Evolutionary Dynamics: Fitness, Cooperation and Gene Expression Noise.

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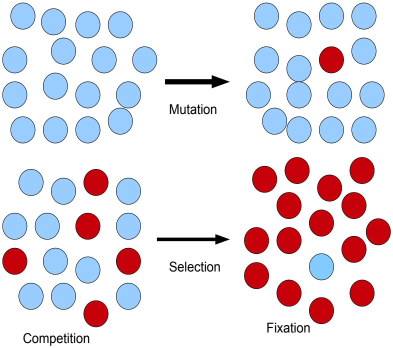
Natural Selection and Fitness

What evolution is?

- Today in colloquial language evolution means, changes over time. From it can be inferred that evolution happens in many things around us: changes in the shapes of mounts, the different leafs of trees across seasons, etc, but evolution in living systems has a key difference, reproduction.
- Biological evolution is changes in the characteristics of populations of organisms over the course of generations. Where these changes are inherited.

Which are the mechanisms that leads to an evolutionary process?. Evolutionary dynamics have three basic mechanisms:

- Replication.
- Mutation: mistakes in genetic replication. Is responsible for generating different types.
- Selection.


Mutation
Selection
Competition
Fixation

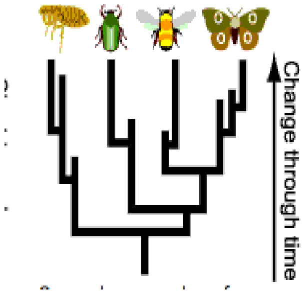


Figure: www.evolution.berkeley.edu

Figure: http://images.yuku.com.s3.amazonaws.com/image/jpg/03616d619a16fb3ae47432d6694ed9f2
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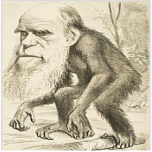
Changes in traits across successive generations is the beginning of the way to explain the diversification in living beings.



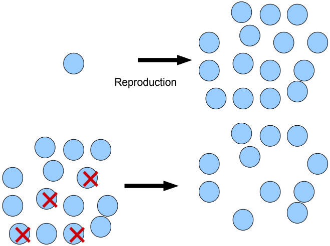
Darwin proposed Natural selection.

Changes in population traits are gradual directional to the fittest trait, and through genetic inheritance the fittest characteristic gets fixed in the population depending on the environment.

- In the early 20th century scientist created approaches to modeling natural selection mathematically.
- A quantity that makes a characteristic more selective than others.
- This quantity is called fitness.

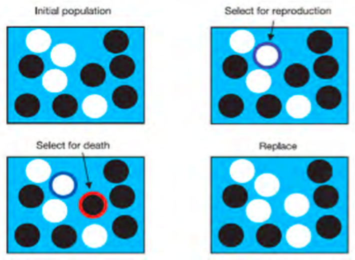
Fitness is usually defined as the average number of offsprings produced by individuals of a certain type and the average number of these that survive.

The per capita growth rate R of a genotype.



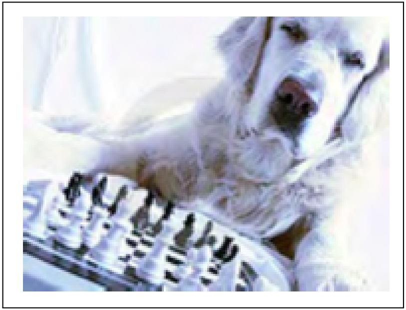
Fitness=(proportion surviving)x(average fecundity). Suppose that an organism lays an average of 60 eggs, and 0.05 of then survive to reproductive age. $f = 0.05 \times 60 = 3$.

Because our constant population N simulation and usually in stochastic model for evolution, fitness is just the reproductive contribution of each individual of a certain type. The death rate is due to the N constant size.



$f_i = offsprings/time$ in our simulation with asexual reproduction.

Fitness is not just due to physical advantages, it have been seen that it also due to social behaviors and altruistic interactions.



Deterministic Model of Reproduction and Selection

Bacterial cells in a perfect environment.

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

Differential equation for exponential growth at rate r. Where the time of cell division is an exponential distribution with average $1/r$.

$$\dot{x} = rx \quad x(t) = x_0 e^{rt}. \tag{2}$$

$$\frac{dN(t)}{dt} = rN(t) - dN(t) - mN(t). \tag{3}$$

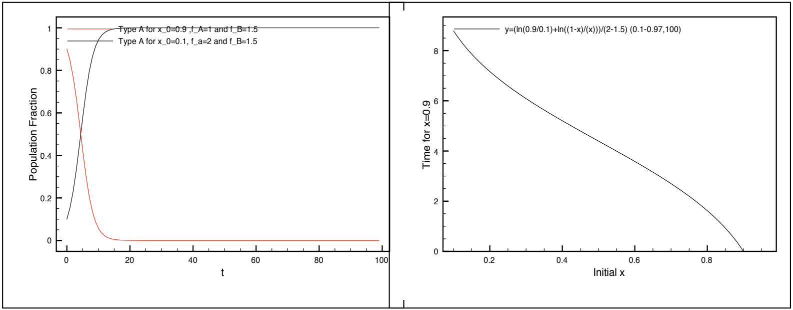
Suppose we have two organism A and B competing, with fitnesses f_A and f_B , frequencies x_A and x_B and size N.

$$\frac{dx_A}{dt} = f_A x_A - \phi, \tag{4}$$

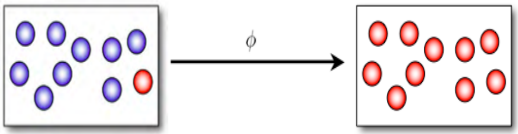
$$\frac{dx_B}{dt} = f_B x_B - \phi. \tag{5}$$

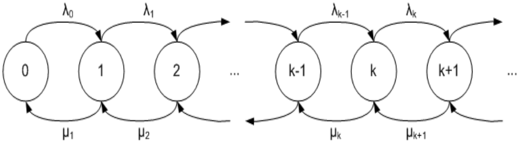
$$\frac{dx_A}{dt} = x_A(1 - \frac{x_A}{N})(f_A - f_B). \tag{6}$$

$$x_A(t) = \frac{x_{A0} e^{(f_A - f_B)t}}{1 - \frac{x_{A0}}{N} + \frac{x_{A0}}{N} e^{(f_A - f_B)t}}. \tag{7}$$



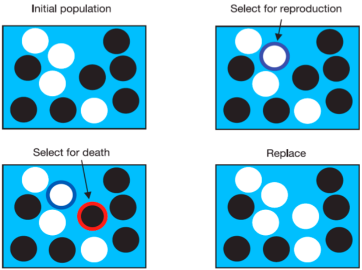
Markov Chain and Moran Process





$$p_0'(t) = \mu_1 p_1(t) - \lambda_0 p_0(t)$$
$$p_k'(t) = \lambda_{k-1} p_{k-1}(t) + \mu_{k+1} p_{k+1}(t) - (\lambda_k + \mu_k) p_k(t)$$

Moran Process



Nowak, Sasaki, Taylor, and Fudenberg, Nature 428, 646 (2004).

Moran Process Simulation

Two types with fitness r and s. At each time step one types i selected for reproduction with probability

$$\frac{ri}{ri + s(n-i)} \tag{8}$$

Then one individual is replaced randomly with the new offspring.

$$\frac{i}{n} \ , \ \frac{n-i}{n} \tag{9}$$

Transition probabilities

$$\begin{aligned} P_{i,i+1} &= \frac{ri}{ri+s(n-i)}\frac{n-i}{n} \\ P_{i,i-1} &= \frac{s(n-i)}{ri+s(n-i)}\frac{i}{n} \end{aligned} \tag{10}$$

The master equation for this system is:

$$\frac{dP_i}{dt} = -\left(\frac{ri}{ir+s(n-i)}\frac{n-i}{n}+\frac{s(n-i)}{ir+s(n-i)}\frac{i}{n}\right)P_i(t)+\frac{r(i-1)}{(i-1)r+(n-i+1)s}\frac{n-i+1}{n}P_{i-1}+\frac{r(i+1)}{(i+1)r+(n-i-1)s} \tag{11}$$

The conditions for fixation probabilities ρ_i are $\rho_0 = 0$, $\rho_n = 1$ and

$$\rho_i = p_{i,i}\rho_i + p_{i,i+1}\rho_{i+1} + p_{i,i-1}\rho_{i-1}. \tag{12}$$

Fixation time $\rho_i^n(t)$:

$$\phi_j t_j^A = \phi_{j-1} T_j^- (t_{j-1}^A + 1) + \phi_j (1 - T_j^- - T_j^+)(t_j^A + 1) + \phi_{j+1} T_j^+ (t_{j+1}^A + 1).$$

Neutral Drift

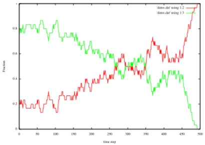
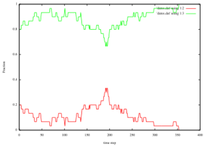
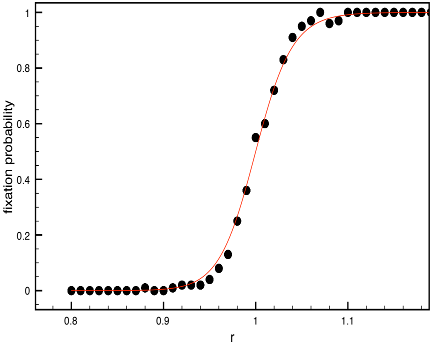


Figure 6: Red line fraction of type 1 and green one fraction of type 0, first round(this was obtained with Basicmoran.cpp).



$$\rho_i = \frac{i}{n}$$

$$\rho_i = \frac{1 - 1/r^i}{1 - 1/r^n}. \tag{13}$$



Game Theory, Cooperation and Fitness

Cooperate or cheating. They can be transfer to the next generation.

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \tag{14}$$

$$P_C = \frac{R(x-1) + S(N-x)}{N-1} \tag{15}$$

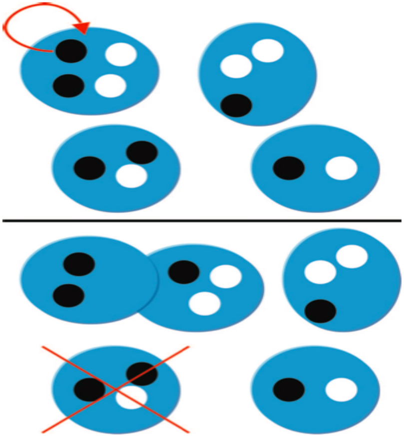
$$P_D = \frac{Tx + P(N-x-1)}{N-1} \tag{16}$$

fitness as function of the payoff.

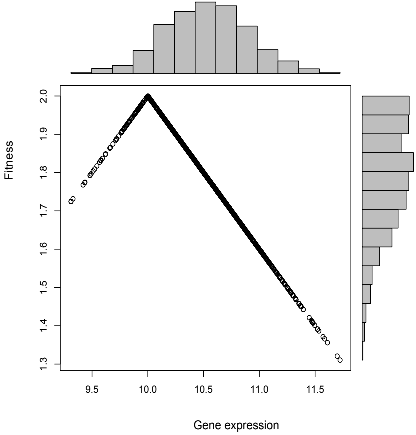
$$f_C = 1 - w + wP_C \quad f_D = 1 - w + wP_D \tag{17}$$

where w is the intensity of selection.

Selection is also at level of groups of the fittest individuals, which will reproduce faster. There is a Moran Process for GOUP SELECTION.



Due to internal noise, fitness is not deterministic.



$$p_{reproduction} = \frac{\sum_{i=1}^{n} f_{1i}}{\sum_{i=1}^{n} f_{1i} + \sum_{j=1}^{N-n} f_{0j}} \tag{18}$$

$$\rho_1 = \left(1 + \sum_{i=2}^{N} \frac{(i-1)!(N-i)!}{(N-1)!} \prod_{j=2}^{i} \frac{\sum\limits_{m=1}^{N-(j-1)} s_m}{\sum\limits_{m=1}^{j-1} r_m} \right)^{-1} \tag{19}$$

Bibliography I