

## Dynamics of populations in a changing environment

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We present an individual-based model of a population that lives in a changing environment. The individuals forming the population are subject to mutations and selection pressure. Using Monte Carlo simulations we have shown that, depending on the values of the mutation rate and selection, the population may reach either an active phase (it will survive) or an absorbing phase (it will become extinct). We have determined that the transition between the two states (phases) is continuous. We have shown that when the selection is weaker the population lives in all available space, while if the selection is stronger, it will move to the regions where the living conditions are better, avoiding those with more difficult conditions. The dependence of the mean time to extinction on the rate of mutations has been determined and discussed.

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### I. INTRODUCTION

Modeling biological evolution already has a long history. Biologists and biologically oriented mathematicians used mostly partial differential equations operating on global variables (see, e.g., [1]). On the other hand, a microscopic approach where individuals are the basic entities has also been considered [2]. It is known that there are several factors that could influence the fate of an evolving population. Among them are (1) accumulation of harmful mutations [3,4], (2) selection pressure [5,6], (3) changing environment [7–9].

Most of the above approaches, except [2], used a mean-field-like, global variables, ignoring individual features of the organisms forming the population.

There are also papers by physicists using an individual-based models to describe the fate of a population under pressure and/or mutations. The colonization process of a neighboring empty niche has been considered in this aspect [10–13]. To the best of our knowledge the question of how a population will react when confronted with a changing climate has not yet been considered within the microscopic approach. Similar problem, using diffusion equations for averaged quantities has been studied in Ref. [7] from a biological point of view while the mean field approach and simulations on global variables were employed in Ref. [14].

Our aim is to determine the fate of a population that initially is adapted to a given environment and then the conditions change for the worse. That may mean either growing skills of predators attacking the population, decreasing supply of food, or climatic changes, such as the coming of the ice age. The changes are irreversible. We want to find out when the population will adapt to the new conditions and when it will try to invade a neighboring empty niche with the old climate. We also want to find out if the role played by the selection pressure and mutation rate are similar. Obviously, we expect that there would be two limit states—the population may either stay alive or become extinct. It would be interesting to know what can be learned about the nature of such a transition.

### II. MODEL

We consider a population composed at time  $t$  of  $N(t)$  individuals. The individuals live in a habitat that has the form of a square lattice of dimensions  $L_x$  along the  $X$  axis and  $L_y$  along the  $Y$  axis. The lattice is divided into three equal parts (denoted regions I, II, and III afterwards), perpendicular to the  $X$  axis. A site could be either empty or occupied by only one individual.

An individual is characterized by its position on the lattice  $\mathbf{j}$  and by its genotype  $g_j$  that is a double string (of 32 positions) of 0's and 1's. It could have the form

$$g_j = \begin{cases} 0010110 \dots \\ 0101101 \dots \end{cases}$$

We have decided on using one pair of homologous chromosomes, since increasing their number with the same number of loci in the genome and the same recombination rate per chromosome would increase the overall, already very high, recombination rate. It could not produce any effect of linkage. It should be noted that in the model one recombination per generation equals one recombination per 32 loci. Some linkage disequilibrium effects were obtained also in Ref. [15] for a single pair of chromosomes and the recombination rate equal, not 1 per generation but 0.001.

From the genotype the phenotype  $f_j$  of the individual is constructed, as a single string (vector) of the same length, according to the following rule. For each position (locus) of the genotype the product of the two values is taken and the result is put at the corresponding place of the phenotype. In biological terms it means that 0 corresponds to a dominant, and 1 to a recessive allele,

$$(00), (01), (10) \rightarrow 0, \quad (11) \rightarrow 1. \quad (1)$$

Hence the phenotype corresponding to the genotype presented above would be

$$f_j = \{0000100 \dots\}. \quad (2)$$

Moreover, each individual is also characterized by its age  $a_j$  which at birth is set equal to 1 and is increased during the simulations (see below). This feature makes the model more

realistic by diminishing the survival probability of an individual with its age and also by eliminating perfectly adapted individuals, who otherwise could live forever and eventually dominate the population.

In constructing our model we aimed for maximum simplicity, within the class describing population dynamics with recombination and phenotype following from the genotype. Suggestions for this type of models were given in Ref. [2]. However in almost all biology papers describing evolution, individuals are characterized simply by their phenotypes.

The algorithm governing the dynamics of our system has the following structure.

- (1) Chose an individual, for example on a site  $\mathbf{j}$ .
- (2) Calculate its survival probability  $p_{\mathbf{j}}$  according to the rule

$$p_{\mathbf{j}} = \exp(-s \cdot a_{\mathbf{j}}/z_{\mathbf{j}}), \quad (3)$$

where  $s$  is a parameter characterizing the selection pressure and  $z_{\mathbf{j}}$  is the fitness of the  $\mathbf{j}$  individual, defined as the agreement between the optimal phenotype (“climate”)  $\mathbf{F}$  and the individual’s phenotype

$$z_{\mathbf{j}} = \frac{1}{32} \sum_{i=1}^{32} [1 - (f_{\mathbf{j}}^i - F^i)^2]. \quad (4)$$

Hence  $z_{\mathbf{j}} \in [0,1]$ . Survival probability defined by Eq. (3) increases with the individual’s fitness but goes down with increasing age and the selection pressure. Since the exact form of the survival probability is not known, exponential or Gaussian dependence on the selection is quite often used by biologists (see, e.g., [5]). It should be noted that the results do not depend quantitatively on the form of the survival probability.

The notion of the optimal phenotype has been known for a long time [2] and it represents here a vector of 32 components taking values equal to either 0 or 1.

- (3) A random number  $r_{\mathbf{j}}$  is chosen. If  $r_{\mathbf{j}} \leq p$  the individual lives; otherwise it is removed from the system and the procedure goes back to 1.

(4) If the individual’s age is greater than 1, it may breed. To do so it must go through the steps listed below

- (5) Find an empty place in the von Neumann neighborhood [16]. On a square lattice used here, it means in the four principal directions N,E,S,W. Only one such search is made (blind ant rule).

(6) After moving to the new place, find a partner in the von Neumann neighborhood of the new position.

(7) The two produce at most four offspring. Each of them receives its own genotype constructed through recombination and formation of two gametes from each parent (genetic shuffling). The process may be described as follows. The two strings of a parent’s genotype are cut at a random place. The resulting four pieces are glued across, forming two gametes. The same is done for the second parent. From each parent one gamete is chosen randomly, thus forming two strings for the genotype of the offspring.

(8) On each site of the chosen gametes a harmful mutation may take place with probability  $p_{mut}$ . This means that if at a given site (locus in biological terms) the value agrees with the value at the corresponding site of the optimal phenotype, it may be changed with that probability. If the value is different from that of the optimal phenotype, no action is taken. Each progeny receives its genotype independently.

(9) From the genotype a phenotype is produced along the lines described above.

(10) For each offspring a search for an empty place is made in the Moore neighborhood [16] of the first parent. On a square lattice it means eight sites, N,NE,E,SE,S,SW,W,NW. If the place is found, the offspring is put there; if not, it lost its chance and is not born.

(11) After choosing as many first parents as there are individuals in the population at that time, one Monte Carlo step (MCS) has been made and the age of all individuals is increased by one.

At the beginning of simulations the optimal phenotype is the same in all three regions and is the most favorable, i.e., it is a string of zeros only (zero is a dominant allele). The initial population is random, i.e., it has random genotypes and the spatial distribution is random, too, but restricted to the first region only, with a given initial concentration. We have checked that if that concentration is above a certain level (about 0.05) its precise value is unimportant, since the population very quickly (about 50 MCS) reaches the same value of about 0.6 and then follows its evolution, depending on the values of the parameters. Regions II and III are empty. The values of the selection pressure  $s$  and mutation rate  $p_{mut}$  are fixed. We let the population adapt to the existing conditions and then we change the optimal phenotype (climate) as follows. At the first change, after 200 MCS after the adaptation, the values at two, randomly chosen, sites in the optimal phenotype in the first region are changed from 0 to 1. Since a zero in the individual’s phenotype can be obtained from three combinations of alleles in the genotype, i.e., (00), (01), and (10), a change from 0 to 1 in the optimal phenotype means that there are less sites in the genotypes that satisfy this condition. One may, therefore, say that the living conditions turned worse. At the second change, which also occurred after 200 MCS, the optimal phenotype in the first region is again changed in the same way, i.e., at two randomly chosen sites, zeros were switched for ones. Now, however, also the optimal phenotype in the second region has been changed. We simply adopted here the previous (changed) optimum phenotype of region I. One may see it as a gradual moving, from the left, of a colder climate. Finally, once again after 200 MCS the climate is changed. Two more sites in the optimal phenotype in region I are switched from 0 to 1, thus it now contains six sites with value 1 and twenty six sites with value 0. In region II the optimal phenotype contains four sites with value 1, and in region III it contains just two sites with values equal to 1. Since the average age of an individual in our simulations oscillates around 3.5 MCS—the changes are made after about 100 generations. We consider here a system with overlapping generations.

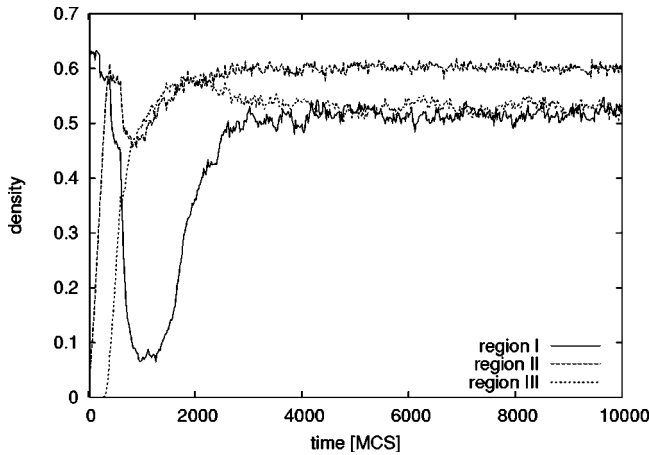


FIG. 1. Colonization of the three regions under the most favorable conditions  $s=0.065$ ,  $p_{mut}=0.001$ . Full line, density of the population in the first region; dashed line, density in the second region; and dotted line, density in the third region.

Although in our model there is no force pushing the individuals into regions II and III, it is not a simple colonization of empty territories. An individual adapted to the climate in the first region finds, after the conditions have changed, a better chance of survival if it follows the climate, hence if it moves into the II or III region. In such a way, region I becomes depopulated. A simple invasion process occurs in our model when the climatic changes are negligible. Then the density in the first region remains approximately the same as in the other two.

For simulations we have used a lattice of the following dimensions,  $L_x=150$ , hence each region was 50 lattice sites long,  $L_y=1000$ . We have checked that increasing the value of  $L_x$  did not change the results, while increasing  $L_y$  led to very long simulations with only slightly better statistics. Typically we let a population evolve for  $5 \times 10^4 - 10^5$  MCS.

### III. RESULTS AND DISCUSSION

In Figs. 1, 2, and 3 we show time dependencies of the densities in the three regions at a given time for a given

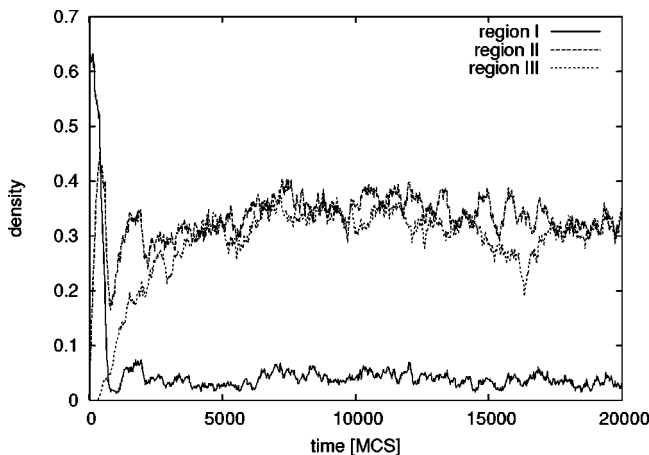


FIG. 2. As in Fig. 1 except that mutation rate is increased to  $p_{mut}=0.003$ .

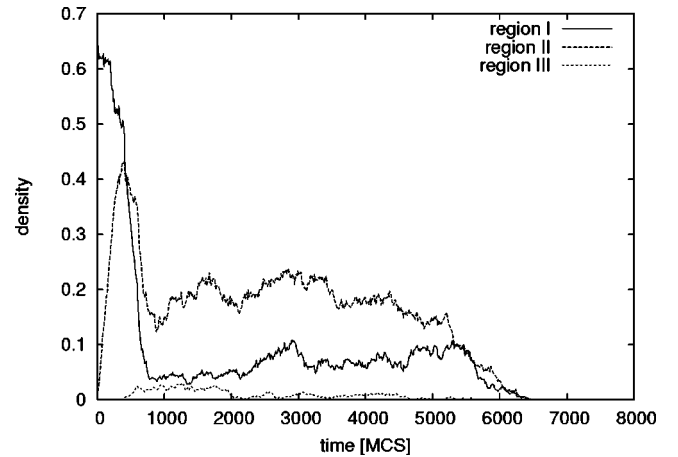


FIG. 3. As in Fig. 1 for still higher mutation rate  $p_{mut}=0.004$ . The population became extinct after 6480 MCS.

value of the selection pressure and mutation rate. There are three possible outcomes. In Fig. 1, where the mutation rate is low, the population survives and colonizes all three regions with similar densities. In Fig. 2, although the population also survives, the mutation rate is so high that life in region I becomes difficult. Hence the population moves to more friendly regions II and III, with only very few individuals remaining in region I. Both cases correspond to the active state. In Fig. 3 the population becomes, after some time, extinct. This is the absorbing state. The fitness of the individuals in the three regions rises very quickly to about 0.8 and remains at that level. We present the results obtained when the mutation rate is changed. Similar curves are produced when the mutation rate is kept constant and the selection pressure is varied. One may note that there is a minimum for the density dependence in the first and second region, hence obviously also in the average value, at around 900 MCS. The minimum seems not to depend on the value of the mutation rate. It does depend, however, on the selection pressure and if it is weak, it disappears. The minimum indicates migration of the population from the first and second regions. If the living conditions in region I are not too difficult, the population will recolonize it and the density will grow there to about 0.5. This is the case illustrated in Figs. 4, where the density dependence on time and some “snapshots,” showing the spatial location of the population, are presented. For better presentation the data were obtained for a smaller system with  $L_y=200$ . If the conditions in region I are difficult (as in Fig. 2), only the border zone between regions I and II is populated and the density in region I remains low.

We have performed a series of simulations keeping either the selection pressure or mutation rate fixed and changing the other parameter. We have found that in each case, for some values of the varying parameter, the population arrived at an active state, while for others it became extinct. Far away from the critical point, i.e., the lowest value of the parameter that was changed (selection or mutation rate) and for which the populations died, average density stabilized pretty quickly. The closer the system was to the critical point, the more the density fluctuated. The fact is well known to biolo-

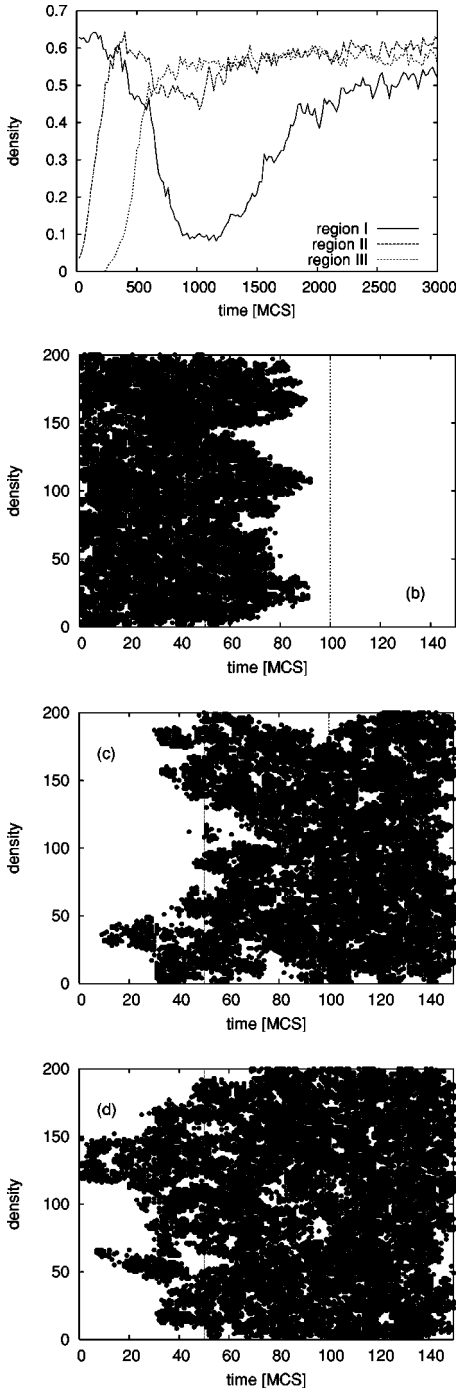


FIG. 4. Density dependence on time (a). Spatial distribution of the population after 160 MCS (b), 1000 MCS (c), 15 000 MCS (d).

gists as a demographic stochasticity, affecting populations of small sizes [4]. Close to the critical point our populations are indeed very small. From the obtained results we have plotted Figs. 5 and 6, which show the final average density of the population as a function of the selection pressure and mutation rate, respectively.

One may easily notice that both show a sharp transition into the absorbing state. To elucidate the nature of the phase transition we have looked for a possible hysteresis in crossing the transition point [17]. Since we have not found such a

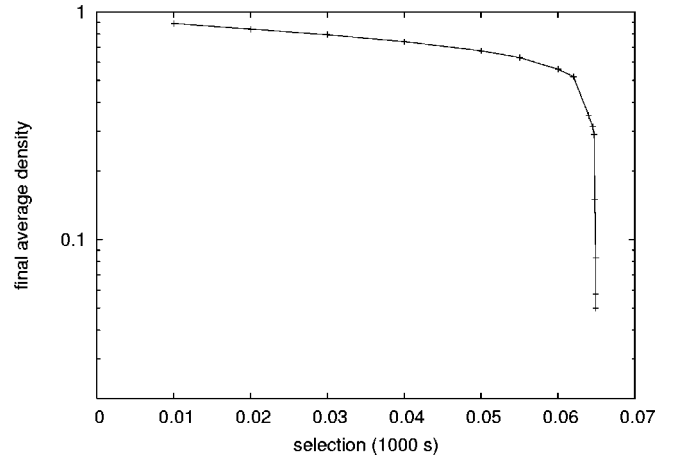


FIG. 5. Asymptotic average density of the population as a function of the selection pressure on the log-normal scale. The mutation rate is  $p_{mut} = 0.0035$ .

hysteresis, we conclude that the transition to the absorbing state is continuous.

We defined the average density,  $\rho_{av}$ , as the total number of individuals living at a given time in all three regions, divided by the available space (number of lattice sites). We have found that after 10 000 MCS the average density depends on the reduced selection  $\Delta s = (s_c - s)/s_c$ , where  $s_c$  is the critical value of the selection pressure, in a power law form

$$\rho_{av} \sim (\Delta s)^\beta. \quad (5)$$

A good fit is obtained for  $0.001 < \Delta s < 0.1$  with  $s_c = 0.0651$  and  $\beta = 0.265 \pm 0.005$ . No such power law was found for the dependence of the average density on the mutation rate.

Examining the final, quasistationary, states obtained from the time dependencies of the density of the populations, we can construct a phase diagram in the (*selection, mutation rate*) plane, presented in Fig. 7. The diagram shows a critical line separating the alive (active) and extinct (absorbing)

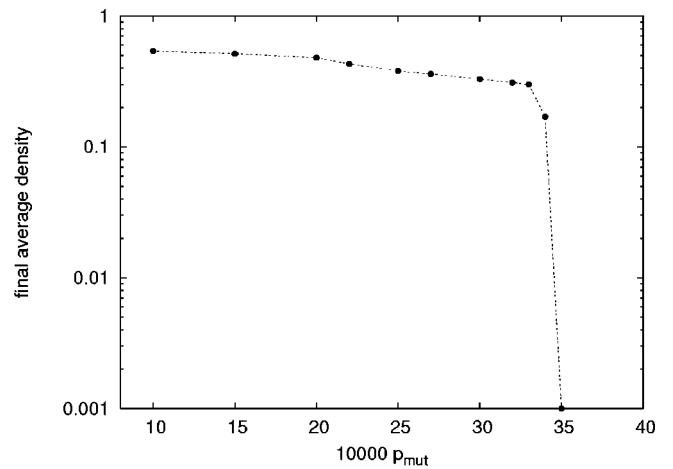


FIG. 6. Asymptotic average density of the population as a function of the mutation rate on the log-normal scale. The selection pressure is  $s = 0.065$ .



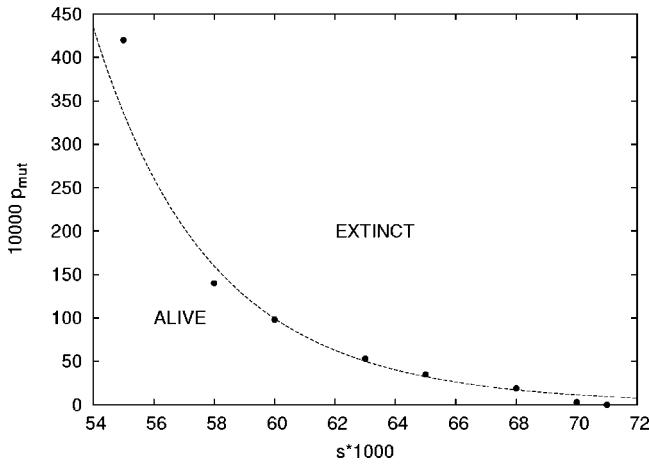


FIG. 7. Phase diagram in the (*selection, mutation*) plane. The line is a guide to the eye only.

phases. The line is not symmetric, since the role played by the two parameters is not equal. Selection acts in the same way in all three regions, while mutation rate affects individuals differently. First of all, if a mutation (there are only harmful mutations) occurred for an individual in region II, then if it migrates to either region I or III, the mutation may turn beneficial, because of different optimal phenotypes there. Next, a mutation changes only one allele in the genotype, and for having an effect on the phenotype, also the second allele at the same locus (site on the genotype) has to be “wrong.” In biological terms it means that if a harmful mutation is to affect the phenotype it has to occur in a heterozygote (different alleles in the same site) at that locus. Third, there is a genetic shuffling, meaning that progeny receive genotypes of the parents changed in the process of recombination.

In many biology papers (see, e.g., [3,4,6]) the average time to extinction is considered. In most cases the parameters are the reproduction rate (number of offspring) and the size of the carrying capacity of the habitat (maximum number of individuals who can live there at the same time). Here we have found that the dependence of the average time of extinction on the mutation rate can be fitted into a dependence  $\langle t_{ext} \rangle \approx p_{mut}^\alpha$ . Since, however, the data covers a rather narrow range, it would be difficult to claim that we have here a true power law.

As seen from Fig. 8, we obtained different slopes for lower selection pressures and a single slope for higher selections. This could be explained in the following way. For strong selection the population has really no chance to develop and changing the mutation rate has no marked effect. Any individual that is not well fit has a very low chance of survival. Therefore, the time to extinction increases with growing mutation rate in more or less the same way. If the selection is weaker, then it matters whether the mutation rate is low or high. If it is low, the population has enough time to grow, since at the beginning there are few mutations. Afterwards the mutations accumulate and the population dies. This behavior is reflected as the upper part of the  $t_{ext}$  vs  $p_{mut}$  curve. If the mutation rate is high, then the population very quickly acquires enough mutations and behaves similarly to

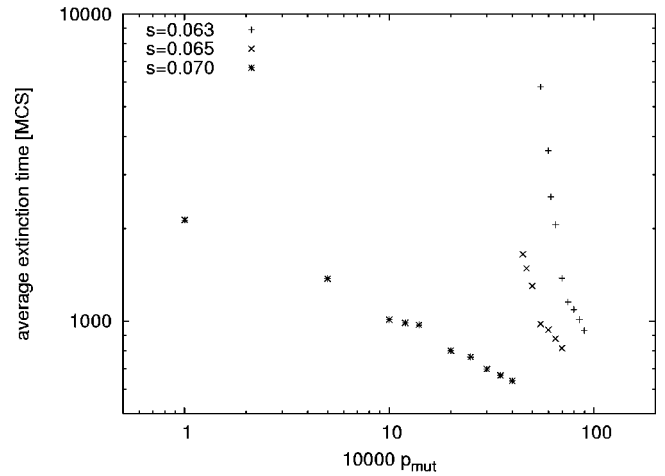


FIG. 8. Average extinction time versus mutation rate on the log-log scale, for several values of the selection pressure.

the case of strong selection, and this is the lower part of the  $t_{ext}$  vs  $p_{mut}$  dependence. A similar kind of dependence of the average extinction time on the selection and mutation could be deduced from the data presented in Ref. [4].

It should be noted that the role of the selection pressure is realized in our model via the survival probability of an individual, and since it depends explicitly on its fitness, it is impossible to describe the model in terms of global variables.

Because in order to produce offspring an individual has to move, find a partner, and find the place for the progeny, there is no need to introduce outside restrictions on the population growth, such as the Verhulst factor, see, e.g., Ref. [1].

We have presented a microscopic model describing the behavior of a population under selection pressure and mutational load living in a changing environment. The population is confronted with a choice: either adapt to new conditions or follow the climate and colonize new territories. We have found that if the selection pressure is not high, the population will spread with similar densities all over the three regions. With increasing selection pressure and rate of mutations the first region will become depleted and regions II and III will contain most of the population, with a slight preference for region II, since there will be immigrants from regions I and III. Finally, if the selection pressure is very strong, the population will die out. In the model the role of the selection pressure seems to be more important because of its global character. We have constructed the phase diagram of the final states of the evolving population—an active state (living population) or an absorbing state (extinct population). We have shown that the transition between the two states is continuous. The dependence of the average time to extinction on the mutation rate shows two different regimes.

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