

Selección de grupo como un mecanismo de evolución de la cooperatividad

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1 2×2 Games

At these games a population of individuals have pairwise interactions with two behavioral strategies to choose from, the elements of the payoff matrix

$$\begin{array}{cc} & C & D \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix} \end{array} \quad (1)$$

are the parameters of the strategies and determine the dynamics of population, for prisoner's dilemma ($T > R > P > S$). There are two ways to simulate these: solving the differential replication equation¹

$$\frac{dx}{dt} = x(x-1)(P_C - P_D) \quad (2)$$

and the stochastic code with a replication probability depending on the average payoff of the two strategies to choose.

The stochastic code works as follow; a population of N individuals with two strategies C (cooperate) and D (defect) where x individuals behave as C and $N-x$ as D , then the average payoffs respect to whole population for a cooperator and a defector are

$$P_C = \frac{R(x-1) + S(N-x)}{N-1} \quad (3)$$

$$P_D = \frac{Tx + P(N-x-1)}{N-1} \quad (4)$$

¹<http://www.univie.ac.at/virtuallabs/TwoByTwo/mixed.html>

With a population of $N = 10000$ and parameters $R = 0.4$ $S = 0$ $T = 0.8$ $P = 0.2$. The plots of P_C and P_D as functions of x are

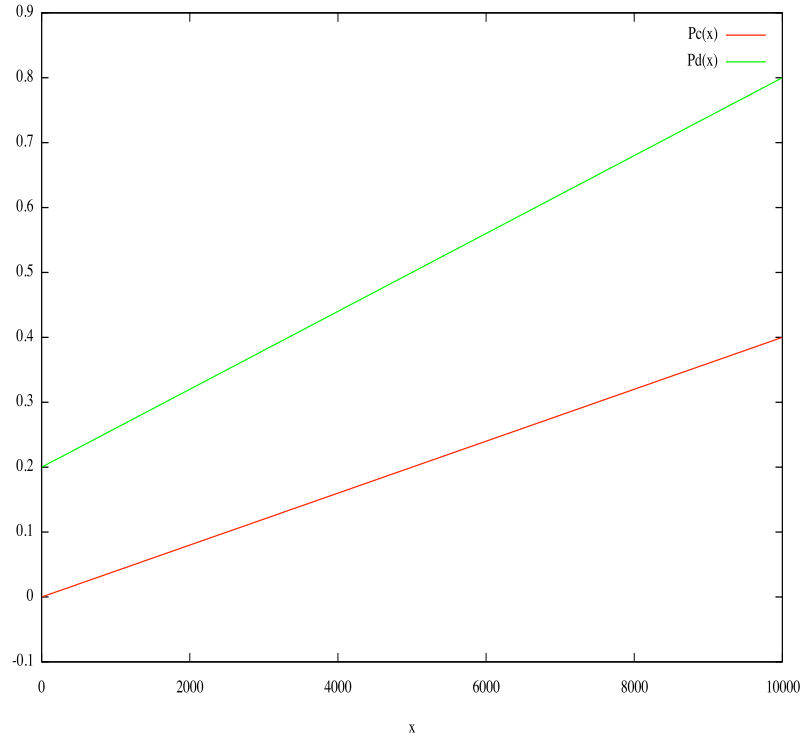


Figure 1: P_C and P_D payoffs plots

The probability of cooperate $\rho_c = P_C/(P_C + P_D)$

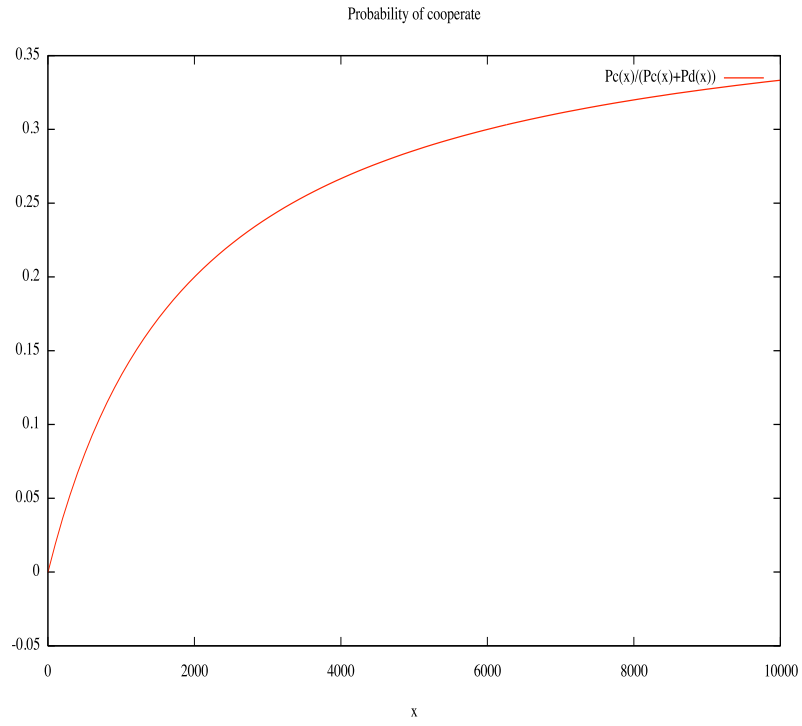


Figure 2: Probability $\rho_c(x)$ of cooperate

The next plot was done with a simulation that works as Monte-Carlo step, if a random number in the range $[0, 1]$ is less than ρ_c the individual cooperates and stay for next iterations(using only if) even the random number is larger than ρ_c .

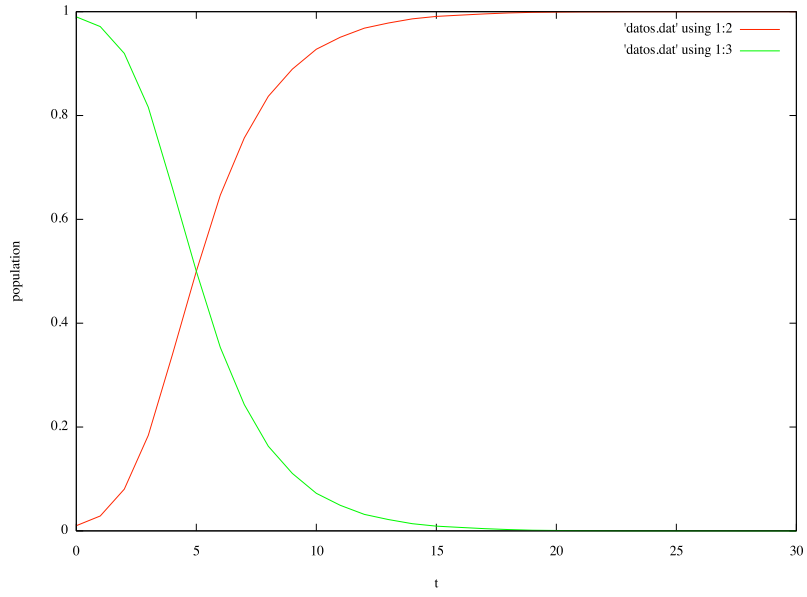


Figure 3: Red line fraction of cooperators and green line fraction of defectors

Now using parameters $R = 1$, $S = 0$, $T = 0.7$ y $P = 0.2$, the expected payoff P_C is less than P_D for low population of cooperators, as show Figure(4).

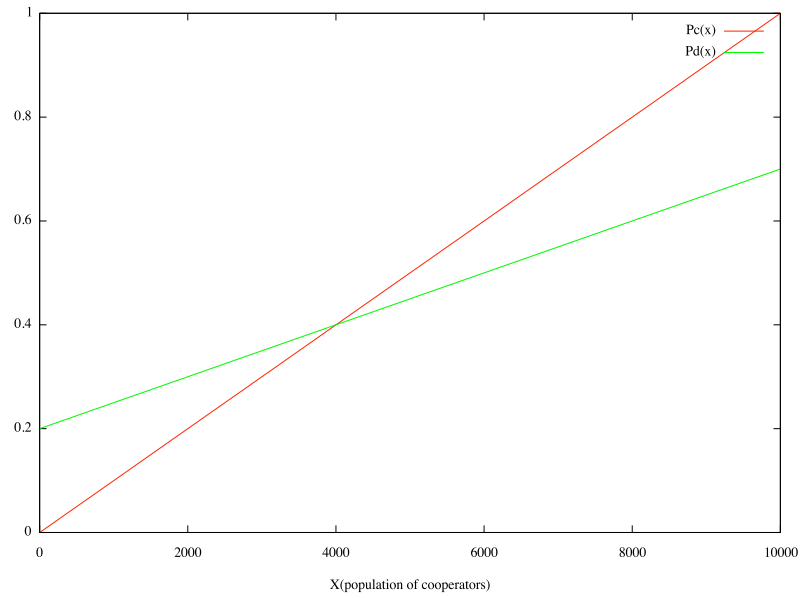


Figure 4: Plots of payoff P_C and P_D

This time the probability for the stochastic process is proportional to the payoffs difference

$$\rho_c = \frac{1}{2} + \frac{(P_C - P_D)}{2MAX_{P_C - P_D}} \quad (5)$$

where $MAX_{P_C - P_D}$ is the highest difference $P_C - P_D$. Including the parameter $0 \leq w \leq 1$ that controls the intensity of selection:

$$\rho_c = \frac{1}{2} + \frac{w(P_C - P_D)}{2MAX_{P_C - P_D}} \quad (6)$$

For $w = 1$ and probability of change for next iterations(using if and else) the result of the simulation was

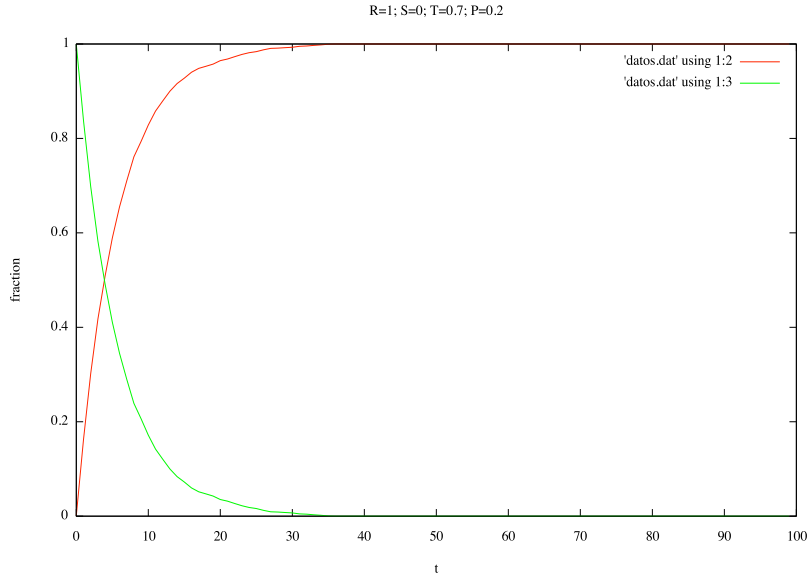


Figure 5: Red line fraction of cooperators and green one fraction of defectors

2 Replicator Dynamics: Moran process

In the Moran process, at each time step one individual of the population is chosen randomly for reproduction, with a probability that depends of its fitness, the new offspring replaces other individual of the population that is chosen randomly. The fitness and probability functions can be implemented in several forms, the fitness is usually a lineal function or an exponential function of the expected payoff and the probability is a function of the difference strategies fitness or the fraction of the total payoff.

The next simulation is the basic Moran process where an individual is chosen for reproduction using an uniform random generator and other random individual is replaced by the new

offspring. The total number of individuals n is fixed and has two types: individuals 0 and 1, the number of 1 individuals is denoted by i . The simulation start whit the initial condition $i > 0$ and stops when one of the two types dominates the population, randomly some times type 1 dominate and others type 0.

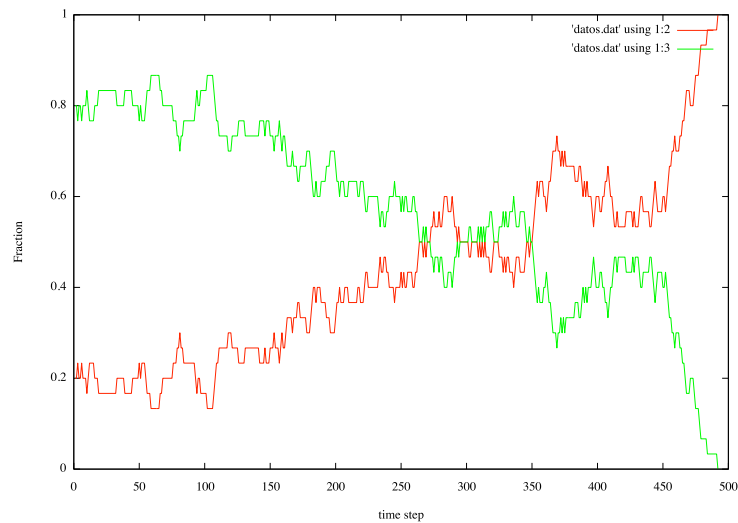


Figure 6: Red line fraction of type 1 and green one fraction of type 0, first round(this was obtained with Basicmoran.cpp).

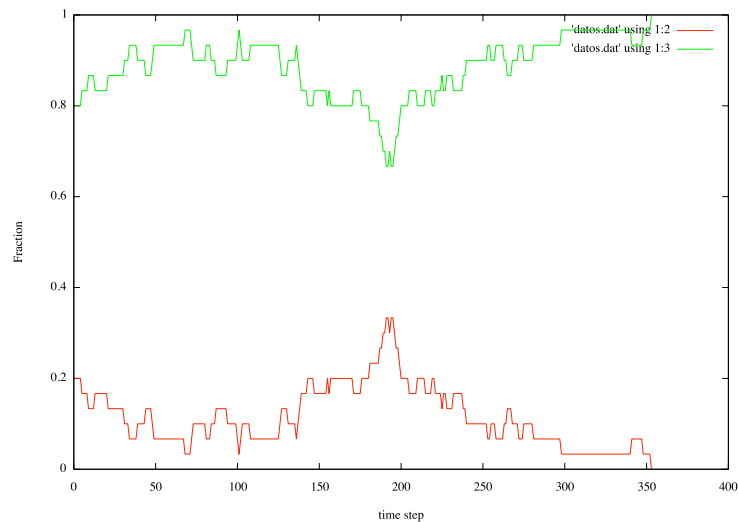


Figure 7: second round(this was obtained with Basicmoran.cpp).

The analytical development to find the probability of dominance is as follow. Whit a

population of size n and i individuals of type 1, the probabilities of choosing are: i/n for type 1 and $(n-i)/n$ for type 0. Then the probability that the population changes from i to $i+1$ is

$$p_{i,i+1} = \frac{i(n-i)}{n^2}, \quad (7)$$

and from i to $i-1$ is

$$p_{i,i-1} = \frac{(n-i)i}{n^2}. \quad (8)$$

The probability ρ_i of fixation or dominance for the initial condition of i individuals of type 1, is $\rho_i = 0$ if $i = 0$ and $\rho_i = 1$ if $i = n$, this is because of when an individual is chosen to dead it is replaced by one of its same type. The probability ρ_i is the sum of the probabilities of dominate from three events, that is

$$\rho_i = p_{i,i}\rho_i + p_{i,i-1}\rho_{i-1} + p_{i,i+1}\rho_{i+1} \quad i = 1, 2, 3, \dots, n-1 \quad (9)$$

deafening the new variables

$$y_i = \rho_i - \rho_{i-1}$$

The series of y_i is a geometric series

$$\sum_{i=1}^n y_i = \rho_n - \rho_0 = 1. \quad (10)$$

Since $p_{i,i-1} = p_{i,i+1}$ and $p_{i,i} = 1 - 2p_{i,i+1}$, let us write equation (9) as

$$\begin{aligned} \rho_i 2p_{i,i+1} &= p_{i,i+1}(\rho_{i-1} + \rho_{i+1}) \\ \rho_i - \rho_{i-1} &= \rho_{i+1} - \rho_i \end{aligned} \quad (11)$$

because $\rho_0 = 0$, then $y_i = \rho_i$ and $\sum_{i=1}^n y_i = \rho_n - \rho_0 = n\rho_1$. To determine ρ_i note that $\rho_i = \sum_{j=1}^i y_j = i\rho_1$, then finally

$$\rho_i = \frac{i}{n}. \quad (12)$$

We can perform the same calculation for the same process as before but assuming that type 1 has fitness r and type 0 fitness 1. Then the probability that 1 is chosen for reproduction is

$$\frac{ri}{ir + n - i} \quad (13)$$

that 1 is chosen for elimination is

$$\frac{i}{n}. \quad (14)$$

Type 0 has probability for reproduction $n-i/(ri+n-i)$ and $n-i/n$ for elimination. Therefore the probabilities of transition are

$$p_{i,i+1} = \frac{ri}{ri + n - i} \frac{n-i}{n} \quad (15)$$

$$p_{i,i-1} = \frac{n-i}{ri+n-i} \frac{i}{n} \quad (16)$$

$$p_{i,i} = 1 - p_{i,i+1} - p_{i,i-1}. \quad (17)$$

Ones again the conditions for fixation probabilities ρ_i are $\rho_0 = 0$, $\rho_n = 1$ and

$$\rho_i = p_{i,i}\rho_i + p_{i,i+1}\rho_{i+1} + p_{i,i-1}\rho_{i-1}. \quad (18)$$

With the new variable $y_i = \rho_i - \rho_{i-1}$ we can write equation (18) as

$$y_i = y_{i+1} \frac{p_{i,i+1}}{p_{i,i-1}} = y_{i+1} \frac{ri}{n-i} \frac{n-i}{i} \quad (19)$$

them $y_{i+1} = \frac{1}{r} y_i$, and these lead to

$$y_i = \frac{1}{r^{i-1}} \rho_1 \quad (20)$$

since $1 = \rho_1(1 + \sum_{m=1}^{n-1} \frac{1}{r^m})$ and $\rho_i = \rho_1(1 + \sum_{j=1}^{i-1} \frac{1}{r^j})$, the fixation probability is

$$\rho_i = \frac{1 + \sum_{j=1}^{i-1} \frac{1}{r^j}}{1 + \sum_{m=1}^{n-1} \frac{1}{r^m}}. \quad (21)$$

In this expression we have telescopic series. The sum value for a telescopic series is

$$\sum_{i=0}^n \frac{1}{x^n} = \frac{1 - \frac{1}{x^{n+1}}}{1 - \frac{1}{x}}. \quad (22)$$

Therefore the probability of fixation for type 1 starting in state i is

$$\rho_i = \frac{1 - 1/r^i}{1 - 1/r^n}. \quad (23)$$

This result can be checked in a Moran process simulation where is measured the fixation probability as a function of r . In the figure below are showed the analytical curve and the stochastic measures.

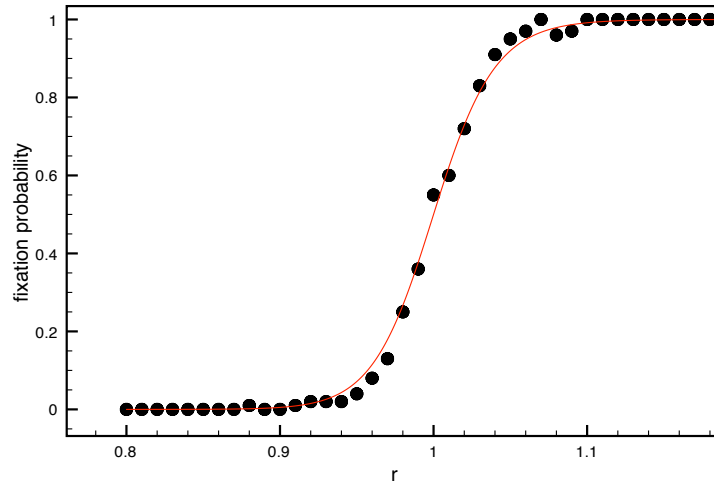


Figure 8: Red line, plot of equation (23) with $i = 50$ and $n = 100$, black points represent the stochastic simulation (this was obtained with RamdonDriftbucle.cpp).

In the next figure there is a plot of ρ_i as a function of i , which shows that the probability ρ_i is 1 for values of i greater than 6.

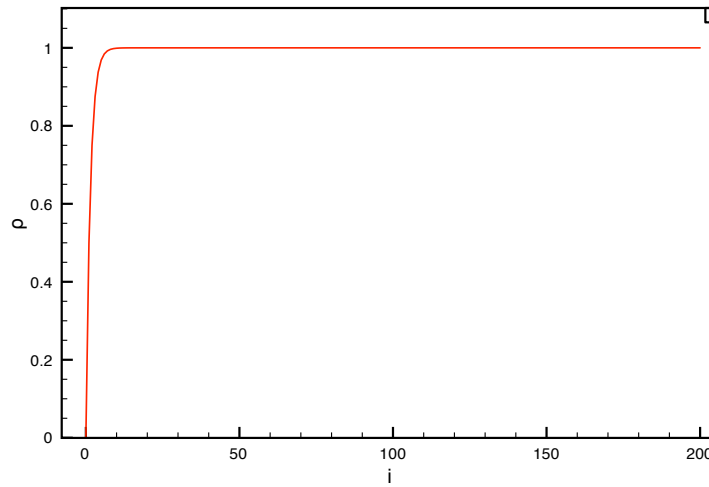


Figure 9: Plot of ρ_i with $n = 1000$ and $r = 2$.

Assuming alleles with fitness r and s , the transition probabilities become

$$\begin{aligned} P_{i,i+1} &= \frac{ri}{ri + s(n-i)} \frac{n-i}{n} \\ P_{i,i-1} &= \frac{s(n-i)}{ri + s(n-i)} \frac{i}{n} \end{aligned} \tag{24}$$

replacing into the recurrence equation for y_i

$$y_{i+1} = y_i \frac{s}{r} \tag{25}$$

which leads to

$$\begin{aligned} y_i &= \left(\frac{s}{r}\right)^{i-1} \rho_1, \\ \rho_1 &= \frac{1 - \left(\frac{s}{r}\right)^i}{1 - \left(\frac{s}{r}\right)^n} \end{aligned} \tag{26}$$

3 Features to make the simulation closer to the experiment conditions and real world

An spacial array with next neighbors and a distribution of fitness for each allele, for this work it is going to be implemented the distribution of fitness which is doing by giving several possible values of fitness to each allele. Then the initial condition will be a gaussian distribution for the individuals of each type of allele. It is known that the phenotype variability of an allele is due to the noise in the expression of its gene and which leads to phenotypes that can share value fitness for different alleles.

In this model model the fitness for the initial populations of the alleles and their offsprings come from a distribution which can be usually gaussian or poisson's, but by simplicity, initially we are going to use the Gaussian distribution.

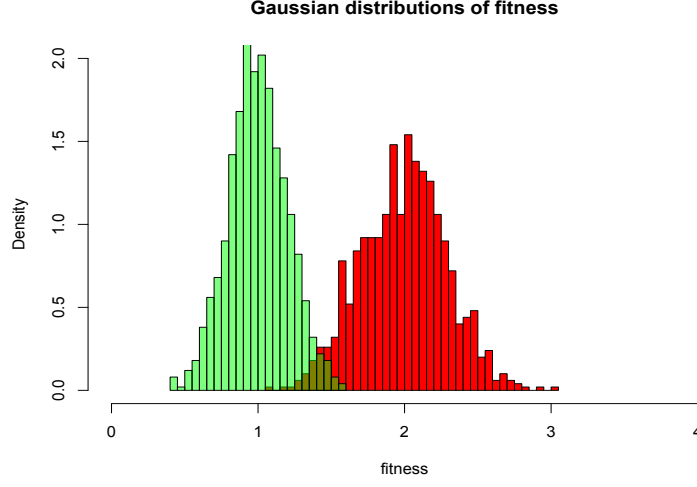


Figure 10: In these figure there is an example where two different alleles produce equals values of fitness

Let individuals of alleles of types 1 and 0 have values of fitness f_{1i} and f_{0j} respectively. Then the probability that type 1 is choosing for reproduction is

$$p_{reproduction} = \frac{\sum_{i=1}^n f_{1i}}{\sum_{i=1}^n f_{1i} + \sum_{j=1}^{N-n} f_{0j}} \quad (27)$$

where n is the initial population of type 1 and N the size of total population. Therefore the probabilities of transition are

$$P_{n,n+1} = \frac{\sum_{i=1}^n f_{1i}}{\sum_{i=1}^n f_{1i} + \sum_{j=1}^{N-n} f_{0j}} \frac{N-n}{N} \quad (28)$$

$$P_{n,n-1} = \frac{\sum_{j=1}^{N-n} f_{0j}}{\sum_{i=1}^n f_{1i} + \sum_{j=1}^{N-n} f_{0j}} \frac{n}{N} \quad (29)$$

replacing them in equation

$$y_n = y_{n+1} \frac{P_{n,n+1}}{P_{n,n-1}}$$

leads to

$$y_n = y_{n+1} \frac{N-n}{n} \frac{\sum_{i=1}^n f_{1i}}{\sum_{j=1}^{N-n} f_{0j}} \quad (30)$$

since $y_1 = \rho_1$, evaluating (31) for $n = 1, 2$ gives

$$\begin{aligned} y_2 &= \frac{\rho_1}{N-1} \frac{\sum_{m=1}^{N-1} s_m}{\sum_{m=1}^{N-1} r_m}, \\ y_3 &= \frac{\rho_1}{N-1} \frac{\sum_{m=1}^{N-1} s_m}{\sum_{m=1}^{N-1} r_m} \frac{2}{N-2} \frac{\sum_{m=1}^{N-2} s_m}{\sum_{m=1}^{N-2} r_m} \end{aligned} \quad (31)$$

then by induction

$$y_i = \rho_1 \frac{(i-1)!(N-i)!}{(N-1)!} \prod_{j=2}^i \frac{\sum_{m=1}^{N-(j-1)} s_m}{\sum_{m=1}^{j-1} r_m}, \quad i \geq 2 \quad (32)$$

from the condition $\sum_{n=1}^N y_n$ can be obtained ρ_1

$$1 = \rho_1 + \sum_{i=2}^N \rho_1 \frac{(i-1)!(N-i)!}{(N-1)!} \prod_{j=2}^i \frac{\sum_{m=1}^{N-(j-1)} s_m}{\sum_{m=1}^{j-1} r_m} \quad (33)$$

$$\rho_1 = \left(1 + \sum_{i=2}^N \frac{(i-1)!(N-i)!}{(N-1)!} \prod_{j=2}^i \frac{\sum_{m=1}^{N-(j-1)} s_m}{\sum_{m=1}^{j-1} r_m} \right)^{-1} \quad (34)$$

In the simulation the time of getting the half of population is similar in both situations: the population with discrete value of fitness and with values from a gauss distribution of fitness figure(11).

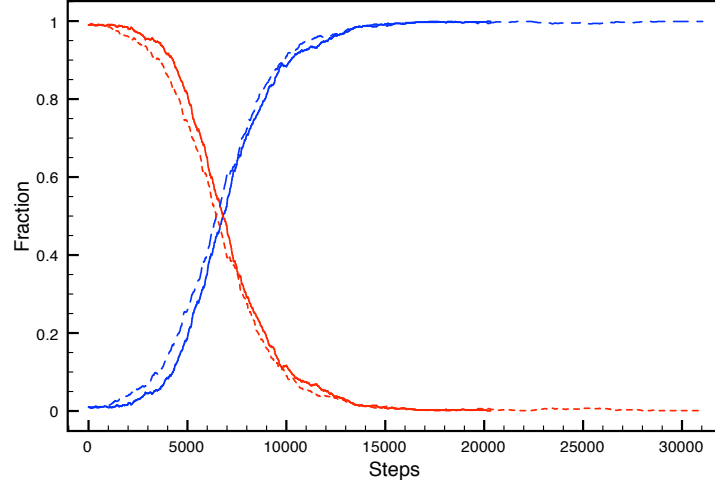


Figure 11: The dashed lines are the population with discrete fitness while the continued lines with gauss distribution fitness. The discrete population has the next parameters $r = 2$ and $s = 1$, and the parameters for the gaussian distribution are $r_{pro} = 2$, $s_{pro} = 1$, $\sigma_r = 0.3$ and $\sigma_s = 0.25$.