + x_n(t) = 1$. The type frequencies are points in the (n − 1)-dimensional probability simplex S_n.
- The average fitness of the population is $\phi = x_1 f_1 + \ldots + x_n f_n$.
- The selection dynamics are

$$x_i' = x_i(f_i - \phi) \qquad i = 1, \ldots, n$$

- This ODE system has a single stable equilibrium: starting from any interior point of the probability simplex, the fittest type will eventually outcompete all other types.

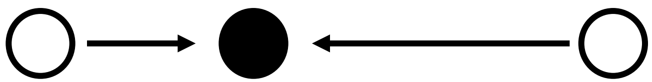
Subexponential and superexponential growth

- Consider two types with $x + y = 1$ and dynamics $x' = ax^c - \phi x$ and $y' = by^c - \phi y$, where $\phi = ax^c + by^c$.
- If $c = 0$, growth is linear (immigration).
- If $c = 1$, growth is exponential.
- If $c < 1$, growth is subexponential.
- If $c > 1$, growth is superexponential.
- The system is equivalent to $x' = x(1 - x)f(x)$, where $f(x) = ax^{c-1} - b(1 - x)^{c-1}$.
- It has fixed points at $x = 0$, $x = 1$, and for $c \neq 1$, there is exactly one additional fixed point $x^* = 1 / (1 + (a/b)^{1/(c-1)})$ between 0 and 1.

c < 1: survival of all

- If c < 1, then x^* is globally stable.
- Even if a > b, B can *invade* A (i.e., an infinitesimal small amount of type B individuals can grow in a population of almost all type A individuals).

all-A
is unstable

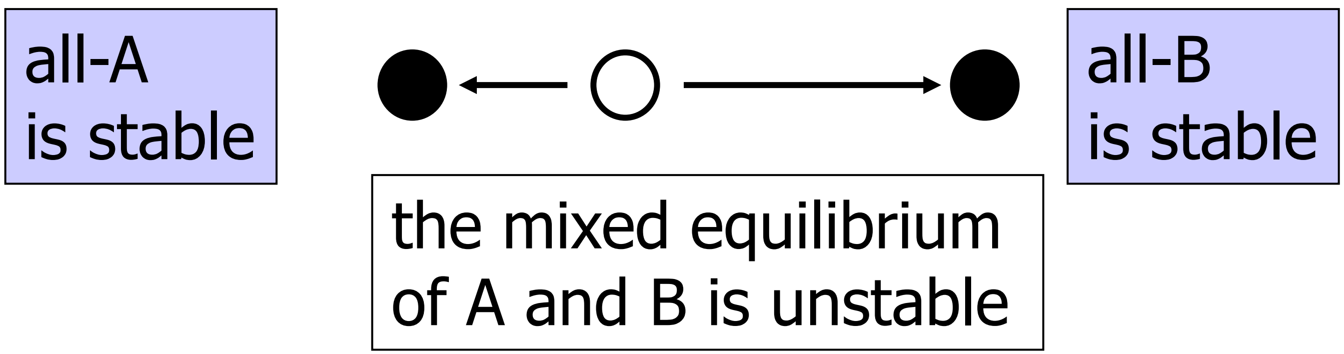


all-B
is unstable

the mixed equilibrium
of A and B is stable

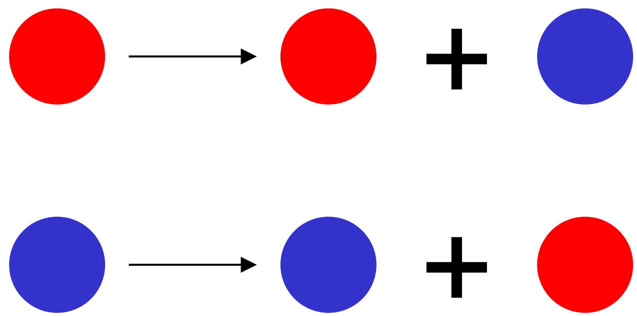
c > 1: survival of the first

- If $c > 1$, then x^* is unstable.
  - If $x > x^*$, then A will outcompete B.
  - If $x < x^*$, then B will outcompete A.
- Even if $a > b$, a B population cannot be invaded by an A mutant.

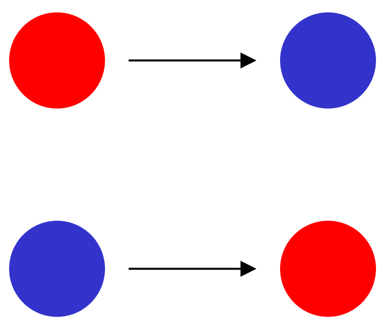


Mutation

Mutation during reproduction :



Mutation without reproduction :



Basic mutation dynamics

- Consider two types of equal fitness $a = b = 1$ with mutation rates $u_1 = \text{Prob}(A \to B)$ and $u_2 = \text{Prob}(B \to A)$ during reproduction.
- We have
$$x' = x(1 - u_1) + yu_2 - \phi x$$
$$y' = xu_1 + y(1 - u_2) - \phi y.$$
- Because $\phi = 1$ and $x + y = 1$, this system is equivalent to $x' = u_2 - x(u_1 + u_2)$ with stable equilibrium $x^* = u_2/(u_1 + u_2)$.
- Mutation leads to coexistence, $x^*/y^* = u_2/u_1$.
- If $u_1 \gg u_2$, we may assume $u_2 = 0$. Then $x' = -xu_1$ and A will go extinct. Thus, even without fitness differences, mutation alone can affect survival.

Mutation dynamics of n types

- Let q_{ij} = Prob(type i $\rightarrow$ type j), i,j = 1, ..., n.
- For all i, we have $q_{i1} + \ldots + q_{in} = 1$.
- Thus, $Q = (q_{ij})$ is a stochastic matrix.
- The n-dimensional mutation dynamics are

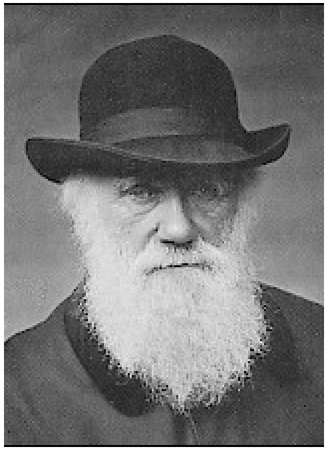
$$x_i' = \sum_{j=1}^{n} x_j q_{ji} - \phi x_i \qquad i = 1, \ldots, n$$

or $x' = xQ - \phi x$ in matrix notation.

- The equilibrium is the left hand eigenvector of Q associated with the largest eigenvalue, 1.

Genetic variation in populations

- Can genetic variation be maintained in the course of evolution?
- Darwin was confronted with the paradox that variation in *continuous traits* should disappear under *blending inheritance*.
- However, biological inheritance is discrete (Mendel; unknown to Darwin)
- Hardy showed mathematically that *particulate inheritance* preserves genetic variation in a diploid population under random mating.



Charles Darwin

Gregor Mendel

Hardy-Weinberg principle

- Consider an infinite population of diploid individuals.
- There are two *alleles*, namely “a” and “A”, with frequencies p and q, respectively.
- Hence there are three different *genotypes*, namely aa, aA, AA, with relative frequencies x, y, z, respectively.
- We have x + y + z = p + q = 1.
- The allele frequencies are:

AA aA
aa AA
AA
aA aA
AA aa AA

$$
\begin{aligned}
p &= x + y/2 \\
q &= z + y/2
\end{aligned}
$$

Hardy-Weinberg principle

- After one round of random mating,

$$x = p^2, \quad y = 2pq, \quad z = q^2$$

and the new allele frequencies p* and q* are

$$\begin{aligned} p^* &= x + y/2 = p^2 + pq = p \\ q^* &= z + y/2 = q^2 + pq = q \end{aligned}$$

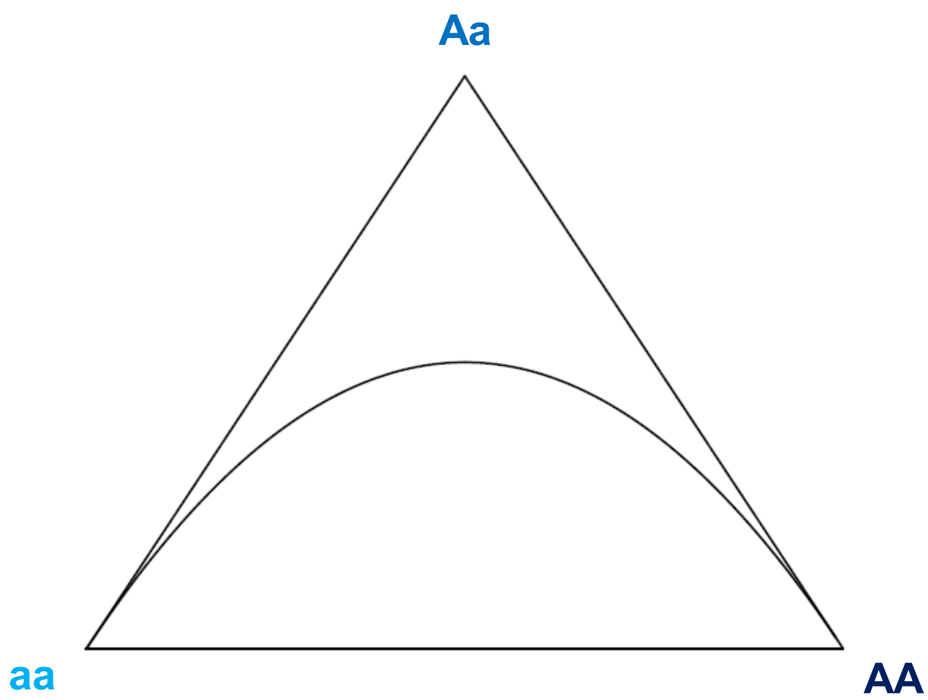
- Thus, after the first mating, the allele frequencies and the genotype frequencies are constant.

Hardy-Weinberg curve

- The set of Hardy-Weinberg equilibria is the intersection of the probability simplex with the algebraic curve

$$4xz - y^2 = 0$$

Godfrey Harold Hardy



Summary

- Evolution requires populations of reproducing individuals.
- Simple models of population growth in discrete time can give rise to very complicated dynamics.
- The fitness of an individual is its relative growth rate. In general, fitter individuals outcompete less fit ones.
- Subexponential growth: survival of all
- Superexponential growth: survival of the first
- Mutation promotes coexistence.
- Asymmetric mutation can result in selection even without growth differences.