

Role of evolution by natural selection in population dynamics

Michel Droz¹ and Andrzej Pękalski²

¹*Institut de Physique Théorique, Université de Genève, quai Ernest Ansermet 24, 1211 Genève 4, Switzerland*

²*Institute of Theoretical Physics, University of Wrocław, plac Maxa Borna 9, 50-204 Wrocław, Poland*

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Using a Monte Carlo approach we study the role of inheritance and natural selection in the dynamics of populations. We show that a population subject to inheritance has a much better chance of survival in a given condition than a population where new generations do not inherit genomes of their parents. The dependence of the survival chance on such factors as selection pressure, fecundity, or carrying capacity of the system is much stronger when selection and inheritance are present. We demonstrate, in accordance with biological observations, that in certain conditions evolution can save a population which would perish without it.

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I. INTRODUCTION

Biological population dynamics became in recent years the object of many studies as well by evolutionary biologists [1–3] as by physicists [4–8]. Tools developed to study dynamics of extended systems, nonequilibrium statistical physics as well as optimization problems (genetic algorithms), provide new ways to approach such problems. Biological population dynamics has many interesting, and still not solved, problems such as conditions for a successful colonization [3,9–11], pattern formation [12,13], or changes in the genotype space [14]. Another problem, which attracted much attention by biologists [1,2,15] but much less by physicists, is the determination of the stability, or extinction time, of a population either in stable or in changing environment [8,16,17].

The conditions when a population may stay alive depend, in general, on such factors as the genetic diversity of the population [18], climate and the rate of its change [19], selection pressure [2], mutation rate [20], the availability of resources often related to the carrying capacity of the system [2], average fertility and dispersion rate [21]. It would be useless to include all those factors into a model, hence the necessity to choose just a few, which are considered most interesting for the investigated problem. There are also many possible approaches to describe dynamics of a population—analytic ones, using most often difference or differential equations of the Lotka - Volterra type, or numerical simulations via either Monte Carlo or cellular automaton technique. Each of the approaches has its own merits and drawbacks, as discussed, in a biological context in Ref. [22,23]. There is still another important problem which received virtually no attention of physicists, namely, the role of natural selection and inheritance in preserving a population. The problem has been studied, in general terms, by evolutionary biologists [1,24]. As could be expected, evolution plays a crucial role in determination of the fate of a population. If there would be no evolution then the average fitness of the population would remain constant in time [1]. In an evolutionary process there is natural selection and inheritance of better genomes to the offspring which increases mean fitness [25].

Shaffer [22] explained that there are four major factors influencing possible extinction of a population—

demographic stochasticity, environmental stochasticity, genetic stochasticity, and natural catastrophes. Demographic stochasticity is the risk coming from events happening to particular members of the population, such as unexpected death and infertility. It is especially important for small populations. In this context quite often the notion of *minimum viable population* is introduced [22] as the smallest population which has a given chance of remaining alive after a given period of time. Since, however, both limits are quite arbitrary, the notion is not very helpful. Environmental stochasticity relates to all random changes in such factors as availability of food, density of predators, and climatic changes. Big scale changes in the habitat fall into the natural catastrophes category. Genetic stochasticity is random changes at the genetic level. It is quite difficult in field studies to determine the role played by each factor in driving a particular population to extinction, as shown by the example of the extinction of the heath hen quoted by Shaffer [22].

In this paper we study the role of inheritance in populations under selection on the survival chance for a population, when the habitat remains constant, both in time and in space. Situation when there is no inheritance we shall call in the following *without evolution*, since the genetic pool at each generation is random and constant in time. We shall study two scenarios—one in which the traits of the parents are passed on to the progeny (*evolution case*) and the second in which there is no heredity (*no evolution*). A population changing in time without heredity is of course rather difficult to find in nature, but one possible realization could be a population in which selection kills phenocopies, which are independent of the genotypes. Selection eliminates worse phenocopies, but that does not change the genetic pool.

The following parameters characterizing the model will be changed—carrying capacity of the system, selection pressure, and fecundity. We shall show that when the evolution is acting, a population has a much better chance to stay alive, and that the chosen variables play important roles in preserving a population from extinction. We shall use Monte Carlo simulations.

II. MODEL

We consider a square lattice of linear dimensions $L \times L$, on sites of which a population composed at time t of $N(t)$

individuals is located. An individual i is characterized by its position on the lattice and its trait (a phenotype) $z_i \in [0, 1]$. One lattice site may be either empty or occupied by at most one individual. The lattice has rigid boundaries, hence any attempt to move an individual outside those borders is unsuccessful. All external factors, such as climatic conditions, density of predators, and prey, influencing an individual are summarized in the optimum $F \in [0, 1]$ [19,21], which in general could change in time and in space. For simplicity we shall consider an environment constant in space and time. The agreement of the individual's trait with the optimum determines the fitness of the individual [21], hence the individual's probability of survival [2] is

$$p_i = \exp[-(z_i - F)^2 s], \quad (1)$$

where s is the selection pressure. Fitness is maximized when $z_i = F$. The individuals may breed, but to do so an individual must first of all move to an empty nearest neighboring site. If there is no such site, no reproduction is possible. After moving the individual must find a partner in the neighborhood of its new position. We do not distinguish sexes in our model, yet a pair of individuals is needed for breeding, like in the simulation model in Ref. [2]. A pair of parents produces at most B offspring (fertility rate), which are located inside a given distance R from the first parent. The fertility rate in our model does not depend either on time or on space. However the number of surviving progeny, as will be explained below, depends on local conditions. When evolution is acting on offspring k receives a trait which is an average of the traits of both parents (i and j) changed slightly due to mutations,

$$z_k = 0.5(z_i + z_j) + r_k m, \quad (2)$$

where r_k is a random number $\in (-1, +1)$ and m is the mutation rate. Hence each progeny resembles both parents, yet it is slightly different. Equation (2) describes the inheritance for an additive quantitative trait (no dominance, epistasis) [27]. Natural selection may increase mean fitness, i.e., lower the average distance between an individual's trait and the optimum. In the absence of genetic variation the trait value is determined solely by random events during development (developmental noise), which we implement by setting the trait of each offspring to an independent random number r_k ,

$$z_k = r_k, \quad (3)$$

taken from a uniform distribution.

The introduced conditions necessary for breeding eliminate the need for an extra factor, such as the Verhulst factor [26], which controls, otherwise unbounded, growth of the population. We shall use the Monte Carlo simulations with the following algorithm. Suppose that at time t there was $N(t)$ individuals in the population, then we have the following.

- (1) An individual j is randomly chosen.
- (2) Its survival chances are calculated from Eq. (1). A random number r_j is generated from a uniform distribution. If $r_j > p_j$ then the individual is removed from the system, and

the program returns to step (1). In order to breed the following steps have to be realized. Otherwise the program returns to the beginning.

- (3) One random search is made in the nearest neighborhood of the chosen individual to find an empty place. If found, the individual is moved there.

(4) One random search is made in the neighborhood of the new position of the individual for a partner. If successful, the pair produces B offspring. For each of them independently one random search is made in a square neighborhood of side $2R+1$ centered at the location of the first parent to find an empty place for the offspring. If found, the progeny receives its trait as calculated from Eq. (2), or Eq. (3), depending on whether the population is subject to evolution or not, and is put there. If the search was not successful, the offspring lost its chance and was not born.

- (5) After picking up $N(t)$ individuals as first partners one Monte Carlo step (MCS) was completed, or alternatively one time unit passed.

To keep the number of parameters at a minimum, we set constant the side of the square around the first partner into which the progeny may be put, at $2R=2$. The initial value of the concentration was set at $c(0)=0.6$. Precise value of the initial concentration, as long as it is not too low, i.e., it does not fall below 0.2, does not play an important role. If the initial concentration, or more precisely, the number of individuals is too low, the population falls below a threshold value where stochastic fluctuations (demographic stochasticity) may lead to its extinction. This is known in population biology as the minimum viable population [22], although it should be stressed that the values taken by biologists as the limit ones are quite arbitrary. In our case it means that if the initial number of individuals is low, and corresponds to about $c(0)=0.2$, the chance that the population will become extinct after just 10–20 MCS increases significantly. The mutation rate was chosen to be $m=0.01$, which is consistent with biological data. Should we take a much larger value, the effect of evolution will be lost, since the progeny traits will be quite different from the parents' ones. Reducing the mutation rate to zero will finally lead to a homogeneous genetic pool. Maximum time of simulations was chosen so as to reach a stationary state. For most of the cases 2000 MCS was enough. Statistical averages from over 10^3 runs to 10^4 for small lattices were performed.

III. RESULTS

Since the optimum is constant in our model, we set it at $F=0$, like in biological papers [1]. We shall investigate the dependence of the extinction time on the carrying capacity of the system (size of the lattice), fertility, and selection pressure. In each case we shall compare the behavior of a population subject to evolution and without it. The extinction time is determined as a time at which there is just one individual left in the system. Since for reproduction two individuals are needed, such a population is doomed. Instead of averaging the extinction time, as is usually done by biologists [2], we shall record the most probable time to extinction, determined

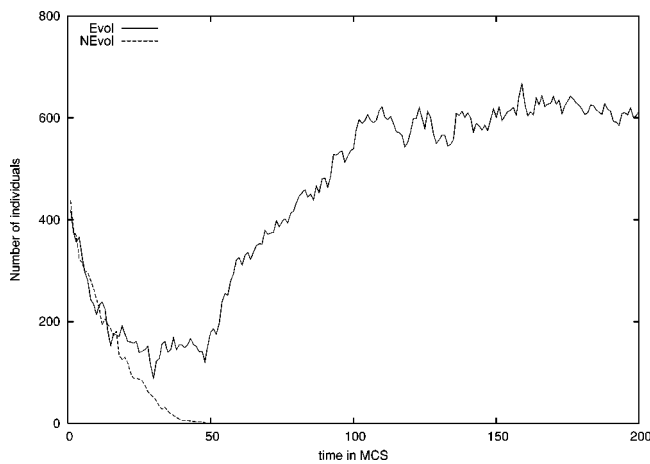


FIG. 1. Number of individuals in a population vs time (in Monte Carlo steps) with and without evolution and with identical initial conditions. Selection pressure $s=2$, carrying capacity $K=900$, and fecundity $B=30$.

as the maximum in the distribution of the extinction times obtained for all simulations. This time is a well-defined quantity not influenced by large but rare statistical fluctuations (presence of very long tails in the distribution). Apart from the extinction time we measure also the survival chance for a population, defined as the number of populations which started from the same initial conditions (same initial density, same fecundity, selection pressure, and lattice size) and survived till the end of simulations, divided by the total number of runs.

In Fig. 1 we present, taken in a single run, the time dependence of the number of individuals in a population in the cases with and without evolution. The values of the selection pressure ($s=2.0$) and carrying capacity ($K=900$) are intermediate. The initial spatial distribution of individuals as well as the values of their traits are identical in the two presented cases. As could be easily seen, the time around 50 MCS is critical for both populations. However only evolution can save the population. This kind of behavior has been also found, using different type of considerations, by biologists [1].

In Fig. 2 we present the dependence of the most probable time to extinction, t_{ext} , on the carrying capacity K for the cases with and without evolution. The dependence has a similar character, and the curves could be fitted by a power-type dependence,

$$t_{ext} = a + bK^c, \quad (4)$$

where the exponent c has two values—slightly larger $c_1 \approx 0.56$ for a larger system and slightly smaller $c_2 \approx 0.45$ for a smaller system. The effect of the demographic stochasticity is not evident here, but it shows better in Fig. 3, where the survival chance is plotted against K . Here heredity leads to several times larger chance of survival for populations with evolution. If there is no evolution then even increasing the size of the system does not help. For the case with evolution there are two distinct regions—below and above $K=900$. Below it demographic stochasticity is clearly seen. For small

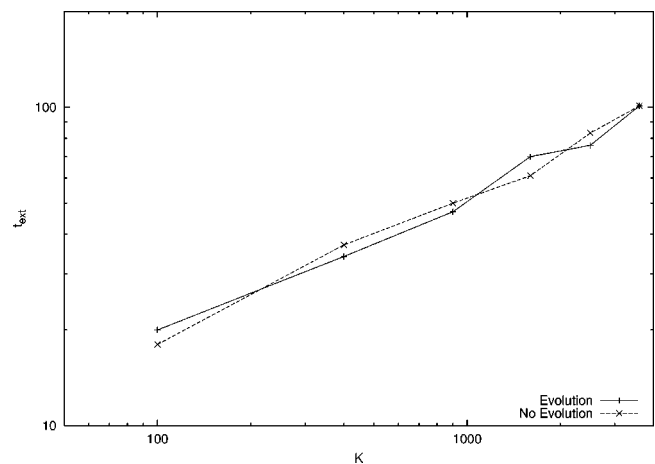


FIG. 2. The most probable time to extinction t_{ext} vs carrying capacity K on a log-log scale. $B=30$, and $s=1.67$.

systems, composed of relatively few individuals, the survival chance drops drastically with decreasing size of the habitat. Even small fluctuations in the number of individuals could have dramatic effects on the whole population. The same effect is also visible, although on a smaller scale, in Fig. 2.

A different behavior of populations living on a small and large systems is reflected also in the distribution of the extinction time, as shown in Figs. 4(a) (with evolution) and 4(b) (without it). For small systems most of the extinctions happen before 50 MCS. For large systems no extinction has been observed till 50 MCS. Therefore not only the maximum of the distribution (the most probable time to extinction) moves with the size of the system but the smallest extinction time moves as well. Small populations, with or without evolution, not only die more often but they also die faster.

Figure 5 presents the dependence of the most probable time to extinction on the selection pressure s . It decreases exponentially as a function of s , independent of whether evolution is acting or not. The behavior of the survival chance as a function of selection pressure has a more complex character (Fig. 6), exhibiting once again two different regimes—for

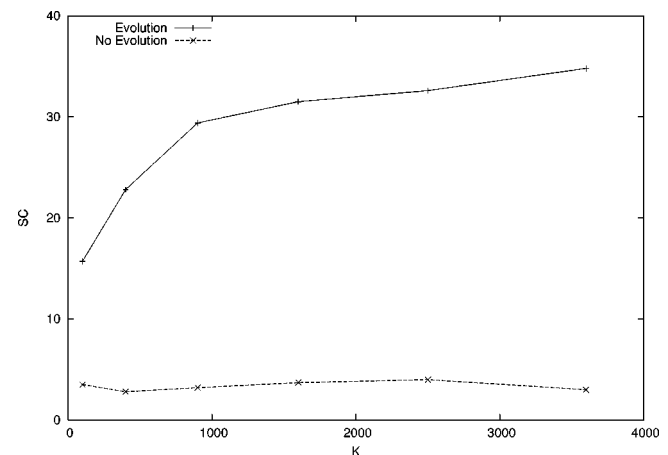


FIG. 3. Survival chance (SC), vs carrying capacity K for populations with and without evolution. Simulation time 2000 MCS. Same values of B and s as in Fig. 2.

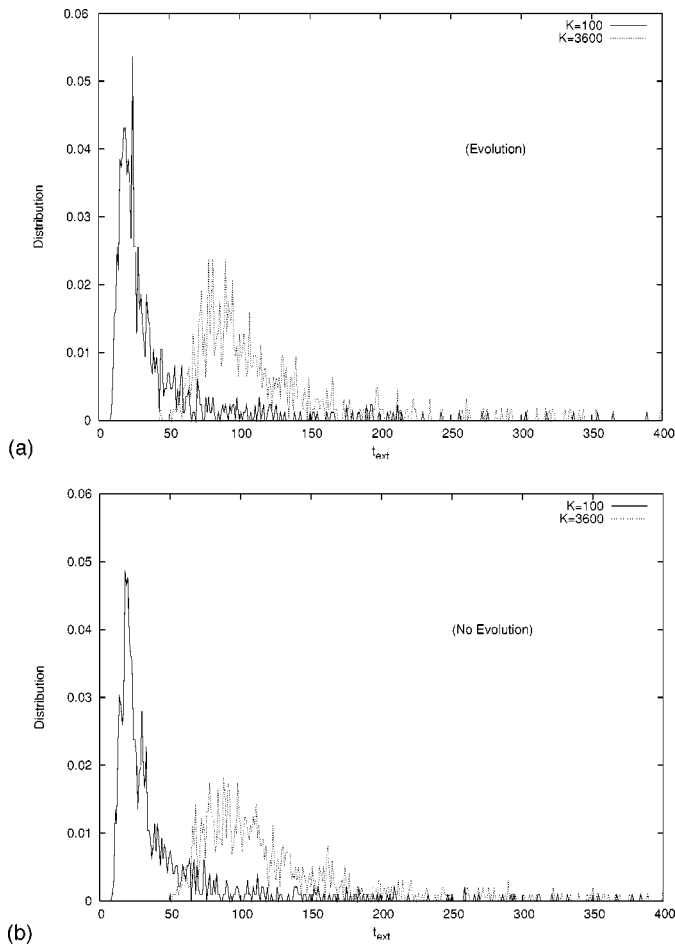


FIG. 4. (a) Distribution of the most probable time to extinction for 1000 independent runs, each till 2000 MCS with evolution. Same values of B and s as in Fig. 2 and 3. (b) The same as in (a), but without evolution.

strong and weak selection, separated by a transition period. For strong selection the increase of the extinction time with diminishing selection is rather slow and the difference between the evolution and no evolution cases is small. At the

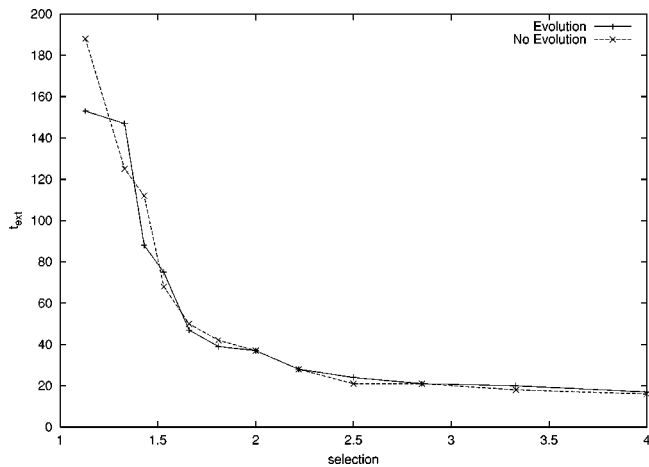


FIG. 5. The most probable time to extinction as a function of selection for dynamics with and without evolution. $K=900$, $B=30$.

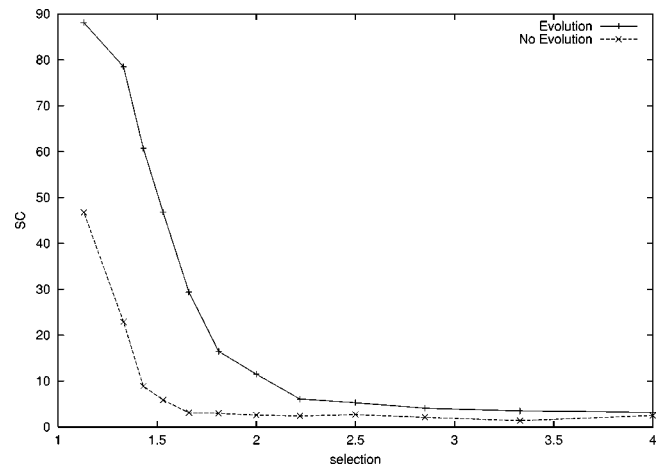


FIG. 6. Survival chance vs selection for dynamics with and without evolution. Same values of K and B as in Fig. 5.

intermediary values of the selection the difference between the two cases is the largest, since for low selection genetic structure plays only a small role [see Eq. (1)] and therefore it does not really matter whether the evolution acts or not. This kind of behavior is indeed what the biologists observe [1]. As could be expected, reduced viability due to deviation from the optimum has a stronger effect on the population dynamics in the absence of heredity because selection cannot bring the population mean fitness closer to the optimum.

Figure 7 showing the average value of the trait, z , obtained at the end of simulations for the surviving populations, as a function of the selection pressure, exhibits the existence of two regions and an intermediary one, between $s=2$ and $s=1.8$ for the case of evolution. Average trait values in this case lie always closer to the optimum than when there is no evolution. This is understandable, since only heredity can help population in approaching the optimum. Since the surviving populations without evolution were composed of just a few individuals, the statistics was very bad, even when an average over 3000 runs was performed. To improve it we first averaged the values of z obtained in a given run over the

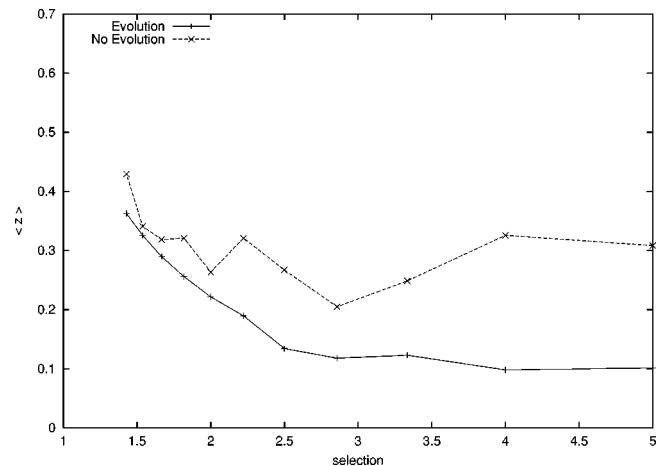


FIG. 7. Averaged over all population value of the trait z vs selection for the cases with and without evolution. Same values of K and B as in Fig. 5.

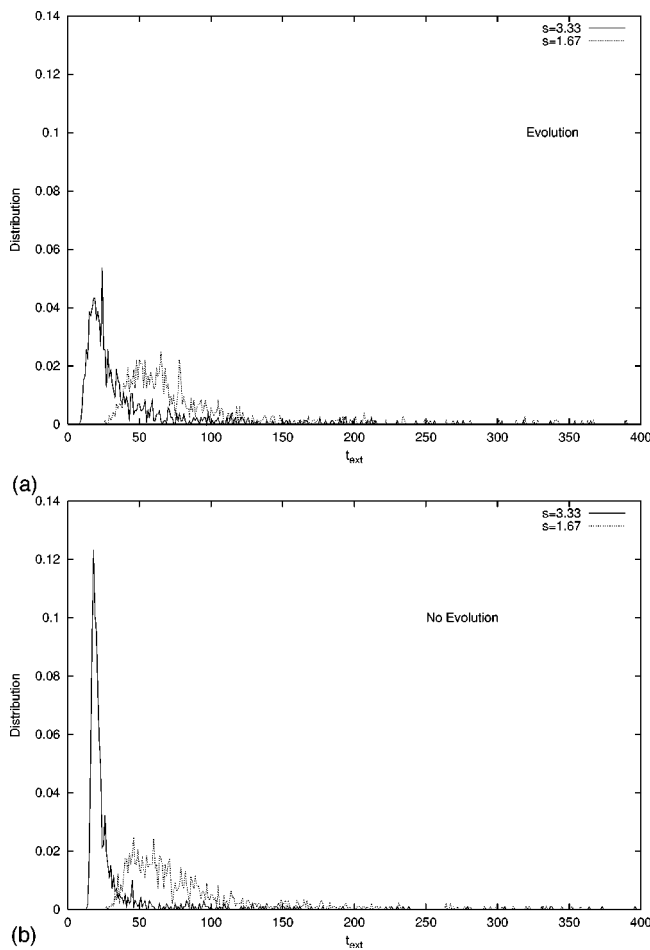


FIG. 8. (a) Distribution of the most probable time to extinction for 1000 independent runs. Two values of selection. Same values of K and B as in Fig. 5. Case with evolution. (b) The same as in (a), but without evolution.

last 500 MCS and then those values were once again averaged over the number of surviving populations.

In Figs. 8(a) (with evolution) and 8(b) (without it) we show the differences in the distribution of the extinction time for smaller and larger selection pressure. Stronger selection leads to populations which are quite similar to one another in the sense that the extinction times are nearly all grouped around one value, while weaker selection permits a wider distribution of extinction times, hence the populations differ more from one another. In each case however populations with evolution die later. For strong selection the very pronounced peak observed in the case without evolution is significantly reduced and the distribution of t_{ext} is wider. Distributions for weak selection are similar, but again it is shifted to longer times for the cases with evolution.

Figure 9 shows the most probable time to extinction versus B , the fecundity. As could be expected, the time grows with B , and the growth could be reasonably well fitted, in the two cases, by a hyperbolic tangent. A similar effect of saturation has been also found in a kind of mean-field model by biologists [2].

The dependence of the survival chance on the fecundity is presented in Fig 10. Again there are strong differences be-

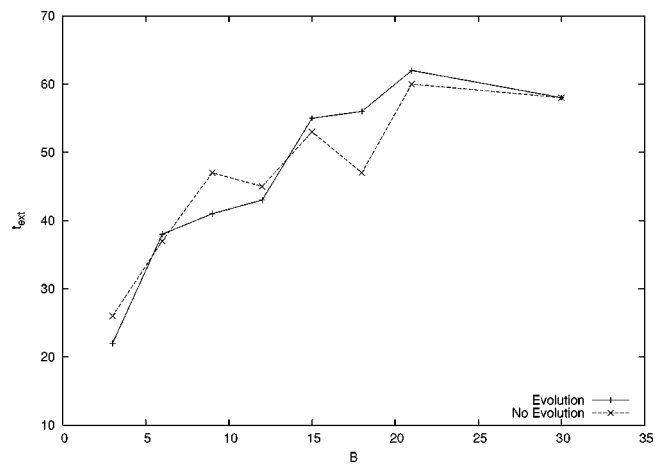


FIG. 9. Most probable time to extinction vs fecundity B for the cases with and without evolution. $K=900$, $s=1.67$.

tween the population dynamics with and without evolution. In the latter the survival chance practically does not depend on the fecundity and it remains well below the values for the population with evolution. As the extinction time, the chance for survival in the case of evolution could be well fitted into a hyperbolic tangent.

IV. FINAL REMARKS

We have presented a model describing dynamics of a population living in a constant environment and we have compared two cases—when evolution by natural selection acts via heredity and when it is absent. Individuals forming the population are characterized by a single value (trait, continuous character, phenotype) which, compared with the optimum characterizing the environment, determines the individual’s probability of survival. Individuals are treated independently, which permits studying the effects of demographic stochasticity in more detail than in the continuous models operating only on quantities averaged over the entire population [1,2]. We have investigated the dependence of the

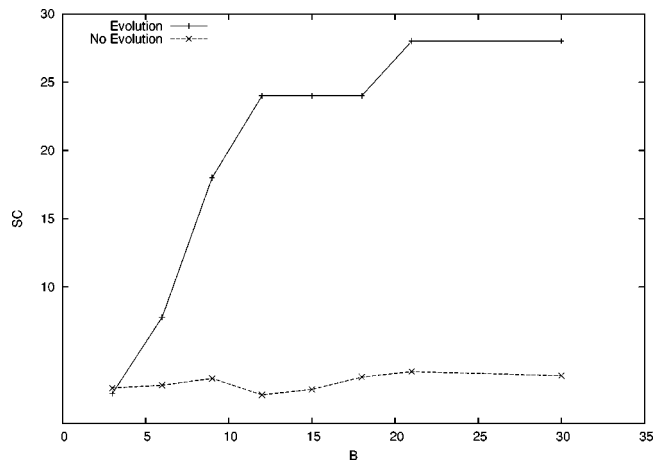


FIG. 10. Chance of survival vs fecundity B for the cases with and without evolution, $K=900$, $s=1.67$

most probable time to extinction and the survival chance of the population on such factors as selection pressure, carrying capacity of the habitat (size of the lattice), and fecundity. We have shown that while the extinction time only weakly differs between the cases with and without evolution, the survival chance is much greater if the evolution acts. Also the surviving populations are much more numerous in this case. Without evolution the survival chance depends very weakly on the investigated parameters—fecundity, selection, and carrying capacity. As can be seen from Fig. 3, if there is no evolution the population remains, even for large values of K , i.e., large habitat, in the vicinity of the minimum viable threshold. The reason may be the fact that the genetic pool of such population is always random and there are no correlations between the individuals forming the population. In this case we have a system with no interactions, on the genetic level, among entities forming the system and the evolution introduces this kind of interactions. Populations which are not satisfactorily adapted will be eliminated in each case, with or without evolution, and at the same rate. Hence there is equal most probable time to extinction, however, when the evolution is acting there will be less such populations, and the survival chance will be much larger in the case of evolution.

The most probable time to extinction and the survival probability are not related, at least not in a straightforward way, as shows the following argument.

We have a probability distribution $p(t_{ext})$ of the extinction time t_{ext} . This distribution has a most probable value t_m and a tail which is crudely exponential. However, this tail may vanish (or not) for a long time t_{max} which depends upon the parameters used.

The survival chance (SC) looks at what is the probability that a population remains alive after a time t_s corresponding to the end of the simulation. SC is thus the probability of survival for a time $t > t_s$. It is thus

$$SC = \frac{\int_{t_s}^{\infty} p(t) dt}{\int_0^{\infty} p(t) dt},$$

but the denominator is 1 by definition and thus

$$SC = \int_{t_s}^{\infty} p(t) dt.$$

In other words, SC is related to the properties of the tail of the distribution of the extinction times, while t_{ext} characterizes the most probable value of this distribution. Thus there is no simple relation between these two quantities.

Our study confirms the findings of Gomulkiewicz and Holt [1] that evolution may save an initially maladapted population. We have also shown that in many dependencies, first of all in the survival chance with evolution acting, two regimes could be found. This reflects the existence of a threshold value for extinction of small populations, as predicted on general grounds by Shaffer [22]. Apart from showing the agreement with the mean-field model of Gomulkiewicz and Holt [1] we have also shown that it is more reasonable to use the most probable time of extinction rather than the average one. We have demonstrated that it is interesting to study another quantity, not yet considered, i.e., the survival chance a population has in a given external condition. From it one could deduce information not present in the studies of the extinction time.

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