



# Adaptation of Mutability in a Computational Evolutionary Model

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## Introduction

Recent computational studies [1-3] have explored the existence of *optimal mutation rates* in evolutionary models. The role of mutation rate in optimizing evolutionary dynamics has already been shown to be critically important in simple experimental organisms [4-7], and is generating increasing interest in light of the ongoing discussion of the "evolution of evolvability" [8]. Here, we investigate whether there exists an optimal maximum mutation size (mutability) in a simple evolutionary model with assortative mating.

## Model

**Environment** – The coordinates of the morphospace, in which our simulated organisms live, are overlaid on a fitness landscape grid, illustrated as the color scale background in Figure 1. The fitness landscape contains discrete values 1-4 which represent the number of offspring a given parent may have. The fitness landscape is generated by assigning a random fitness value to 144 points of a 12x12 grid. Interpolation is then performed within the 12x12 grid to construct a smoother 45x45 grid (2025 points) which is then used in the simulation. Every two generations, the landscape is shifted toward the right so that the last column of the 12x12 grid is removed and a new column is generated along the first column. The interpolation is then performed again.

**Organisms** – The morphospace is initially populated with 300 randomly distributed organisms. In addition to being assigned a position within the morphospace, each organism is assigned a mutability  $\mu$ , selected with uniform probability from the range  $0 < \mu < 1$ .

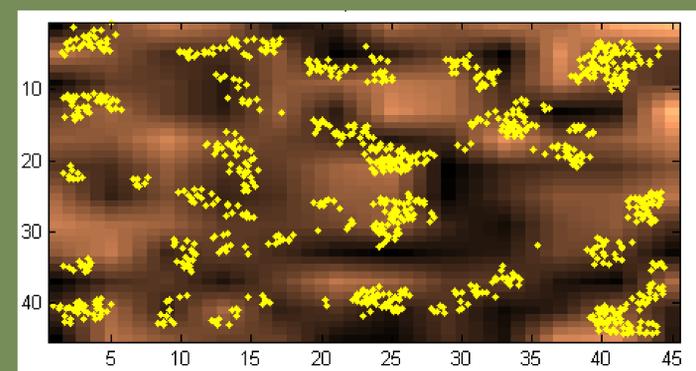


Figure 1: Example of the output of the model. The color scale indicates the fitness landscape, with the darkest regions corresponding to a minimum fitness (one offspring per parent) and the lightest regions corresponding to a maximum fitness (four offspring per parent). Yellow diamonds show the locations of organisms. (From Ref. [9])

**Mating** – Mating between organisms is strictly with the nearest neighbor in morphospace (i.e., an assortative mating scheme). Each organism is selected as a reference organism (RO) once in each generation. The organism mates with its nearest neighbor and produces a number of offspring corresponding to the fitness of the landscape nearest to its location. The offspring are placed according to a uniform random distribution within a region determined by the  $\mu$  value corresponding to the RO parent, as shown in Figure 2. The mutability  $\mu$  thus represents the maximum mutation size available to the offspring. The mutability of the RO is assigned to each of its offspring. After all organisms have been an RO, they are removed, leaving only their offspring for the next generation.

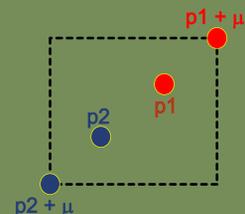


Figure 2: Given two parents,  $p_1$  and  $p_2$ , and with  $\mu$  defined as the mutability of the parent who serves as a reference organism (RO), the offspring will lie at a random location within the outlined region. The mutability assigned to the offspring will be that of the RO parent.

**Overcrowding** – After all the organisms have reproduced, any offspring which occur at a distance less than 0.25 units from any other newly-generated organism are removed.

**Random Removal** – In addition to removal based on overcrowding, the system is further randomized by the removal of a random number of organisms (between 0 and 70% of the existing organisms). The percentage of organisms to be removed is randomly selected at each generation.

**Competition Experiments** – Each simulation was run until either (1) all values of  $\mu$  had become extinct except one surviving value, or (2) the simulation had run for 1000 generations. All simulations were performed on PCs using a custom-written program in MATLAB. All random numbers were generated using the pseudo random number generator, Mersenne Twister.

For a more detailed description of the algorithms used, see [9].

## Results

In 462 of 518 simulations, a single  $\mu$  value achieved fixation before 1000 generations. In the remaining simulations, only two  $\mu$  values survived at generation 1000 in all cases except one, where three  $\mu$  values remained. Thus, stable coexistence of multiple values of  $\mu$  is strongly selected against in this model. An example of the distribution of  $\mu$  values in a typical simulation, over multiple generations, is shown in Figure 3.

While a single value of  $\mu$  typically dominated each simulation, no single value of  $\mu$  was consistently the "winner" from one simulation to the next, as shown in Figure 4. Most simulations reached fixation (survival of a single value of  $\mu$ ) within less than 400 generations (Figure 5).

Figure 6 shows the *time to fixation* as a function of *surviving value of  $\mu$*  (for the 462 runs where a single value of  $\mu$  remained). Larger values of  $\mu$  reach fixation much faster than the smaller values, and values below  $\mu \sim 0.3$  do not survive at all (though see Figure 7). The Spearman rank correlation coefficient was determined between the surviving  $\mu$  value and the time to fixation, giving  $r = -0.9108$ ,  $p < 0.0001$ .

For the 56 simulations which did not achieve fixation by the 1000<sup>th</sup> generation, every simulation had one value of  $\mu$  between 0.2 and 0.35, and another value in the range 0.35 to 1. The distribution of these surviving values of  $\mu$  is shown in Figure 7.

## Discussion and Conclusions

The observation that one value of  $\mu$  typically survives while the others become extinct is not necessarily surprising, since once a value of  $\mu$  becomes extinct, it cannot reappear in the present model. More striking are the observations that higher values of  $\mu$  reach fixation more quickly, and that surviving values of  $\mu$  show a sharp cutoff below  $\mu \sim 0.3$ . These observations may relate to other key features of the model, illustrated in Figures 8 and 9.

Figure 8 shows time to fixation of the descendants of one member of an original population, as a function of  $\mu$ . This simulation was similar to that performed above, but the value of  $\mu$  was held constant for all individuals in each simulation. The time to fixation defined as the first generation when all organisms shared some lineage with an original "labeled" organism. Note the sharp peak just above  $\mu = 0.3$ . For small  $\mu$ , while fixation does occur, the system quickly reaches extinction due to overcrowding (all organisms are related to the "labeled" one, but the entire population dies).

As illustrated in Figure 9, in the model where  $\mu$  is held fixed for all organisms in each simulation, critical phase-transition-like behavior is observed for this range of  $\mu$  values. Here, the number of clusters (which can be considered analogous to the number of species [9]) undergoes a sharp jump for intermediate values of  $\mu$ . Other variables such as the mean population also show sharp transitions for this range of  $\mu$  values (data not shown, see [9]).

Results in [9] suggest that this critical range of  $\mu$  values changes when the constraints of the model are varied, as, for example, when new organisms are randomly generated within the outlined region in Figure 2 according to a normal rather than a uniform distribution. Thus the particular value of the mutability where the critical behavior occurs is dependent on the model.

Finally, comparison of Figures 6 and 7 reveals an unresolved conundrum. The surviving values of  $\mu$  in the simulations where fixation was not reached by generation 1000 include a large proportion of  $\mu$  values below the level of the observed asymptote at  $\mu \sim 0.3$ . Were the simulation allowed to continue for as many generations as needed in order for fixation to be achieved, it is possible that these low  $\mu$  populations would become extinct; their survival would change the asymptotic shape of the curve shown in Figure 6.

Future work will include (1) modifying the model in order to allow values of  $\mu$  to be regenerated, (2) verifying that the observed asymptotic behavior in Figure 6 is maintained in simulations allowed to run for as many generations as necessary in order to achieve fixation, (3) investigating the effect of feedback between the population and the fitness landscape, (4) comparing the asymptotic behavior in the cases where new offspring arise according to a normal rather than a uniform distribution, and (5) characterizing the underlying phase transition behavior in the model.

AS and SB thank their colleague Dr. Nathan Dees for his help in designing the initial version of the model used here.

## References

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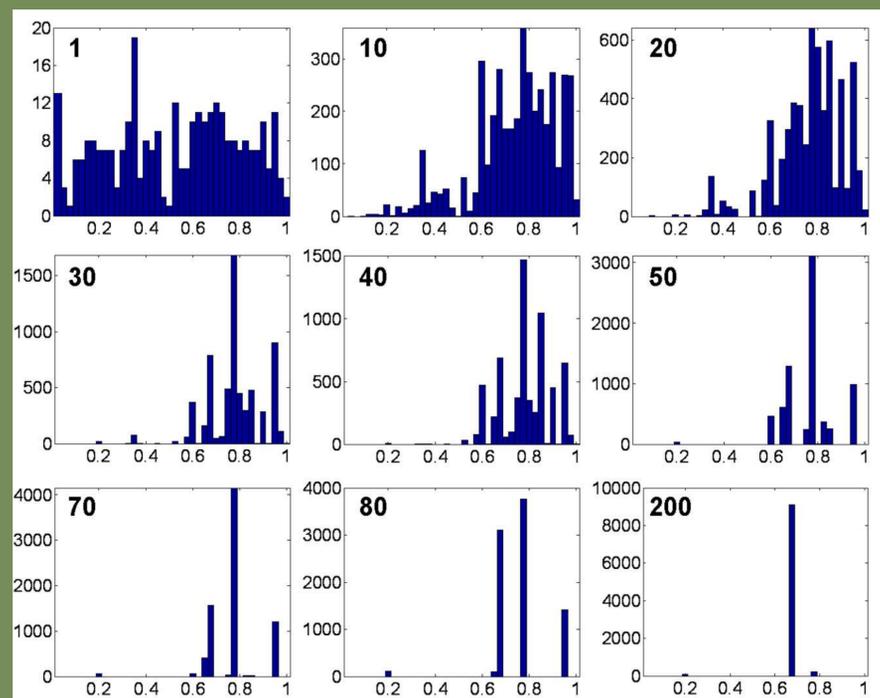


Figure 3: Distribution of values of  $\mu$  in a competition experiment. The generation number is shown in bold face at the top of each histogram. From Ref. [9].

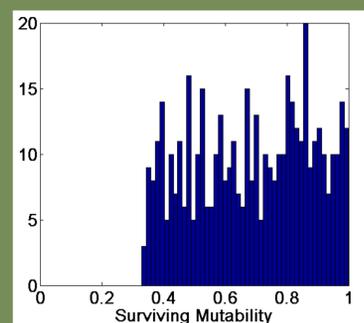


Figure 4: Distribution of surviving values of  $\mu$  for all simulations which reached fixation before 1000 generations.

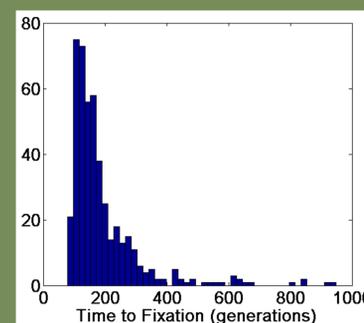


Figure 5: Distribution of times to fixation for all simulations which reached fixation before 1000 generations.

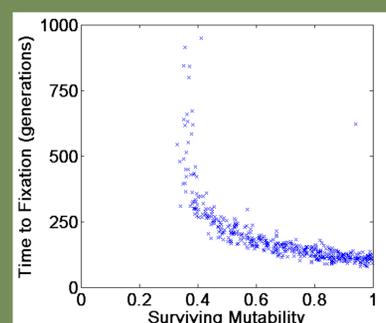


Figure 6: Time to fixation vs. surviving mutability for the 462 simulations which ended before generation 1000.

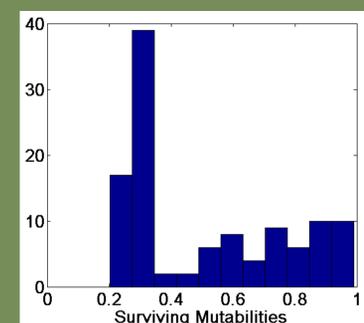


Figure 7: Distribution of surviving mutabilities for the 56 simulations which had multiple mutabilities present at 1000 generations. There are 113 mutabilities counted here.

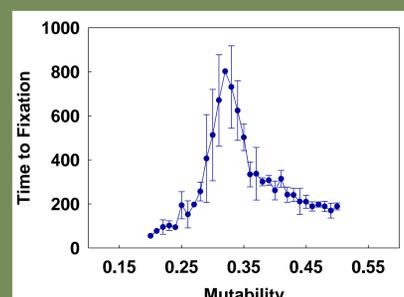


Figure 8: In the non-competing simulations, organisms with mutability in the range  $\mu \sim 0.3$  take the longest time to proliferate throughout the entire population. Error bars show standard deviation over five separate simulations at each value of  $\mu$ .

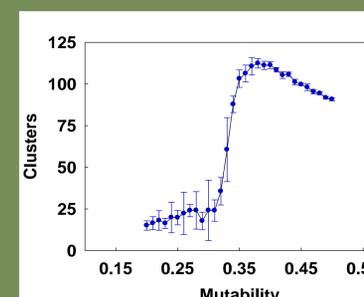


Figure 9: Number of clusters of organisms as a function of mutability in non-competing simulations suggests a phase transition around 0.3. From Ref. [9]. Error bars show standard deviation over five separate simulations at each value of  $\mu$ .