The role of mutation rate in a simple colonization model

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Abstract

We study the effect of mutations in a simple model of colonization, based on Montecarlo simulations. When the population colonizes the whole available habitat, a maximum population density is reached, which depends on the mutation rate. Depending on the values of other parameters, such as selection pressure, fecundity and mobility, there is an optimal value for the mutation rate for which the colonization reaches the highest density. We also investigate the survival probabilities under different conditions and its relation to the mutation rate.

Key words: Population dynamics; evolution; Montecarlo simulation

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1 Introduction

Modeling biological evolution has a long tradition among biologists and applied mathematicians. More recently, the physics community has been attracted to this area because of the rich and complex behavior that arises from these systems, and the possibility to use the available tools from statistical mechanics and computer simulations.

There are many interesting questions that one encounters when dealing with the evolution of populations. Under what conditions can a population successfully colonize a new habitat? What are the factors that most strongly influence this process? Why species do not spread indefinitely into a new territory? Some of the factors that have been studied are the accumulation of harmful mutations (1; 2; 3), selection pressure (4; 5) and changing environment (6; 7), among others.

In this paper we use a model very similar to that recently introduced by Pękalski (8). We study the process of colonization of a habitat by a population initially living on a small region of the habitat. We consider the climate to be spatially varying through this habitat. The individuals are characterized by a single feature, their phenotype, which determines the survival chances by comparison with the ideal conditions imposed by the habitat climate. In this work we are primarily interested in the role played by mutations in the colonization process. We investigate the optimal rate of mutation and its dependence on several model parameters: fecundity, selection pressure, and mobility.
2 Model

The habitat is considered to be a lattice of size $x = 200 \times y = 100$. At most one individual can occupy a lattice site at a given time. The climate is defined by assigning to each lattice site a real number $F(x)$ between 0 and 1. The variation is linear from $x = 0$ to $x = 200$. The adaptation or fitness of a given individual to the environment can be measured by the difference between its phenotype, which is also a single real number $z$ between 0 and 1, and the ideal one, $F(9; 10; 11)$. Following Pękalski (8), the fitness of an individual $i$ at position $x_i$ is calculated as

$$p_i = e^{-\alpha|z_i - F(x_i)|},$$

where $\alpha$ is the selection pressure. The climate $F$ varies from 0 on the leftmost part of the habitat ($x = 0$) to a value of 1 to the right. Individuals are hermaphrodites, thus the only condition for mating is that they are nearest neighbors. Effects of inbreeding are also neglected in this model. The parents die after reproduce. We have not implemented an aging mechanism to keep the model as simple as possible.

The simulation proceeds as follows:

1. An individual $i$ is picked at random.

2. Its survival probability $p_i$ is calculated. A random number $r$ is generated and if $p_i < r$ the individual dies and the process returns to step 1. Otherwise:

3. The individual moves to an adjacent site. If it is occupied, the individual dies and the process returns to step 1. If it is empty then:
4. If no mating partner can be found among the nearest neighbors the individual dies and the process returns to step 1. Otherwise, the couple produces $N$ offspring. Each of them receives a phenotype which is the average of the parents' phenotypes, plus a random mutation rate which can be either positive or negative. This factor is normally smaller than 1 and different for each offspring. In case it happens to be greater than 1, it is set equal to 1. Similarly, if it is less than 0, it is set equal to 0. They are placed at a distance from the parents that must be within a radius given by the mobility parameter. If the site is occupied, the offspring dies.

5. The parents die.

We consider an initial population of $P$ individuals with random phenotypes. They are randomly placed in a $20 \times 20$ square in the center of the lattice, which defines an initial population density. Then we let the population evolve according to the above rules.

3 Results

In Fig. 1 we show the population density at the stationary state as function of the mutation rate for a certain set of parameters. These values have been calculated by letting the initial population of $P = 250$ individuals evolve and colonize the habitat. After the population stabilizes and stops growing, we average the density for a sufficiently long time to obtain the maximum population density. This maximum does not depend on the value of $P$. Instead, the initial population influences the survival probability, as will be seen later. As is well known, the final density depends on the value of the mutation rate.
and this has an optimal value for which the density is maximum. Given the simplicity of the model, we make no attempt here to compare our results with real values for the mutation rate, but rather we want to emphasize the existence of the effect in this model and its dependence on other parameters from a qualitative point of view.

Our simulations have been done by varying the selection pressure from 1 to 3, mobility from 2 to 5 and fecundity from 6 to 8. For each combination of these parameters, a search is made for the value of the mutation rate which maximizes the final density.

Figure 2a shows the optimal mutation rates as function of selection pressure for different fecundities and a mobility value of 3. It can be seen that for higher selection a lower mutation rate is needed in order for the population to attain its maximum density. This is so because at a high selection the individuals can easily die if their fitness is not good enough, so their phenotype must closely match that of the landscape. Once the population has colonized the habitat and the individuals have adjusted their phenotype to that of the local landscape, a large mutation will bring the individual to a point where his fitness is not good enough to survive, so the mutation must be low. This characteristic is independent of the number of offspring and this can be seen in the figure, the three curves for different fecundities almost match.

In figure 2b, the optimal mutation rate as function of selection pressure is shown. Each curve corresponds to a different mobility, and we have averaged the values for different fecundities since as we mentioned above, the dependence on fecundity is negligible. Here we note that for higher mobility, the optimal mutation is larger. This behavior can be explained by noting that a
large mobility means that the offspring can be put at a position which is far from the parents from whom they inherited their phenotype, which in the stationary state is close to the optimal one. Since they are now in a region where the climate is different, their fitness is not good unless a mutation changes the phenotype to a value that matches that of the habitat. The larger the distance between the offspring and the parents, the mutation that is needed will be larger. This can be estimated noting that the change in the optimal phenotype from site to site in the lattice of size $200 \times 100$ is 0.005. Therefore if we increase the mobility by one, the mutation rate must increase by that factor, and indeed the difference between the curves in figure 2b is on the average 0.005.

We now turn attention to the behavior of the maximum density. Figure 3 shows the maximum density obtained at the optimal mutation rate for a mobility of 3 and different fecundities, as function of the selection pressure. As expected, the maximum density increases with fecundity. Selection pressure only plays a minor effect in lowering the maximum density for higher selection. Since this dependence is linear, we take an average over the different values of selection to reduce the number of parameters. In figure 4 we can see the values of maximum density, averaged over the selection, as function of the mobility, for the three different values of fecundity. From these curves we infer that the principal factor affecting the final density is the fecundity.

Another feature that we examine is the initial condition for the system, that is, the survival probability of the initial population and its relation to the model parameters, in particular the influence of the mutation rate.

We start the simulations as before, but now we let the initial population $P$ vary
from 4 to 150 individuals. The simulation stops when all the individuals die or when they have occupied 30% of the available space, when it is considered that the initial population survived at the specified initial density. For each set of the parameters, selection pressure, fecundity and mobility we perform \( 1.5 \times 10^3 \) independent runs in order to obtain a survival probability for the specified set of parameters.

Figure 5 shows the results obtained from the model for a fecundity of 6 and mobility 3. As expected, high selection pressure lowers the survival probability and vice versa. Similarly, the survival probability is higher when the fecundity increases. A similar plot is obtained in this case. In general, small populations have less chances of survival independently of other parameters like selection, as the figure shows. This vulnerability of small populations is a behavior well known to biologists. Actually one can define a minimum viable population, that is, the smallest isolated population having a 99% chance of remaining extant for 1000 years. This concept was originally introduced by Shaffer (12; 13; 14).

In order to better compare different sets of parameters we reduce each of the curves shown to a single point by averaging the survival probability over all initial populations. Figure 6a compares the results for selection pressures from 1 to 3 as function of the mobility and fecundity fixed at 7, and Fig. 6b is analogous but the different curves correspond to different values of fecundity at a fixed selection pressure of 1.5. It is found that an optimal mobility of 3 exists, which is independent of the selection pressure and fecundity. The existence of a maximum can be expected since a low mobility produces overcrowding near the parents and the offspring die because of lack of space in general. On the other hand, if the mobility is too large, the offspring have more difficulty finding a mating partner and also die, therefore, there should be an optimal
value in between.

Now we shall discuss the role played by the mutation rate on these probabilities. All the simulations above were done at the optimal mutation rates for each set of parameters.

Depending on several factors, a population that starts to evolve can be on benign or adverse conditions. By benign conditions we mean large fecundity, small selection pressure and a small difference between the individual’s phenotype $z_i$ and the climate $F(x_i)$.

Our simulations show that if conditions are benign, the mutation rate has a negligible effect on the survival probability. On the contrary, if conditions are adverse, the mutation rate does affect the fate of the initial population.

In figure 7 we show the survival probability as a function of the mutation rate for a population initially at the left, and with a low fertility of 6, thus the individuals must survive in an adverse environment. As can be seen, the survival probability in this case is greater for larger mutation rate, up to a maximum value and then decreases. This can be explained in the following way: if the conditions are adverse, the individuals must adapt (that is, change their phenotype to match the ideal one) as soon as possible before the whole population dies. The only way to do this is by having a large mutation rate. Of course if the mutation is too high the contrary effect is obtained, since harmful mutations become more probable. In contrast, a population that develops under conditions of high fertility and a benign habitat shows a very weak dependence on the mutation rate.

Finally, a phase transition exists with respect to the fecundity. In order to show
that, we modified the fecundity in order to become a continuous variable using a Poisson distribution. In figure 8, the curves for the survival probability as function of time for different fecundities are shown. The central curve which is a straight line represents the critical point of the system, above that value of fecundity all populations survive, and below, all populations disappear. The critical fecundity of course depends on other parameters of the model, and therefore a survival-extinction phase diagram can be constructed as in (6).

4 Conclusions

We have used the model of Pękalski (8) to study the influence of the mutation rate in the colonization process. We found that, even in this simple model, there is an optimal mutation rate for which the final population achieves its maximum density. We also give the dependence of this maximum with the model’s parameters such as mobility, fecundity and selection pressure. We found that the optimal mutation rate is practically independent on the fecundity, decreases when selection pressure increases, and increases approximately linearly with the mobility. Finally, we show that the initial development of the population also depends on the mutation rate. The more adverse the living conditions are, the higher the mutation rate must be in order for the population to adapt quickly before it dies. We want to point out that in this case, if the mutation rate is high and the population survives and colonizes the habitat, it will do it with a non optimal mutation rate, therefore the final density will be lower than the maximum possible one. It would be interesting to study the colonization process under the assumption of a mutation rate that is itself subject to mutation. We are currently working on these issues.
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FIGURE CAPTIONS

Figure 1. Final density as function of the mutation rate using a selection pressure of 3, mobility 2, and fecundity 6.
Figure 2. a) Optimal mutation rate as function of selection pressure. The different curves correspond to fecundities of 6 (solid circles), 7 (open circle) and 8 (asterisks). The mobility has a value of 3. b) Optimal mutation rate as function of selection pressure. The lower curve corresponds to a mobility value of 2, the next one to a mobility of 3, and so on. Here each curve is an average of the curves for different fecundities.

Figure 3. Maximum population density when the whole habitat has been colonized. The curves are for fecundity 6 (solid circles), 7 (open circles), and 8 (open squares). The mobility is set to 3.

Figure 4. Same as figure 3, but averaged over the selection pressure as function of the mobility.

Figure 5. Survival probability plotted as function of the initial population. The leftmost curve is for a selection pressure of 1 and the next ones for values of 1.5, 2, 2.5 and 3 in that order. The mobility is 3 and the fecundity is 6.

Figure 6. a) Averaged survival probability as function of mobility for a fecundity of 7. The uppermost curve corresponds to a selection pressure of 1, and the next ones in descending order are for values of 1.5, 2, 2.5 and 3. b) Same as a) but the different curves are for fecundities of 6 (solid circles), 7 (open circles) and 8 (asterisks). The selection pressure is fixed at 1.5.

Figure 7. Survival probability as function of the mutation rate. The upper curve corresponds to a population that evolves at the center of the habitat, with a fertility of 8 and selection pressure 1 (benign conditions). The lower curve has fertility 6, selection pressure 1.5 and is initially placed at the left of the habitat (adverse conditions).
Figure 8. Survival probability of populations as function of time. The different curves represent fecundities of 5.7, 5.705, 5.71, 5.715 and 5.72, from bottom to top. The central curve (5.71) gives approximately the critical point of the system. A lattice of size $800 \times 400$ has been used and results are averaged over $10^6$ realizations.
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Fig. 6. R. Huerta-Quintanilla and M. Rodríguez-Achach
Fig. 7. R. Huerta-Quintanilla and M. Rodríguez-Achach
Fig. 8. R. Huerta-Quintanilla and M. Rodríguez-Achach