EVOLUTIONARY DYNAMICS

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Competition

Evolution of a population

Mean population at time t:

$$\boldsymbol{n}(t) = \left(n_1(t), \ldots, n_r(t)\right)$$

$$\boldsymbol{n}(t) = \boldsymbol{n}(0)\,\boldsymbol{M}(t) = \boldsymbol{n}(0)\exp(\boldsymbol{A}t)$$

$$\frac{d\boldsymbol{n}}{dt} = \boldsymbol{n}\boldsymbol{A}$$

generalized Malthus law

Population growth

$$N(t) = \boldsymbol{n}(t) \cdot \mathbf{1} = \sum_{i=1}^{r} n_i(t)$$

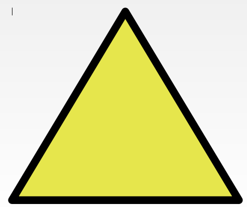
$$\frac{dN}{dt} = \frac{d\boldsymbol{n}}{dt} \cdot \mathbf{1} = \boldsymbol{n}\boldsymbol{A}\mathbf{1}$$

$$\frac{dN}{dt} = N\phi(\boldsymbol{x}) \qquad \phi(\boldsymbol{x}) \equiv \boldsymbol{x}\boldsymbol{A}\mathbf{1}$$

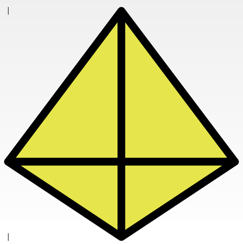
Evolution of the composition

$$\boldsymbol{x}(t)=\frac{\boldsymbol{n}(t)}{N(t)} \qquad \sum_{k=1}^{r} x_k(t)=1 \qquad x_k(t)\geqslant 0$$

$r=2$



$r=3$



$r=4$

$$\frac{d\,\boldsymbol{x}}{d\,t}=N^{-1}\frac{d\,\boldsymbol{n}}{d\,t}-\boldsymbol{n}\,N^{-2}\frac{d\,N}{d\,t}$$

$$\frac{d\,\boldsymbol{x}}{d\,t}=\boldsymbol{x}\,\boldsymbol{A}-\phi(\boldsymbol{x})\,\boldsymbol{x}$$

Asymptotic growth

Steady state of composition:

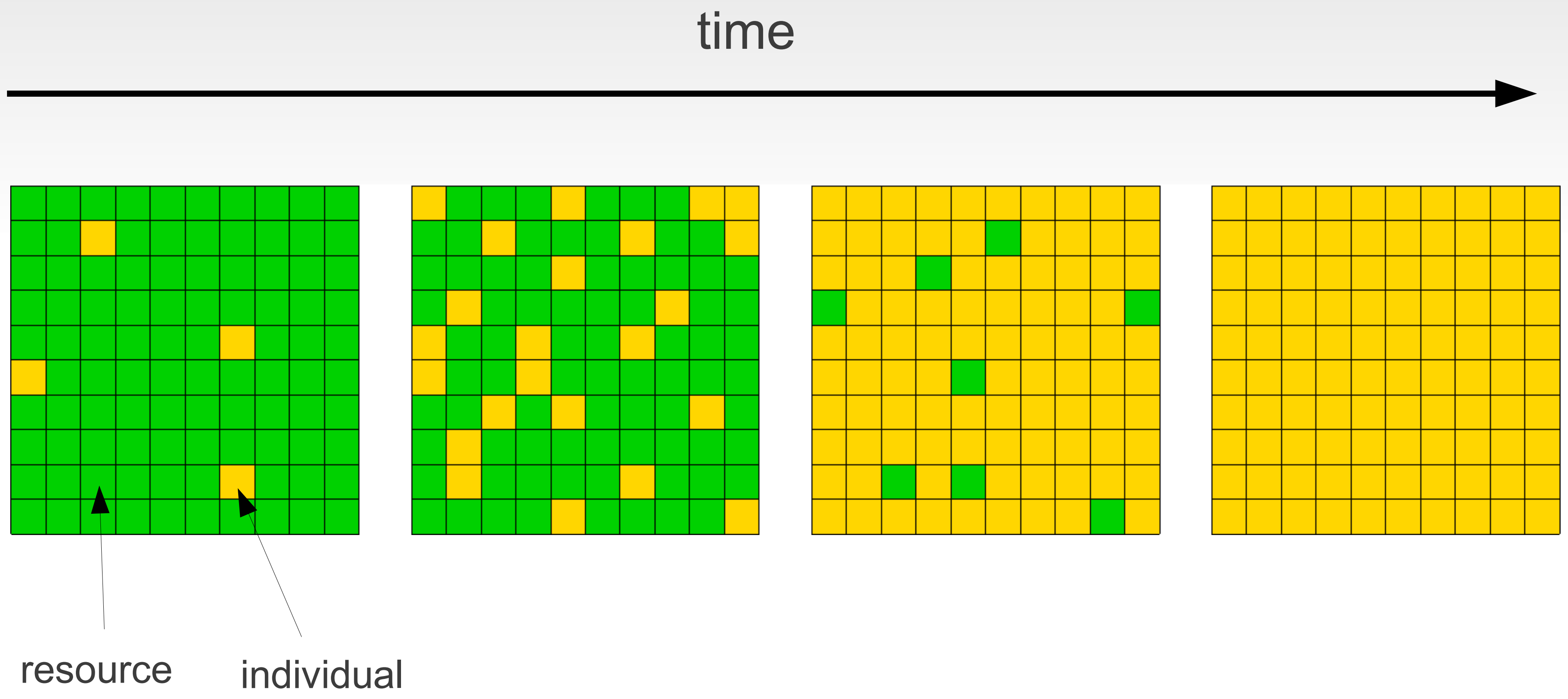
$$\boldsymbol{v}\,\boldsymbol{A} = \phi(\boldsymbol{v})\,\boldsymbol{v} \quad \Rightarrow \quad \phi(\boldsymbol{v}) = a$$

$$\lim_{t \to \infty} \boldsymbol{x}(t) = \frac{\boldsymbol{v}}{\boldsymbol{v} \cdot \mathbf{1}}$$

Exponential growth of population:

$$\frac{dN}{dt} \sim N\,\phi(\boldsymbol{v}) \quad \Rightarrow \quad N(t) \sim C\,e^{at}$$

Exhaustion of resources



Exhaustion of resources

$K \rightarrow$ carrying capacity of the environment $\left(N(t) \leqslant K\right)$

uniform death rate

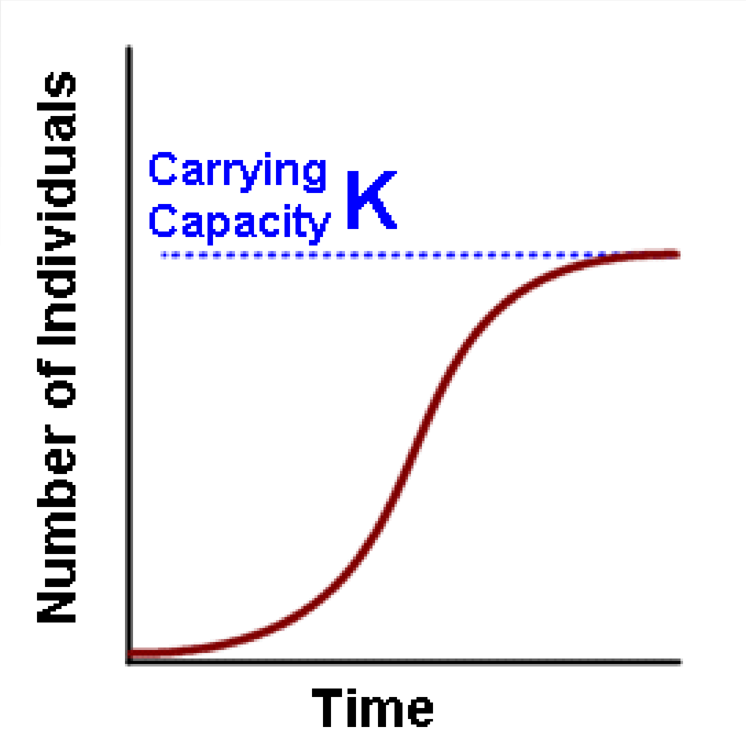
$$\frac{d\boldsymbol{n}}{dt} = \boldsymbol{n}A - \phi(\boldsymbol{x})\frac{N}{K}\boldsymbol{n}$$

population growth rate

fraction of “used” resources

Exhaustion of resources

$$\frac{dN}{dt} = N\phi(\boldsymbol{x})\left(1 - \frac{N}{K}\right)$$



but

$$\frac{d\boldsymbol{x}}{dt} = \boldsymbol{x}A - \phi(\boldsymbol{x})\boldsymbol{x}$$

Fitness and mutations

$$\boldsymbol{A} = \boldsymbol{F} + \boldsymbol{Q}$$

$$\boldsymbol{F} = \mathrm{diag}\{f_1, \cdots, f_r\} \qquad f_i = \sum_{j=1}^{r} a_{i,j}$$

$$\boldsymbol{Q} \equiv (q_{i,j}) = \boldsymbol{A} - \boldsymbol{F} \qquad \sum_{j=1}^{r} q_{i,j} = 0 \qquad q_{i,j} \geqslant 0 \quad (i \neq j)$$

f_i → average growth rate of “species” i (fitness)

$q_{i,j}$ → average mutation rate from species i to species j

Fitness and mutations

$$\phi(\boldsymbol{x}) = \boldsymbol{x}\boldsymbol{A}\mathbf{1} = \boldsymbol{x}\boldsymbol{F}\mathbf{1} + \boldsymbol{x}\underbrace{\boldsymbol{Q}\mathbf{1}}_{\mathbf{0}} = \boldsymbol{x}\boldsymbol{F}\mathbf{1}$$

$$\phi(\boldsymbol{x}) = \sum_{k=1}^{r} f_k x_k$$

average fitness of the population

Survival of the fittest

A　　　　　　　　B

$x_A = x$　　　　$x_B = 1 - x$

$\boldsymbol{F} = \mathrm{diag}\{f_A, f_B\}$　　　　$\boldsymbol{Q} = \boldsymbol{0}$

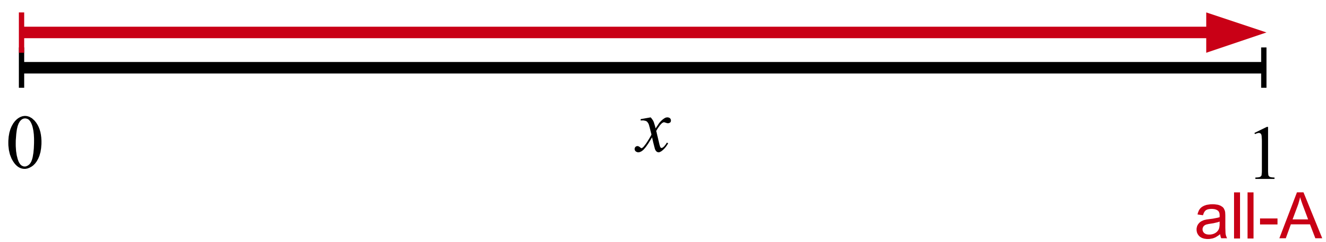
$$\frac{dx}{dt} = x\left(f_A - \phi(x)\right) \qquad \phi(x) = x f_A + (1-x) f_B$$

$$\frac{dx}{dt} = x(1-x)(f_A - f_B)$$

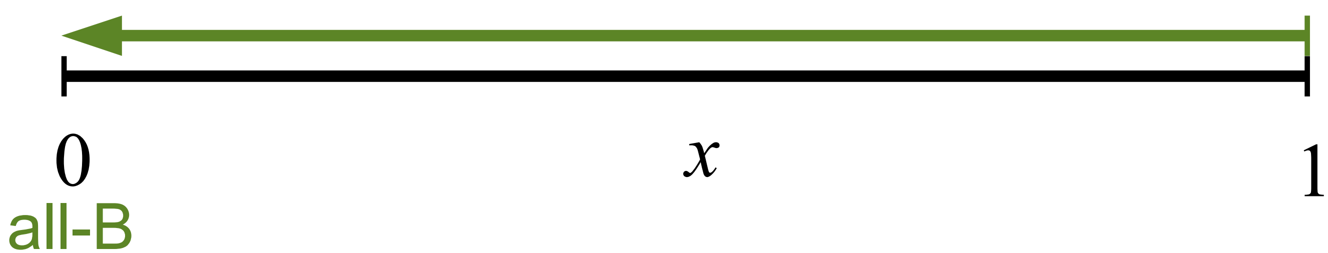
Survival of the fittest

$$\frac{dx}{dt} = x(1-x)(f_A - f_B)$$

$$f_A > f_B$$



$$f_A < f_B$$



Survival of the fittest

$$\frac{dx_k}{dt} = x_k\left(f_k - \sum_{j=1}^{r} x_j f_j\right) = x_k \sum_{j=1}^{r} x_j (f_k - f_j)$$

assume $f_k > f_j \quad \forall\, j \neq k$

↓

$$\lim_{t\to\infty} x_k(t) = 1 \qquad \lim_{t\to\infty} x_j(t) = 0 \quad (j \neq k)$$

Fisher's fundamental theorem of natural selection

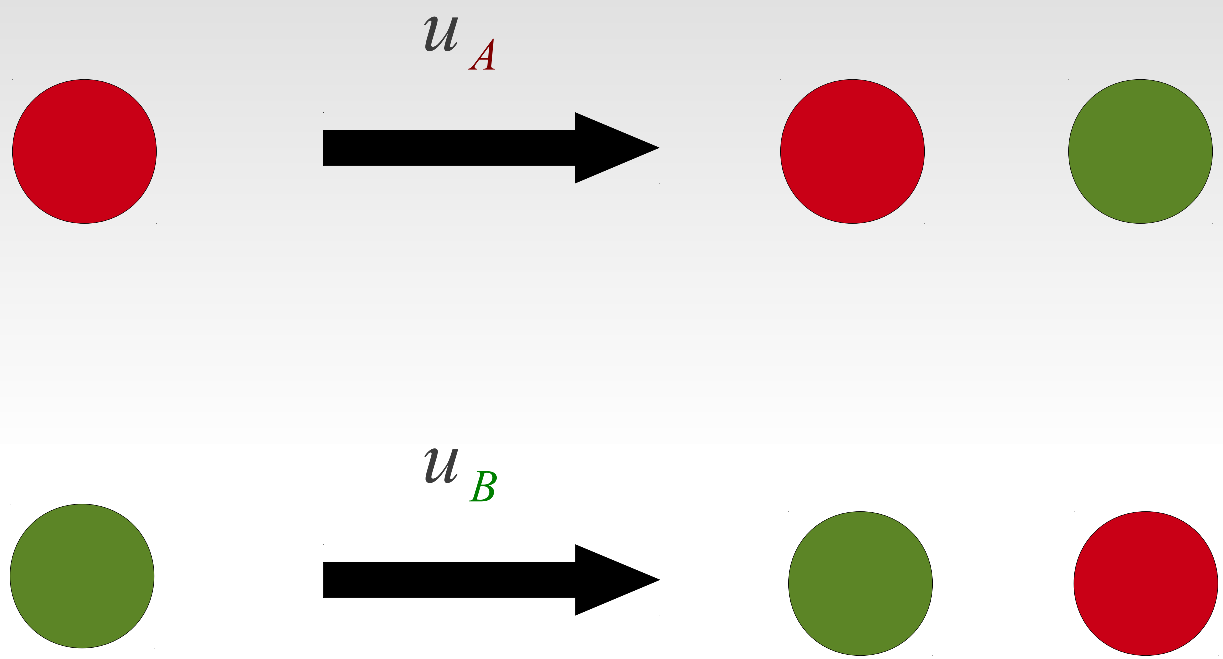
$$\frac{d\phi}{dt} = \sum_{k=1}^{r} f_k \frac{dx_k}{dt} = \sum_{k=1}^{r} f_k x_k (f_k - \phi) = \sum_{k=1}^{r} x_k (f_k - \phi)^2 \equiv \sigma_f^2$$

$$\frac{d\phi}{dt} = \sigma_f^2$$

- Average fitness increases as long as population is diverse
- The more diverse the population the faster it increases
- Average fitness reaches a maximum when population becomes homogeneous

Mutation

Replication with error



$$F = \begin{pmatrix} f_A & 0 \\ 0 & f_B \end{pmatrix} \qquad Q = \begin{pmatrix} -u_A & u_A \\ u_B & -u_B \end{pmatrix}$$

Replication with error

$$\frac{dx}{dt} = x\left(f_A - u_A - \phi(x)\right) + (1-x)u_B$$
$$= x(1-x)(f_A - f_B) + (1-x)u_B - x u_A$$

$$x^* \approx 1 - \frac{u_A}{f_A - f_B} < 1 \qquad f_A > f_B$$

$$x^* \approx \frac{u_B}{f_B - f_A} > 0 \qquad f_A < f_B$$

$$x^* = \frac{u_B}{u_A + u_B} \qquad f_A = f_B$$

mutation is the source of variability

Mutation-selection equilibrium

$$\frac{dx}{dt} = xF + xQ - \phi(x)x \qquad Q\mathbf{1} = \mathbf{0} \qquad \phi(x) = xF\mathbf{1}$$

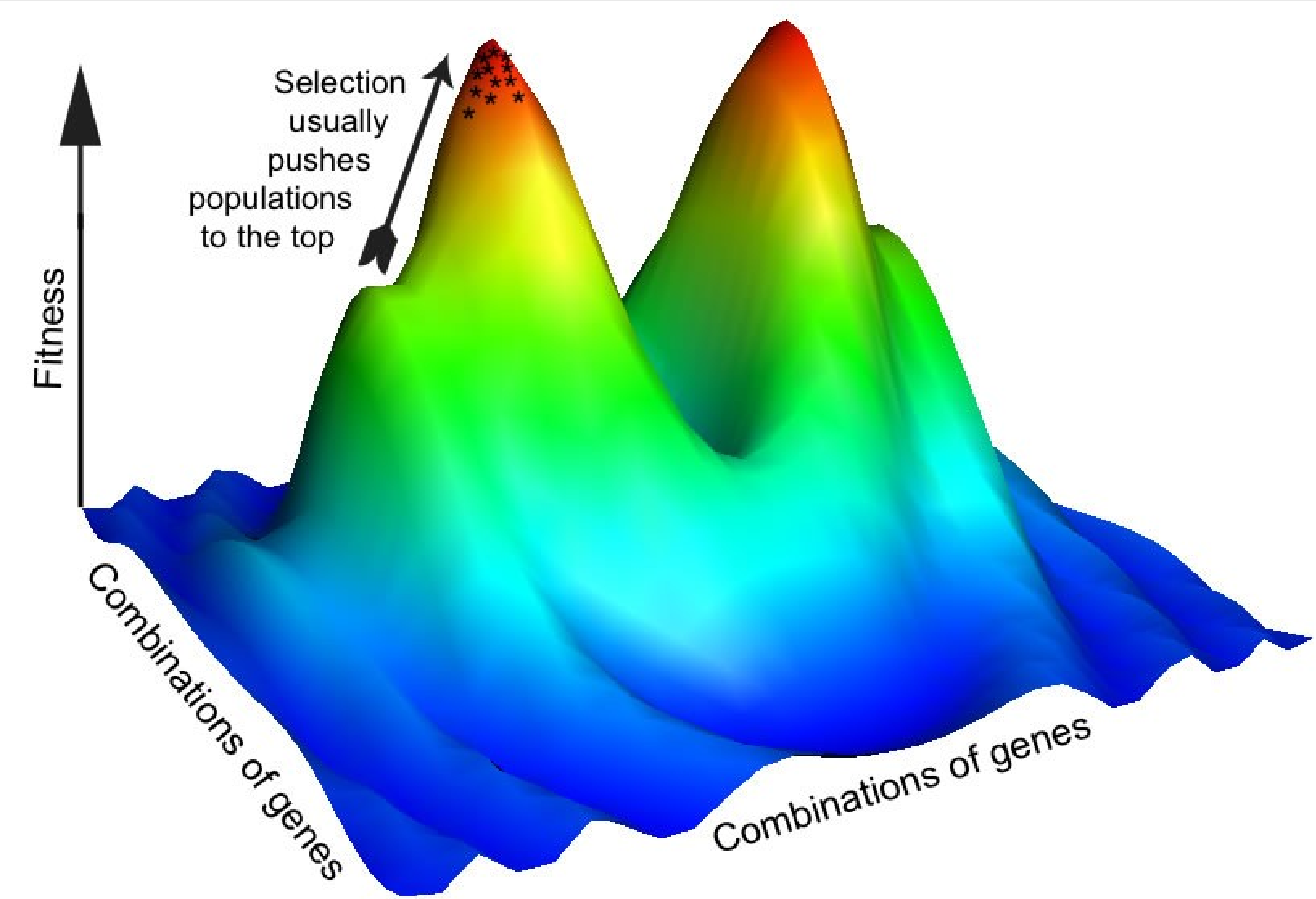
equilibrium $\rightarrow x^*(F+Q) = \phi(x^*)x^*$

Q primitive $\rightarrow x^* > \mathbf{0}$ (nonhomogeneous population)

$\rightarrow \phi(x^*)$ largest eigenvalue of $F + Q$

$\rightarrow \phi(x^*)$ is no longer a maximum ($\sigma_f > 0$)

Mutation-selection equilibrium



The quasi-species model

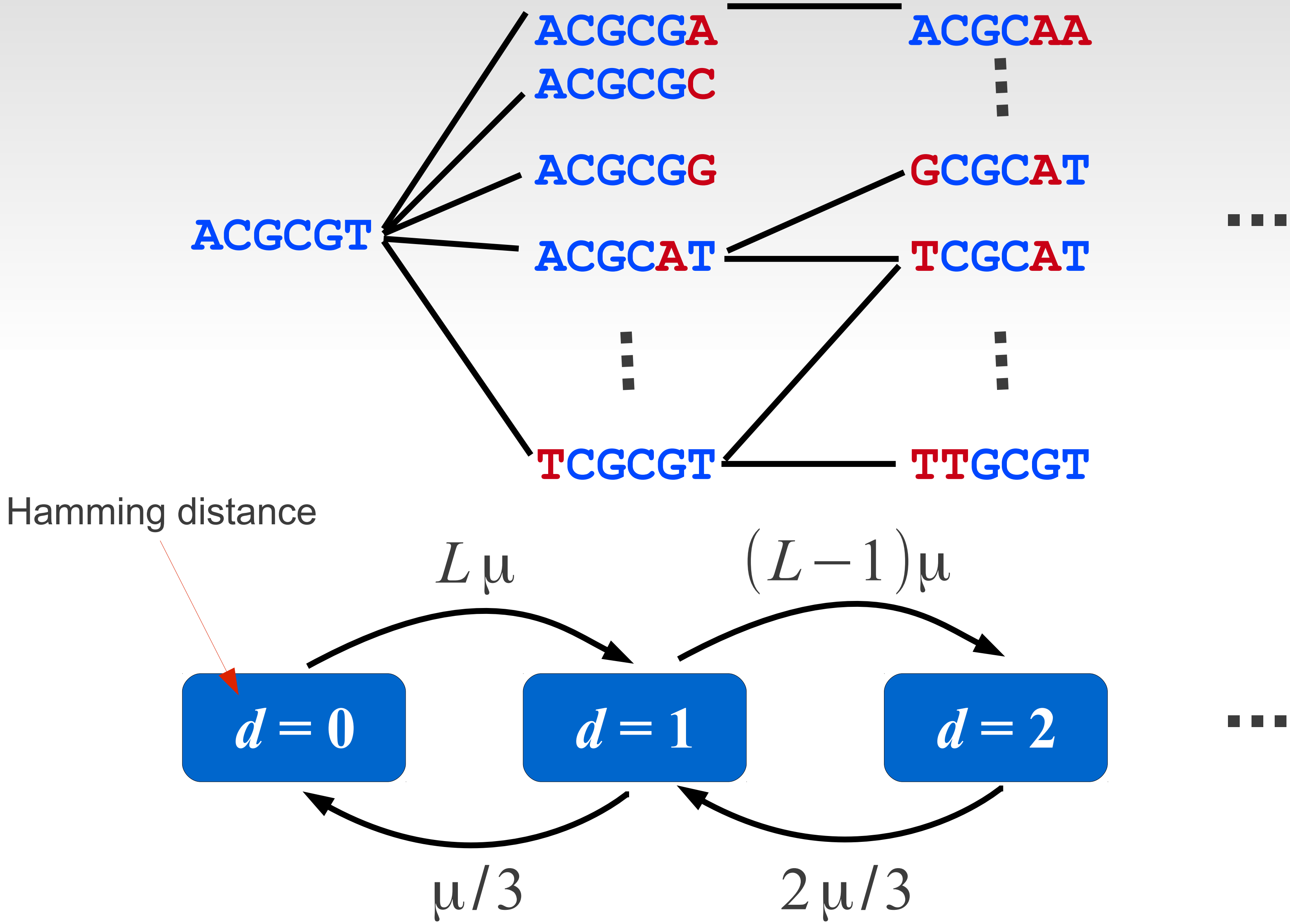
Manfred Eigen

ATTTGGAAATGCCGCAATTTACGGGA
ACTTGCAAATTCCGCAAATTTCGGGG
AGTTGGAACTTCCGCAATTCTCGGGA
ACTTGGACATTCCGATATTCTCGGGA
GGTTGGAAATACCCCAATTTTCGGGA
ACTTTGAAATTCCGCAACGGTCGGGA
ACATGGAAATTCCGCAATTTTCGGGA

ACTTGGAAATTCCGCAATTTTCGGGA

consensus sequence
(optimal)

The quasi-species model



The quasi-species model

Grouping by Hamming distance:

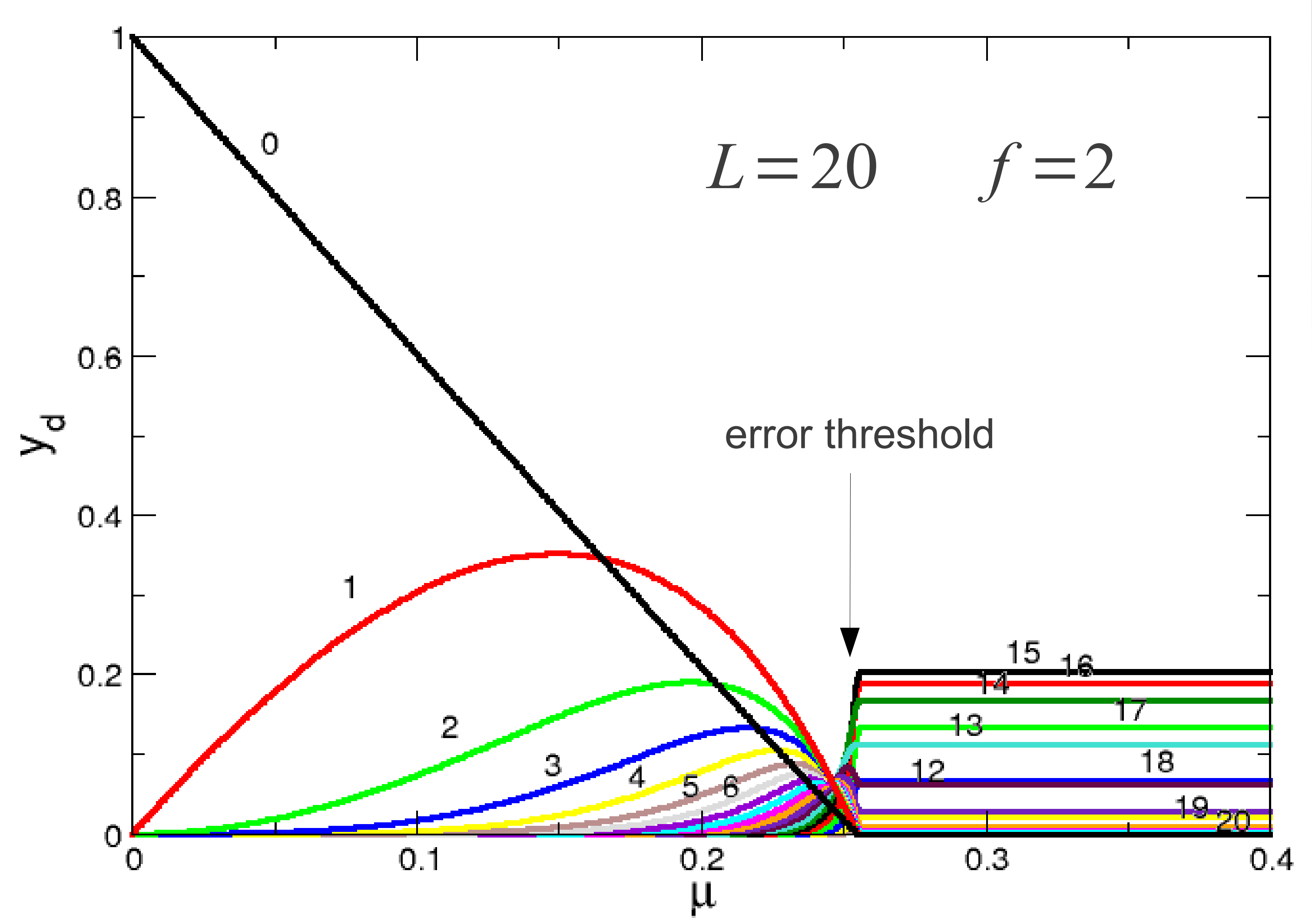
$$y_d = \sum_{i:d(i,0)=d} x_i \qquad \sum_{d=0}^{L} y_d = 1$$

$$f_0 = \boldsymbol{f} > 1 = f_1 = \cdots = f_L$$

$$q_{d,d+1} = f_d (L-d)\mu \qquad q_{d,d-1} = f_d d\mu/3$$

$$q_{d,d} = -q_{d,d-1} - q_{d,d+1}$$

The quasi-species model



The quasi-species model

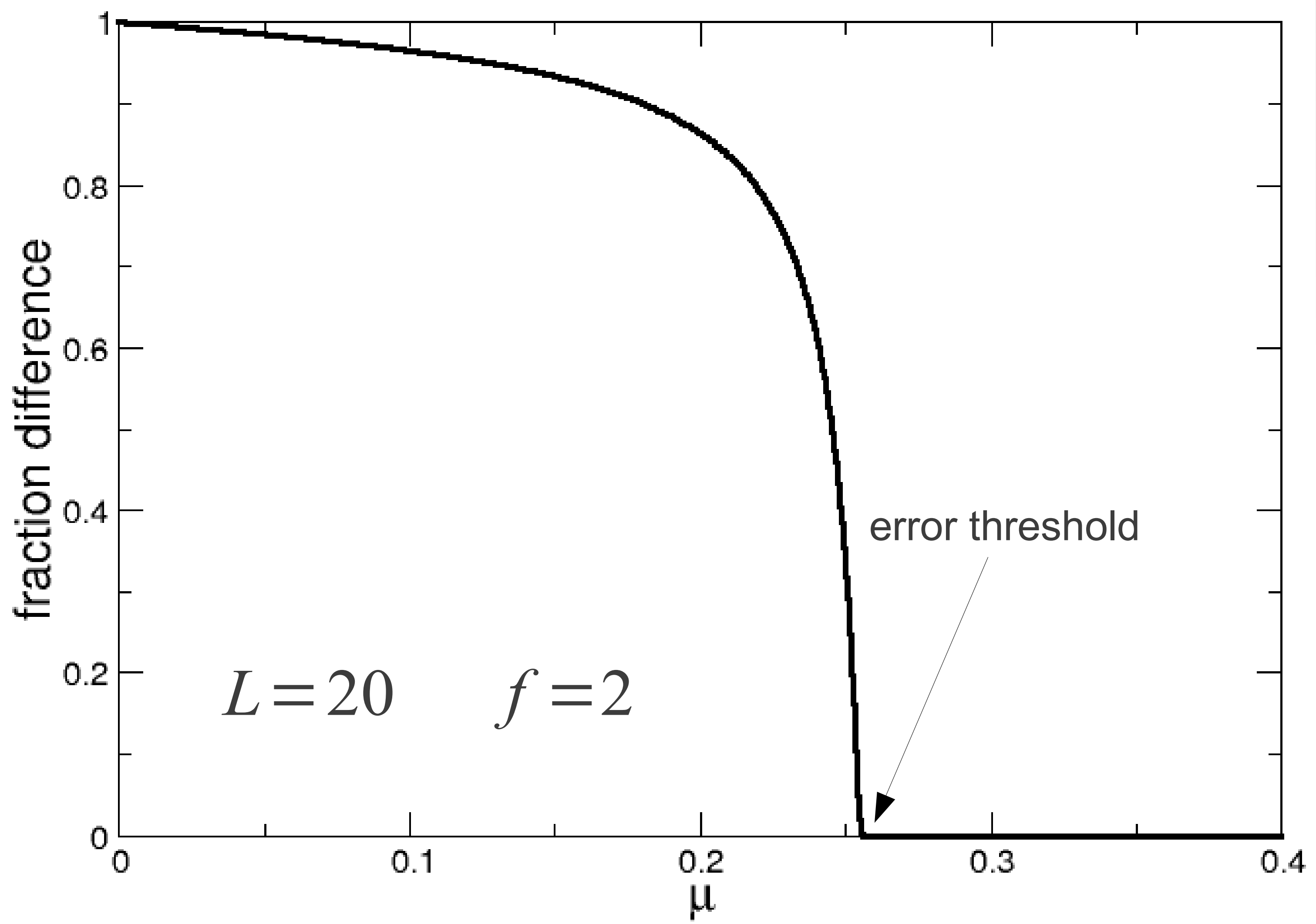
Fraction of sequences with the consensus base at a given position:

$$\sum_{d=0}^{L} \frac{3^d \binom{L-1}{d}}{3^d \binom{L}{d}} y_d = 1 - \sum_{d=0}^{L} \frac{d}{L} y_d$$

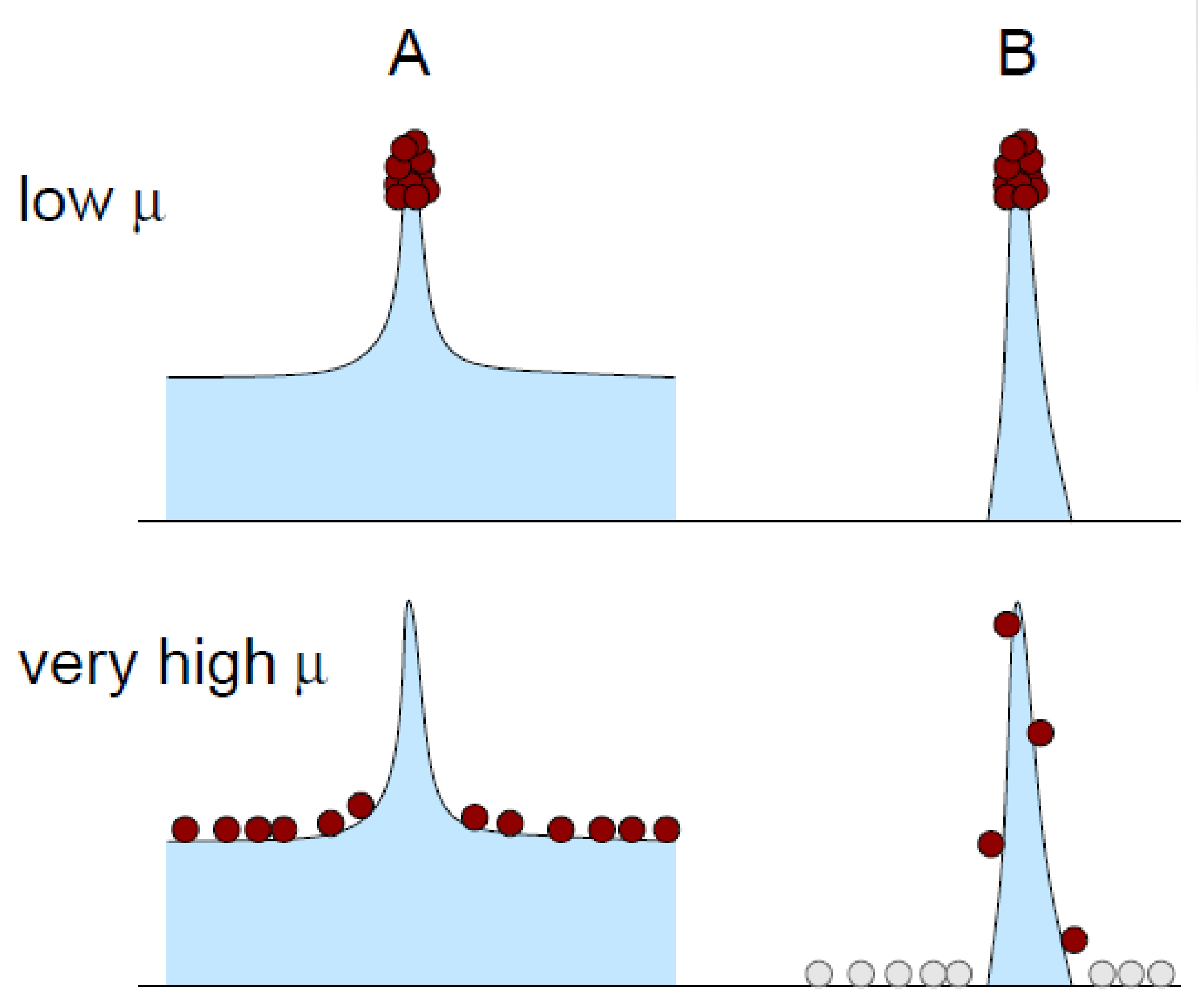
Fraction difference between sequences with the consensus base and sequences with any other base at a given position:

$$\left(1 - \sum_{d=0}^{L} \frac{d}{L} y_d\right) - \frac{1}{3} \sum_{d=0}^{L} \frac{d}{L} y_d = 1 - \frac{4}{3} \sum_{d=0}^{L} \frac{d}{L} y_d$$

The quasi-species model



The quasi-species model



Interaction

Ecological fitness

The presence of other species influences the replication rate:

$$f_k = f_k(\boldsymbol{x})$$

Example: two species

$$f_A(x) = f + \alpha_A(1 - x)$$

$$f_B(x) = f + \alpha_B x$$

symbiosis

$$\alpha_A > 0$$
$$\alpha_B > 0$$

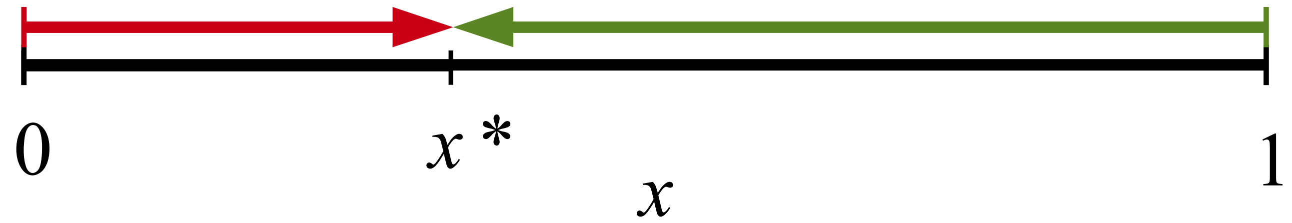
competition

$$\alpha_A < 0$$
$$\alpha_B < 0$$

Symbiotic coexistence

$$\frac{dx}{dt} = (\alpha_A + \alpha_B)\,x\,(1-x)(x^* - x) \qquad x^* = \frac{\alpha_A}{\alpha_A + \alpha_B}$$

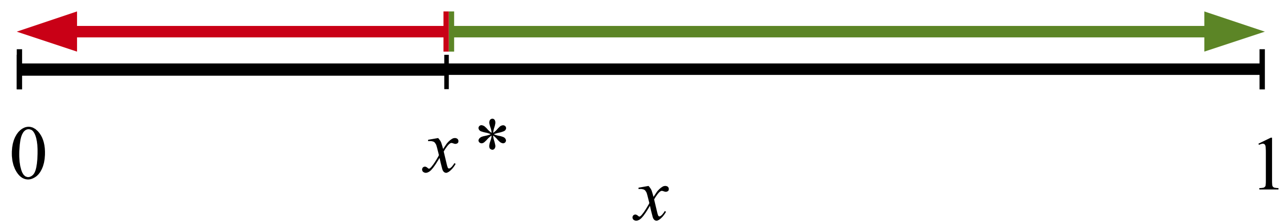
$$\alpha_A > 0$$
$$\alpha_B > 0$$



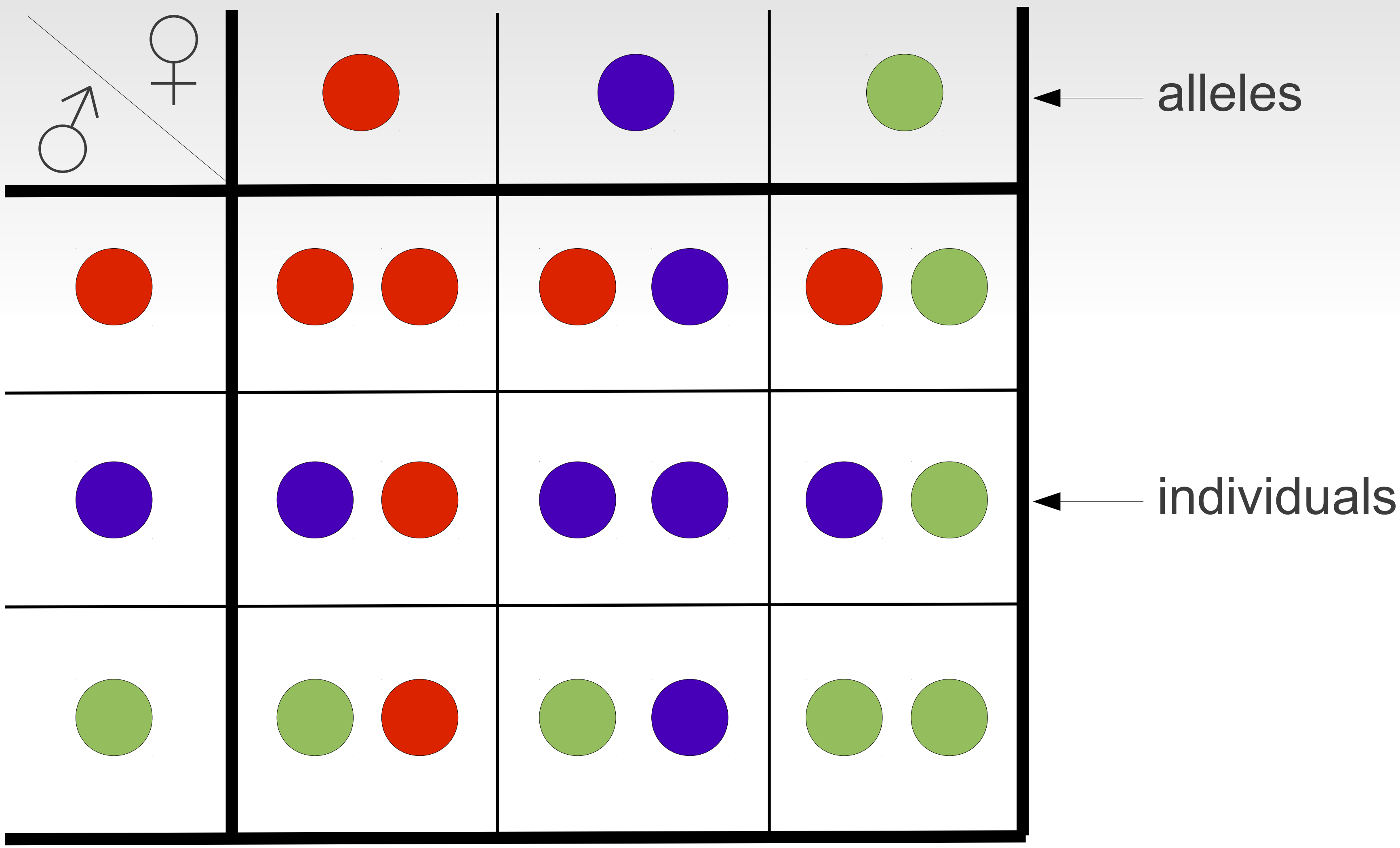
Competitive exclusion

$$\frac{dx}{dt} = (\alpha_A + \alpha_B)\, x\, (1 - x)(x^* - x) \qquad x^* = \frac{\alpha_A}{\alpha_A + \alpha_B}$$

$$\alpha_A < 0$$
$$\alpha_B < 0$$



Population genetics



Population genetics

$f_{i,j} \to$ fitness of individual (i, j) $\quad (f_{i,j} = f_{j,i})$

$$\frac{d\,x_{i,j}}{d\,t} = x_{i,j}\left(f_{i,j} - \phi\right) \qquad \phi = \sum_{i,j=1}^{a} x_{i,j} f_{i,j}$$

$$x_i = \frac{1}{2}\sum_{j=1}^{a}\left(x_{i,j} + x_{j,i}\right) \qquad i = 1, \ldots, a$$

frequency of allele i

Population genetics

random mating $\rightarrow \quad x_{i,j} = x_i x_j$

$$\frac{d x_i}{d t} = \frac{1}{2}\left(\frac{d x_{i,j}}{d t} + \frac{d x_{i,j}}{d t}\right) = x_i \sum_{j=1}^{a} x_j \left(f_{i,j} - \phi(\boldsymbol{x})\right)$$

$$\frac{d x_i}{d t} = x_i \left(f_i(\boldsymbol{x}) - \phi(\boldsymbol{x})\right)$$

$$f_i(\boldsymbol{x}) = (\boldsymbol{F}\boldsymbol{x})_i \qquad \phi(\boldsymbol{x}) = \boldsymbol{x}\boldsymbol{F}\boldsymbol{x} \qquad \boldsymbol{F} \equiv (f_{i,j})$$