Mathematics of evolution

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Grupo **I**nterdisciplinar de **S**istemas **C**omplejos

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DARWIN200

12 February 1809 – 12 February 2009

Summary

(1) A bit of history

(2) Fundamentals of evolution

(3) Genetic drift

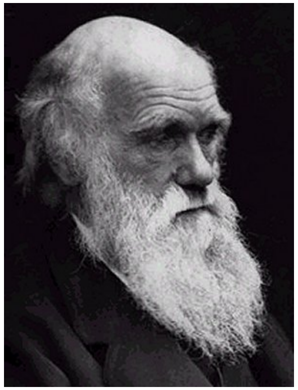
(4) Sequences and fitness landscapes

(5) Game theory

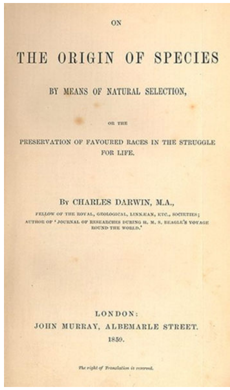
(6) Evolutionary game theory

A little bit of history

Lamarck (1744-1829)



Darwin (1809-1882)



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

BY CHARLES DARWIN, M.A.,

FELLOW OF THE ROYAL, GEOLOGICAL, LINNÆAN, ETC., SOCIETIES; AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:

JOHN MURRAY, ALBEMARLE STREET.

1859.

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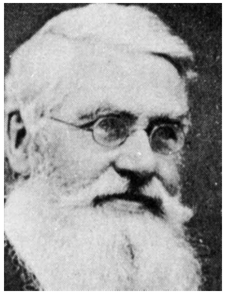
1859

Malthus (1766-1834)

farmer breeding



Wallace (1823-1913)

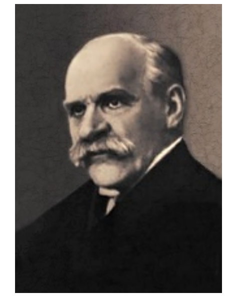
Beagle (1831-1836)

Neodarwinism


Mendel (1744-1829)


Wright (1889-1988)


Fisher (1890-1962)

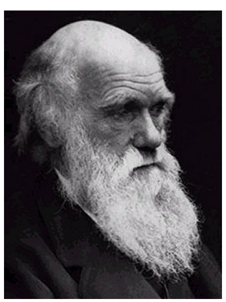

Haldane (1892-1964)


Kimura (1924-1994)

population genetics


Huxley (1887-1975)

biology

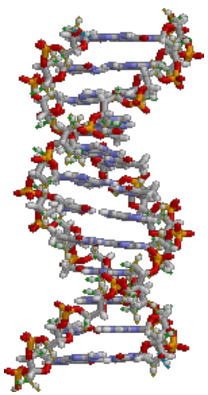

Darwin (1809-1882)


Morgan (1866-1945)


Dobzhansky (1900-1975)

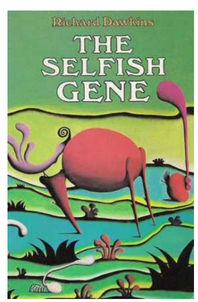

Mayr (1904-2005)

The modern era



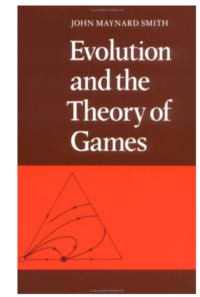
selfish genes

Dawkins (1941-)

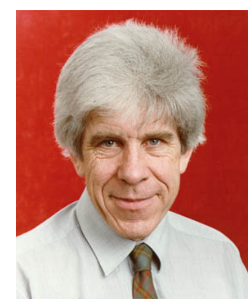


1976

evolutionary game theory



Maynard-Smith (1920-2004)



Hamilton (1936-2000)

FUNDAMENTALS OF EVOLUTION

Evolution: building blocks

- Replication
- Selection
- Mutation

Evolution: building blocks

- Replication
- Selection
- Mutation

Replication

Bacterial reproduction:

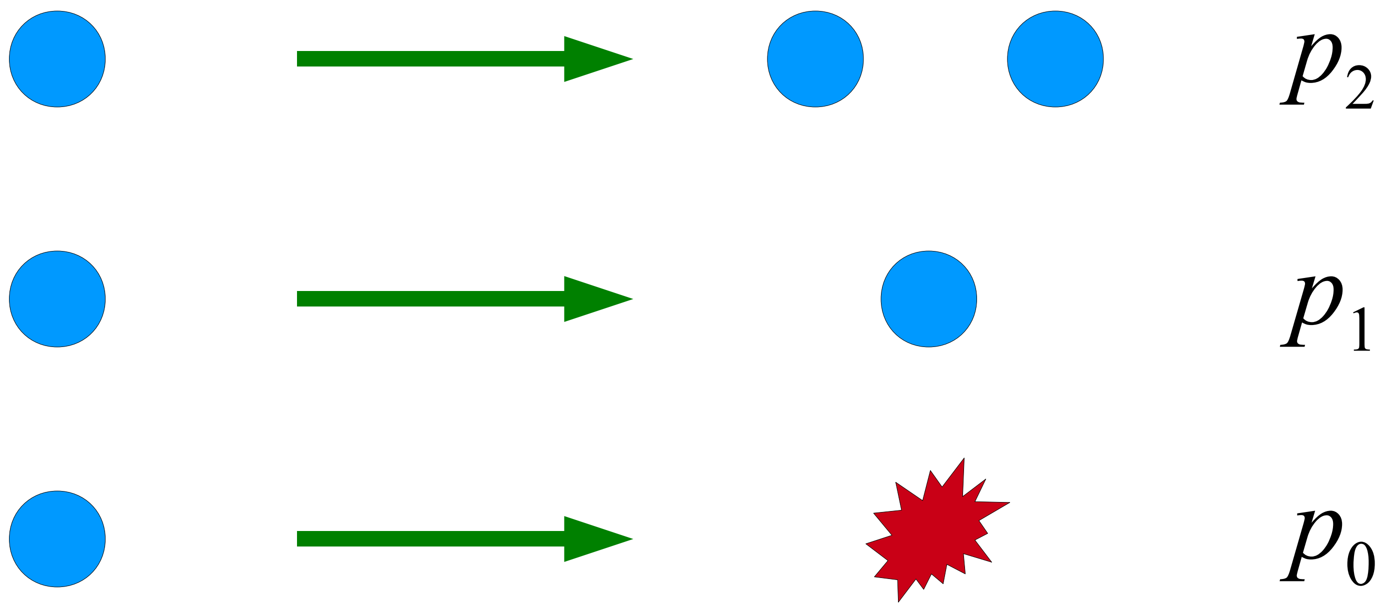
$$x_{t+1} = 2x_t \qquad\qquad x_t = 2^t x_0$$

3 divisions / hour = 144 divisions / 2 days

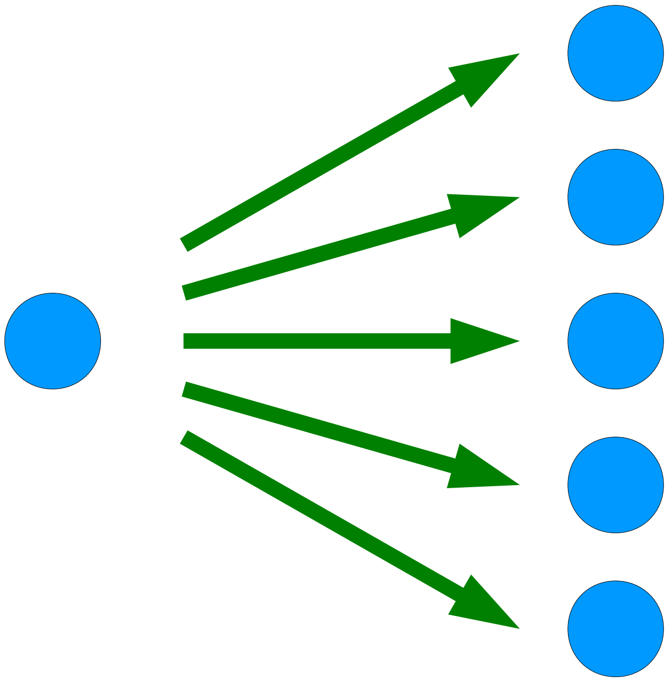
$2^{144} \approx 2 \times 10^{43} \approx 2 \times 10^{28}\, kg \approx 3000$ earths!

Refining the argument

check every τ secs << 20 min



Galton-Watson process

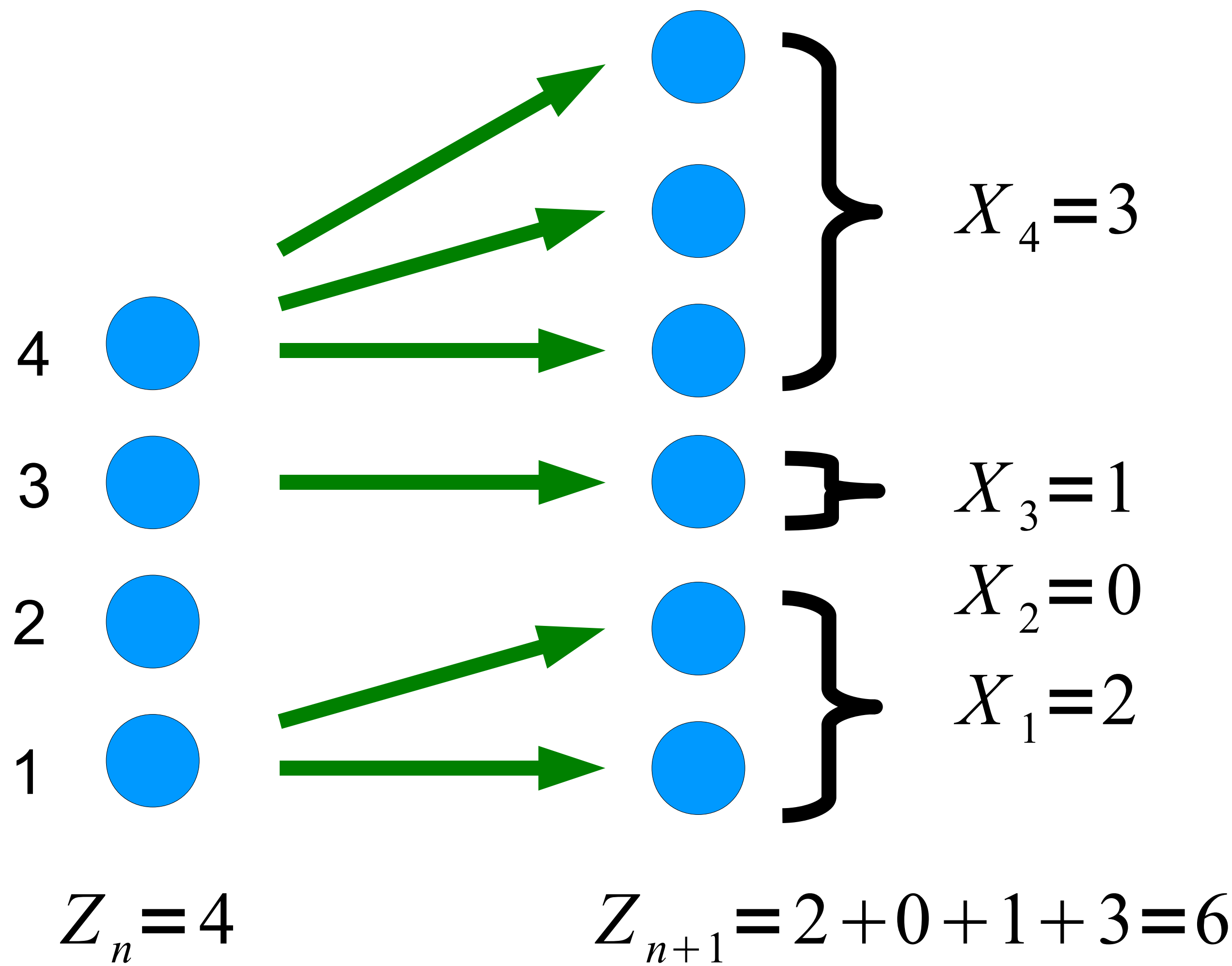


$$P\{X=k\}=p_k$$
$$k=0,1,2\ldots$$

$$F(s)=\sum_{k=0}^{\infty} p_k s^k$$

$$F(1)=1 \qquad F'(1)=m \qquad F''(1)=\sigma^2+m^2-m$$

Galton-Watson process



Galton-Watson process

$$Z_0 = 1 \qquad Z_n = X_1 + X_2 + \cdots + X_{Z_{n-1}} \qquad (n > 0)$$

$$\mathrm{P}\{Z_n = k\} = p_k^{(n)} \qquad k = 0,1,2\ldots$$

$$F_n(s) = \sum_{k=0}^{\infty} p_k^{(n)} s^k$$

Markov process:

$$\mathrm{P}\{Z_{n+1} = k \mid Z_n = j\} = P_{j,k} \qquad j,k = 0,1,2\ldots$$

Galton-Watson process

$$G_j(s) = \sum_{k=0}^{\infty} P_{j,k} s^k = [F(s)]^j$$

$$F_{n+1}(s) = \sum_{j=0}^{\infty} p_j^{(n)} [F(s)]^j = F_n(F(s))$$

$$F_0(s) = s \qquad F_{n+1}(s) = F(F_n(s))$$

Galton-Watson process

$$F'_n(1) = F'(1)\,F'_{n-1}(1) = m\,F'_{n-1}(1)$$

$$\boxed{m_n = m^n}$$

$$F''_n(1) = F''(1)\left[F'_{n-1}(1)\right]^2 + F'(1)\,F''_{n-1}(1)$$
$$= F''(1)\,m^{2n-2} + m\,F''_{n-1}(1)$$

$$\sigma_n^2 = \sigma^2 \frac{m^{n-1}(m^n - 1)}{m-1} \qquad m \neq 1$$

$$\sigma_n^2 = n\sigma^2 \qquad m = 1$$

Galton-Watson process

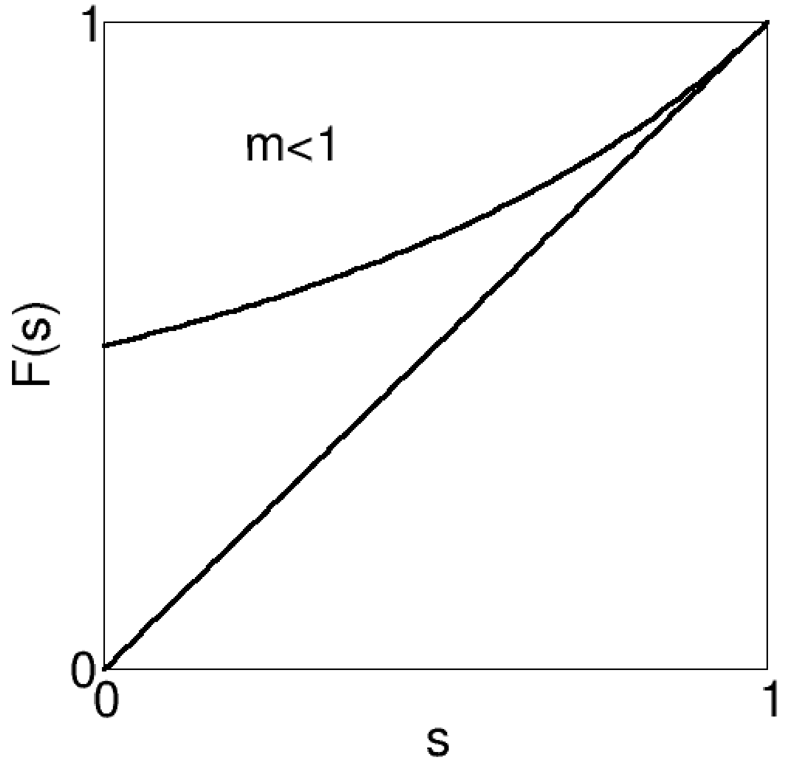
$$F(1) = 1 \qquad F(0) = p_0 \qquad F'(1) = m$$

$$p_0 + p_1 < 1$$

$$\Downarrow$$

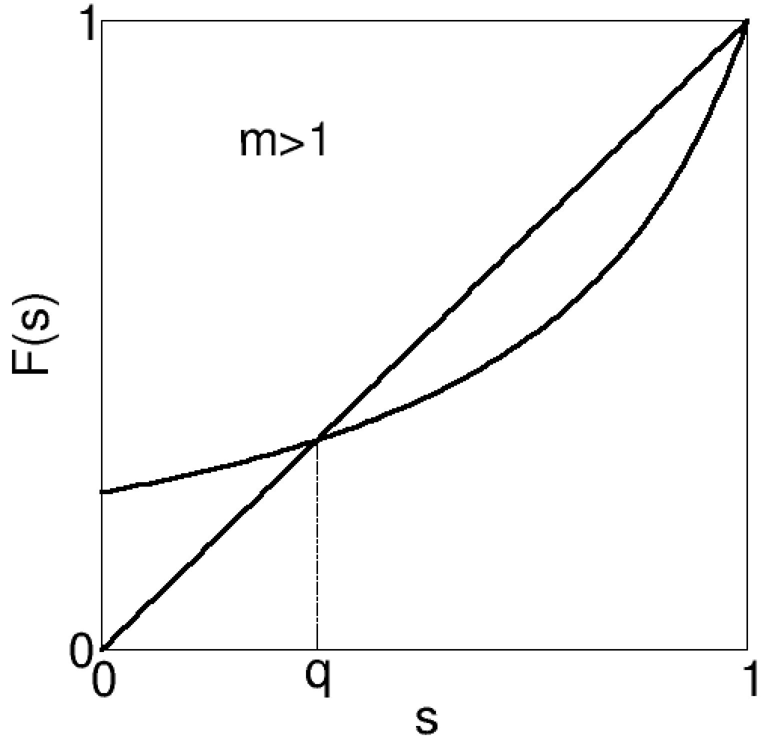
$$F'(s) > 0 \qquad F''(s) > 0 \qquad s \in [0,1]$$

Galton-Watson process



subcritical

Galton-Watson process



supercritical

Galton-Watson process

extinction probability:

$$q = \lim_{n \to \infty} F_n(0)$$

$$F_{n+1}(0) = F(F_n(0)) \qquad \Rightarrow \qquad q = F(q)$$

$$\begin{array}{lcl} m \leqslant 1 & \Rightarrow & q = 1 \\ m > 1 & \Rightarrow & q < 1 \end{array}$$

Bacterial growth revisited

$$F(s) = p_0 + p_1 s + p_2 s^2$$
$$= s + (1-s)(p_0 - p_2 s)$$

$$m = 1 + p_2 - p_0$$

$$q = 1 \qquad p_2 \leqslant p_0$$

$$q = \frac{p_0}{p_2} \qquad p_2 > p_0$$

$$m_n = (1 + p_2 - p_0)^n \approx e^{n p_2 (1-q)}$$

Continuous Galton-Watson process

$$p_k(\tau) = \tau \lambda p_k + o(\tau) \qquad k \neq 1$$

$$p_1(\tau) = 1 - \tau \lambda (1 - p_1) + o(\tau)$$

$$F(s;\tau) = \sum_{k=0}^{\infty} p_k(\tau) s^k = s + \tau \lambda \overbrace{\left[F(s) - s \right]}^{U(s)} + o(\tau)$$

$$\lim_{\tau \to 0} p_k^{(t/\tau)} = p_k(t) \qquad \lim_{\tau \to 0} F_{t/\tau}(s) = F(s,t)$$

Continuous Galton-Watson process

$$F_{t/\tau+1}(s) = F(F_{t/\tau}(s);\tau)$$

$$\frac{F_{t/\tau+1}(s) - F_{t/\tau}(s)}{\tau} = \lambda U(F_{t/\tau}(s)) + o(1)$$

$$\boxed{\frac{\partial F(s,t)}{\partial t} = \lambda U(F(s,t))}$$

backward Kolmogorov eq.

Continuous Galton-Watson process

$$F_{t/\tau+1}(s) = F_{t/\tau}(F(s;\tau))$$

$$\frac{F_{t/\tau+1}(s) - F_{t/\tau}(s)}{\tau} = \frac{F_{t/\tau}(s + \lambda\tau U(s) + o(\tau)) - F_{t/\tau}(s)}{\tau}$$

$$\boxed{\frac{\partial F(s,t)}{\partial t} = \lambda U(s) \frac{\partial F(s,t)}{\partial s}}$$

forward Kolmogorov eq.

Evolution of the mean

$$\lim_{s\to 1}\frac{\partial}{\partial s}F(s,t)=m(t) \qquad U'(1)=m-1\equiv r/\lambda \qquad U(1)=0$$

$$\frac{\partial}{\partial t}\frac{\partial F(s,t)}{\partial s}=\lambda U'(s)\frac{\partial F(s,t)}{\partial s}+\lambda U(s)\frac{\partial^2 F(s,t)}{\partial s^2}$$

$$\boxed{\frac{d\,m(t)}{dt}=r\,m(t)}$$

Malthus law

Bacterial growth again

$$U(s) = (1-s)(p_0 - p_2 s)$$

$$F(s,0) = s \qquad p_2 > p_0 \qquad r \equiv \lambda(p_2 - p_0)$$

$$F(s,t) = \frac{p_0(1-s) - (p_0 - p_2 s)e^{-rt}}{p_2(1-s) - (p_0 - p_2 s)e^{-rt}}$$

$$\mathrm{P}\{T_{ext} \leqslant t\} = p_0(t) = F(0,t) = \frac{p_0 - p_0 e^{-rt}}{p_2 - p_0 e^{-rt}}$$

mean extinction time of realizations that go extinct:

$$\mathrm{E}\{T_{ext}\} = \frac{-\ln(1-q)}{\lambda p_0} = \frac{1}{\lambda p_2}\left[1 + \frac{q}{2} + o(q)\right]$$

Saturation

$$\frac{dm}{dt} = r\,m\left(1 - \frac{m}{K}\right)$$

carrying capacity

$$m(t) = \frac{K\,m_0\,e^{rt}}{K + m_0\left(e^{rt} - 1\right)} \qquad \lim_{t\to\infty} m(t) = K$$

saturation maintains a constant population

Evolution: building blocks

- Replication
- Selection
- Mutation

Fitness

fitness: mean number of adult offspring in the next generation (separated generations)

fitness: mean growth rate (mixed generations)

$$\frac{dm}{dt} = r\,m$$

fitness

Competition

$$\frac{dm_A}{dt} = r_A m_A \qquad \frac{dm_B}{dt} = r_B m_B$$

$$x = \frac{m_A}{m_A + m_B} \qquad y = \frac{m_B}{m_A + m_B} = 1 - x$$

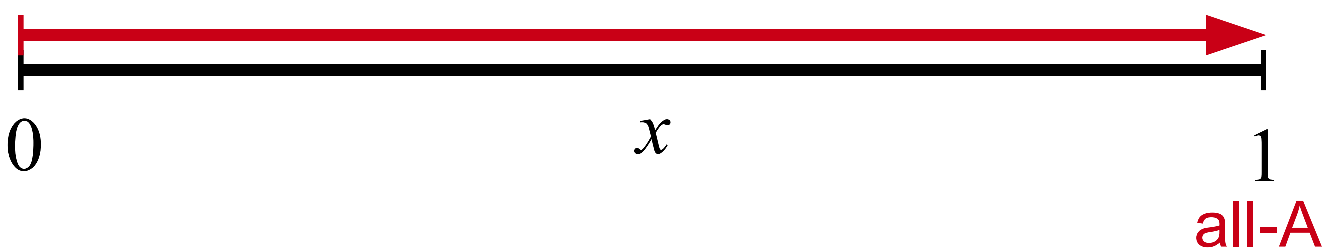
$$\frac{dx}{dt} = x(r_A - \phi) \qquad \frac{dy}{dt} = y(r_B - \phi)$$

average fitness: $\phi = x r_A + y r_B$

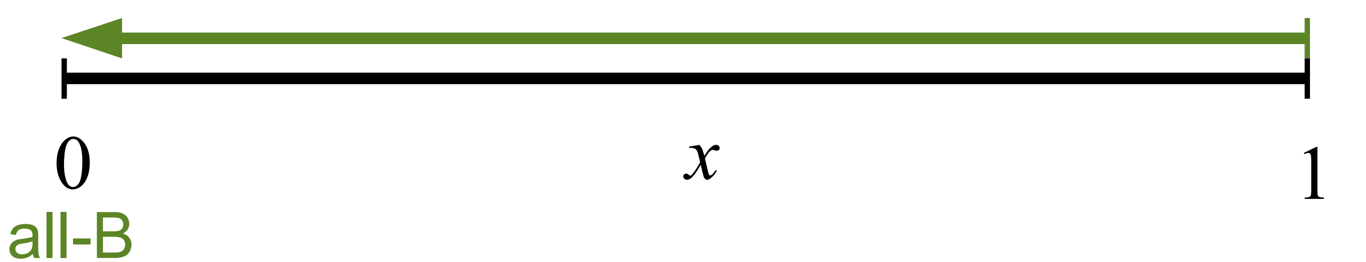
Survival of the fittest

$$\frac{dx}{dt} = x(1-x)(r_A - r_B)$$

$$r_A > r_B$$



$$r_A < r_B$$

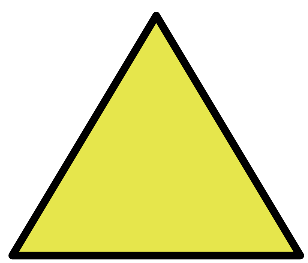


Survival of the fittest

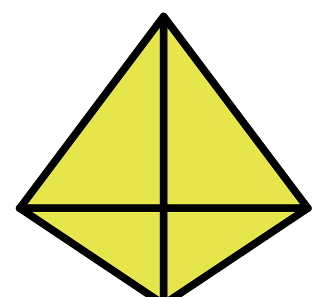
$$\frac{d\,x_k}{d\,t} = x_k\left(f_k - \phi\right) \qquad \phi = \sum_{k=1}^{n} x_k f_k$$

$$\sum_{k=1}^{n} x_k = 1 \quad \forall\, t$$

$n = 2$



$n = 3$



$n = 4$

Survival of the fittest

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

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

$$\Downarrow$$

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

Fundamental theorem of natural selection

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

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

- Mean fitness never decreases ($\sigma_f^2 \geqslant 0$)
- The spead of increase is determined by the variation within the population

Composition-dependent fitness

$$f_k = f_k(x_1, \ldots, x_n) \equiv f_k(\boldsymbol{x})$$

Example: two species

$$r_A(x, y) = r + \alpha_A y$$
$$r_B(x, y) = r + \alpha_B x$$

symbiosis

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

competition

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

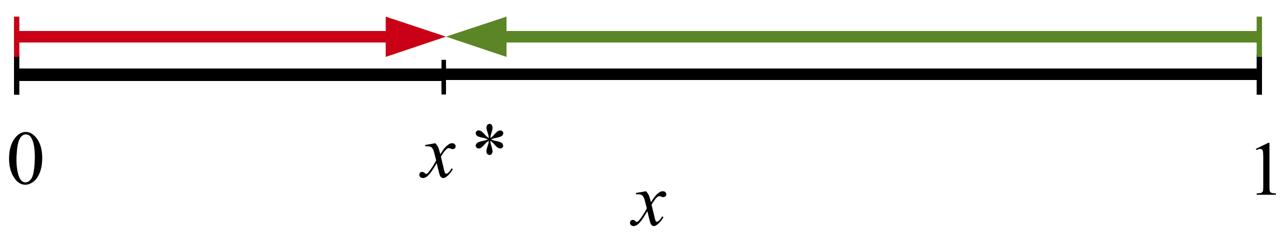
Symbiotic coexistence

$$\frac{dx}{dt} = x(1-x)[\alpha_A - (\alpha_A + \alpha_B)x]$$

$$\alpha_A > 0$$

$$\alpha_B > 0$$

$$x^* = \frac{\alpha_A}{\alpha_A + \alpha_B}$$

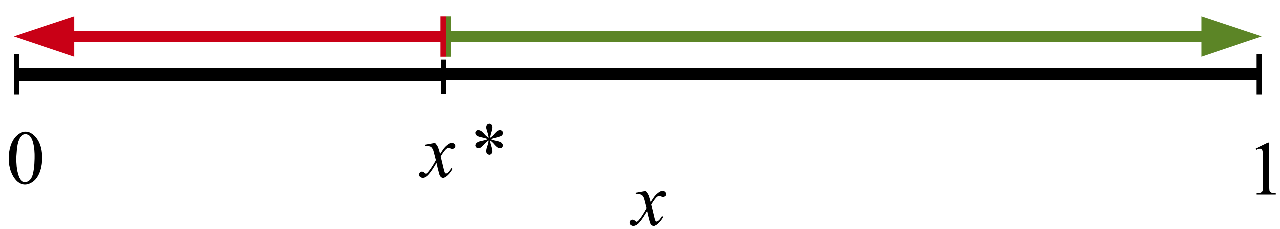


Competitive exclusion

$$\frac{dx}{dt} = x(1-x)[\alpha_A - (\alpha_A + \alpha_B)x]$$

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

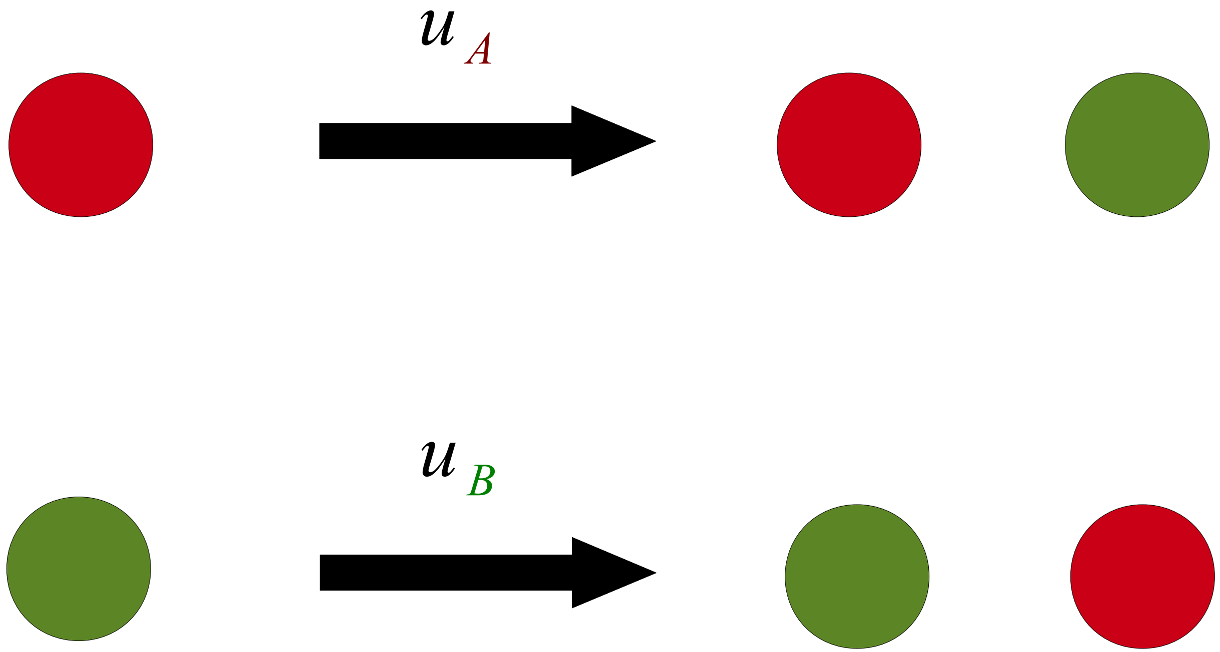
$$x^* = \frac{\alpha_A}{\alpha_A + \alpha_B}$$



Evolution: building blocks

- Replication
- Selection
- Mutation

Replication with error



Replication with error

$$\frac{dx}{dt} = x r_A (1 - u_A) + y r_B u_B - \phi x$$

$$\frac{dy}{dt} = x r_A u_A + y r_B (1 - u_B) - \phi y$$

$$\phi = x r_A + y r_B$$

$$\frac{dx}{dt} = x(1 - x)(r_A - r_B) + (1 - x) r_B u_B - x r_A u_A$$

$x = 0 \quad x = 1$ are not equilibria

Replication with error

$$x^* \approx 1 - \frac{r_A u_A}{r_A - r_B} \qquad r_A > r_B$$

$$x^* \approx \frac{r_B u_B}{r_B - r_A} \qquad r_A < r_B$$

$$x^* = \frac{u_A}{u_A + u_B} \qquad r_A = r_B$$

mutation is the source of variability

Evolution with mutation

mutation matrix $Q = (q_{ij})$ $\qquad$ $\boldsymbol{u} = (1, \ldots, 1)$

$$\sum_{j=1}^{n} q_{ij} = 1 \quad \Leftrightarrow \quad Q\,\boldsymbol{u}^T = \boldsymbol{u}^T$$

$$R = \begin{pmatrix} r_1 & & 0 \\ & \ddots & \\ 0 & & r_n \end{pmatrix} \qquad W \equiv RQ$$

mutation-selection matrix

$$\frac{d\boldsymbol{x}}{dt} = \boldsymbol{x}W - \phi\,\boldsymbol{x} \qquad \phi = \boldsymbol{x}W\boldsymbol{u}^T = \sum_{j=1}^{n} x_j r_j$$

quasispecies equation

Evolution with mutation

fundamental theorem

may be negative!

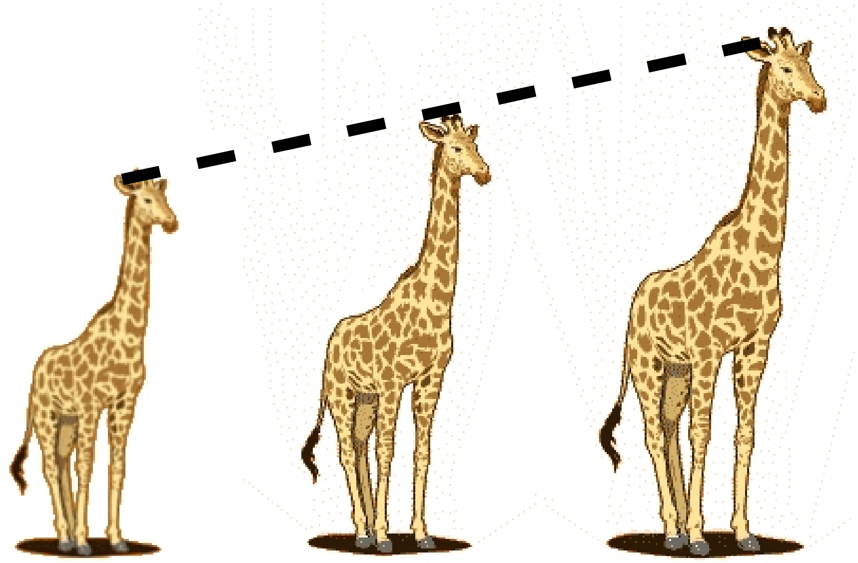
$$\frac{d\phi}{dt} = \frac{d\boldsymbol{x}}{dt} W \boldsymbol{u}^T = \boldsymbol{x} W^2 \boldsymbol{u}^T - \phi^2 = \boldsymbol{x}(W - \phi I)^2 \boldsymbol{u}^T$$

equilibria: $\boldsymbol{x}^* W = \phi^* \boldsymbol{x}^*$

if Q is irreducible, ϕ^* is the largest eigenvalue of W

as $\boldsymbol{x}^*$ normally corresponds to a mixed population, ϕ^* need not be the absolute maximum

The paradox of mutation reversion



“classical” theory of inheritance:

$$X_{n+1} = \frac{1}{2}\left(X_n^{(1)} + X_n^{(2)}\right) + Z_n$$

$N(0, \sigma)$

The paradox of reversion

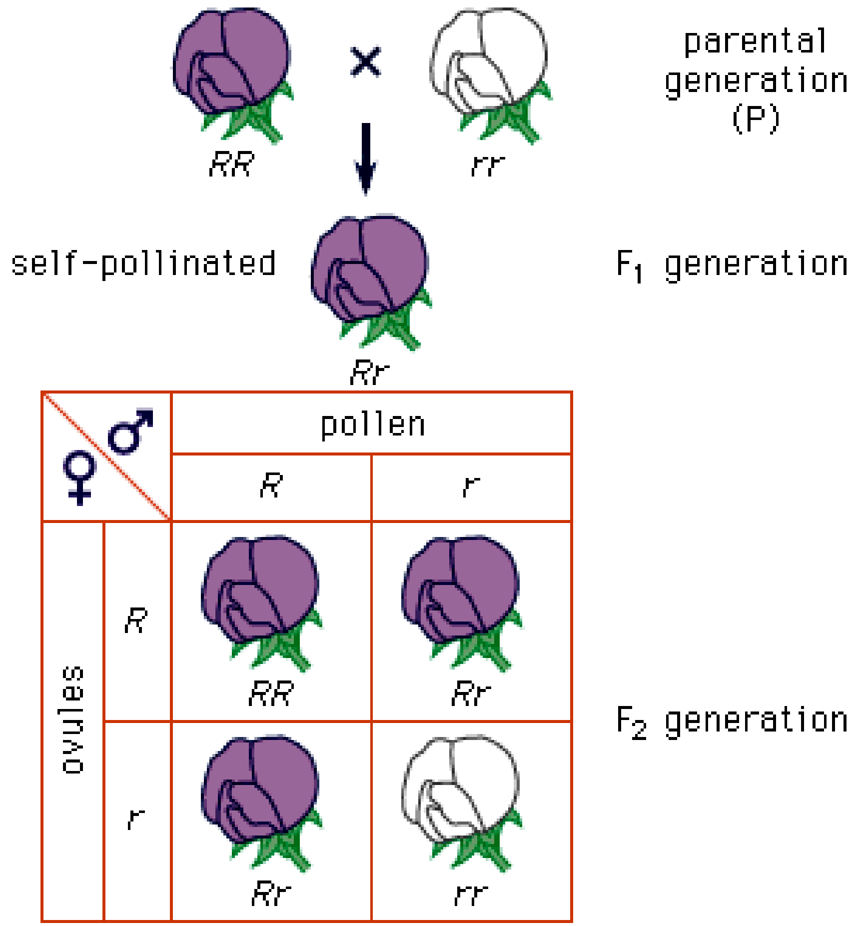
$$\mathrm{P}\{X_n \leqslant x\} = P_n(x) \qquad F_n(q) = \int e^{iqx}\, d\, P_n(x)$$

$$\log F_n(q) = i\, q\, m_n + \sum_{k=2}^{\infty} \kappa_n^{(j)} \frac{(i\, q)^j}{j\,!}$$

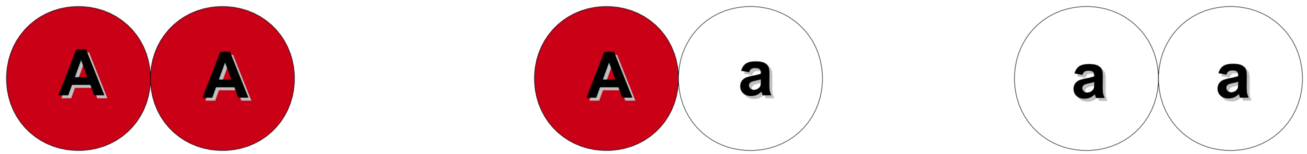
$$F_{n+1}(q) = F_n(q/2)^2\, e^{-\sigma^2 q^2/2} \qquad \Leftrightarrow \qquad \begin{cases} m_{n+1} = m_n & \\ \sigma_{n+1}^2 = \dfrac{\sigma_n^2}{2} + \sigma^2 & \\ \kappa_{n+1}^{(j)} = \dfrac{\kappa_n^{(j)}}{2^{j-1}} & j > 2 \end{cases}$$

$$\lim_{n\to\infty} F_n(q) = e^{iq\, m_1 - \sigma^2 q^2} \qquad \Rightarrow \qquad \lim_{n\to\infty} P_n(x) = N(m_{1,} \sqrt{2}\, \sigma)$$

“Quantum” theory of inheritance



Hardy-Weinberg law



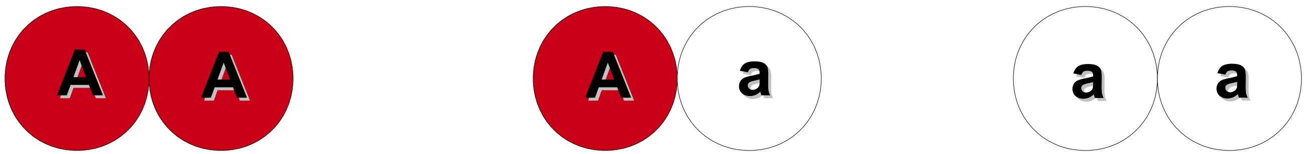
$$X_0 \quad + \quad Y_0 \quad + \quad Z_0 \quad = 1$$

$$X_1 = X_0^2 + X_0 Y_0 + \frac{Y_0^2}{4}$$

$$Y_1 = X_0 Y_0 + \frac{Y_0^2}{2} + 2 X_0 Z_0 + Y_0 Z_0$$

$$Z_1 = \frac{Y_0^2}{4} + Y_0 Z_0 + Z_0^2$$

Hardy-Weinberg law



X_0 Y_0 Z_0

$$X_1 = \left(X_0 + \frac{Y_0}{2} \right)^2$$

$$Y_1 = 2\left(X_0 + \frac{Y_0}{2} \right)\left(Z_0 + \frac{Y_0}{2} \right)$$

$$Z_1 = \left(Z_0 + \frac{Y_0}{2} \right)^2$$

Hardy-Weinberg law

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$$p_0 + q_0 = 1$$

$$X_1 = p_0^2 \qquad p_0 = X_0 + \frac{Y_0}{2}$$

$$Y_1 = 2p_0 q_0$$

$$Z_1 = q_0^2 \qquad q_0 = Z_0 + \frac{Y_0}{2}$$

Hardy-Weinberg law

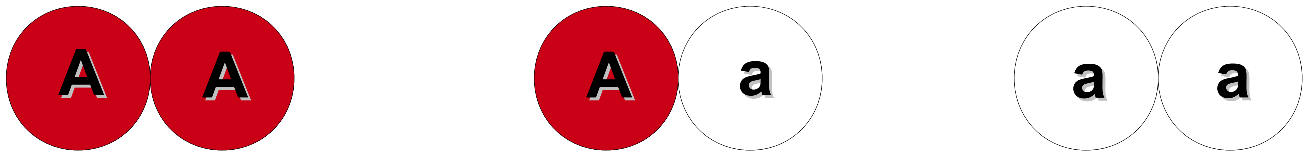
$$p_0 \quad + \quad q_0 \quad = 1$$

$$p_1 = X_1 + \frac{Y_1}{2} = p_0^2 + p_0 q_0 = p_0$$

$$q_1 = Z_1 + \frac{Y_1}{2} = q_0^2 + p_0 q_0 = q_0$$

$$\Rightarrow \quad X_2 = X_1, \quad Y_2 = Y_1, \quad Z_2 = Z_1$$

Hardy-Weinberg law



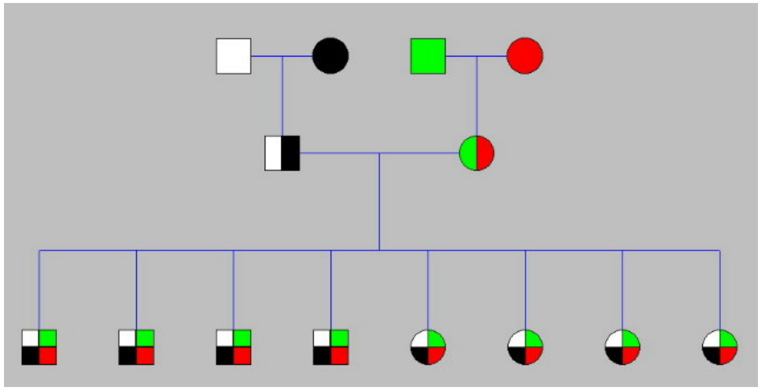
$$X_n = p_0^2 \qquad Y_n = 2 p_0 q_0 \qquad Z_n = q_0^2$$

$$p_0 = X_0 + \frac{Y_0}{2} \qquad q_0 = Z_0 + \frac{Y_0}{2}$$

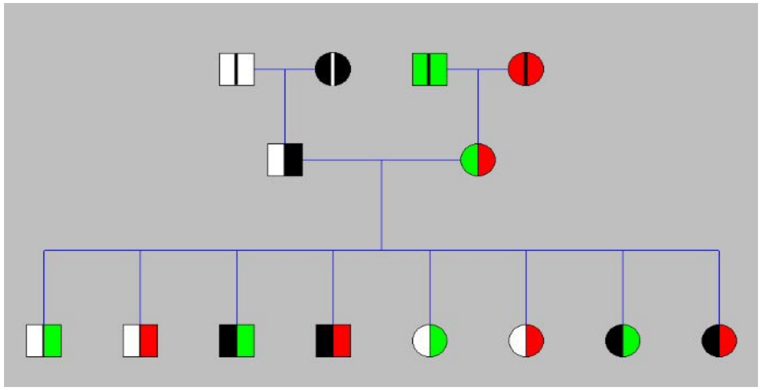
no reversion of the mutant
sustainment of variability

Classical vs. quantum inheritance

pre-Mendel (Galton)



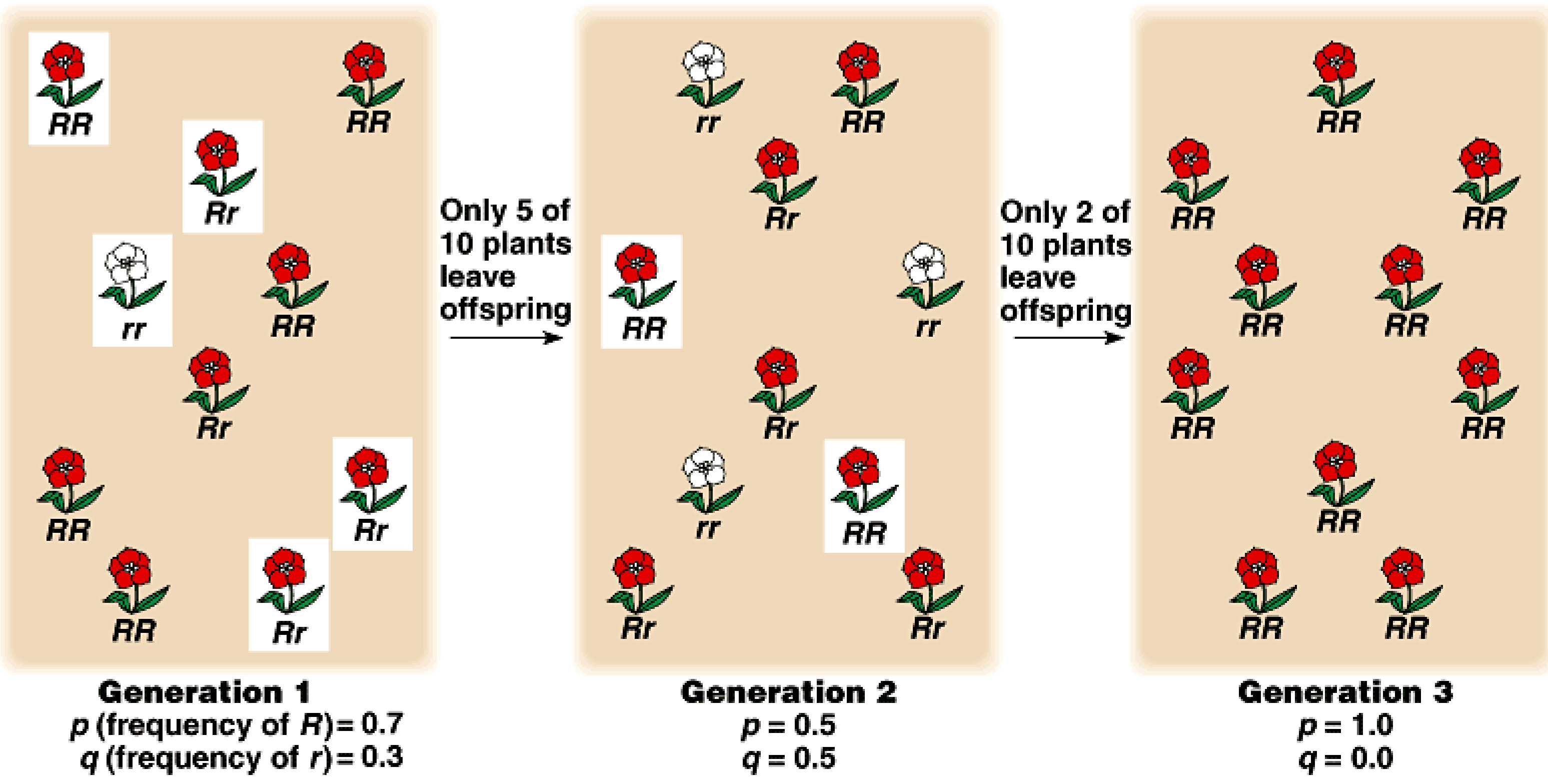
Mendel



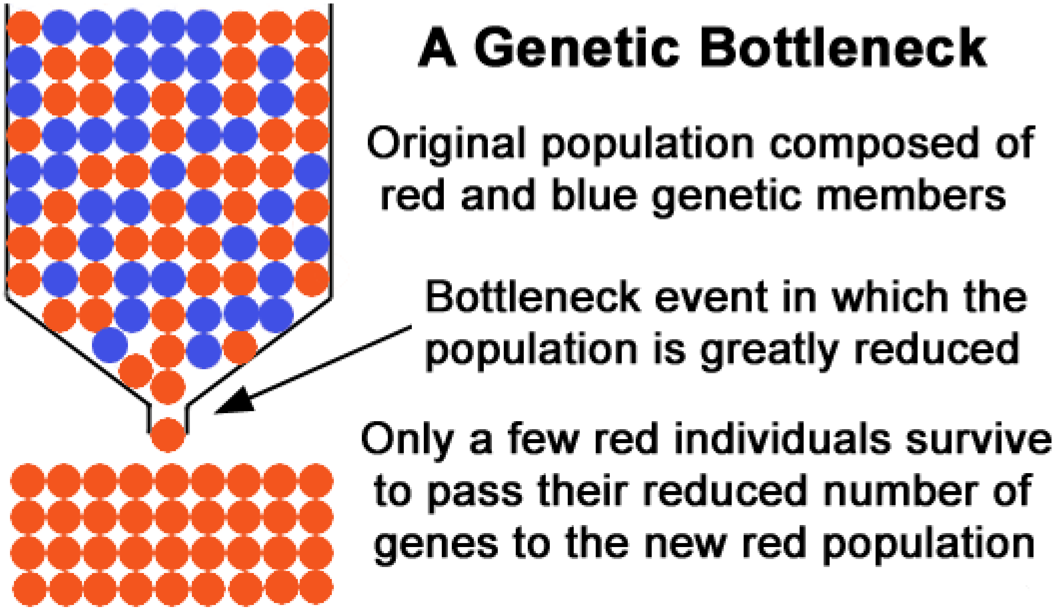
GENETIC DRIFT

Genetic drift

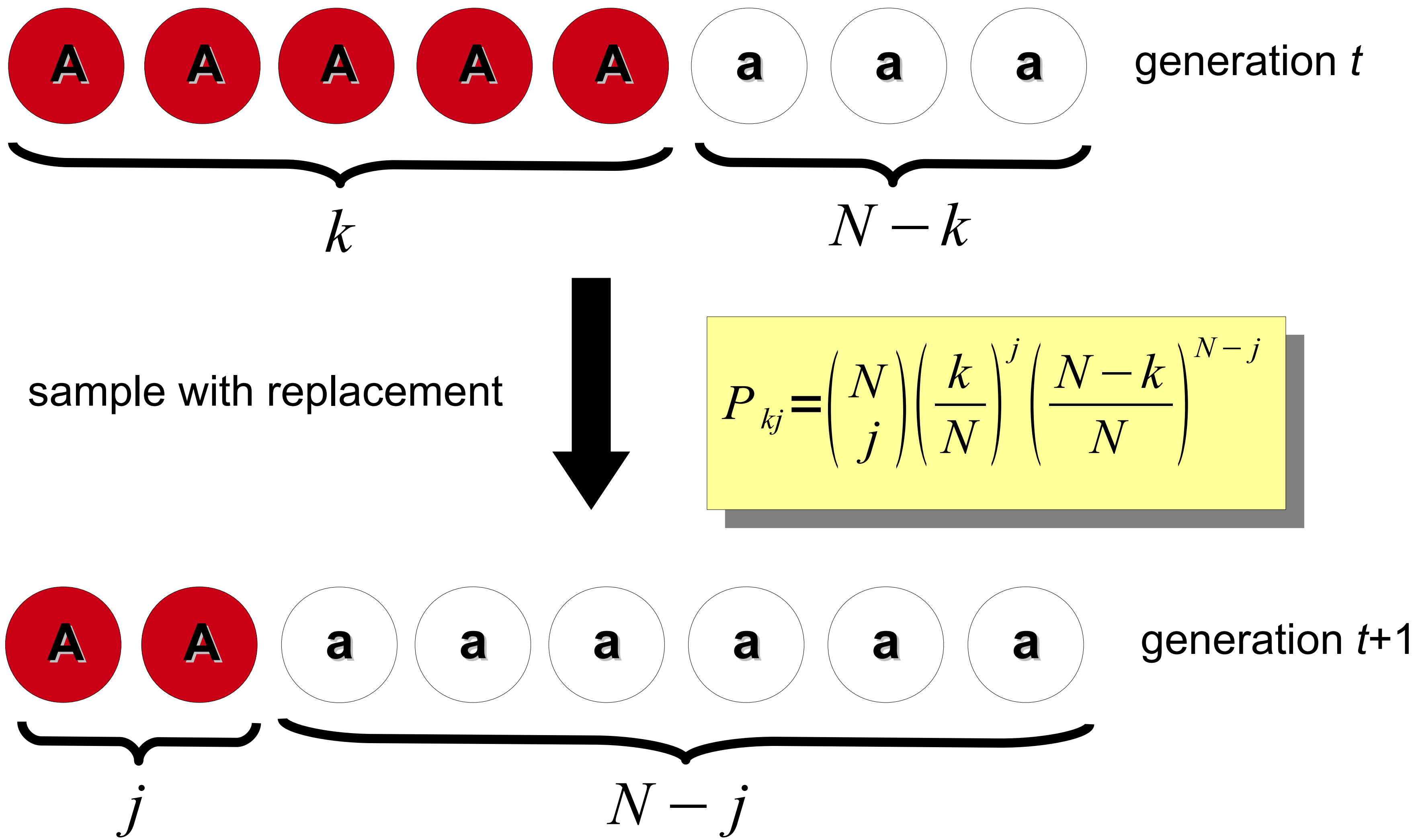
neutral evolution (no selection, no mutation)



Small populations: bottlenecks

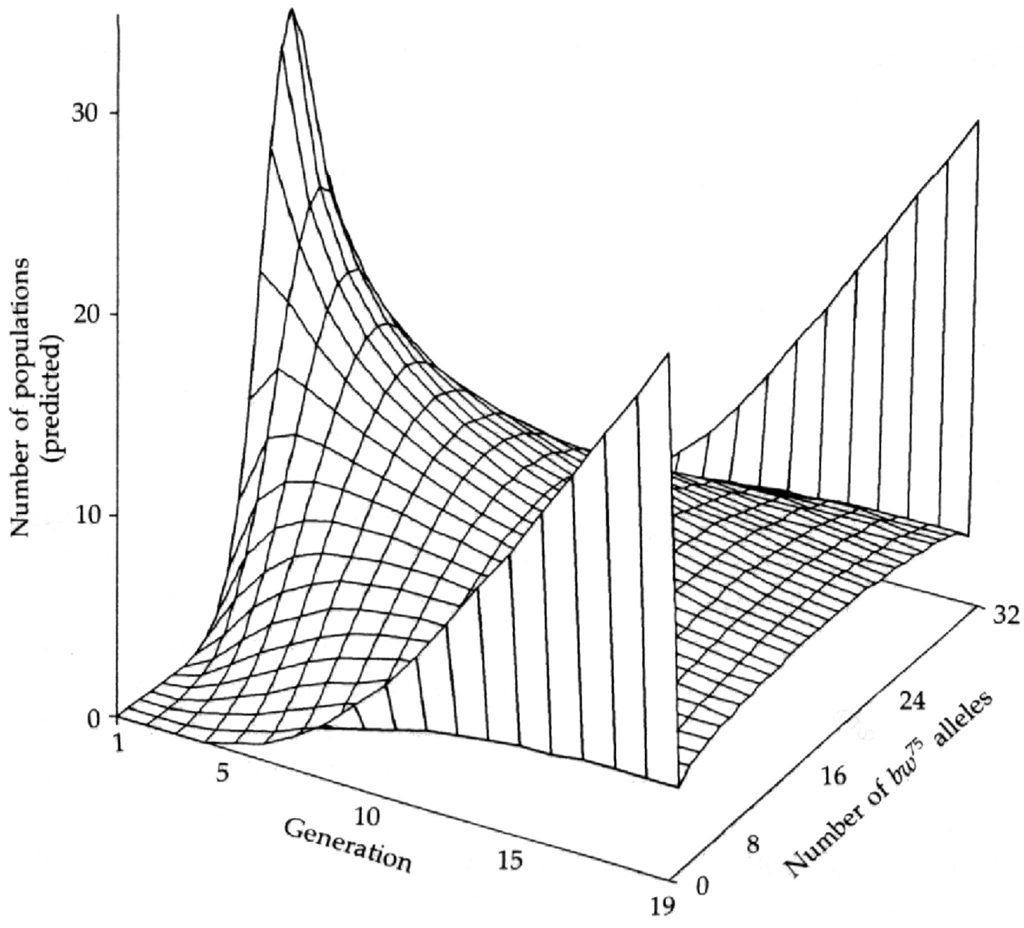


Fisher-Wright model



$$P_{kj} = \binom{N}{j} \left(\frac{k}{N}\right)^{j} \left(\frac{N-k}{N}\right)^{N-j}$$

Fisher-Wright model



Fisher-Wright model

two absorbing states:

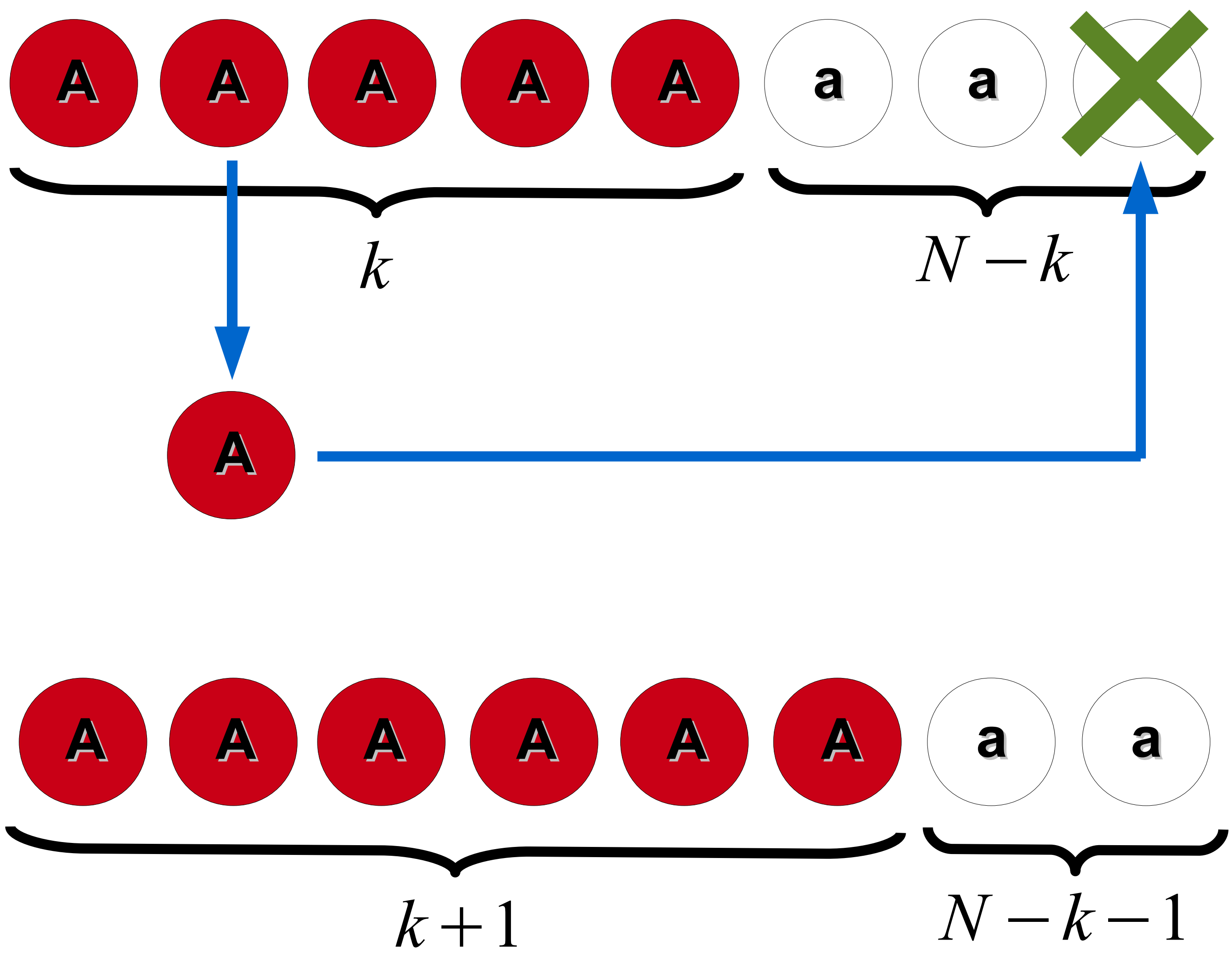
$$k = N \qquad\qquad k = 0$$

$$\pi_i = \mathrm{P}\left\{ \lim_{t \to \infty} X_t = N \,\middle|\, X_0 = i \right\}$$

$$\pi_i = \sum_{j=0}^{N} P_{ij} \pi_j \qquad \pi_0 = 0 \qquad \pi_N = 1$$

$$\mathrm{E}\{ X_{t+1} | X_t = k \} = k \qquad \Rightarrow \qquad \boxed{\pi_i = \frac{i}{N}}$$

Moran model



Moran model

$$P_{k,k\pm 1} = \frac{k(N-k)}{N^2}$$

$$P_{k,k} = \frac{(N-k)^2 + k^2}{N^2}$$

$$P_{k,j} = 0 \qquad \text{if } |k-j| > 1$$

birth-death process with
two absorbing states

Birth-death processes

$$q_0 = 1 \qquad q_j = \prod_{k=1}^{j} \frac{P_{k,k-1}}{P_{k,k+1}} \qquad Q_i = \sum_{j=0}^{i-1} q_j$$

if absorption

$$\pi_i = \mathrm{P}\left\{ \lim_{t \to \infty} X_t = N \,\middle|\, X_0 = i \right\}$$

$$t_{ij} = \sum_{n=0}^{\infty} \left(P^n\right)_{ij} \qquad T = PT + I \qquad t_{0j} = t_{Nj} = 0$$

if ergodic

$$w = wP$$

Birth-death processes

two absorbing states (0 & N)

$$\pi_i = \frac{Q_i}{Q_N}$$

$$t_{ij} = \frac{Q_N (1-\pi_i)\pi_j}{q_j P_{j,j+1}} \quad \text{if } j \leqslant i$$

$$t_{ij} = \frac{Q_N \pi_i (1-\pi_j)}{q_j P_{j,j+1}} \quad \text{if } j > i$$

one absorbing state (N)

$$t_{ij} = \frac{Q_N - Q_i}{q_j P_{j,j+1}} \quad \text{if } j \leqslant i \qquad t_{ij} = \frac{Q_N - Q_j}{q_j P_{j,j+1}} \quad \text{if } j > i$$

no absorbing state

$$w_i = \frac{(q_i P_{i,i+1})^{-1}}{\sum_{j=0}^{N} (q_j P_{j,j+1})^{-1}}$$

Moran model

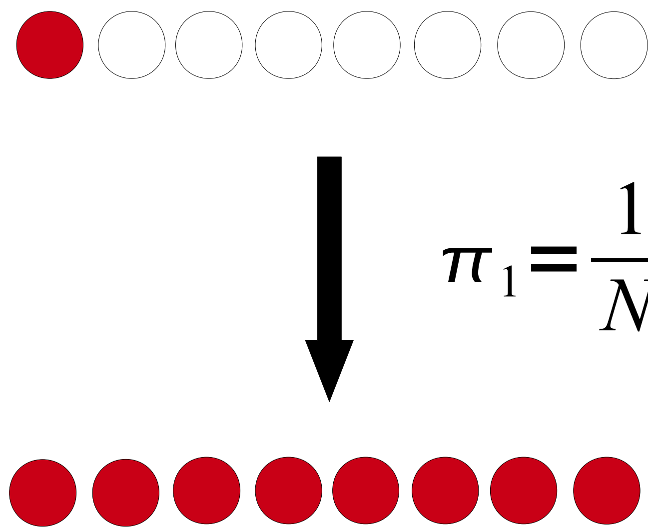
$$q_i = 1 \qquad Q_i = i \qquad \pi_i = \frac{i}{N}$$

$$t_{ij} = N\left(\frac{N-i}{N-j}\right) \quad \text{if} \quad j \leqslant i \qquad\qquad t_{ij} = N\left(\frac{i}{j}\right) \quad \text{if} \quad j > i$$

mean absorption time

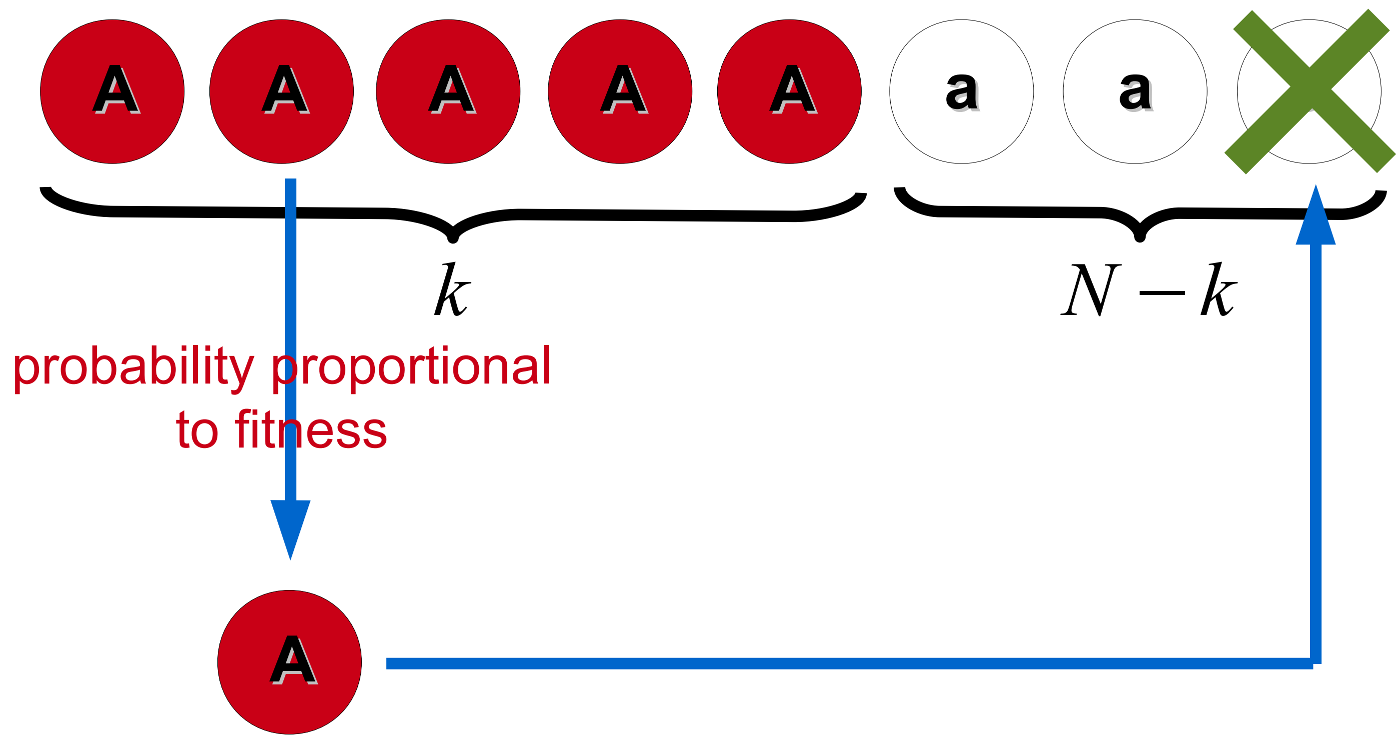
$$t_i = \sum_{j=1}^{N-1} t_{ij} = O(N)$$

Fixation of a mutant allele



$$\pi_1 = \frac{1}{N}$$

Genetic drift under selection



Genetic drift under selection

$$P_{k,k+1} = \frac{N-k}{N} \frac{k f_A}{k f_A + (N-k) f_a}$$

$$P_{k,k-1} = \frac{k}{N} \frac{(N-k) f_a}{k f_A + (N-k) f_a}$$

$$\frac{P_{k,k-1}}{P_{k,k+1}} = \frac{f_a}{f_A} \equiv r^{-1}$$

$$\boxed{\pi_i = \frac{1-r^{-i}}{1-r^{-N}}}$$

Fixation of a mutant allele under selection

$$\rho_A = \frac{1-r^{-1}}{1-r^{-N}} \qquad \rho_a = \frac{1-r}{1-r^{N}}$$

- If $r>1$ selection favors **A** over neutral case
- If $r<1$ selection favors **a** over neutral case

Diffusion approximation

$$\boldsymbol{w}(t+1)=\boldsymbol{w}(t)P$$

master equation

$$\boxed{w_i(t+1)-w_i(t)=\sum_j w_j(t)P_{ji}-w_i(t)\sum_j P_{ij}}$$

birth-death process

$$\Delta w_i(t)=\sum_{\pm}\left[w_{i\pm 1}(t)P_{i\pm 1,i}-w_i(t)P_{i,i\pm 1}\right]$$

Diffusion approximation

$$x \equiv \frac{i}{N} \qquad w_i(t) \equiv N\, f(x,t) \qquad \Delta t \equiv (\Delta x)^2 = \frac{1}{N^2}$$

$$a(x) \equiv P_{i,i+1} - P_{i,i-1} \qquad b(x) \equiv P_{i,i+1} + P_{i,i-1}$$

forward Kolmogorov (Fokker-Planck) equation

$$\frac{\partial f(x,t)}{\partial t} = -N \frac{\partial}{\partial x}[a(x) f(x,t)] + \frac{1}{2}\frac{\partial^2}{\partial x^2}[b(x) f(x,t)]$$

Diffusion approximation

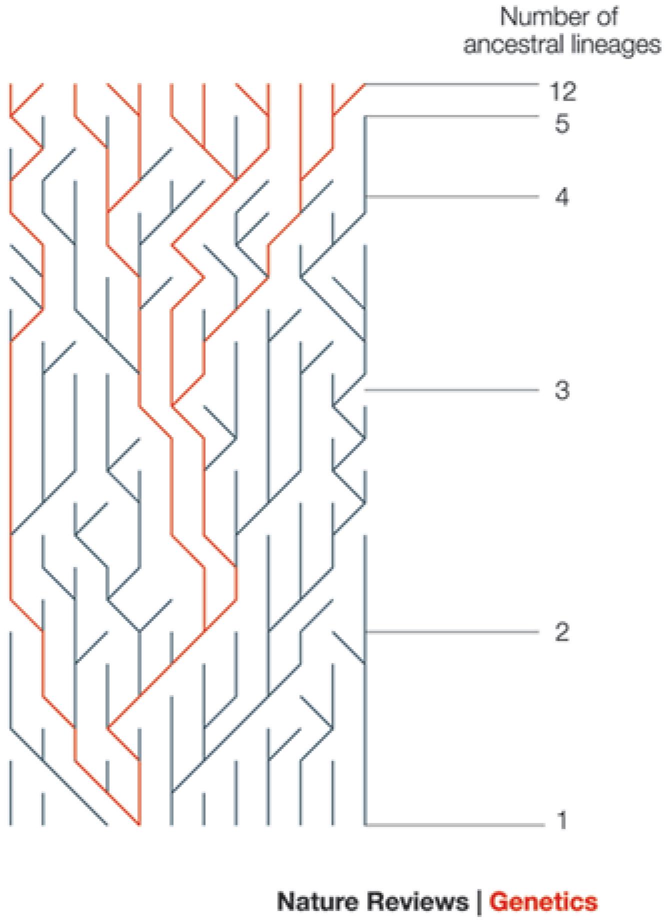
absorption probability

$$0 = -N a(x) \pi'(x) + \frac{1}{2} b(x) \pi''(x)$$

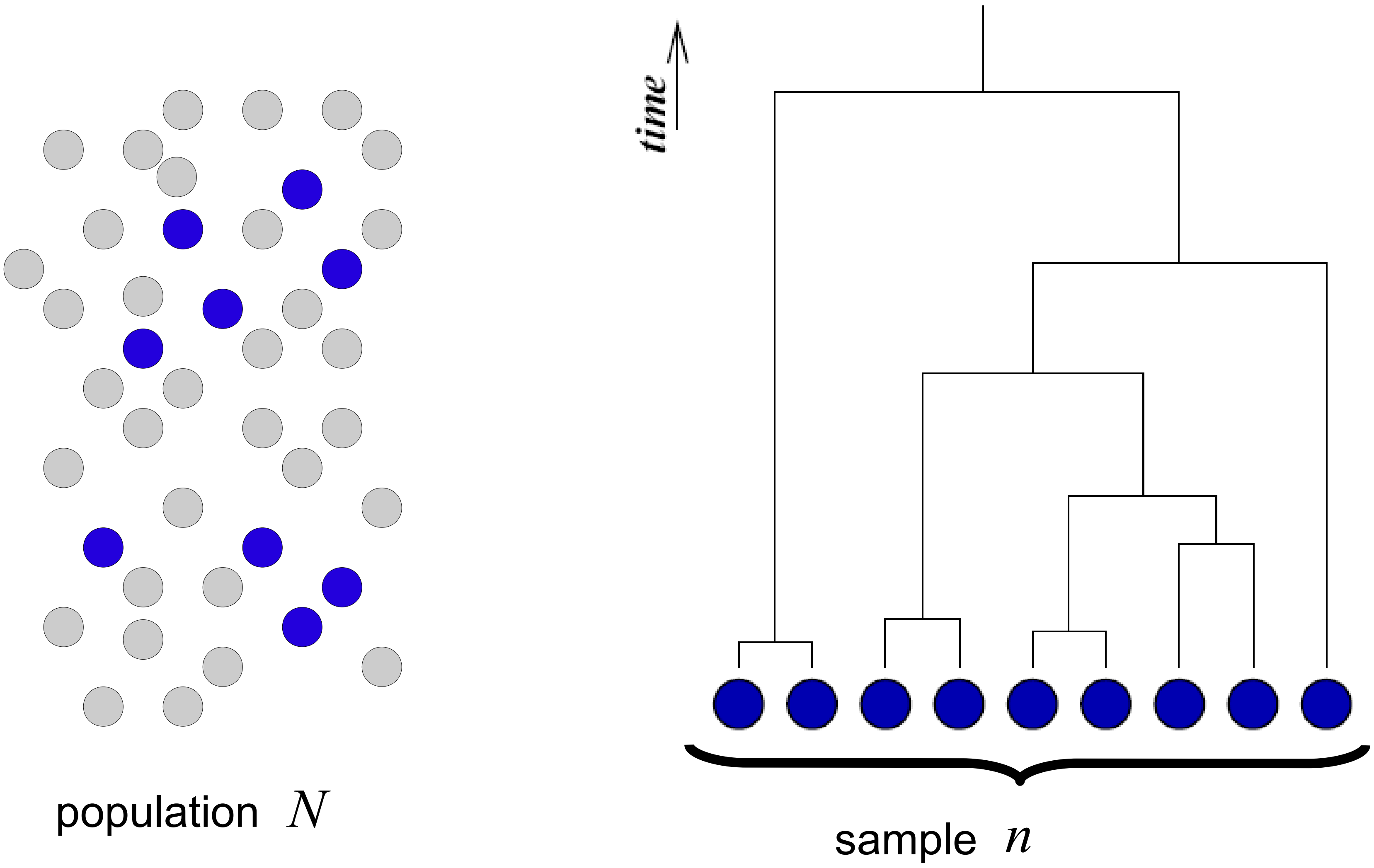
mean absorption time

$$-1 = -N a(x) \tau'(x) + \frac{1}{2} b(x) \tau''(x)$$

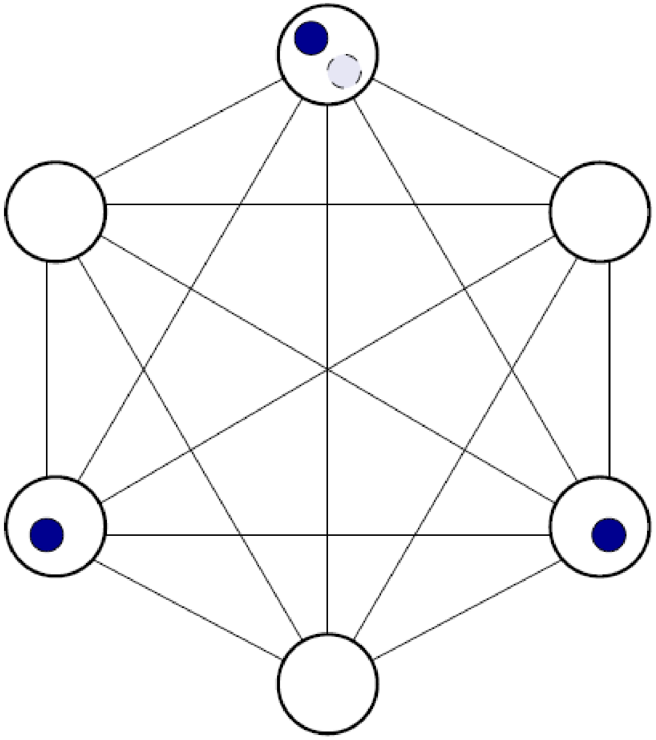
The coalescent



The coalescent



The coalescent



The coalescent

$$P\{j-1, t+\delta t \mid j, t\} = \frac{j(j-1)}{2}\delta t$$

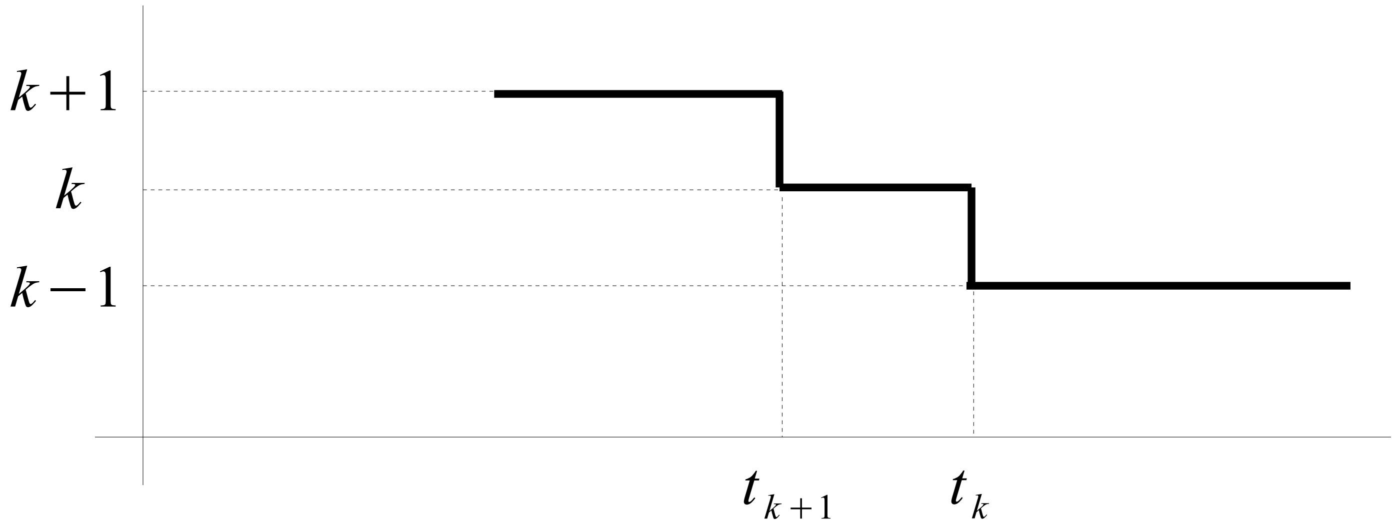
$$1 < j \leqslant n$$

Wright-Fisher: $\delta t = \frac{1}{N}$ $\quad n \ll N$

Moran: $\delta t = 1$ $\quad n \leqslant N$

$$P\{n, t \mid n, 0\} = \exp\left\{-\frac{n(n-1)}{2}t\right\}$$

Distribution of branching times



$$\Pi(t_n, t_{n-1}, \ldots, t_k) = \prod_{j=k}^{n} \exp\left\{ -\frac{j(j-1)}{2}(t_l - t_{l+1}) \right\}$$

$$(t_{k+1} \equiv 0)$$

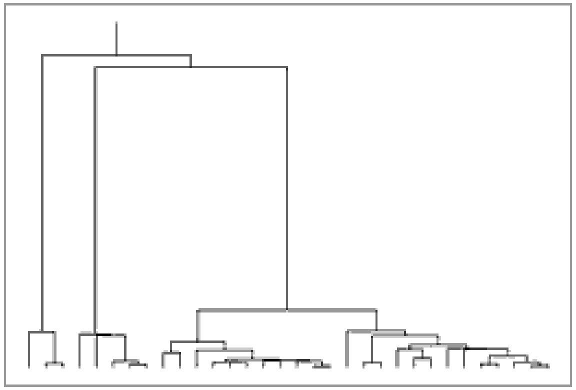
Expected times

$$E\{t_{j\to j-1}\} = \frac{2}{j(j-1)}$$

$$E\{t_{n\to m}\} = 2\sum_{j=m+1}^{n} \frac{1}{j(j-1)} = 2\left(\frac{1}{m} - \frac{1}{n}\right)$$

$$T_{\mathrm{MRCA}} \equiv E\{t_{n\to 1}\} = 2\left(1 - \frac{1}{n}\right) \approx 2$$

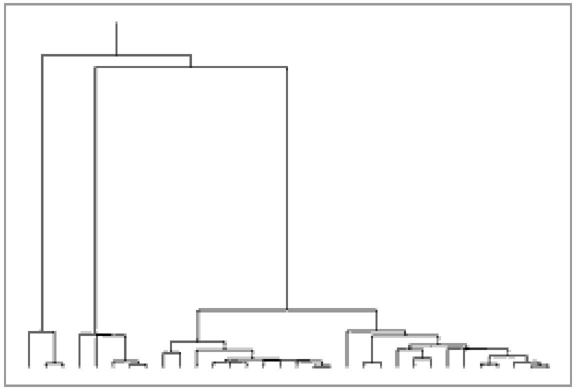
Most Recent Common Ancestor



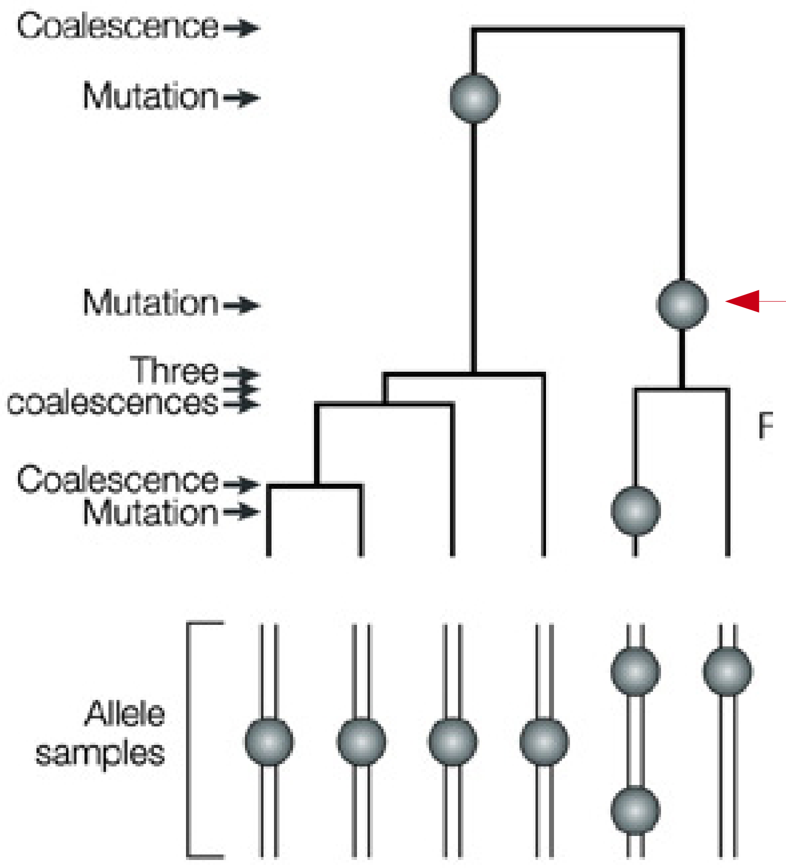
Variances

$$\mathrm{Var}\left\{t_{j\to j-1}\right\} = \frac{4}{j^2(j-1)^2}$$

$$\mathrm{Var}\left\{t_{n\to 1}\right\} = 4\sum_{j=1}^{n-1}\frac{1}{j^2(j+1)^2} \approx 1.16$$

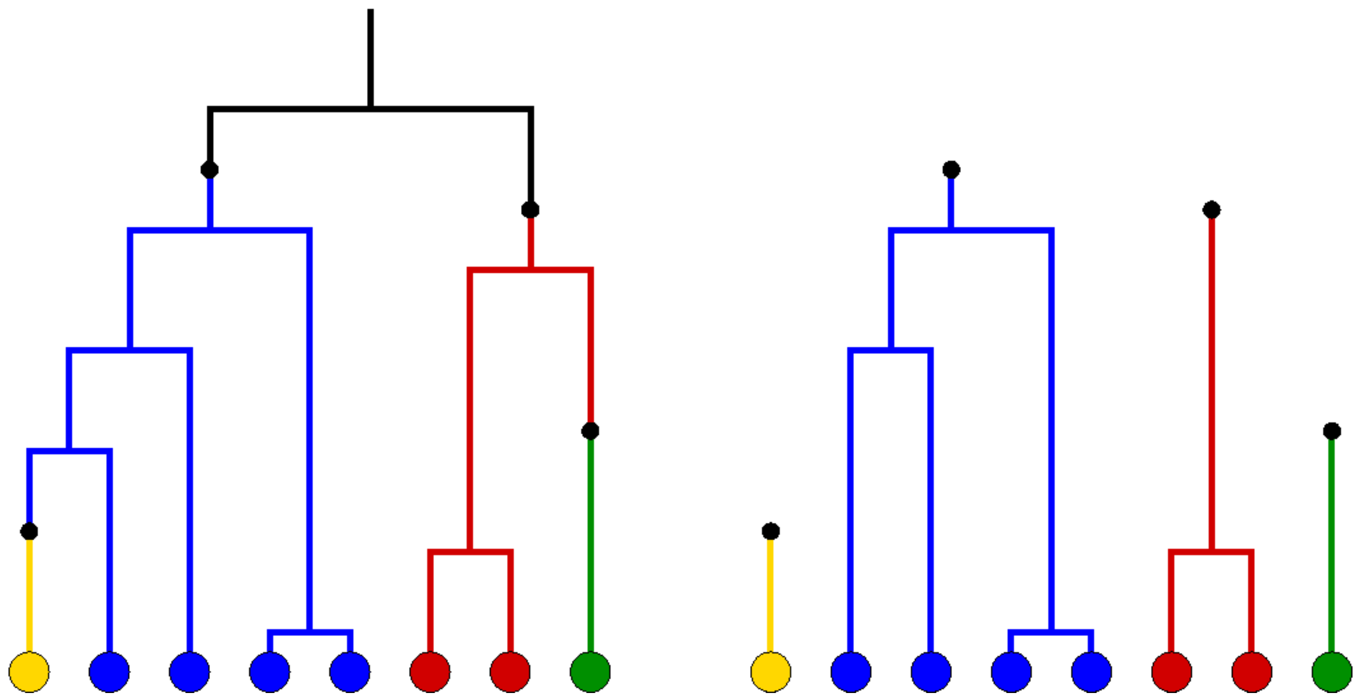


Coalescent with mutations



$$\text{Prob} = \frac{\theta}{2}\delta t$$

Coalescent with mutations



$$P\{j-1,\, t+\delta t \mid j,\, t\} = \frac{j(j-1)}{2}\delta t + j\frac{\theta}{2}\delta t = \frac{j(j+\theta-1)}{2}\delta t$$

Expected times

$$\mathrm{E}\{t_{j\to j-1}\} = \frac{2}{j(j+\theta-1)}$$

$$\mathrm{E}\{t_{n\to 1}\} = \frac{2}{\theta} + 2\sum_{j=2}^{n} \frac{1}{j(j+\theta-1)}$$

$$T_{\mathrm{MRCA}}(\theta) = 2\sum_{j=1}^{n} \frac{1}{j(j+\theta-1)}$$

$$\theta < 2 \quad \Rightarrow \quad T_{\mathrm{MRCA}}(\theta) > T_{\mathrm{MRCA}}$$

$$\theta = 2 \quad \Rightarrow \quad T_{\mathrm{MRCA}}(\theta) = T_{\mathrm{MRCA}} + O\left(\frac{1}{n^2}\right)$$

$$\theta > 2 \quad \Rightarrow \quad T_{\mathrm{MRCA}}(\theta) < T_{\mathrm{MRCA}}$$

Number of different types

$$\mathrm{P}\{\text{mutation} \mid j \to j-1\} = \frac{\theta j/2}{j(j+\theta-1)/2} = \frac{\theta}{j+\theta-1}$$

$$\mathrm{E}\{\text{different types in sample}\} = \sum_{j=1}^{n} \frac{\theta}{j+\theta-1}$$

$$\mathrm{P}\{k \text{ types in sample}\} = \left[\begin{matrix} n \\ k \end{matrix}\right] \frac{\theta^k}{S_n(\theta)} \qquad 1 \leqslant k \leqslant n$$

unsigned Stirling
numbers of first kind

$$S_n(\theta) = \theta(\theta+1)\cdots(\theta+n-1)$$
$$= \sum_{k=1}^{n} \left[\begin{matrix} n \\ k \end{matrix}\right] \theta^k$$

$$\left[\begin{matrix} n+1 \\ k \end{matrix}\right] = n\left[\begin{matrix} n \\ k \end{matrix}\right] + \left[\begin{matrix} n \\ k-1 \end{matrix}\right] \qquad n > 0$$

$$\left[\begin{matrix} n \\ 0 \end{matrix}\right] = 0 \qquad \left[\begin{matrix} n \\ n \end{matrix}\right] = 1$$

Cycles in permutations

$$\begin{pmatrix} 1 & 2 & 3 & 4 & 5 \\ 2 & 5 & 4 & 3 & 1 \end{pmatrix} = (1 \quad 2 \quad 5)(3 \quad 4) = (3 \quad 4)(1 \quad 2 \quad 5) = (3 \quad 4)(5 \quad 1 \quad 2)$$

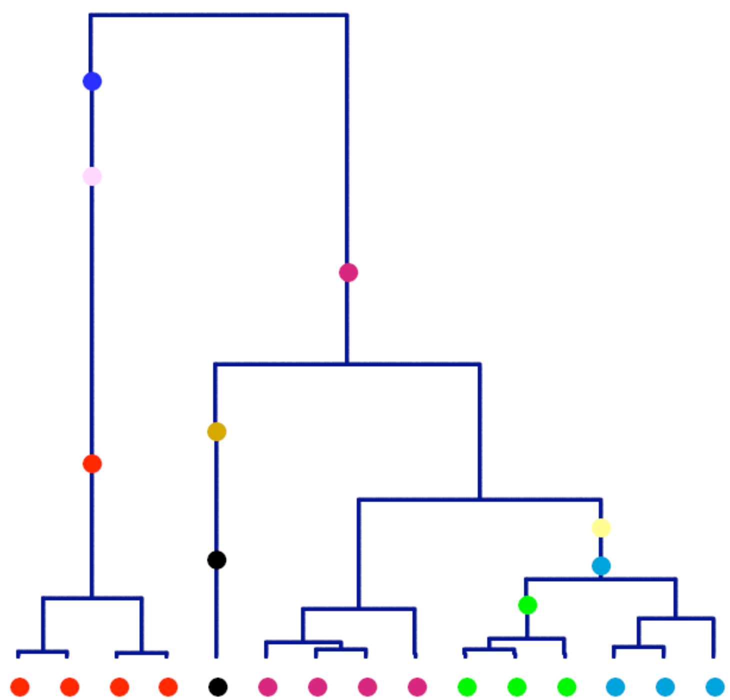
there are $\left[\begin{matrix} n \\ k \end{matrix} \right]$ permutations of n elements into k cycles

permutations of n elements into c_1 cycles with 1 element, c_2 cycles with 2 elements, etc.

$$\frac{n!}{1^{c_1} \cdots n^{c_n} c_1! \cdots c_n!} \qquad \sum_{j=1}^{n} j c_j = n \qquad \sum_{j=1}^{n} c_j = k$$

Ewens' sampling formula

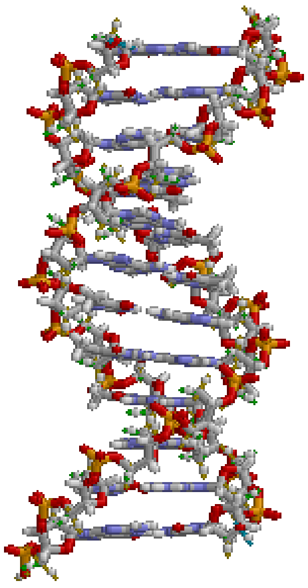
$$P\left\{c_1,\ldots,c_n \,\middle|\, \sum_{j=1}^{n} j c_j = n\right\} = \prod_{j=1}^{n}\left[\frac{j}{\theta+j-1}\frac{(\theta/j)^{c_j}}{c_j!}\right]$$

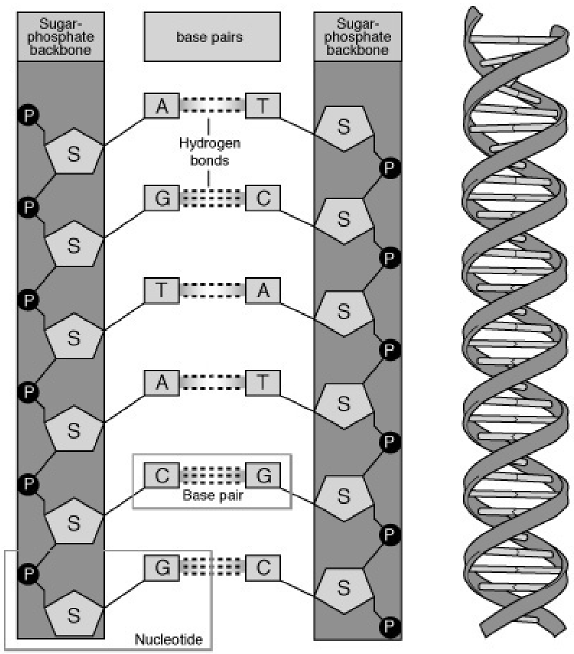


Sample configuration of alleles 4 A_1, 1 A_2, 4 A_3, 3 A_4, 3 A_5

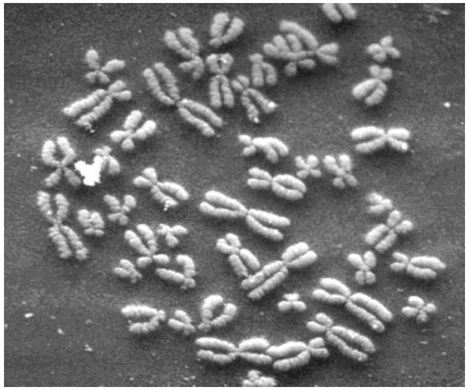
SEQUENCES
AND
FITNESS LANDSCAPES

Sequences: DNA





Chromosomes



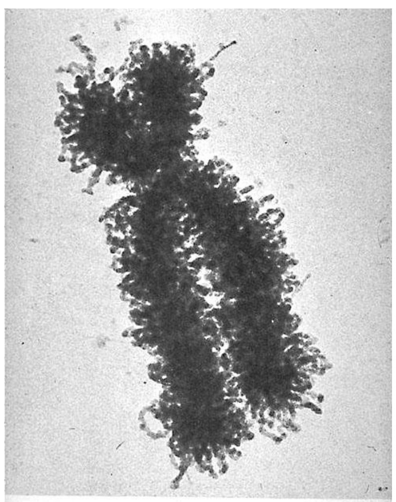
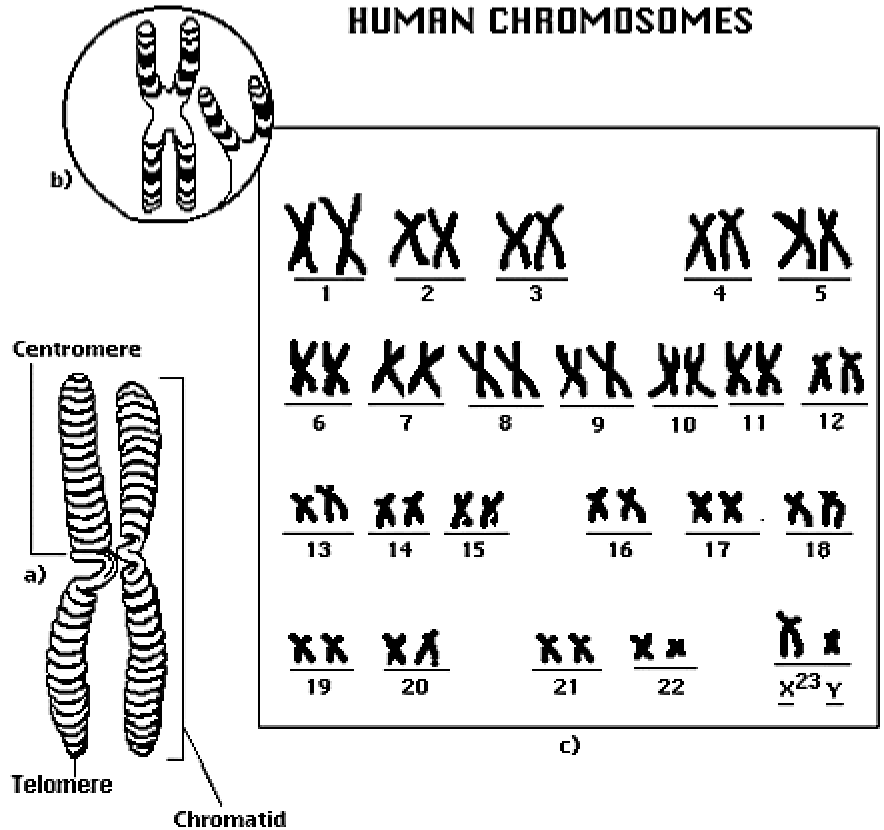
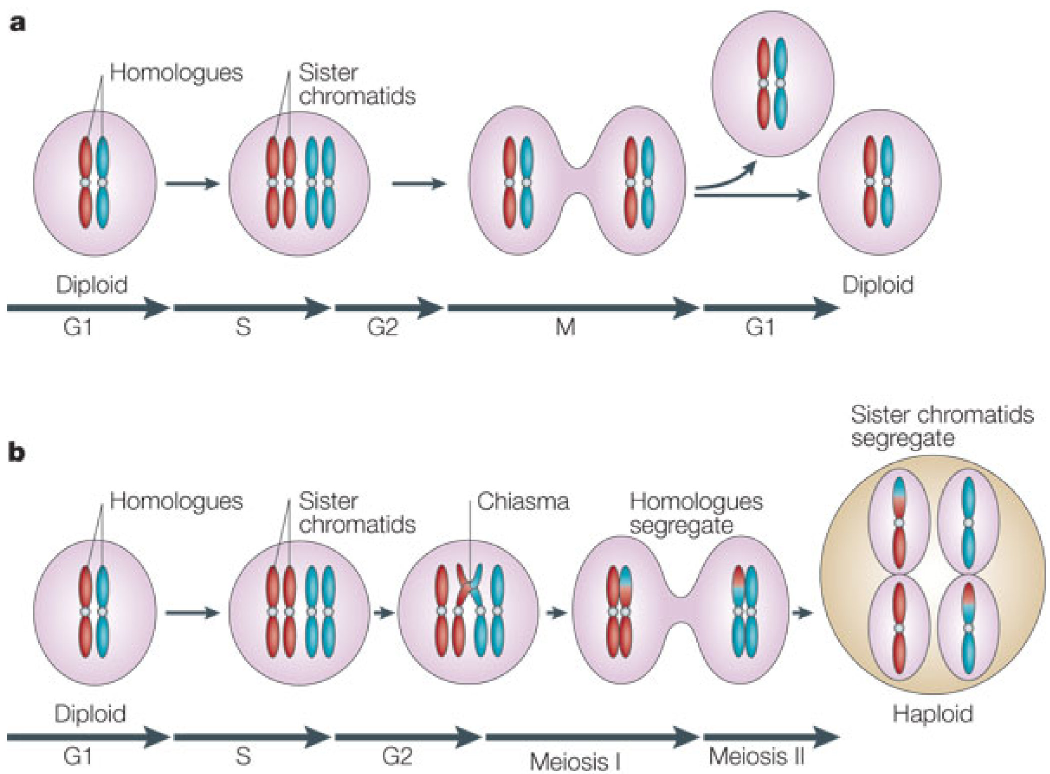


FIGURE 1-14
An electron micrograph of a human chromosome. Chromosome XII from a HeLa cell culture. (Courtesy of Dr. E. Du Praw.)



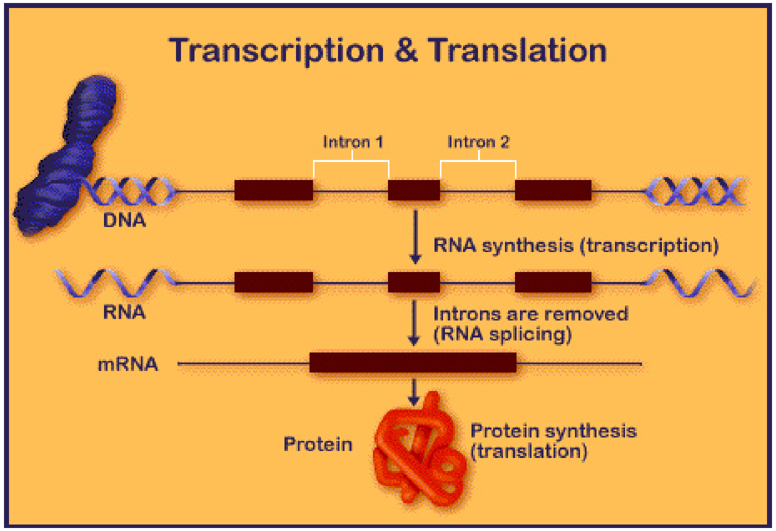
http://www.accessexcellence.org/AB/GG/human.html

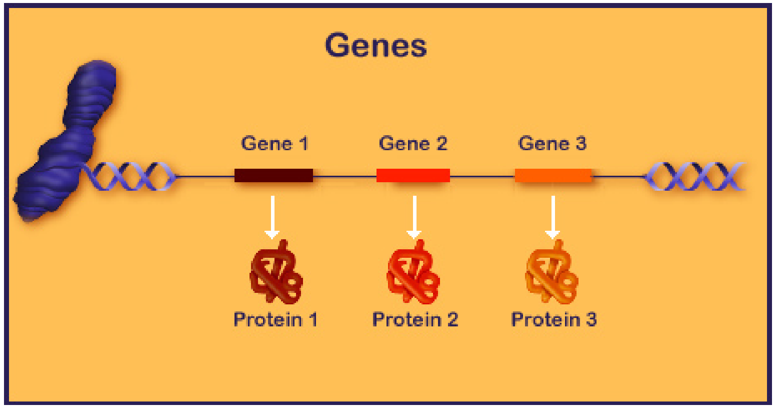
Mitosis & meiosis

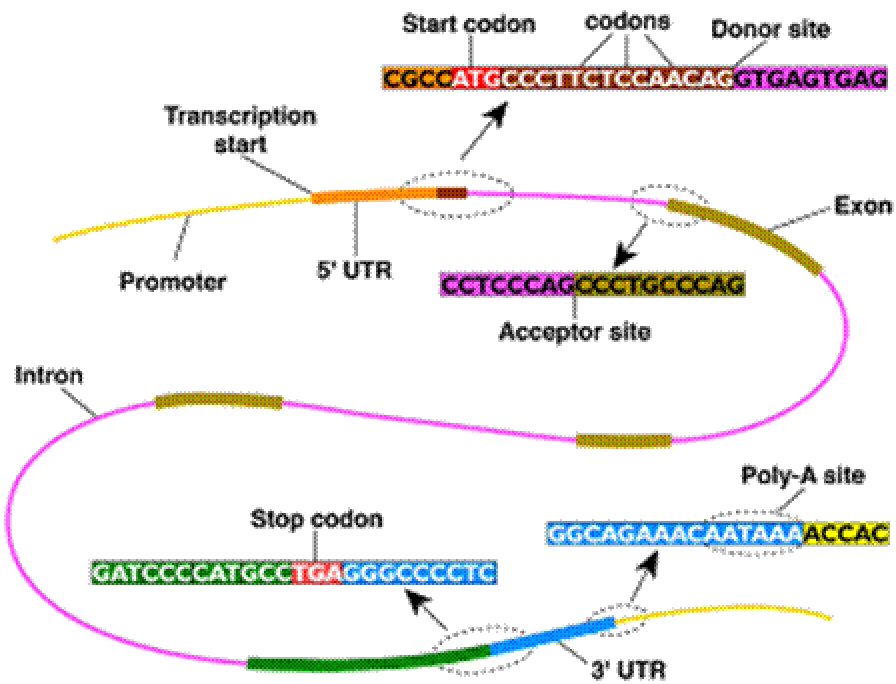


Nature Reviews | Molecular Cell Biology

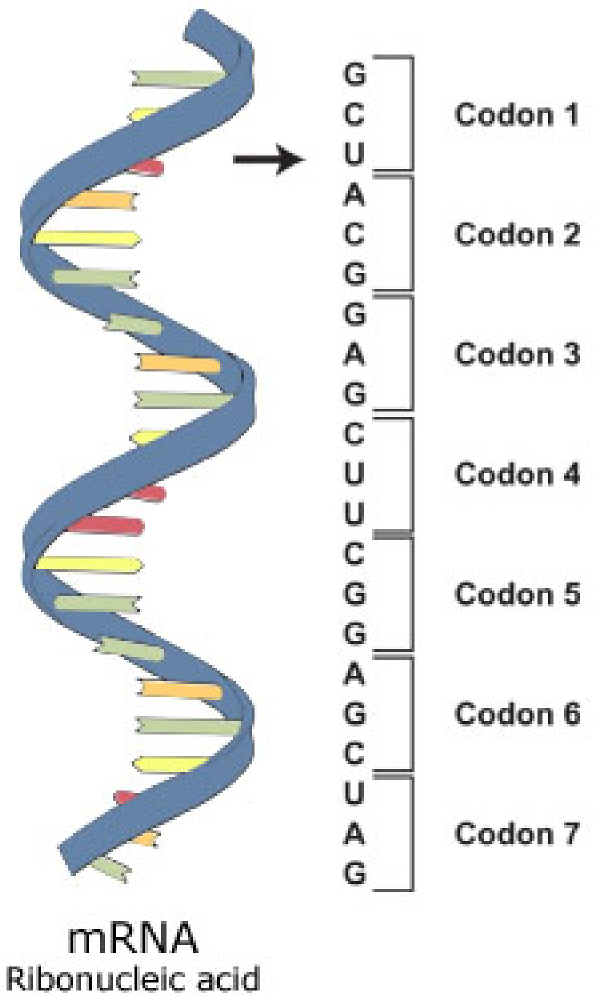
Genes


Transcription & Translation
Intron 1
Intron 2
DNA
RNA synthesis (transcription)
RNA
Introns are removed
(RNA splicing)
mRNA
Protein
Protein synthesis
(translation)


Genes
Gene 1
Gene 2
Gene 3
Protein 1
Protein 2
Protein 3


Start codon
codons
Donor site
CGCCATGCCCTTCTCCAACAGGTGAGTGAG
Transcription
start
Exon
Promoter
5' UTR
CCTCCCAGCCCTGCCCAG
Acceptor site
Intron
Poly-A site
Stop codon
GGCAGAAACAATAAAACCAC
GATCCCCATGCCTGAGGGCCCCTC
3' UTR

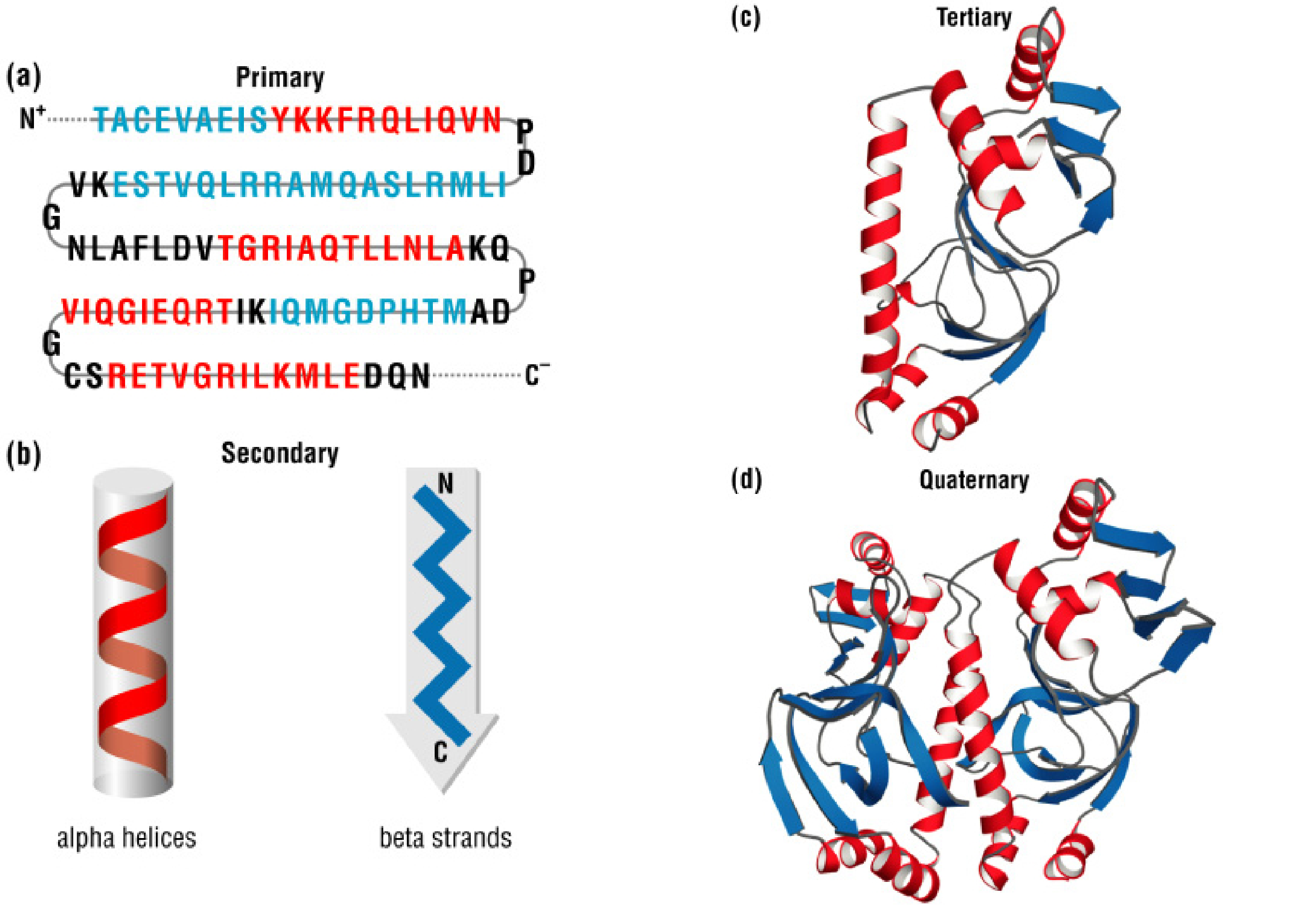
Transcription: genetic code



Second Base

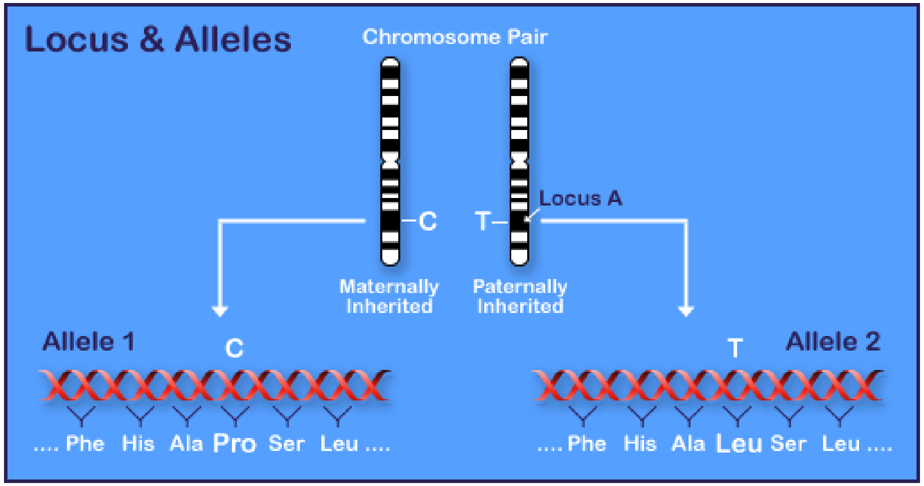
First Base	U	C	A	G	Third Base
U	UUU Phe	UCU Ser	UAU Tyr	UGU Cys	U
U	UUC Phe	UCC Ser	UAC Tyr	UGC Cys	C
U	UUA Leu	UCA Ser	UAA Stop	UGA Stop	A
U	UUG Leu	UCG Ser	UAG Stop	UGG Trp	G
C	CUU Leu	CCU Pro	CAU His	CGU Arg	U
C	CUC Leu	CCC Pro	CAC His	CGC Arg	C
C	CUA Leu	CCA Pro	CAA Gln	CGA Arg	A
C	CUG Leu	CCG Pro	CAG Gln	CGG Arg	G
A	AUU Ile	ACU Thr	AAU Asn	AGU Ser	U
A	AUC Ile	ACC Thr	AAC Asn	AGC Ser	C
A	AUA Ile	ACA Thr	AAA Lys	AGA Arg	A
A	AUG Met / Start	ACG Thr	AAG Lys	AGG Arg	G
G	GUU Val	GCU Ala	CAU Asp	GGU Gly	U
G	GUC Val	GCC Ala	GAC Asp	GGC Gly	C
G	GUA Val	GCA Ala	GAA Glu	GGA Gly	A
G	GUG Val	GCG Ala	GAG Glu	GGG Gly	G

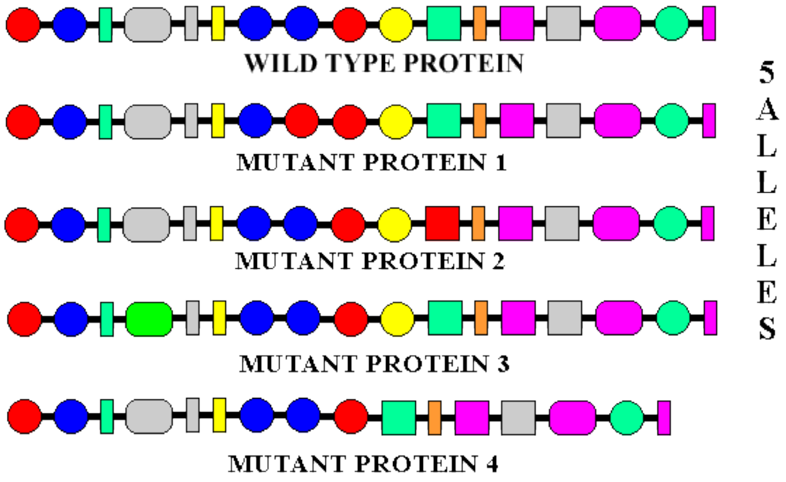
Proteins



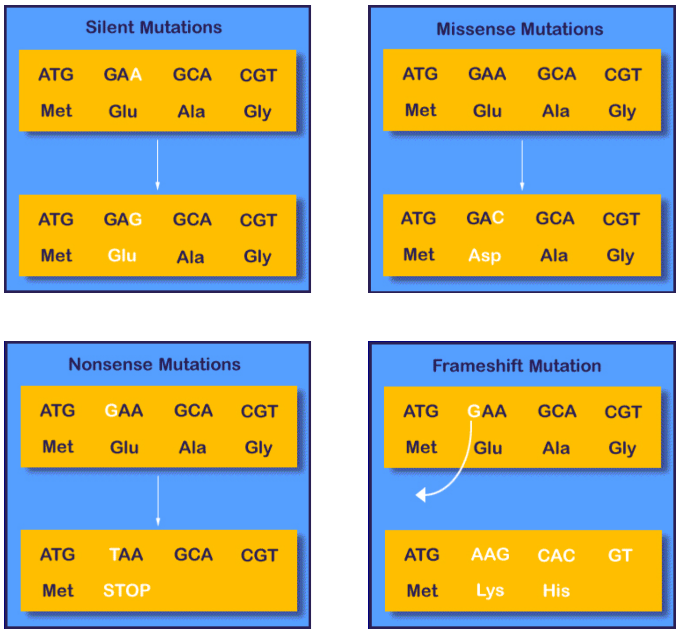
(a)
Primary
N+
TACEVAEISYKKFRQLIQVN
P
D
VKESTVQLRRAMQASLRMLI
G
NLAFLDVTGRIAQTLLNLAKQ
P
VIQGIEQRTIKIQMGDPHTMAD
G
CSRETVGRILKMLEDQN
C−
(b)
Secondary
N
C
alpha helices
beta strands
(c)
Tertiary
(d)
Quaternary

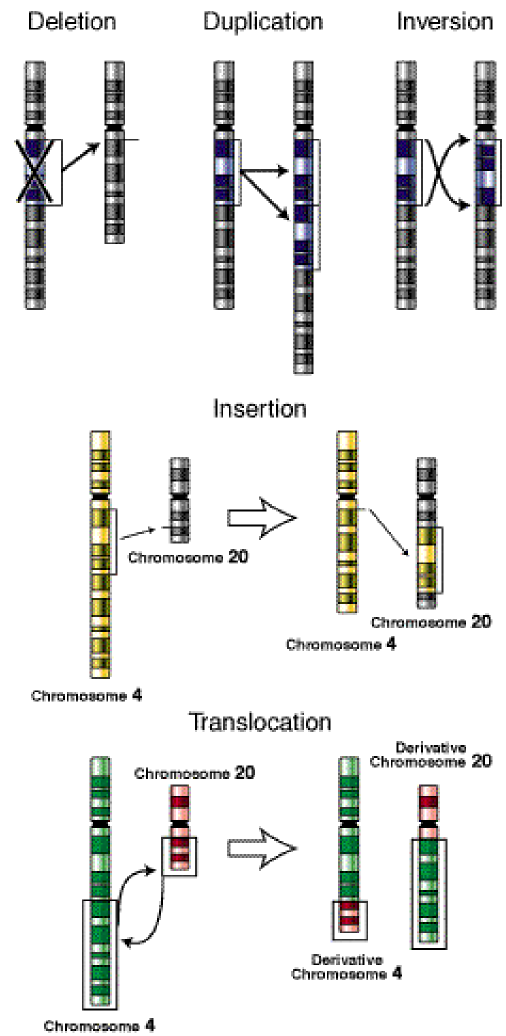
Locus & alleles

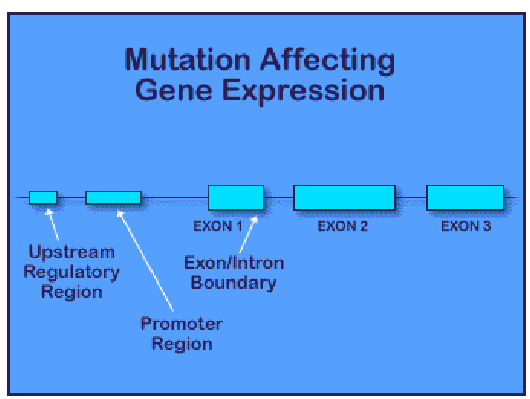




Types of mutation



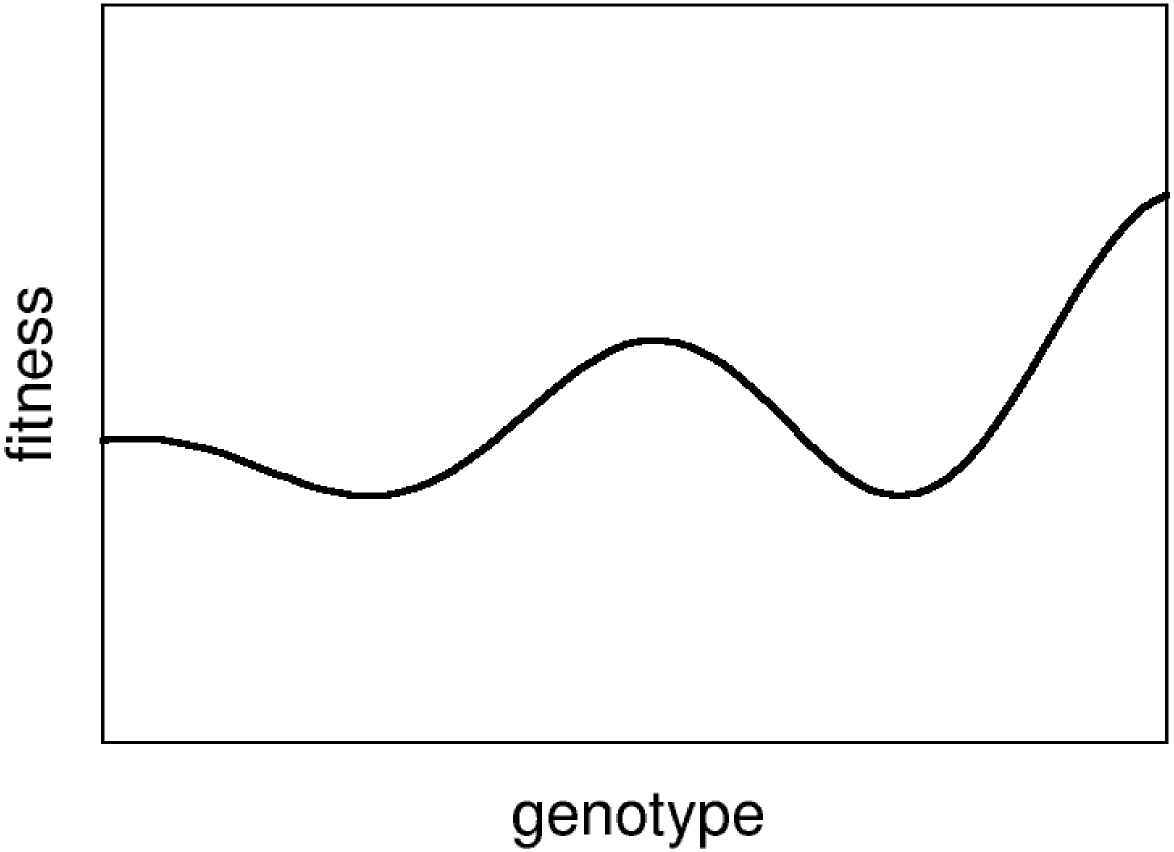




Fitness landscapes

- Metaphor introduced by Wright (1932)
- Representation of fitness of individuals or population
- Key points:
  - Fitness is affected by environment (external factors)
  - Fitness depends on phenotype, which is determined by genotype (permanent factor)

Fitness landscapes



Working example:
1 locus, 2 alleles, random mating

Working example:
1 locus, 2 alleles, random mating

$$x = [\mathrm{A}] \qquad y = [\mathrm{a}]$$

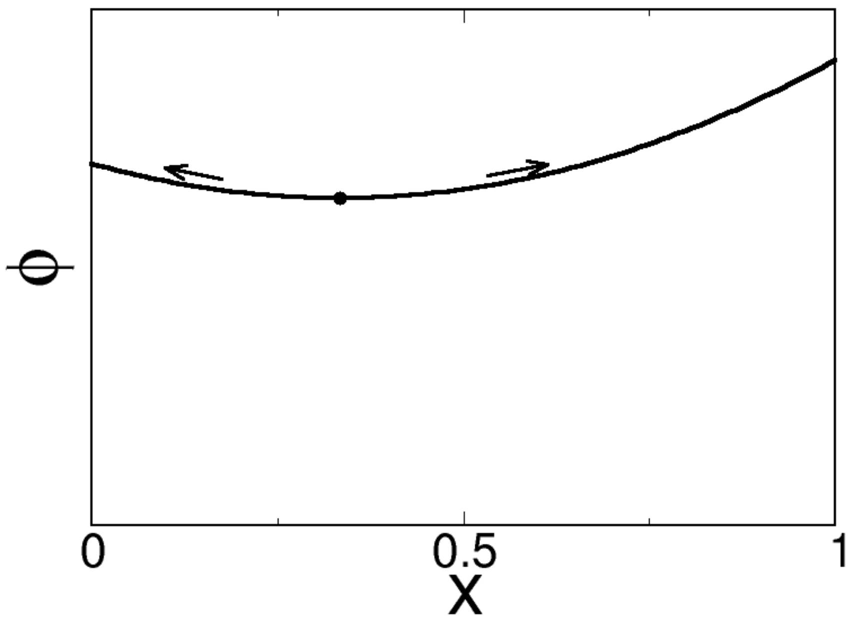
Hardy-Weinberg law:

$$[\mathrm{AA}] = x^2 \qquad [\mathrm{Aa}] = 2\,x\,y \qquad [\mathrm{aa}] = y^2$$

$$f_{\mathrm{A}}(x) = f_{\mathrm{AA}}\,x + f_{\mathrm{Aa}}\,y \qquad f_{\mathrm{a}}(x) = f_{\mathrm{Aa}}\,x + f_{\mathrm{aa}}\,y$$

$$\phi(x) = f_{\mathrm{AA}}\,x^2 + f_{\mathrm{Aa}}\,2\,x\,y + f_{\mathrm{aa}}\,y^2$$

Working example:
1 locus, 2 alleles, random mating

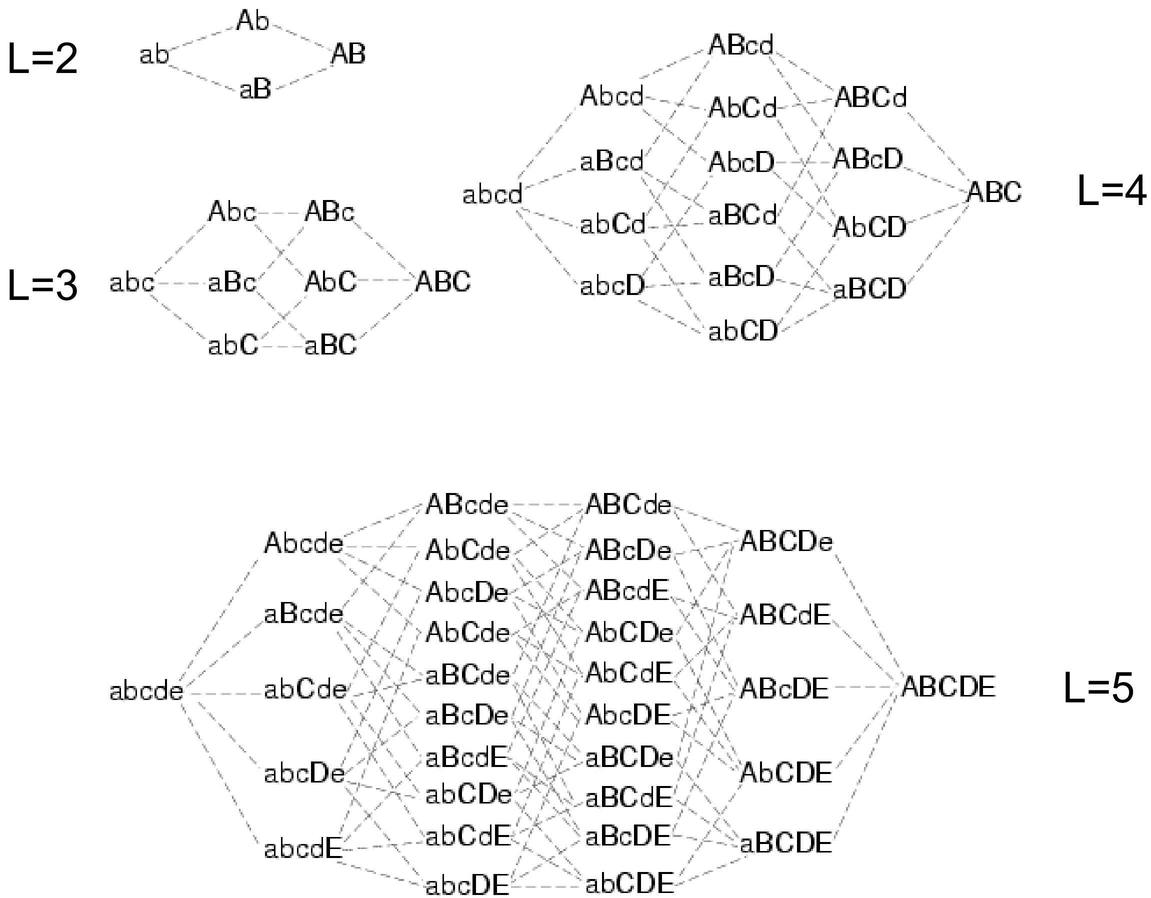


$$\frac{dx}{dt} = x\,y\,[f_{\mathrm{A}}(x) - f_{\mathrm{a}}(x)] = \frac{1}{2}\,x\,y\,\frac{d\,\phi(x)}{dx}$$

Remarks

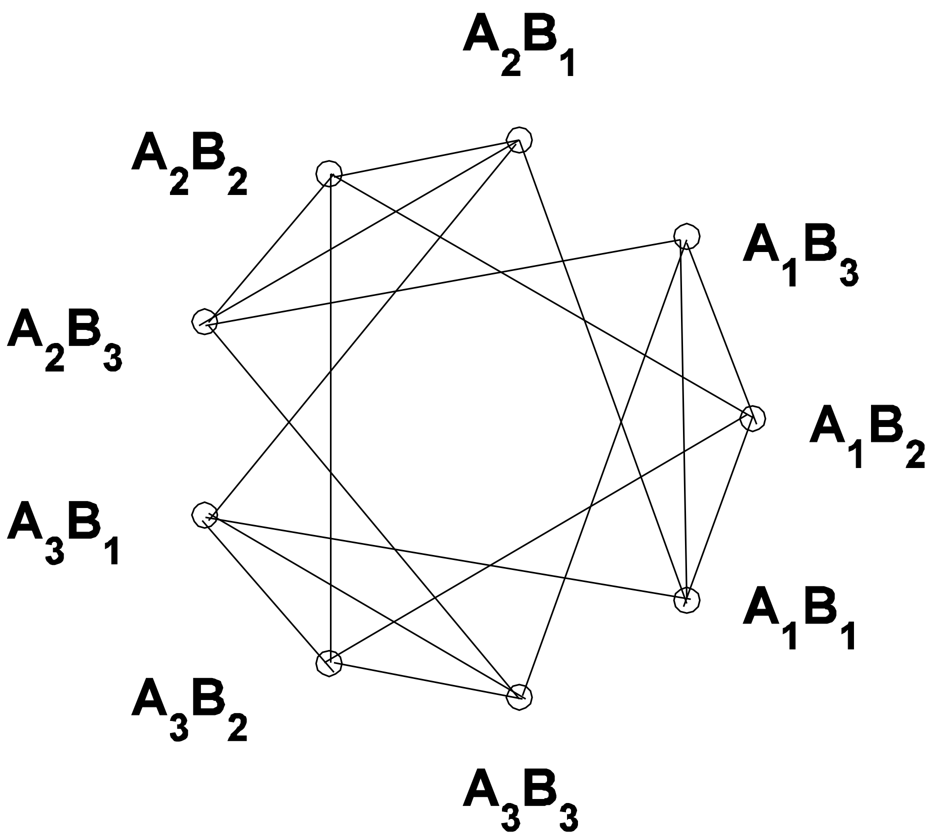
- First representation is a fundamental one:
  - Individuals sit at their genotypic positions
  - Population at every position changes in time
- Second representation is not because:
  - Depends on evolution law
  - Assumes maximization of mean fitness (not always true; e.g. mutations)
  - Can't be generalized to multilocus models

Genotype space



vertices of L-dimensional hypercubes

Genotype space



L=2 (loci), A=3 (alleles)

different genotypes for L loci and A alleles:

$$G = A^L$$

dimensionality (number of nearest neighbors):

$$D = L(A-1)$$

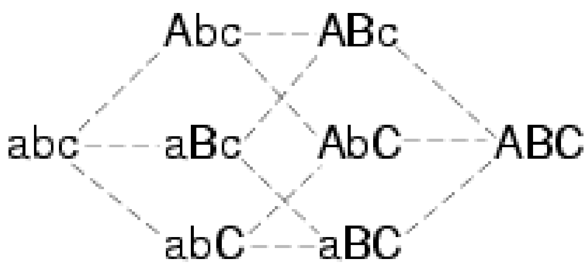
e.g. L=100, A=2:

$$D = 100 \qquad G \approx 10^{30}$$

Hamming distance

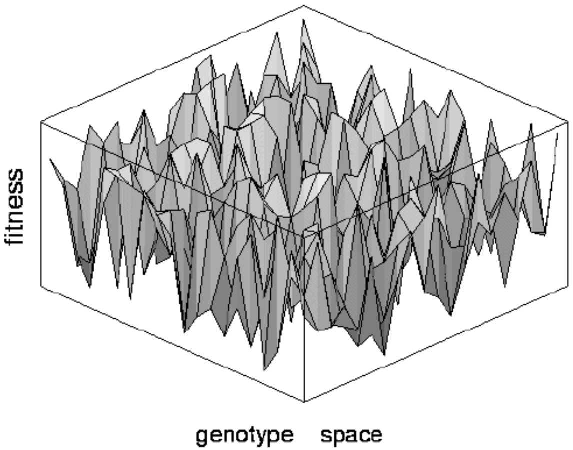
$$\boldsymbol{s}^a = s_1^a s_2 \cdots s_L^a$$
$$\boldsymbol{s}^b = s_1^b s_2^b \cdots s_L^b$$

$$d\left(\boldsymbol{s}^a, \boldsymbol{s}^b\right) = \sum_{i=1}^{L} \delta\left(s_i^a, s_i^b\right)$$

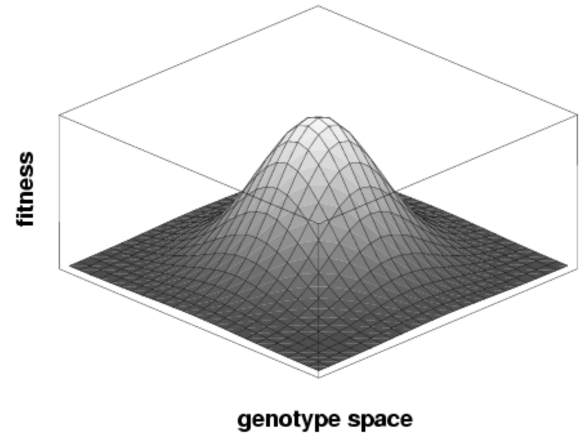


$$d(\text{abc}, \text{aBC}) = 2$$
$$d(\text{Abc}, \text{aBC}) = 3$$

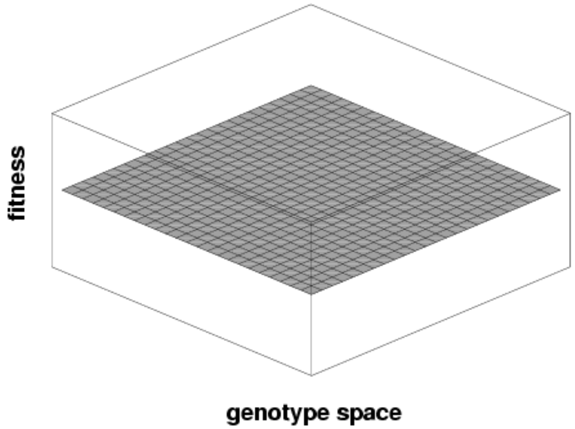
The metaphor



rugged (Wright)



Fujijama (Fisher)



flat (Kimura)

Quasispecies

ATTTGGAAATGCCGCAATTTACGGGA

ACTTGCAAATTCCGCAAATTTCGGGG

AGTTGGAACTTCCGCAATTCTCGGGA

ACTTGGACATTCCGATATTCTCGGGA

GGTTGGAAATACCCCAATTTTCGGGA

ACTTTGAAATTCCGCAACGGTCGGGA

ACATGGAAATTCCGCAATTTTCGGGA

ACTTGGAAATTCCGCAATTTTCGGGA

consensus sequence

Quasispecies

11001010100110011011000100
10001110101110011111100101
11001010001110011010100100
10001011101110101010100100
01001010100111011011100100
10000010101110011100100100
10101010101110011011100100

10001010101110011011100100

consensus sequence

Quasispecies equation

$$Q = (q_{ij}) \qquad \boldsymbol{u} = (1, \ldots, 1) \qquad Q\boldsymbol{u}^T = \boldsymbol{u}^T$$

$$F = \begin{pmatrix} f_1 & & 0 \\ & \ddots & \\ 0 & & f_n \end{pmatrix} \qquad W \equiv FQ$$

$$\frac{d\boldsymbol{x}}{dt} = \boldsymbol{x}W - \phi\boldsymbol{x} \qquad \phi = \boldsymbol{x}W\boldsymbol{u}^T = \sum_{j=1}^{n} x_j f_j$$

Point mutations

probability of a point mutation: $\mu \ll 1$

$$q_{ij} = \mu^{d_{ij}} (1-\mu)^{d_{ij}}$$

d_{ij} Hamming distance

$$i, j = 0, \ldots, n \qquad (n \equiv 2^L - 1)$$

$$f_0 > 1 = f_1 = f_2 = \cdots = f_n$$

$$x_0 = x \qquad x_1 + x_2 + \cdots + x_n = 1 - x$$

$$\frac{d\boldsymbol{x}}{dt} = \boldsymbol{x} W - \phi \boldsymbol{x} \qquad \phi = \boldsymbol{x} W \boldsymbol{u}^T = \sum_{j=1}^{n} x_j f_j$$

Error catastrophe

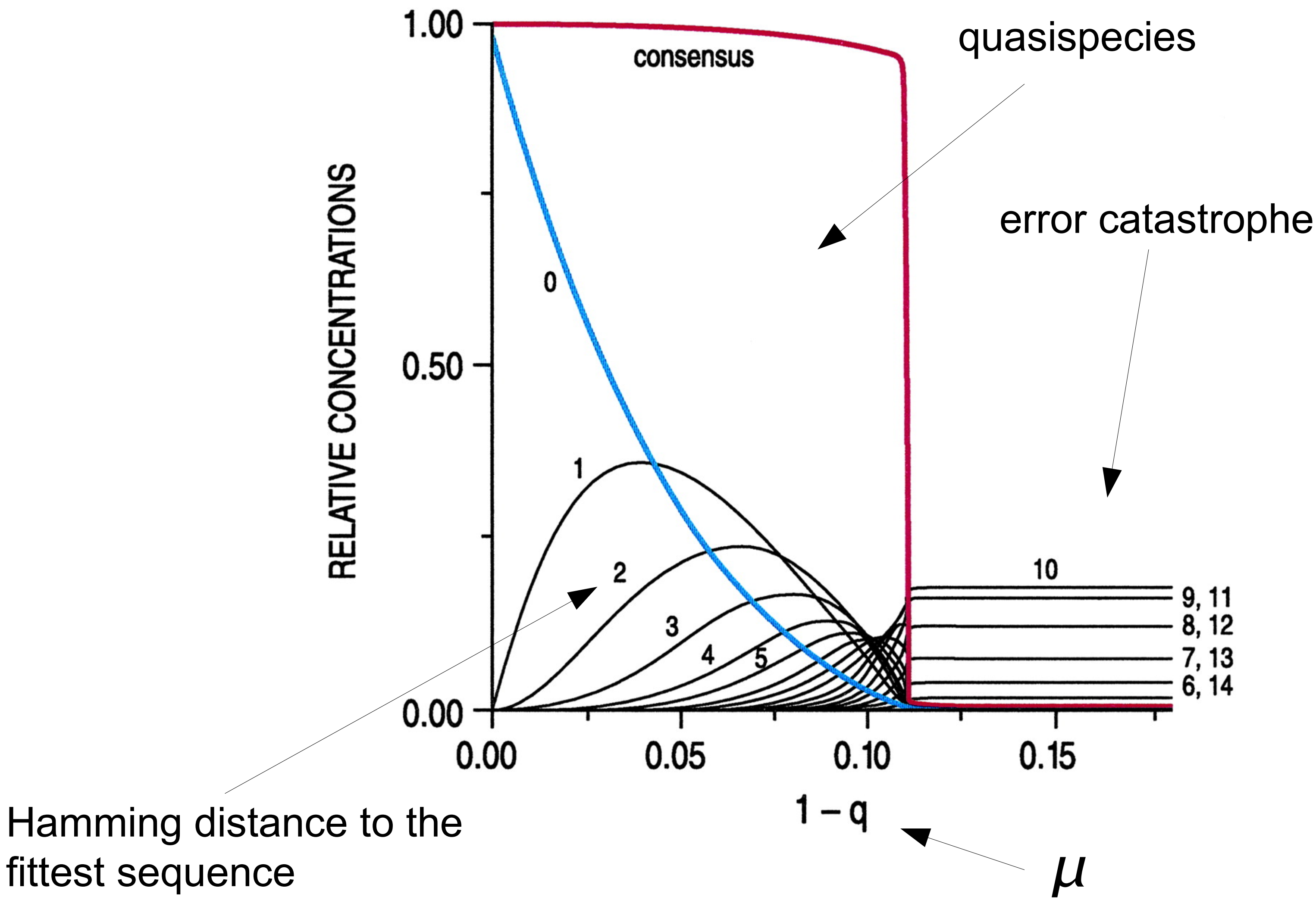
$$\frac{dx_i}{dt} = \sum_{j=0}^{n} x_j f_j q_{ji} - \phi x_i \qquad \phi = f x + 1 - x$$

$$\frac{dx}{dt} = x\left[f \underbrace{(1-\mu)^L}_{\approx e^{-\mu L}} - 1 - (f-1)x\right] + O(\mu)$$

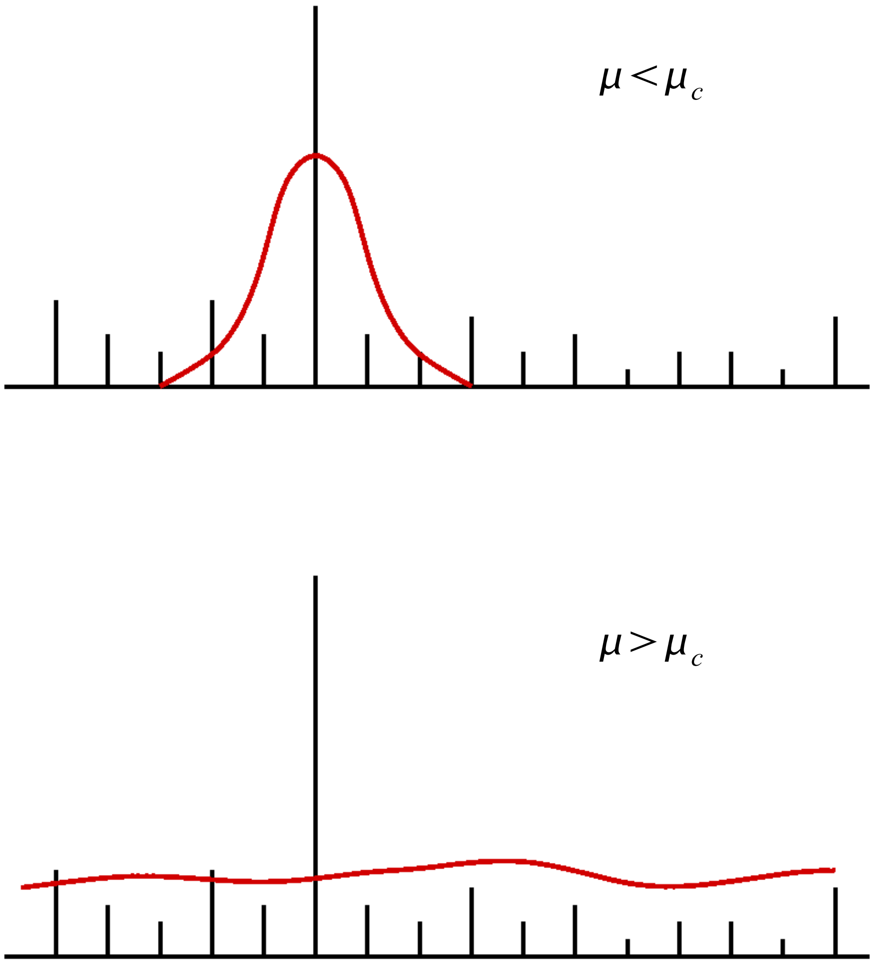
$$x^* \approx \frac{f}{f-1} e^{-L\mu} \qquad \text{if} \quad \mu < \frac{\log f}{L}$$

$$x^* = O(\mu) \qquad \text{if} \quad \mu > \frac{\log f}{L}$$

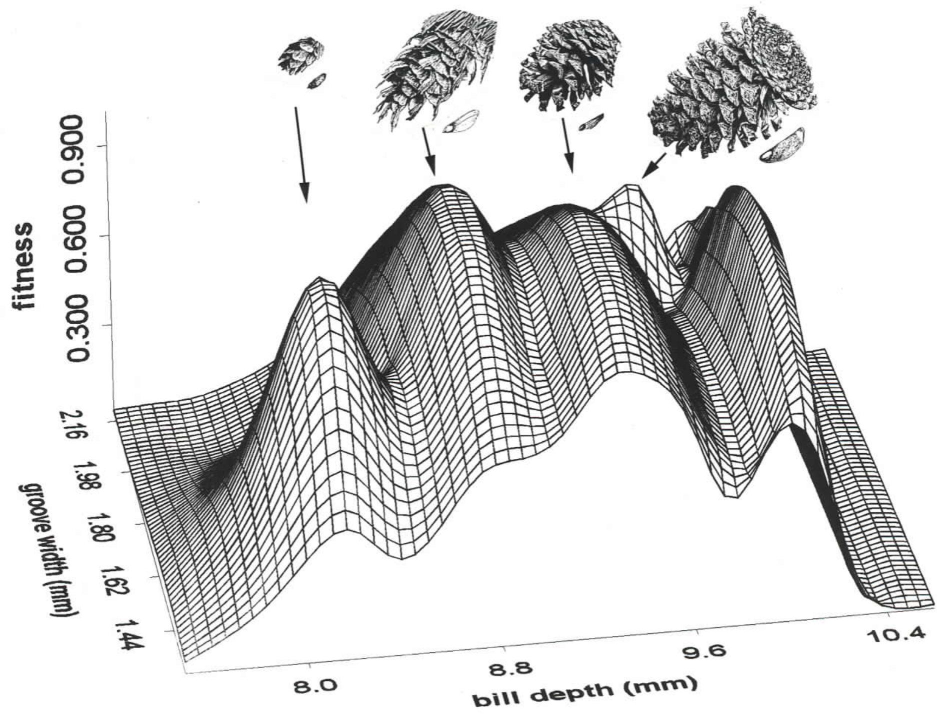
Error catastrophe

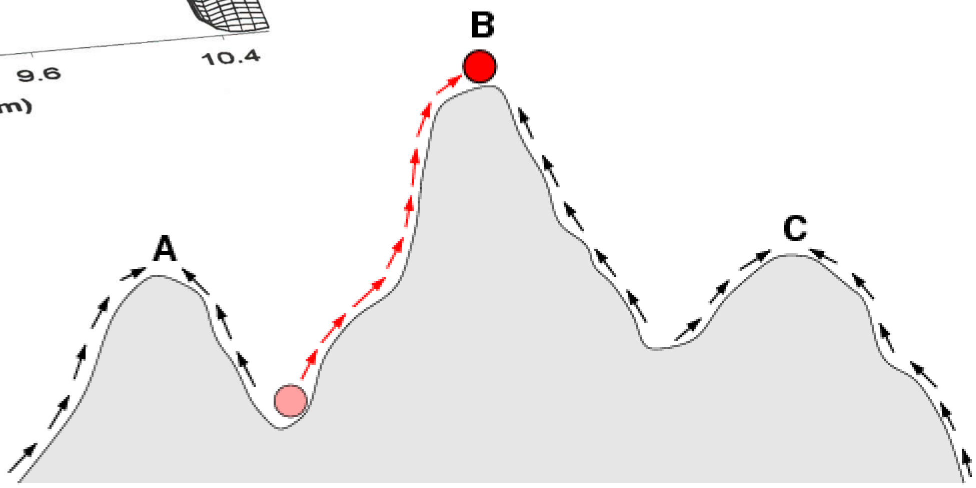


Error catastrophe

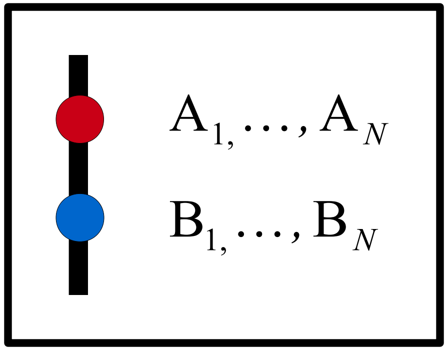


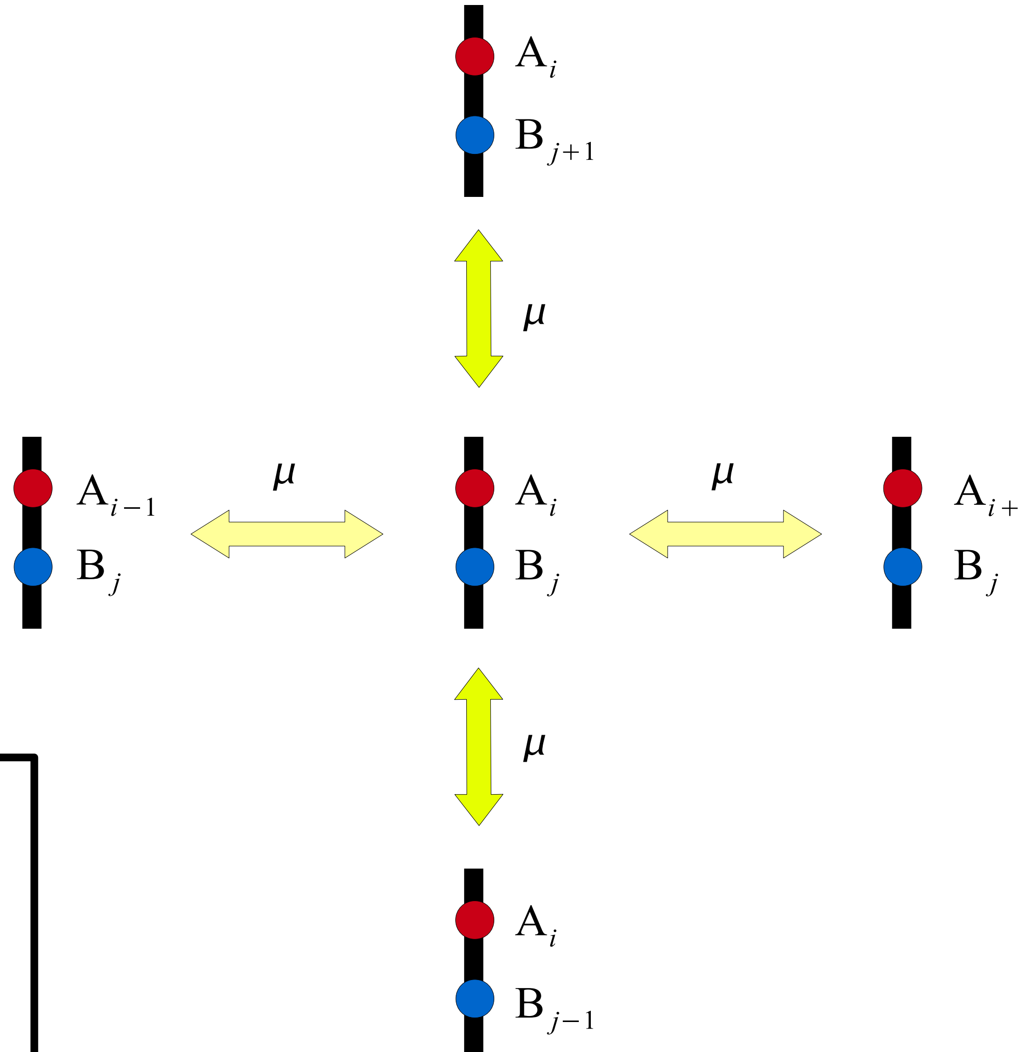
Speciation in rough landscapes

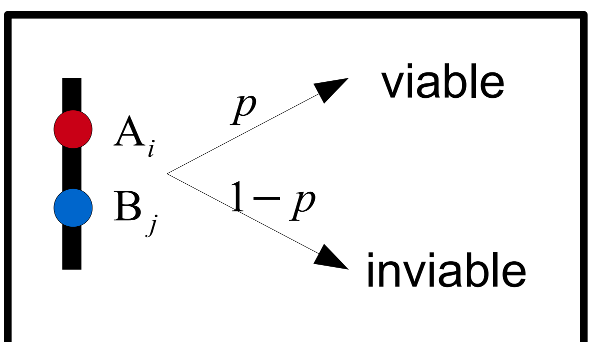




Russian roulette model



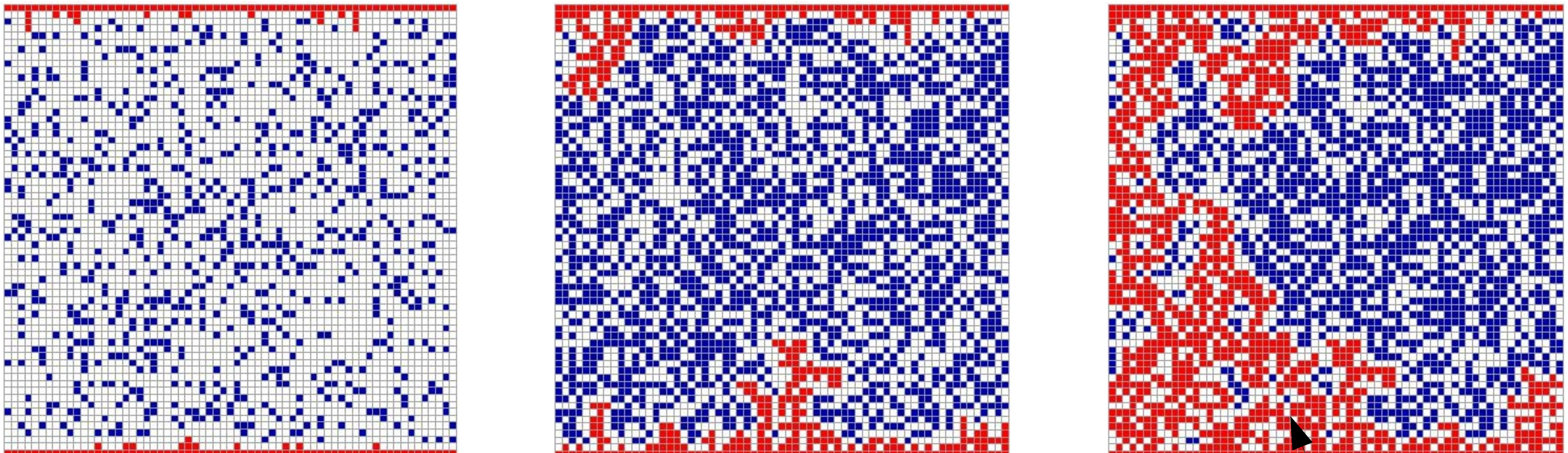




Russian roulette model

2D site percolation

p=0.2 p=0.51 p=0.594

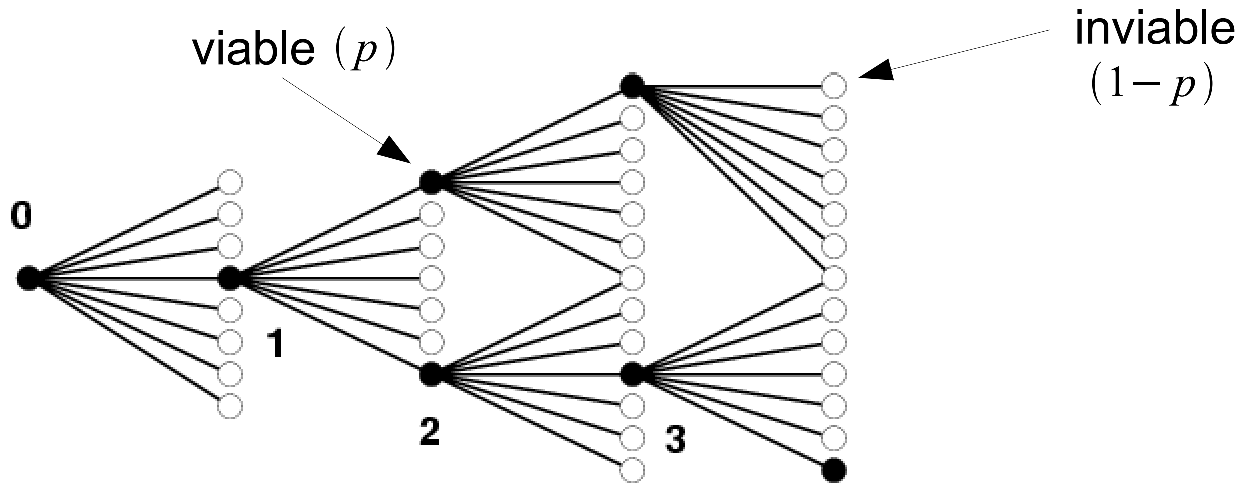


size=65x65 p_c=0.592746

neutral network

Russian roulette for sequences

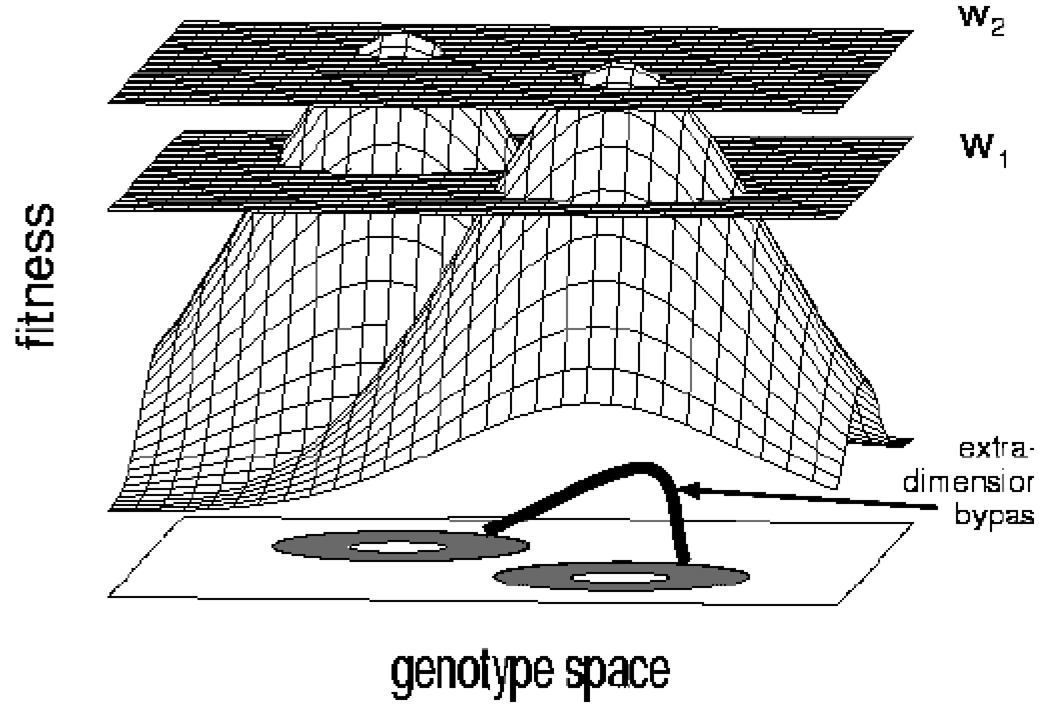
$$D = L(A-1) \qquad L \gg 1$$



branching process $p_k = \binom{D-1}{k} p^k (1-p)^{D-1-k}$

$$E\{k\} = (D-1)\,p \qquad \Leftrightarrow \qquad p_c = \frac{1}{D-1} \approx \frac{1}{D}$$

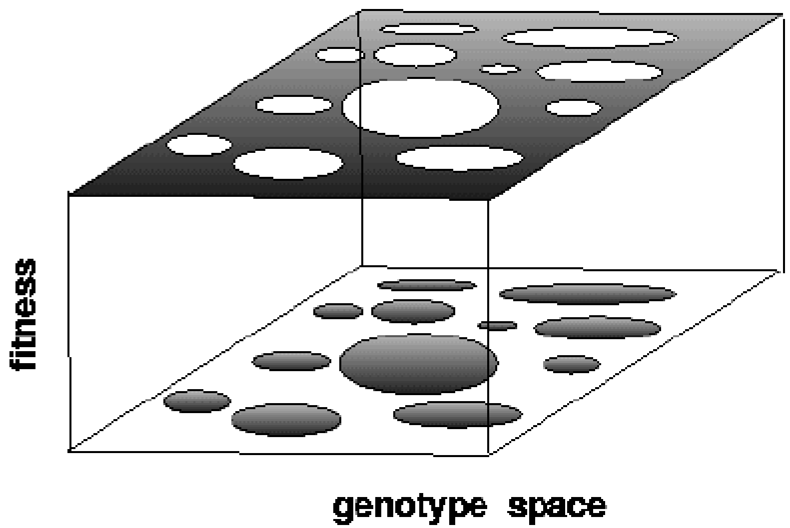
More general rugged lanscapes



$$\int_{w_1}^{w_2} f(w)\,dw > \frac{1}{D} \qquad \Rightarrow$$ quasi-neutral network

fitness distribution

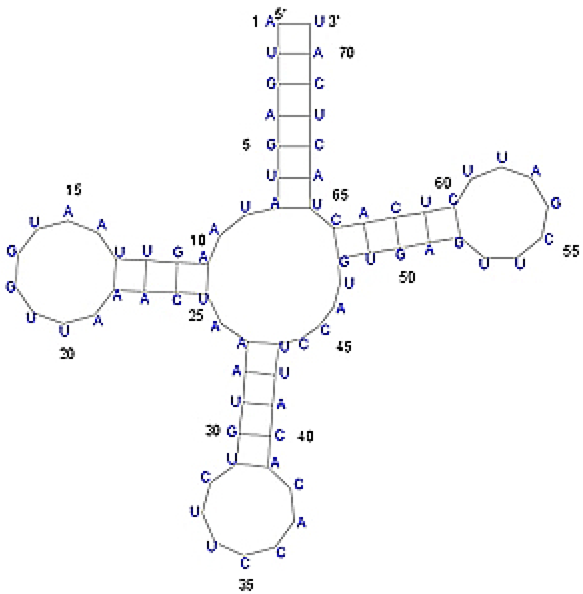
New metaphor of fitness landscapes



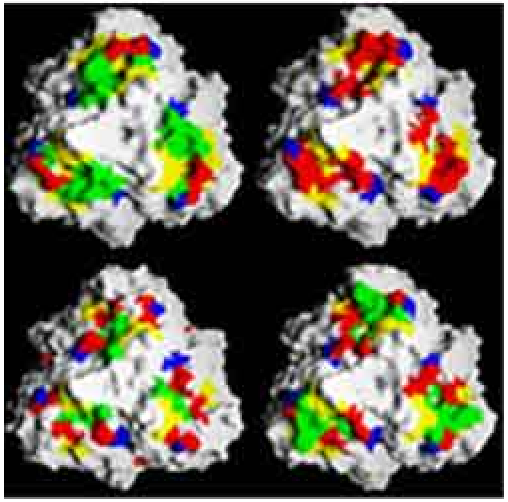
most evolutionary steps are neutral *(Kimura)*

Neutral networks

WORD → WORE → GORE → GONE→ GENE



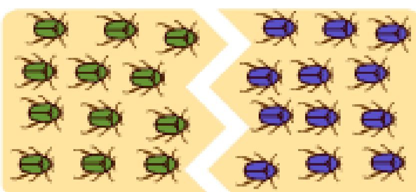
RNA



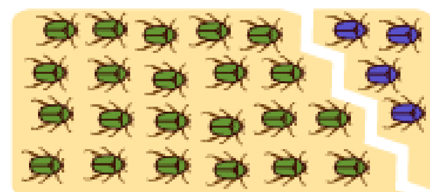
proteins

Speciation

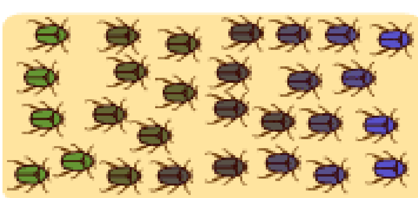
speciation proceeds mostly trough random drift



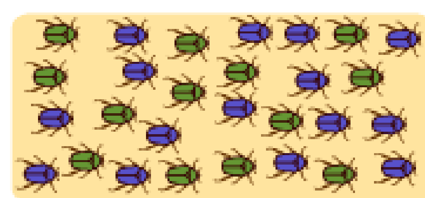
allopatric



peripatric

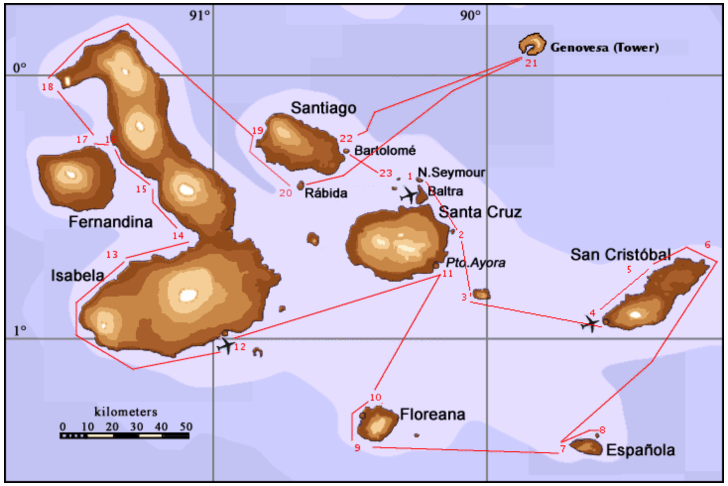


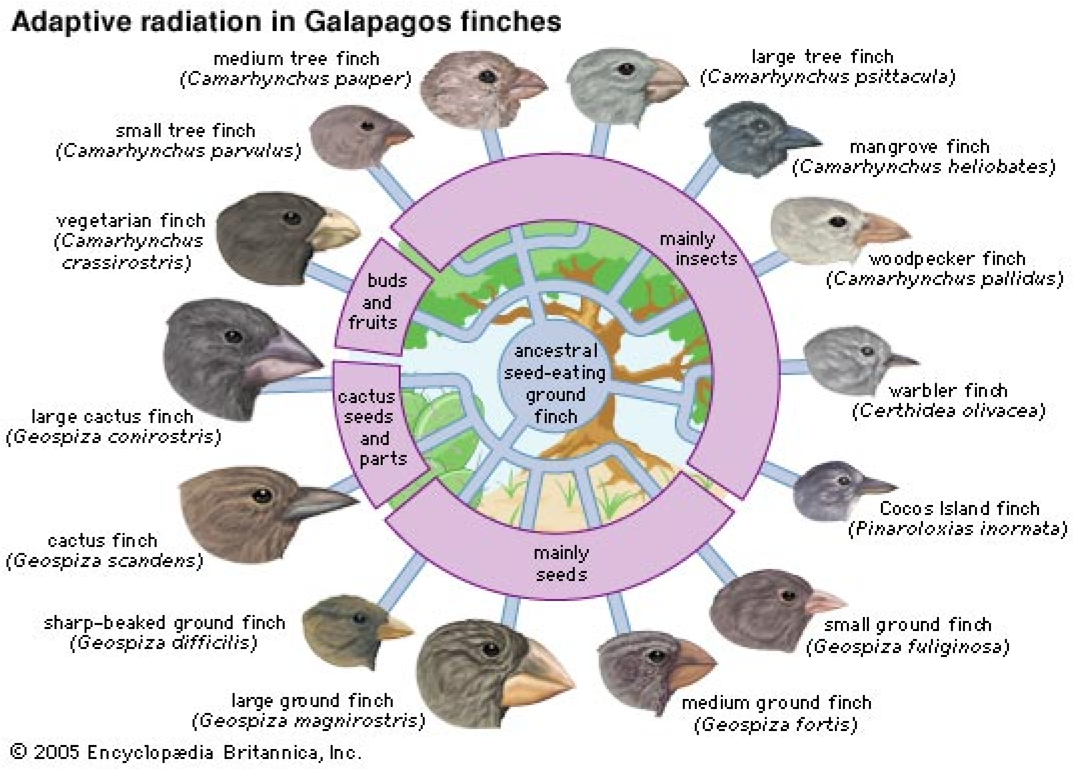
parapatric



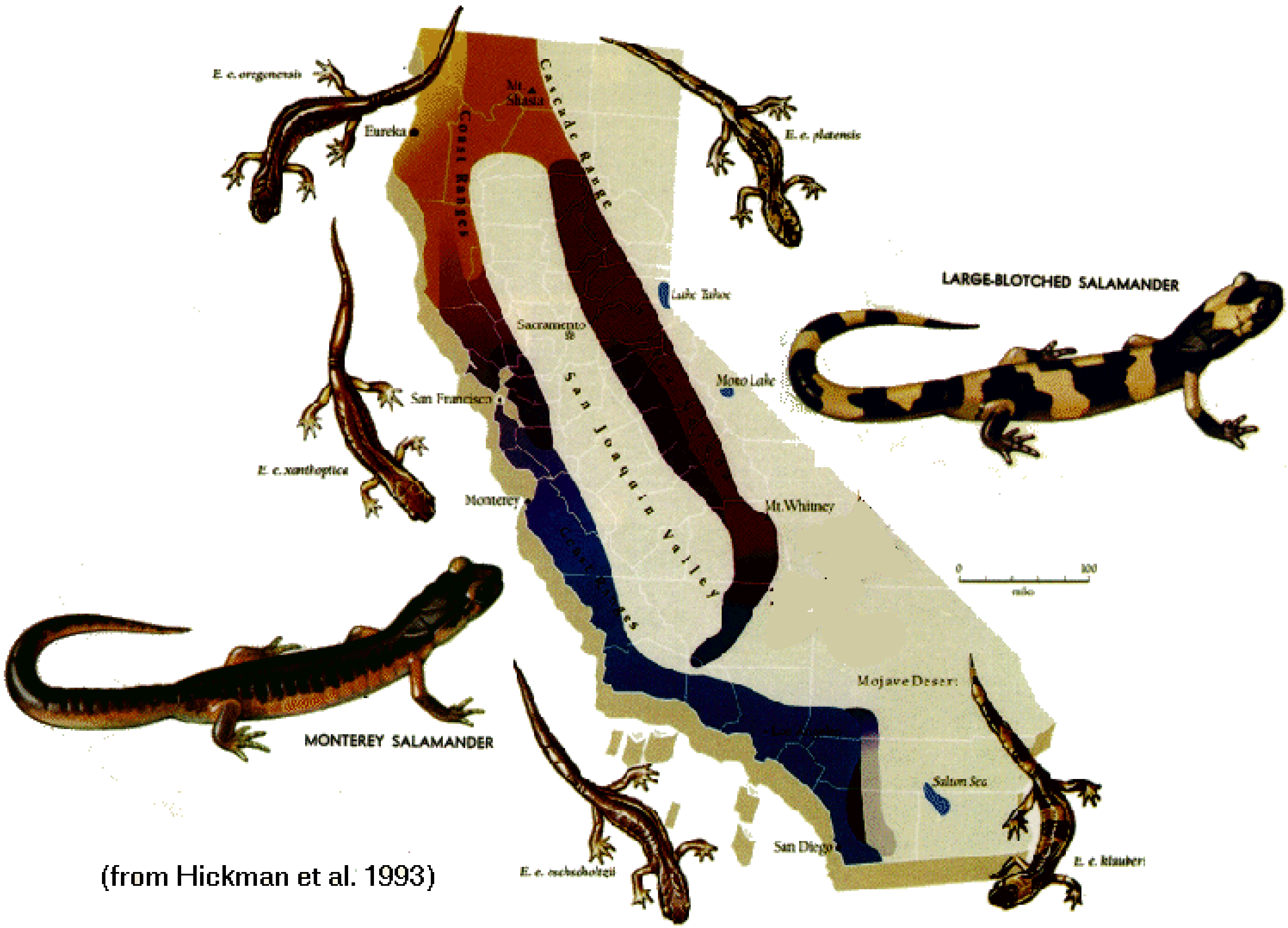
sympatric

Allopatric speciation





Paratric speciation



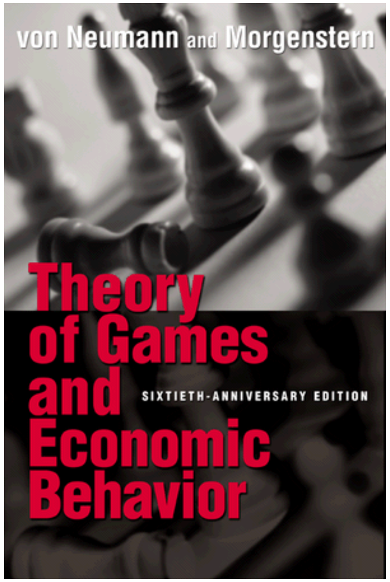
(from Hickman et al. 1993)

GAME THEORY

Game theory

Von Neumann
(1903-1957)

Morgenstern
(1902-1977)



1944

Game

- Players $i = 1, \ldots, N$
- Set of strategies S_i, $|S_i| = n_i$
- Strategy profile

$$\boldsymbol{s} = (s_{1}, \ldots, s_N) \in \boldsymbol{S} \equiv S_1 \times \cdots \times S_N$$

- Payoff (utility) functions

$$W_i : \boldsymbol{S} \to \mathbb{R}$$

$$\boldsymbol{s} \to W_i(\boldsymbol{s}) \qquad i = 1, \ldots, N$$

Two-player games

$$\mathbf{W}^{(1)} = \{ W_1(s_1, s_2) \}_{\{s_i \in S_i\}} \qquad \mathbf{W}^{(2)} = \{ W_2(s_2, s_1) \}_{\{s_i \in S_i\}}$$

$\mathbf{W}^{(1)} =$

a11	a12	a13
a21	a22	a23

$\mathbf{W}^{(2)} =$

b11	b12
b21	b22
b31	b32

symmetric game $\quad \mathbf{W}^{(1)} = \mathbf{W}^{(2)}$

Zero-sum games

one player's gain is the other player's loss

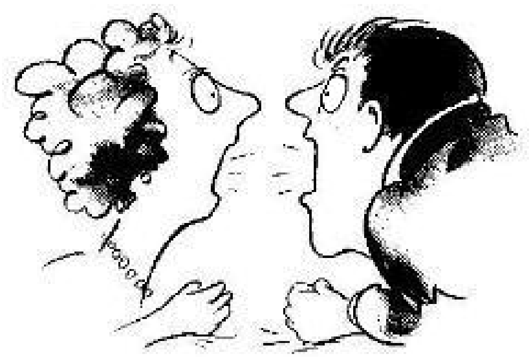
matching pennies

	≠ player 1	≠ player 2
= player 1	1,-1	-1,1
= player 2	-1,1	1,-1

Coordination games

doing the same as the other player

battle of the sexes



		him	
		opera	**soccer**
her	**opera**	2,1	0,0
	soccer	0,0	1,2

Coordination games

doing the same as the other player

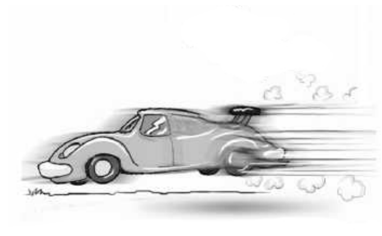
stag-hunt

		hunter 2	
		stag	**hare**
hunter 1	**stag**	3,3	0,2
	hare	2,0	1,1

Anti-coordination games

doing the opposite to the other player

chicken / snowdrift



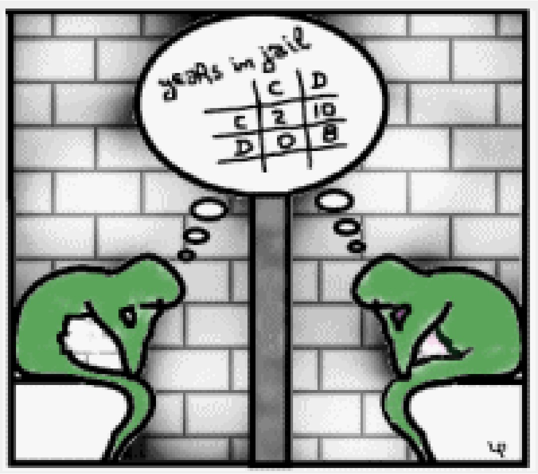
player 2

player 1

	stay	quit
stay	-1,-1	2,0
quit	0,2	0,0

Dilemmatic games

prisoner's dilemma



		prisoner 2	
		coop.	**defect**
prisoner 1	**coop.**	3,3	0,4
	defect	4,0	1,1

Principle of perfect rationality

Every player will always aim at maximizing its payoff

Common knowledge

Dominated strategies

player 2

player 1

	L	M	R
U	2,2	1,1	4,0
D	1,2	4,1	3,5

Dominated strategies

player 2

player 1

	L	M	R
U	2,**2**	1,**1**	4,0
D	1,**2**	4,**1**	3,5

Dominated strategies

		player 2	
	L	**M**	**R**
player 1 **U**	2,2	1,1	4,0
D	1,2	4,1	3,5

Dominated strategies

player 2

player 1

	L	M	R
U	2,2	1,1	4,0
D	1,2	4,1	3,5

Dominated strategies

		player 2	
player 1			
		L	**M**	**R**
	U	2,2	1,1	4,0
	D	1,2	4,1	3,5

Dominated strategies

player 2

player 1

	L	M	R
U	2,2	1,1	4,0
D	1,2	4,1	3,5

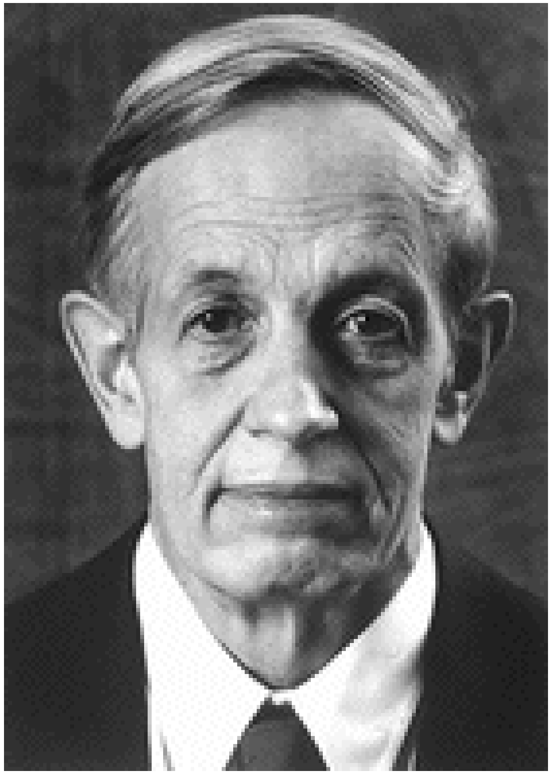
Dominated strategies

		player 2	
player 1		L	M	R

	L	M	R
U	2,2	1,1	4,0
D	1,2	4,1	3,5

player 1 / player 2

Nash equilibria



Nash (1928-)

Master thesis: 1949 - Nobel Prize in Economics: 1994

Nash equilibria in pure strategies

$$W_i(\mathbf{s}^*) \geqslant W_i(s_i, \mathbf{s}_{-i}^*) \qquad \forall s_i \in S_i \qquad \forall i = 1, \ldots, N$$

NEPS

- Games may have 0, 1 or more than 1 NEPS
- Iterative elimination of dominated strategies leads to a NEPS when it converges

Zero-sum games

one player's gain is the other player's loss

matching pennies

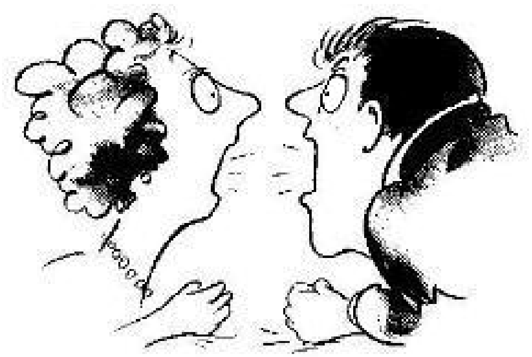
≠ player

= player		1	2
	1	1,-1	-1,1
	2	-1,1	1,-1

Coordination games

doing the same as the other player

battle of the sexes



		her	
		opera	**soccer**
him	**opera**	2,1	0,0
	soccer	0,0	1,2

Coordination games

doing the same as the other player

stag-hunt

risk dominant

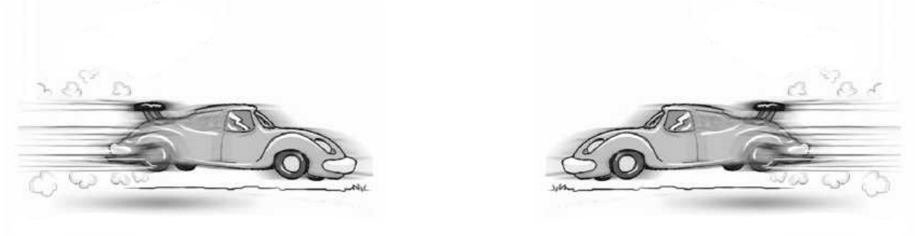
Pareto dominant

		hunter 2	
		stag	**hare**
hunter 1	**stag**	3,3	0,2
	hare	2,0	1,1

Anti-coordination games

doing the opposite to the other player

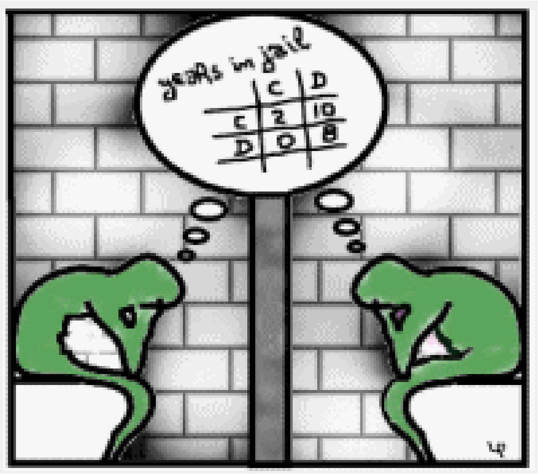
chicken / snowdrift



		player 2	
		stay	**quit**
player 1	**stay**	-1,-1	2,0
	quit	0,2	0,0

Dilemmatic games

prisoner's dilemma



maximizes welfare

		prisoner 2	
		coop.	**defect**
prisoner 1	**coop.**	3,3	0,4
	defect	4,0	1,1

Mixed strategies

$$p_i : S_i \to [0,1] \qquad \sum_{s \in S_i} p_i(s) = 1$$

$$\boldsymbol{p} = (p_1, \ldots, p_N)$$

$$W_i(\boldsymbol{p}) = \sum_{s_1 \in S_1} \cdots \sum_{s_N \in S_N} p_1(s_1) \cdots p_N(s_N) W_i(s_1, \ldots, s_N)$$

Nash equilibria

$$W_i(\boldsymbol{p}^*) \geqslant W_i(p_i, \boldsymbol{p}_{-i}^*) \qquad \forall\, p_i \text{ mixed strategy}$$
$$\forall\, i = 1, \ldots, N$$

NE

Every finite game has at least one NE
(Nash (1950) PNAS **36**, 48)

Fundamental theorem

$$W_i(s_i, \boldsymbol{p}_{-i}^*) = W_i(\boldsymbol{p}^*) \qquad \forall\, p_i^*(s_i) > 0$$

Example

player 2

		L	R
player 1	U	1,1	0,4
	D	0,2	2,1

$$p_1{*} = \alpha\,\mathbf{U} + (1-\alpha)\,\mathbf{D} \qquad p_2{*} = \beta\,\mathbf{L} + (1-\beta)\,\mathbf{R}$$

$$W_1(\mathbf{U}, p_2{*}) = W_1(\mathbf{D}, p_2{*}) \iff \beta = 2(1-\beta) \iff \beta = \frac{2}{3}$$

Example

		player 2	
		L	**R**
player 1	**U**	1,1	0,4
	D	0,2	2,1

$$p_1{*} = \alpha \mathbf{U} + (1-\alpha)\mathbf{D} \qquad p_2{*} = \frac{2}{3}\mathbf{L} + \frac{1}{3}\mathbf{R}$$

$$W_2(p_1{*}, \mathbf{L}) = W_2(p_2{*}, \mathbf{R}) \iff \alpha + 2(1-\alpha) = 4\alpha + (1-\alpha)$$

$$\iff \alpha = \frac{1}{4}$$

Example

player 2

player 1

	L	R
U	1,1	0,4
D	0,2	2,1

$$p_1{}^* = \frac{1}{4}\mathbf{U} + \frac{3}{4}\mathbf{D} \qquad p_2{}^* = \frac{2}{3}\mathbf{L} + \frac{1}{3}\mathbf{R}$$

Matching pennies

$$p_i^* = \frac{1}{2}\mathbf{1} + \frac{1}{2}\mathbf{2}$$

≠ player

= player		1	2
	1	1,-1	-1,1
	2	-1,1	1,-1

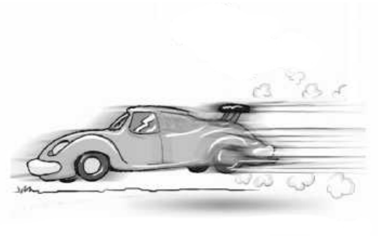
Stag-hunt

$$p_i^* = \frac{1}{2}\mathbf{S} + \frac{1}{2}\mathbf{H}$$

hunter 2

hunter 1		**stag**	**hare**
	stag	3,3	0,2
	hare	2,0	1,1

Chicken / snowdrift

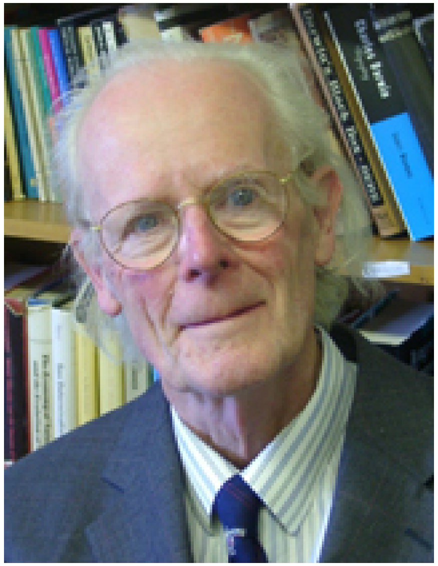


$$p_i{}^* = \frac{2}{3}\mathbf{S} + \frac{1}{3}\mathbf{Q}$$

		player 2	
		stay	**quit**
player 1	**stay**	-1,-1	2,0
	quit	0,2	0,0

EVOLUTIONARY GAME THEORY

Games and evolution



Maynard-Smith
(1920-2004)

NATURE VOL. 246 NOVEMBER 2 1973 15

The Logic of Animal Conflict

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Conflicts between animals of the same species usually are of "limited war" type, not causing serious injury. This is often explained as due to group or species selection for behaviour benefiting the species rather than individuals. Game theory and computer simulation analyses show, however, that a "limited war" strategy benefits individual animals as well as the species.

In a typical combat between two male animals of the same species, the winner gains mates, dominance rights, desirable territory, or other advantages that will tend toward transmitting its genes to future generations at higher frequencies than the loser's genes. Consequently, one might expect that natural selection would develop maximally effective weapons and fighting styles for a "total war" strategy of battles between males to the death. But instead, intraspecific conflicts are usually of a "limited war" type, involving inefficient weapons or ritualized tactics that seldom cause serious injury to either contestant. For example, in many snake species the males fight each other by wrestling without using their fangs[1,2]. In mule deer (*Odocoileus hemionus*) the bucks fight furiously but harmlessly by crashing or pushing antlers against antlers, while they refrain from attacking when an opponent turns away, exposing the unprotected side of its body[3]. And in the Arabian oryx (*Oryx leucoryx*) the extremely long, backward pointing horns are so inefficient for combat that in order for two males to fight they are forced to kneel down with their heads between their knees to direct their horns forward[4]. (For additional examples, see Collins[5], Darwin[6], Hingston[6], Huxley *et al.*[7], Lorenz[8] and Wynne-Edwards[9].)

How can one explain such oddities as snakes that wrestle with each other, deer that refuse to strike "foul blows", and antelope that kneel down to fight?

The accepted explanation for the conventional nature of contests is that if no conventional methods existed, many individuals would be injured, and this would militate against the survival of the species (see, for example, Huxley[7]). The difficulty with this type of explanation is that it appears to assume the operation of "group selection". Although one cannot rule out group selection as an agent producing adaptations, it is only likely to be effective in rather special circumstances[10-12]. Consequently it seems to us that group selection cannot by itself account for the complex anatomical and behavioural adaptations for limited conflict found in so many species, but there must also be individual selection for these, which means that a "limited war" strategy must be differentially advantageous for individuals.

We consider simple formal models of conflict situations, and ask what strategy will be favoured under individual selection. We first consider conflict in species possessing offensive weapons capable of inflicting serious injury on other members of the species. Then we consider conflict in species where serious injury is impossible, so that victory goes to the contestant who fights longest. For each model, we seek a strategy that will be stable under natural selection; that is, we seek an "evolutionarily stable strategy" or ESS. The concept of an ESS is fundamental to our argument; it has been derived in part from the theory of games, and in part from the work of MacArthur[13] and of Hamilton[14] on the evolution of the sex ratio. Roughly, an ESS is a strategy such that, if most of the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness.

A Computer Model

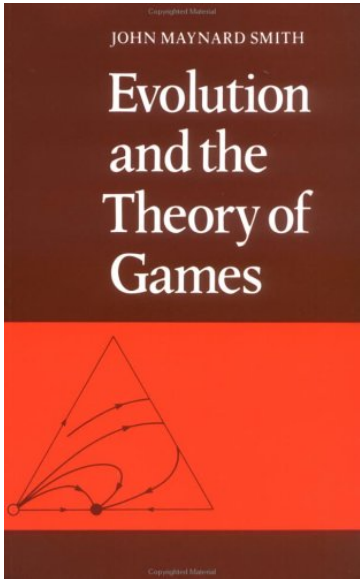
A main reason for using computer simulation was to test whether it is possible even in theory for individual selection to account for "limited war" behaviour.

We consider a species that possesses offensive weapons capable of inflicting serious injuries. We assume that there are two categories of conflict tactics: "conventional" tactics, *C*, which are unlikely to cause serious injury, and "dangerous" tactics, *D*, which are likely to injure the opponent seriously if they are employed for long. (Thus in the snake example, wrestling involves *C* tactics and use of fangs would be *D* tactics. In many species, *C* tactics are limited to threat displays at a distance, without any physical fighting. We consider a conflict between two individuals to consist of a series of alternate "moves". At each move, a contestant can employ *C* or *D* tactics, or retreat, *R*. If a contestant employs *D* tactics, there is a fixed probability that his opponent will be seriously injured: a contestant who is seriously injured always retreats. If a contestant retreats, the contest is at an end and his opponent is the winner. A possible conflict between contestants *A* and *B* can be represented in this way:

A's move *C C C C C C C C C C C D C C C C C C C D*
B's move *C C C C C C C C C C C D C C C C C C C R*

If a contestant plays *D* on the first move of a contest, or plays *D* in response to *C* by his opponent, this is called a "probe" or a "provocation". A probe made after the opening move is said to "escalate" a contest from *C* to *D* level. A contestant who plays *D* in reply to a probe is said to "retaliate". In the example shown above, *A* probes on his twelfth and twentieth moves; *B* retaliates after the first probe, but retreats after the second, leaving *A* the winner. At the end of a contest there are "pay-offs" to each contestant. The pay-offs are taken as measures of the contribution the contest has made to the reproductive success of the individual. They take account of three factors: the advantages of winning as compared with losing, the disadvantage of being seriously injured, and the disadvantage of wasting time and energy in the contest.

Nature, 1973

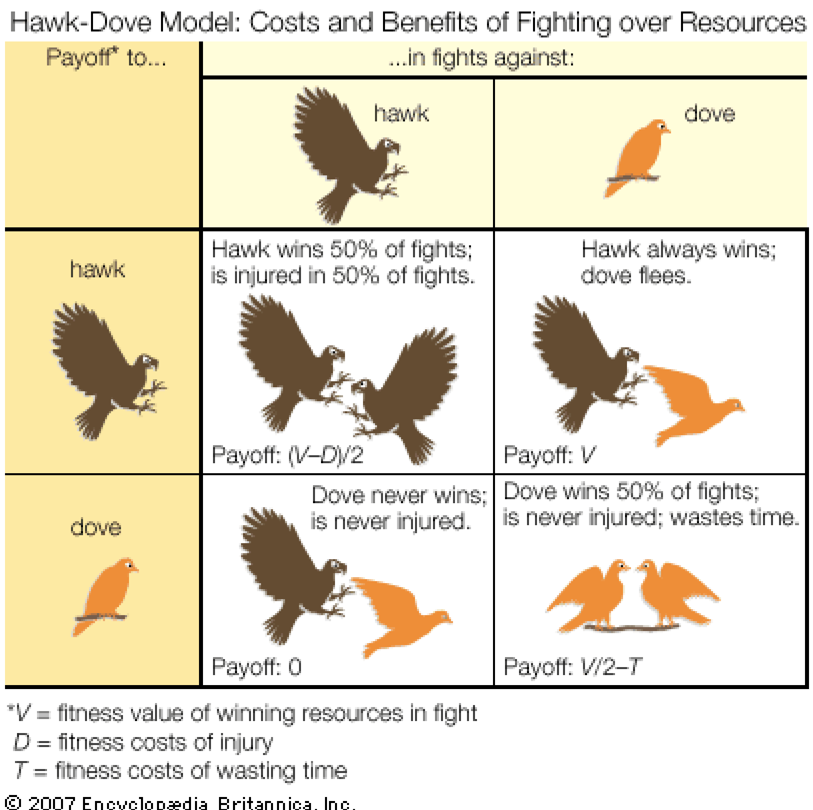


1982

New setup

	classic GT	evolut. GT
players	rational	irrational
strategies	chosen from a set	inherited (phenotypes)
interaction	all at once	random sampling of population
equilibria	Nash equilibria	Evolutionary Stable Strategies

Hawk & doves



Nash equilibrium

$$\text{if } \; V > D + 2\mathrm{T}$$

$$p_i^* = \mathbf{H}$$

$$\text{if } \; V < D + 2\mathrm{T}$$

$$p_i^* = \frac{V}{D + 2\mathrm{T}}\mathbf{H} + \frac{D + 2\mathrm{T} - V}{D + 2\mathrm{T}}\mathbf{D}$$

Connection with evolution

- Species interact by playing games
- Fitness increases with game payoffs
- Simplest setting:

$$f_i \propto W_i + \underbrace{\gamma}_{\text{normalizing term}}$$

Hawk & doves

$$[\text{hawks}] = x \qquad [\text{doves}] = 1 - x$$

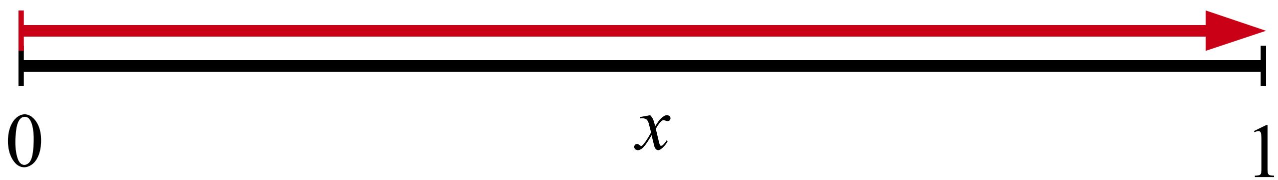
$$f_{\mathrm{h}}(x) = W_{\mathrm{hh}} x + W_{\mathrm{hd}}(1 - x)$$
$$f_{\mathrm{d}}(x) = W_{\mathrm{dh}} x + W_{\mathrm{dd}}(1 - x)$$

$$f_{\mathrm{h}}(x) = \frac{V - D}{2} x + V(1 - x)$$
$$f_{\mathrm{d}}(x) = \left(\frac{V}{2} - T\right)(1 - x)$$

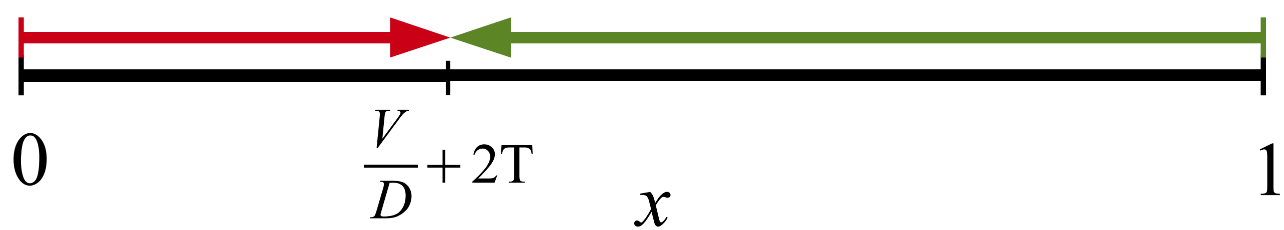
Hawk & doves

$$\frac{dx}{dt} = x(1-x)\left(f_{\mathrm{h}}(x) - f_{\mathrm{d}}(x)\right) = \frac{1}{2}x(1-x)\left[V - (D+2\mathrm{T})x\right]$$

$V > D + 2\mathrm{T}$



$V < D + 2\mathrm{T}$



Replicator dynamics

number of species

$$f_i(\boldsymbol{x}) = W_i(\boldsymbol{x})$$

$$= \sum_{j_2=1}^{S} \cdots \sum_{j_S=1}^{S} x_{j_2} \cdots x_{j_n} \overbrace{W(i, j_2, \ldots, j_n)}^{n\text{-player game's payoff}}$$

fraction of population

$$\phi(\boldsymbol{x}) = \sum_{i=1}^{S} x_i W_i(\boldsymbol{x})$$

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

Equilibria

$$\frac{dx_i}{dt} = x_i\left[f_i(\boldsymbol{x}) - \phi(\boldsymbol{x})\right]$$

$$x_i = 0 \qquad \text{or} \qquad f_i(\boldsymbol{x}) = \phi(\boldsymbol{x})$$

$$\Updownarrow$$

mixed-strategies Nash equilibria

Equilibria

$$x_i \left[f_i(\boldsymbol{x}) - \phi(\boldsymbol{x}) \right] = 0$$

$$\Updownarrow$$

$$x_i = 0 \qquad \text{or} \qquad f_i(\boldsymbol{x}) = \phi(\boldsymbol{x})$$

$$\Updownarrow$$

mixed-strategies Nash equilibria

2 species

$$\begin{array}{cc} & \begin{array}{cc} \mathrm{A} & \mathrm{B} \end{array} \\ W = & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \begin{array}{c} \\ \mathrm{A} \\ \mathrm{B} \end{array}$$

[A]

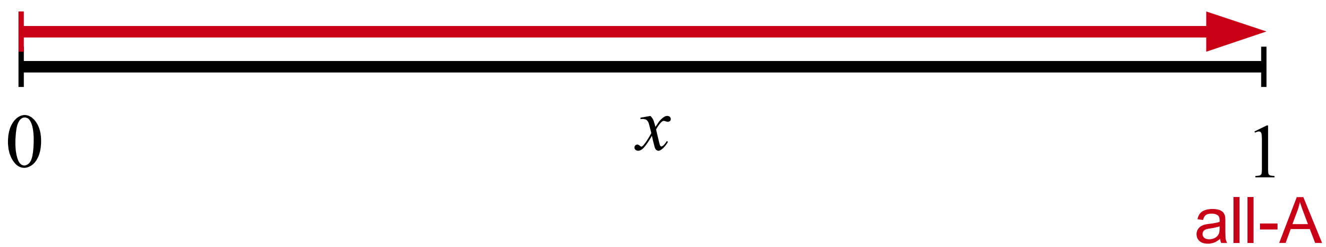
$$f_{\mathrm{A}}(x) = a\,x + b\,(1 - x)$$
$$f_{\mathrm{B}}(x) = c\,x + d\,(1 - x)$$

$$\frac{d\,x}{d\,t} = x\,(1 - x)\big[(b - d) - (b - d + c - a)\,x\big]$$

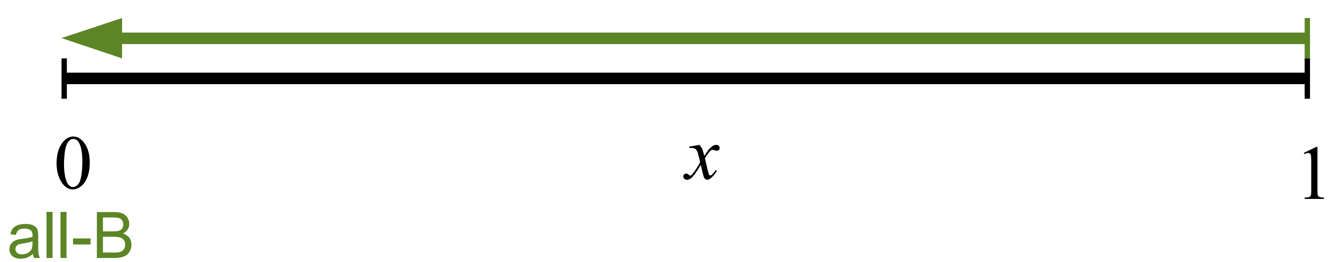
2 species

$$(b-d)(c-a)<0 \quad \Leftrightarrow \quad \text{1 species dominates}$$

$$(b-d)>0$$



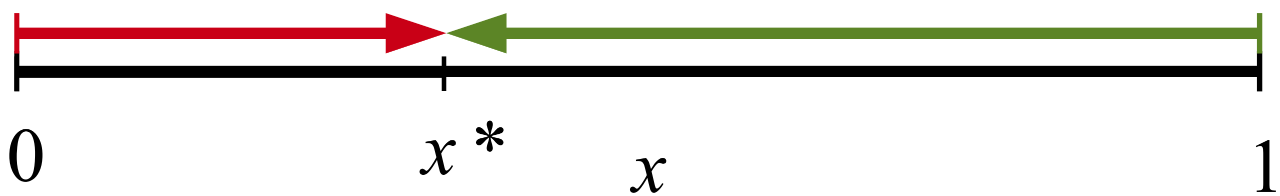
$$(b-d)<0$$



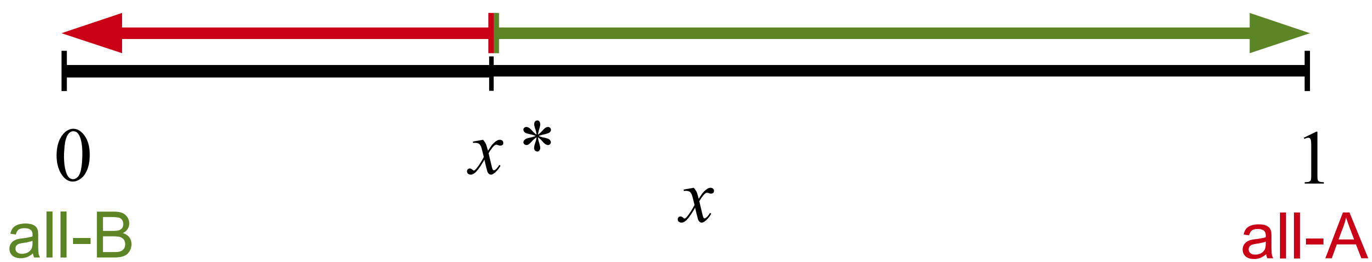
2 species

$$(b-d)(c-a)>0 \quad \Leftrightarrow \quad x^* = \frac{b-d}{b-d+c-a}$$

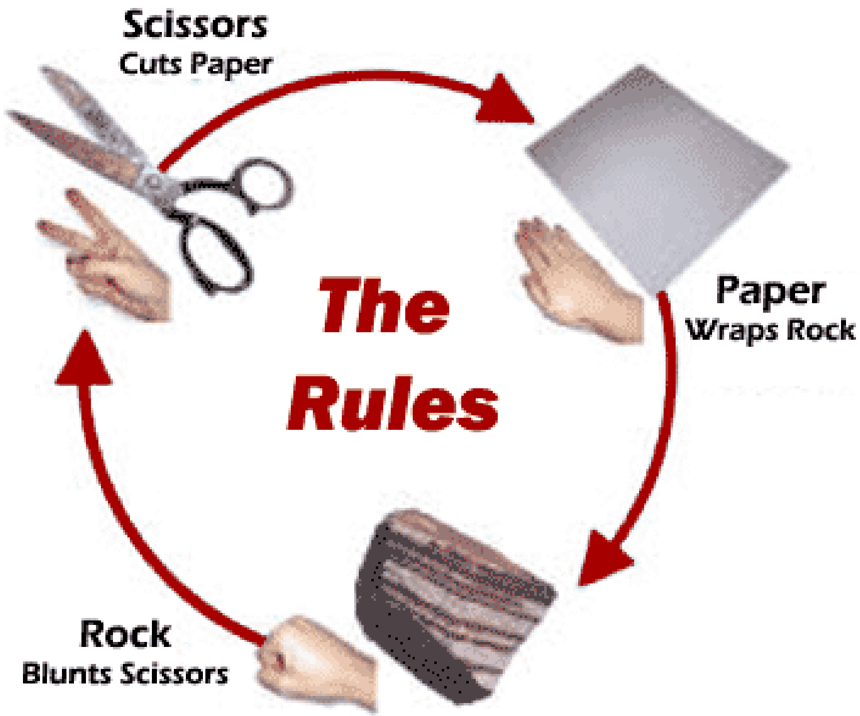
$$(b-d)>0$$



$$(b-d)<0$$



3 species: Rock-Paper-Scissors

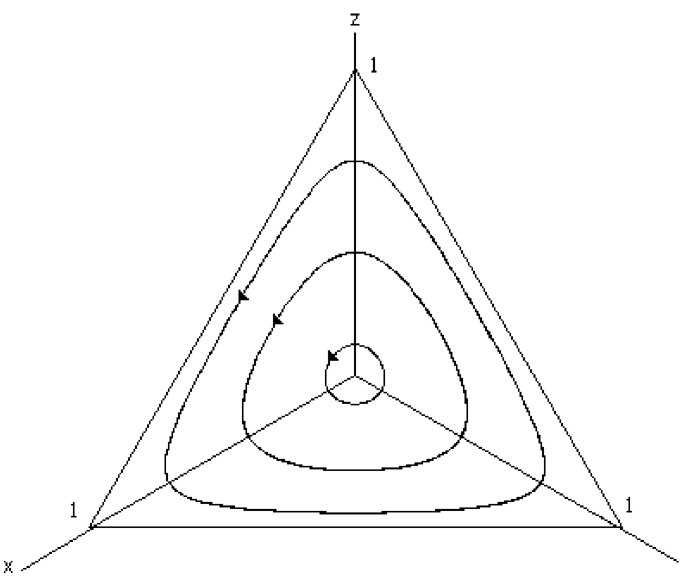


Dynamics of RPS

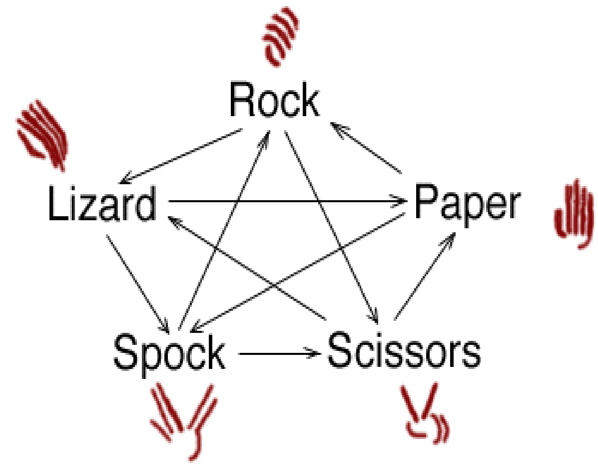
$$\begin{array}{cc} & \begin{array}{ccc} R & P & S \end{array} \\ W = & \begin{pmatrix} 0 & -1 & 1 \\ 1 & 0 & -1 \\ -1 & 1 & 0 \end{pmatrix} \end{array} \begin{array}{c} R \\ P \\ S \end{array}$$

$$\phi = 0$$

$$\prod_{i=1}^{3} x_i = c \leqslant \frac{1}{9}$$



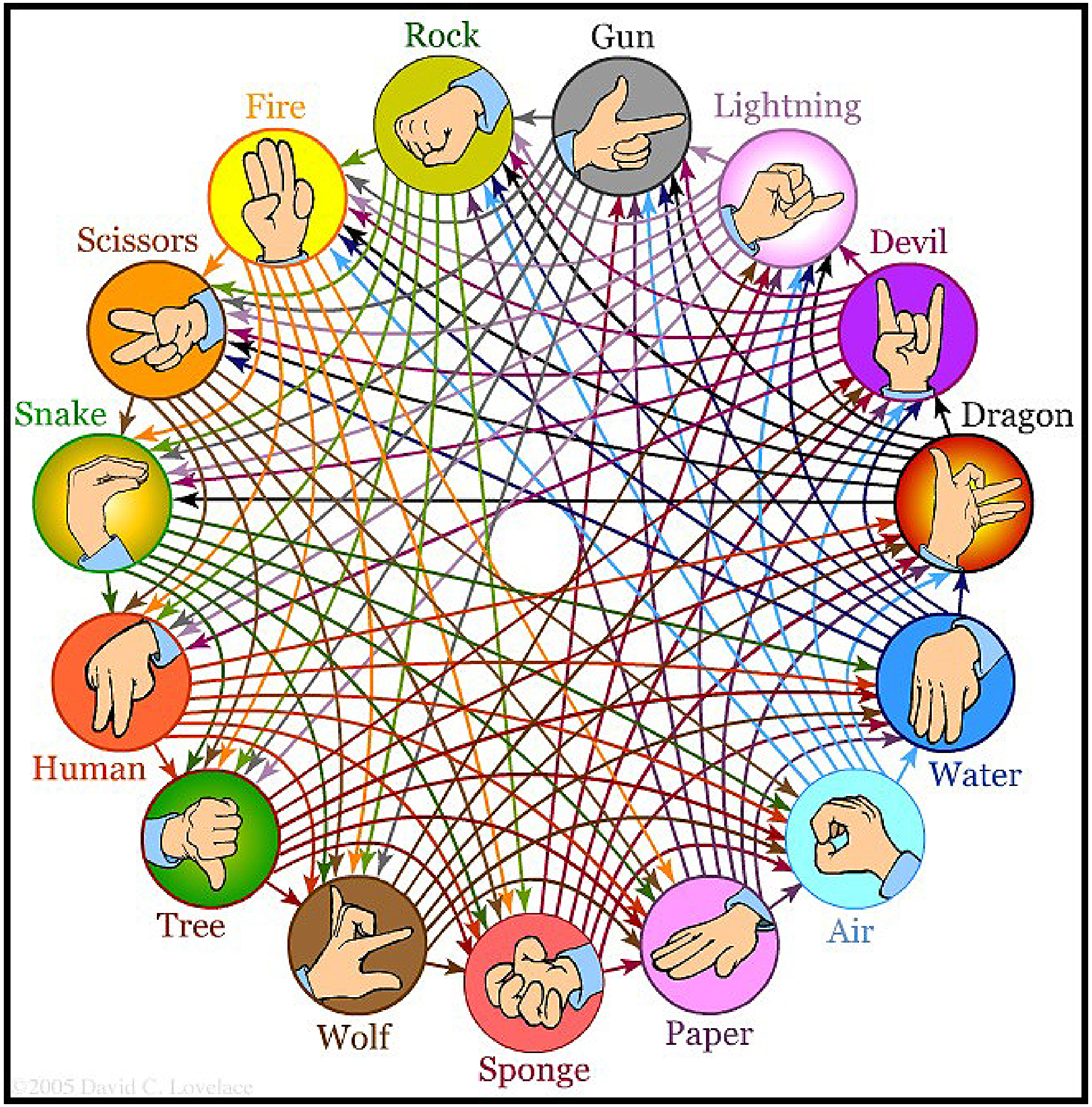
Some "variants"



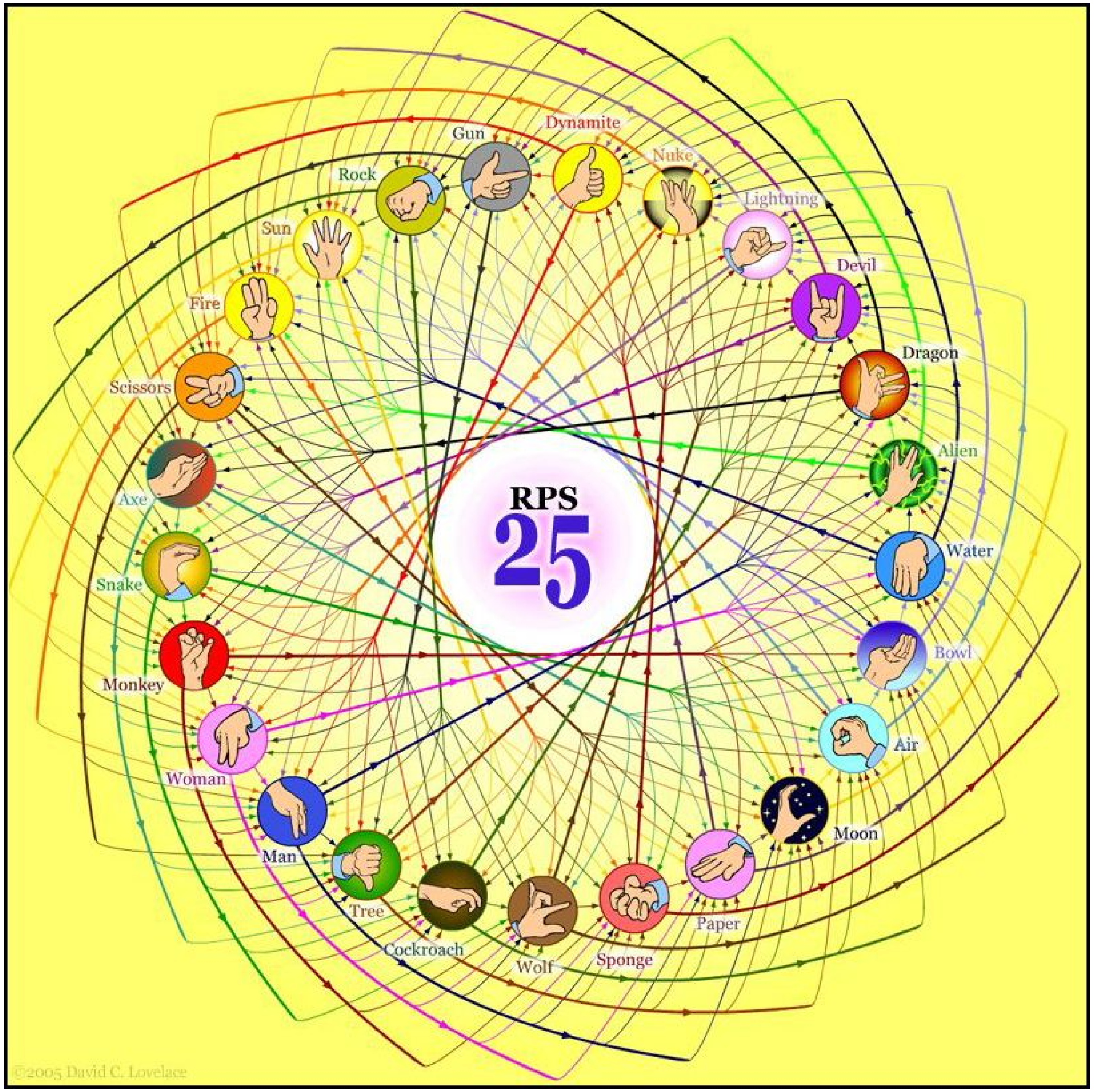
Scissors cuts Paper covers Rock crushes Lizard poisons Spock smashes Scissors decapitates Lizard eats Paper disproves Spock vaporizes Rock crushes Scissors.

$$\prod_{i=1}^{2n+1} x_i = c$$

Some "variants"

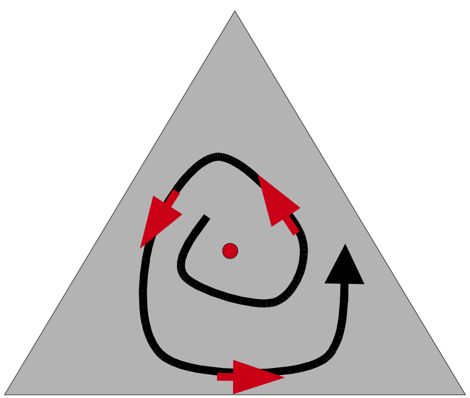


Some "variants"

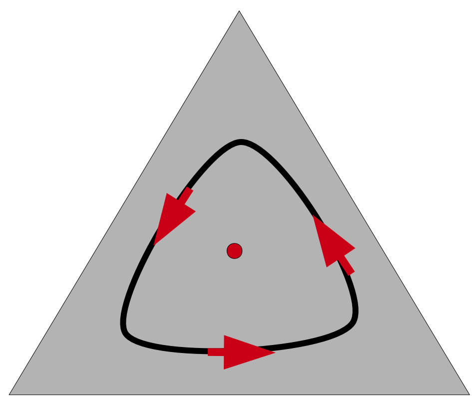


Generalized RPS

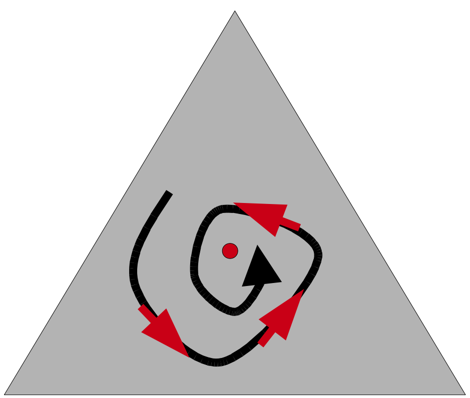
$$W = \begin{array}{c} \\ \\ \end{array}\begin{array}{cc} \begin{array}{ccc} R & P & S \end{array} & \\ \begin{pmatrix} 0 & -a_2 & b_3 \\ b_1 & 0 & -a_3 \\ -a_1 & b_2 & 0 \end{pmatrix} & \begin{array}{c} R \\ P \\ S \end{array} \end{array}$$



$|W| < 0$
$(a_1 a_2 a_3 > b_1 b_2 b_3)$

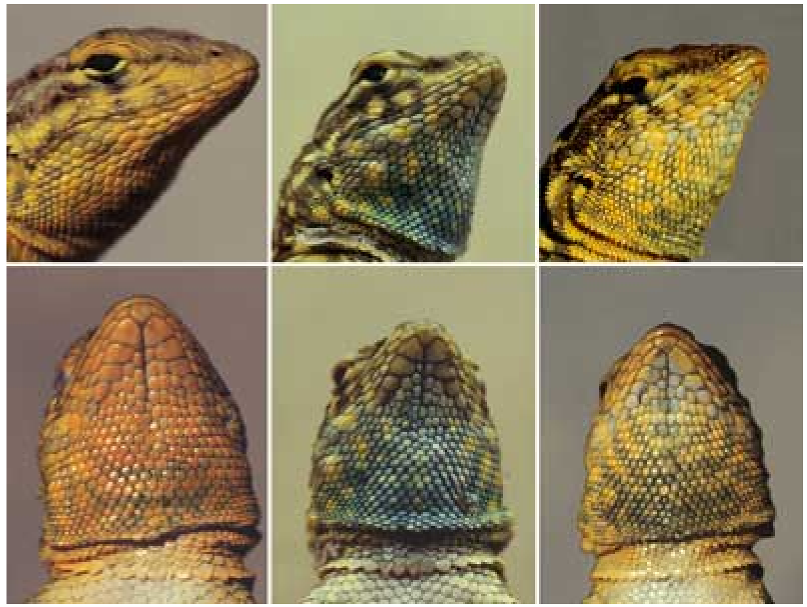


$|W| = 0$
$(a_1 a_2 a_3 = b_1 b_2 b_3)$

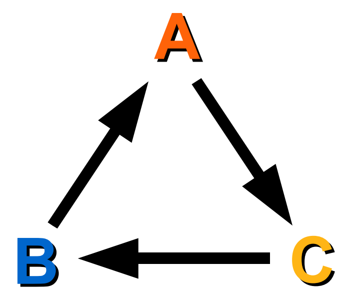


$|W| > 0$
$(a_1 a_2 a_3 < b_1 b_2 b_3)$

A live RSP: *Uta stansburiana*



A B C



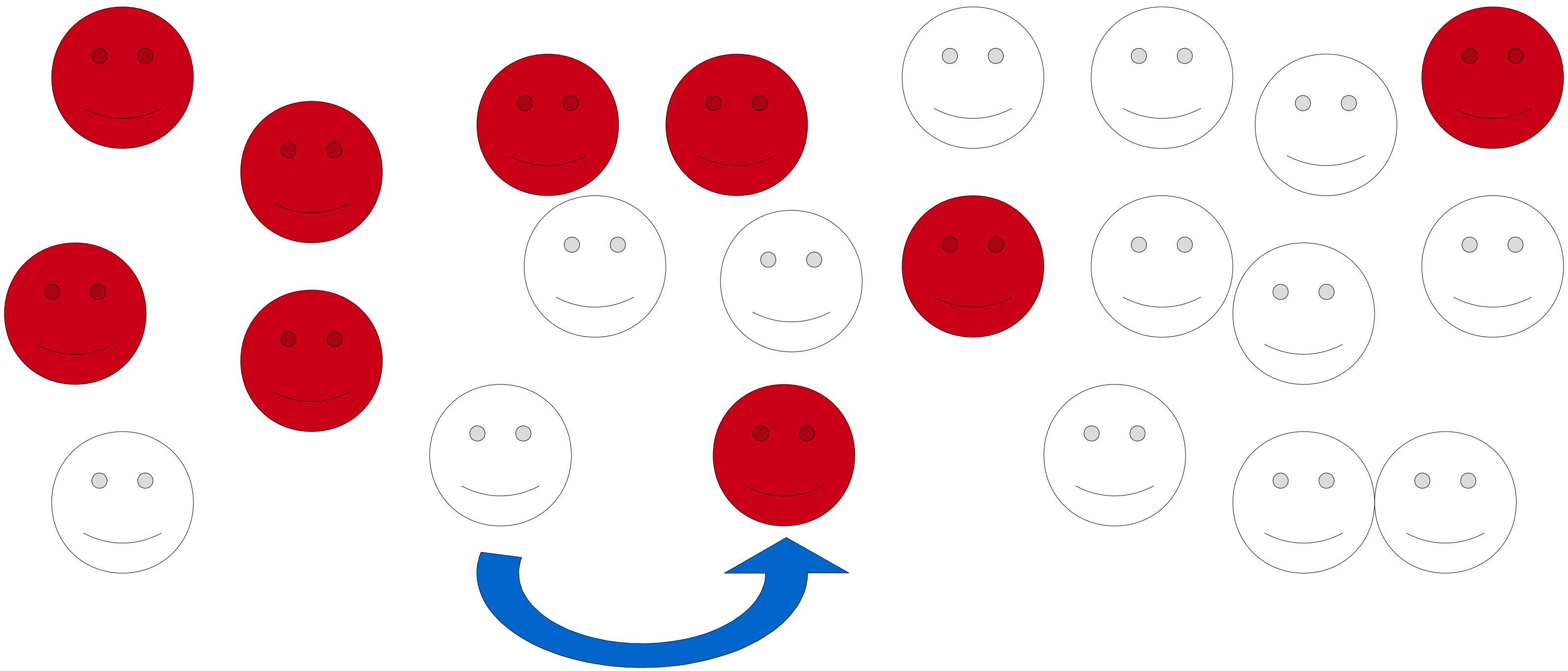
A monogamous, jelous

B polygamous

C sneaky mating

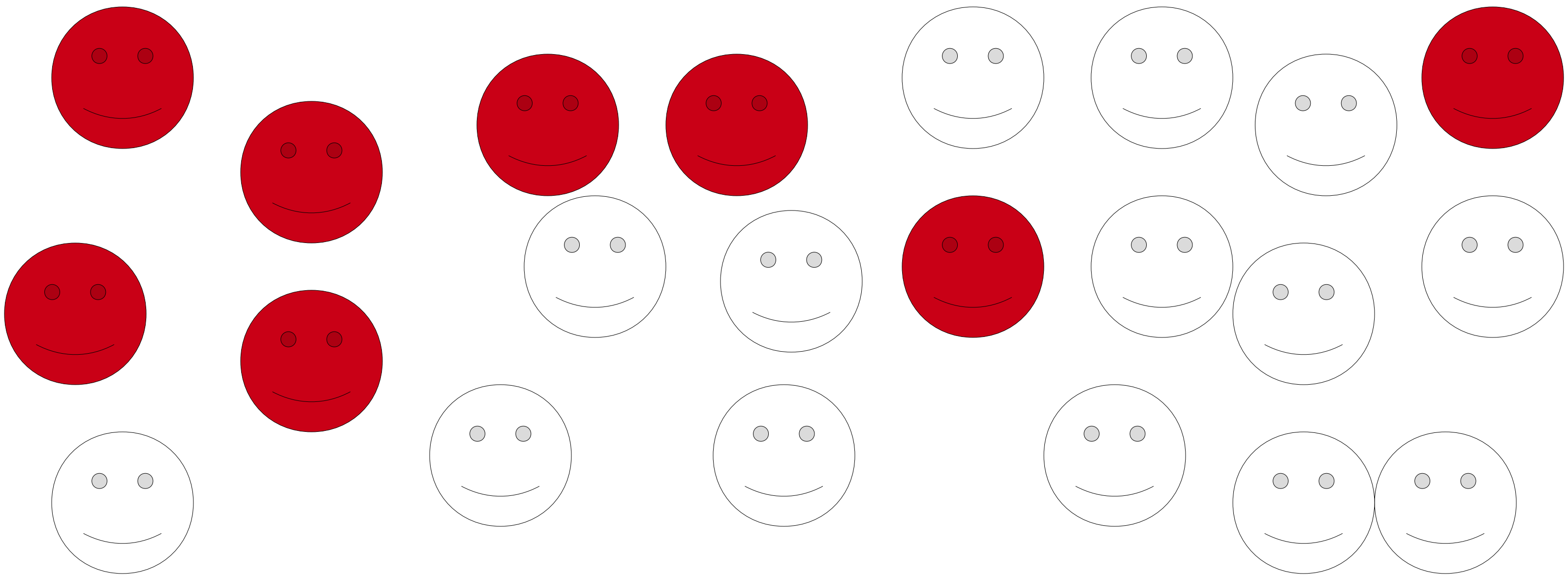
Zamudio & Sinervo, PNAS **97**, 14427-14432 (2000)

Social dynamics: imitation



$$T_{j\to i} \equiv f_{ij}(\boldsymbol{x})$$

Social dynamics: imitation



$$\frac{d x_i}{d t} = \sum_{j=1}^{n} \left[f_{ij}(\boldsymbol{x}) - f_{ji}(\boldsymbol{x}) \right] \underbrace{x_i x_j}_{\text{meeting probability}}$$

Social dynamics: imitation

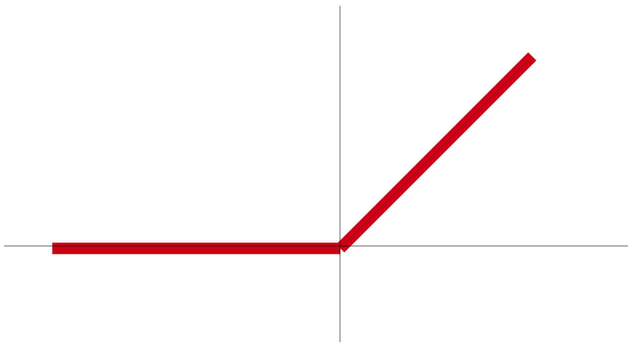
Assumptions:

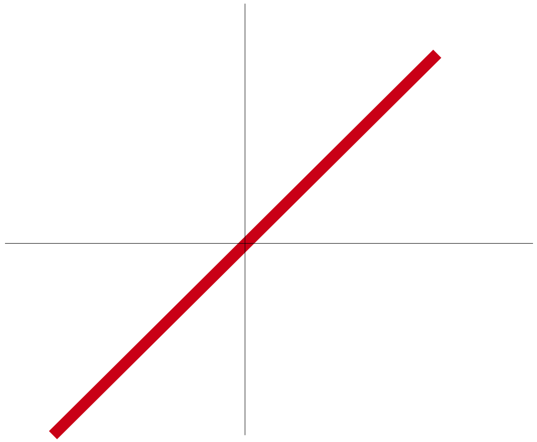
- $f_{ij}(\boldsymbol{x}) = F((W\boldsymbol{x})_i, (W\boldsymbol{x})_j)$
- $F(u, v) = \phi(u - v)$
- $\psi(z) = \phi(z) - \phi(-z)$

$$\frac{dx_i}{dt} = x_i \sum_{j=1}^{n} \psi\left[(W\boldsymbol{x})_i - (W\boldsymbol{x})_j\right] x_j$$

Social dynamics: imitation

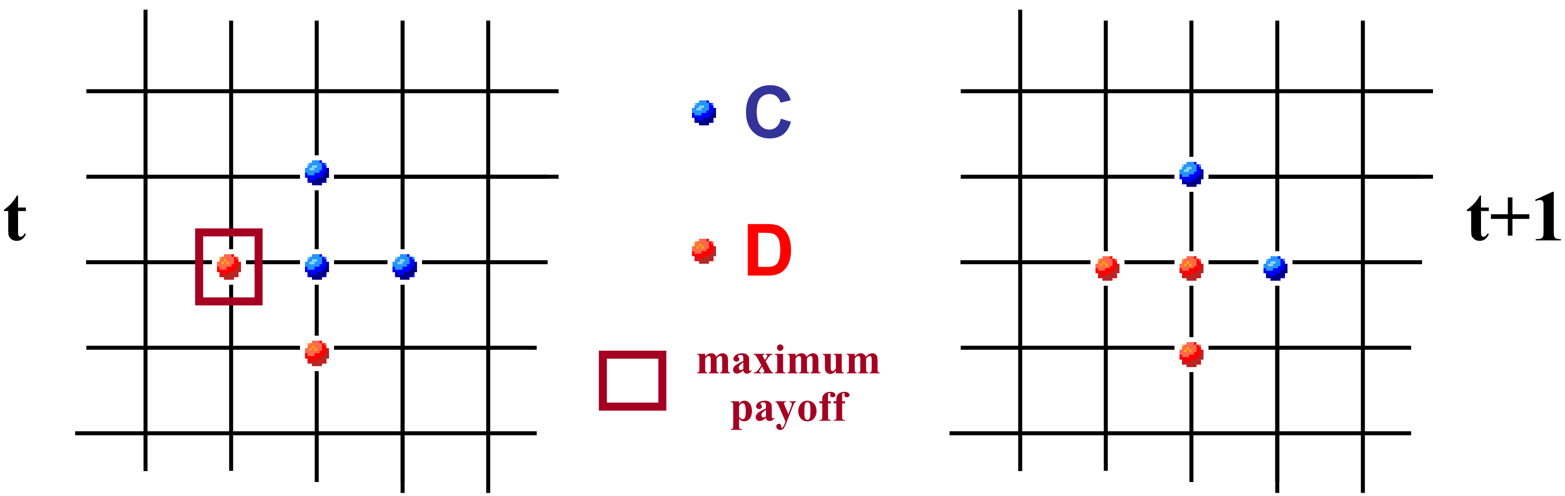
$$\phi(z) = (z)_+ \quad \Rightarrow \quad \psi(z) = z$$



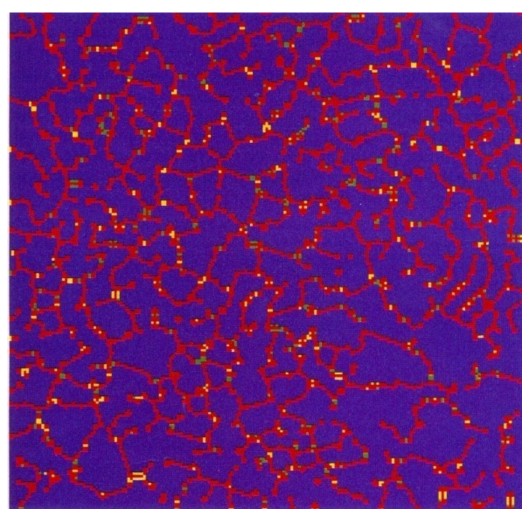


$$\frac{dx_i}{dt} = x_i[(W\boldsymbol{x})_i - \boldsymbol{x}^T W \boldsymbol{x}]$$

Spatial prisoner's dilemma



C->C
D->D
C->D
D->C



M. A. Nowak and R. M. May
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