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Model of evolution with sexual and non-sexual reproduction

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Abstract. Using a previously introduced model (Refs. [9,10]) of biological evolution, we study the role of the reproduction pattern on the fate of an evolving population. Each individual is under the selectional pressure from the environment and random harmful mutations. The habitat ("climate") is changing periodically. Evolution of populations following three reproduction patterns are compared – an asexual one (without recombination) and two with recombination – asexual (meiotic parthenogenesis) and sexual. We show, *via* Monte-Carlo simulations, that sexual reproduction leads to a better adaptation to the environment, slightly better survival rates for the individuals and higher probability that the population will not become extinct in difficult external conditions. The benefits of sexual reproduction are enhanced by higher birth rates and lower mutation rates. In the case of low birth rates and high mutation rates there is a small preference for the meiotic parthenogenesis.

PACS. 05.10.Ln Monte Carlo methods – 87.23.Cc Population dynamics and ecological pattern formation – 87.23.Kg Dynamics of evolution

1 Introduction

One of the biological problems studied by biologists and recently also by theoretical physicists is the question why some organisms reproduce in a sexual way. Basically there are three different ways to produce offspring. The simplest one, used in haploid organisms (having just one set of chromosomes) is to give to each of the offspring a copy of the parential genotype. This is called *asexual reproduction* (AR). The next one applies to diploid organisms (having a double set of chromosomes). Genetic information is passed on to the progeny with the use of recombination. In the case of *meiotic parthenogenesis* (MP) each of the parent's chromosomes is cut at the same, random place and the strings are cross-glued, forming two gametes. Strictly speaking, it is one of the few possible forms of parthenogenesis [12]. Another process using recombination is found in *sexual reproduction* (SR) where each of the parents provides one gamete obtained as for the MP, and the two form the genotype of an offspring.

In each case the progeny's genotypes are modified by random point mutations, which are harmful, *i.e.* they lower the individual's chances for survival.

Clearly the AR is the fastest mechanisms and the SR is the most complicated one. Why then in many cases has nature chosen the SR? No definite answer is given yet to the question neither by biologists [1,2] nor by physicists [3,4]. Computer simulations, based generally on the Penna model [3,5,7,8] have shown that sexual reproduction leads to populations with larger variety of genotypes, although the survival rates for asexual reproduction could be the same [4]. In particular Sá Martins and Moss de Oliveira [6] have shown that the SR gives a better survival chances for a population in the case of a natural disaster.

Since all models of biological evolution are, by necessity, very simple, a question may be asked to what extent the findings of the Brazilian group [3,6] and Stauffer [7] depend on the models they used: the Penna model [5] for ageing or the Redfield model [2], modified by making distinction between recessive and dominant mutations [7].

In this paper we study the problem of possible advantages of either of the three above mentioned reproduction mechanisms, using a different model [9,10]. We shall show also what is the effect of changes of the environment on the populations following the three ways of reproduction.

2 The model

We assume that the modeled biological system is composed, at time t, of $N(t)$ individuals, each characterized by its genotype. In the case of AR (haploid organisms) it is a single string of L sites (*loci*). For MP and SR (diploid organisms) an individual has two such strings (chromosomes) read in parallel. On each locus there might be one of two possible forms of a gene (*alleles*) – a dominant one (1) or a recessive one (0). Thus a genotype is a single, or double for diploid organisms, string of zeros and ones.

From a genotype a phenotype is constructed. It is also a string of L loci. For haploid organisms the phenotype is identical with the genotype. For diploid individuals the rule is the following. If on a locus on the two chromosomes

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are two zeros (*recessive homozygote*) then there is a zero at the same locus in the phenotype. Otherwise, *i.e.* for heterozygotes and dominant homozygotes, there is a one in the phenotype. The rule is simple, but biologically acceptable. It may be mentioned that also the problem of expressing a genotype as a phenotype has not been solved by biologists yet. Another feature characterizing an individual j, is its age, w_j, which is put to 1 at birth and then increased after terminating each Monte-Carlo step.

The population lives in a habitat which is putting selectional pressure on the individuals. In this model it is realized by comparing the individual's phenotype with a certain optimal one which guarantees the best survival chances for its owner. Similar concepts has been already introduced by biologists [11]. At the beginning of the simulations we set the optimal phenotype to all 1's.

The population is also subject to random point mutations affecting genotypes of the offspring. Since the vast majority of mutation in nature are harmful, we consider here only mutations which reduce the adaptation of the individual.

The initial population has its genotypes taken randomly from a uniform distribution. The evolution runs along the following steps:

1. An individual i is randomly chosen. If its age is at least equal 2, it is accepted and its adaptation a_i *i.e.* agreement with the optimal phenotype, is calculated in the following way: the two phenotypes are compared, locus by locus. Each time the two alleles match, adaptation is increased by one. Finally the result is divided by the number of loci L, hence $a_i \in [0, 1]$.
2. Using the individual's adaptation and its age, its survival probability is calculated as

$$p_i = \exp\left(\frac{-\alpha w_i}{a_i}\right), \tag{1}$$

where α is a parameter controlling the speed of the process. Then p_i is compared with a random number r. If $r > p_i$ the process returns to 1. Otherwise the individual has survived.
In the case of SR a mate is chosen at random (*panmictic population*), its adaptation and survival chances are calculated as above. If the mate was not eliminated, the two give birth to m offspring. In AR and MP populations no mate is needed and the parent also gives birth to m offspring, where m is calculated from

$$m = E\left[M\left(1 - \frac{N(t)}{N}\right)\right]. \tag{2}$$

E means taking the integer part of [...], M is the maximum number of offspring permitted in the model (*physiological birth rate*) and the expression in the bracket is the Verhulst factor, limiting the number of offspring according to the actual size, $N(t)$, of the population and the carrying capacity, N, of the habitat.
3. Each offspring receives independently its genotype. The way it is created depends on the kind of population we are considering. When the reproduction is asexual without recombination the baby inherits the genotype of its parent, changed only by mutations. In the case of MP the two strings of the parent's genotype are cut at a random position and glued criss-cross to make the two chromosomes for the diploid offspring's genotype. Then the mutation procedure is applied. For SR each parent provides a pair of gametes, from which one is randomly chosen to make the genotype for the offspring.
Mutations are realized in the following way. A locus in the new genotype is randomly chosen and if it contains a "good gene", *i.e.* the same as in the optimal phenotype, it is changed with a probability p.
Phenotypes of the offspring are constructed from the genotypes according to the rule given above.
4. After selecting $N(t)$ individuals one Monte-Carlo step (MCS) has been completed and the age of each individual is increased by one. There is no maximum age an individual may live, only its survival probability goes down with age.

The changes of the environment are realized as modifications of the optimum phenotype, *i.e.* by changing a 1 at a random locus into a 0. Such changes occur periodically, after each 50 MCS.

The quantities which are registered during the simulations are:

1. The concentration, $c(t)$, of the population $c(t) = N(t)/N$,
2. normalized concentration, *i.e.* $c(t)$ divided by its maximum value,
3. average adaptation of the population,
4. average age of the population,
5. survival rate [3]

$$S(t) = \frac{N(t+1)}{N(t)},$$

6. genetic diversity, defined [6] for the SR and MP cases as the smallest difference between both strings of the genotypes of any two individuals (four combinations). In the AR case each individual is haploid and the comparison is made between two strings only.

The following parameters of the model have been kept constant: carrying capacity N (= 1000 in simulations), initial size $N(0)$ (= 300) of the population, number of loci in the genotypes L (= 20), rate of the process α (= 0.13). We have checked that varying those parameters around the above given values does not influence the results in a significant way. Hence, the system is stable in the Lyapunov sense – small changes of the parameters produce only small changes of the characteristics of the system.

The remaining two parameters of the model – physiological birth rate M (maximum number of offspring) and the probability of mutations p – have a qualitative influence on the evolution of the populations. In the simulations we took the following values of the free parameters: $M = 4$, 5, 7 and $p = 0.005$, 0.001, 0.0005. Relating it to the length of the genotype we get the probability of mutation per gene (*pmg*), a quantity often used by biologists.

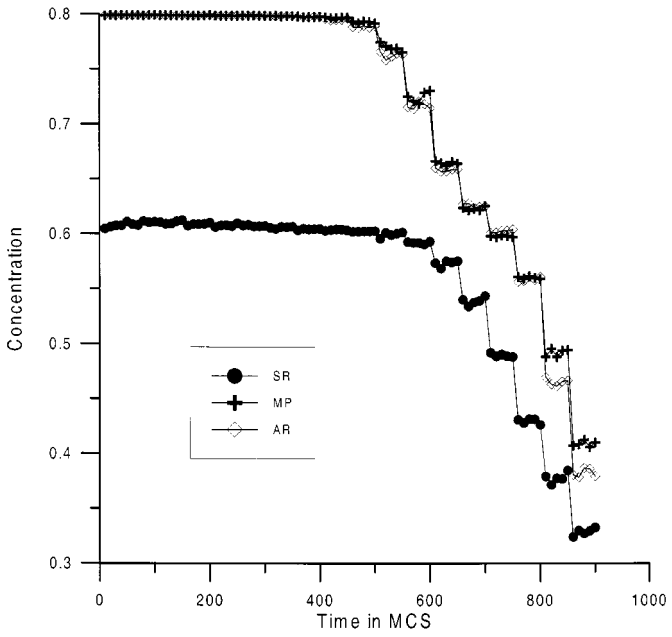

Fig. 1. Concentration *versus* time (in MCS). The following values of the parameters and the notation are the same for Figures 1–6. $M = 5$, $p = 0.001$, average over 100 runs. Three reproduction patterns: AR (empty diamonds), MP (crosses) and SR (full circles).

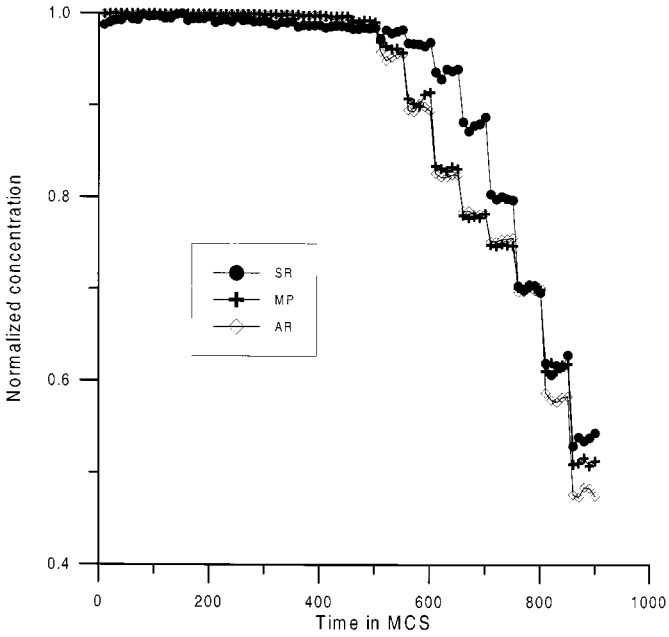

Fig. 2. Concentration (normalized by its maximum value) *versus* time.

Then our parameters are $pmg = 2.5 \times 10^{-4}$, 5×10^{-5}, 2.5×10^{-5}.

3 Results

In Figures 1–6 the data for the three reproduction scenarios (AR, MP, SR) and "mean" values of the parameters ($M = 5, p = 0.001$) are presented. The averaging was over 100 independent runs. Figure 1 shows the time dependence of the concentration, while in Figure 2 each concentration is normalized by its maximum value.

Changing a 1 into a 0 in the optimal phenotype corresponds to making the habitat more difficult to live in, since a 1 in an individual's phenotype comes from either a (0,1), (1,0) or (1,1) in the genotype, whereas a 0 only from (0,0). This is the main reason why the concentration is diminishing in time, and sometimes even leads to extinction of a population.

It can be seen from Figures 1 and 2 that at the beginning, regardless of the method of reproduction, the population adjusts easily to the changes of the environment. However when the "climate" becomes more "harsh", each subsequent change results in a drop of the concentration. The population recovers, but not quite.

The concentration at the initial stages is lower for SR since in order to produce offspring both parents must survive. Sexual reproduction ensures however that the flat part with nearly constant concentration at the beginning of the simulations is maintained longer, *i.e.* such populations are more robust against environmental changes, than the asexual ones. This is clearly seen in Figure 2. The length of the plateau does not depend neither on the mutation nor the birth rates.

One can see in Figure 2 that when the conditions for living are indeed very tough – after 800 MCS the model phenotype contains already 80% of 0's – SR does better than AR or PM. This difference, which is rather small for the illustrated case, becomes quite significant if the maximum number of offspring (M) is increased. Our data for $M = 7$, not shown here, indicate that at 900 MCS the non-normalized concentration for SR is about 0.75, whereas for AR (or PM) it is just 0.6.

Figures 3 and 4 show the average adaptation and average age of the population, respectively. At the initial stages of the process the adaptation rises at the same rate for the three cases. Then SR ensures better adaptation then the remaining two, which are virtually equal. The characteristic saw-teeth pattern follows from adjustment of the population to new conditions. Like in the case of concentration, the adaptation is poorer and poorer. Until some 60% of changes in the optimum phenotype the AR and PM lead to populations of longer living individuals, but later on, in a more demanding habitat, the sexually reproducing individuals live longer on the average. These advantages in the adaptation and average age show up in the dominating SR curve in Figure 2. General features of the adaptation and age *versus* time dependence remain the same for other values of the M and p parameters.

So far both types of asexual reproduction – the simple haploid AR and more refined MP, lead to the same results. They are different, as seen in the survival rate and genetic diversity plots, presented in Figures 5 and 6, respectively.

The survival rate drops with age, as it should, and for older individuals SR gives a slightly better survival chance. MP although yielding lower survival rates than

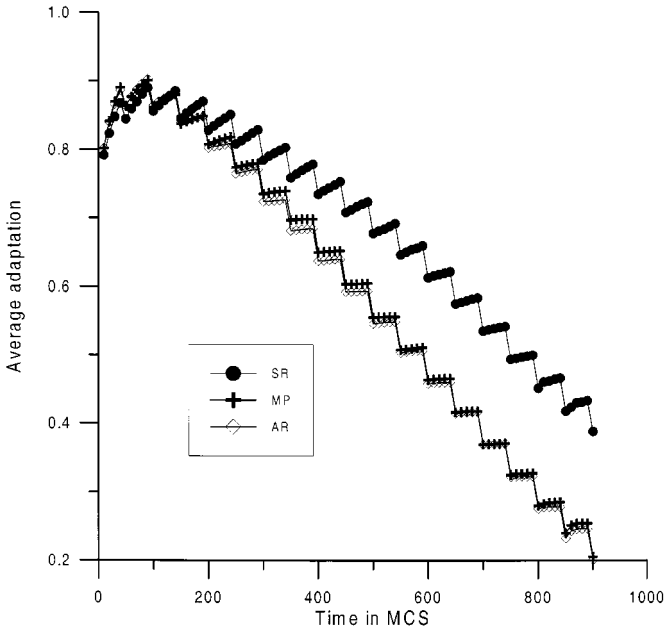

Fig. 3. Average adaptation *versus* time.

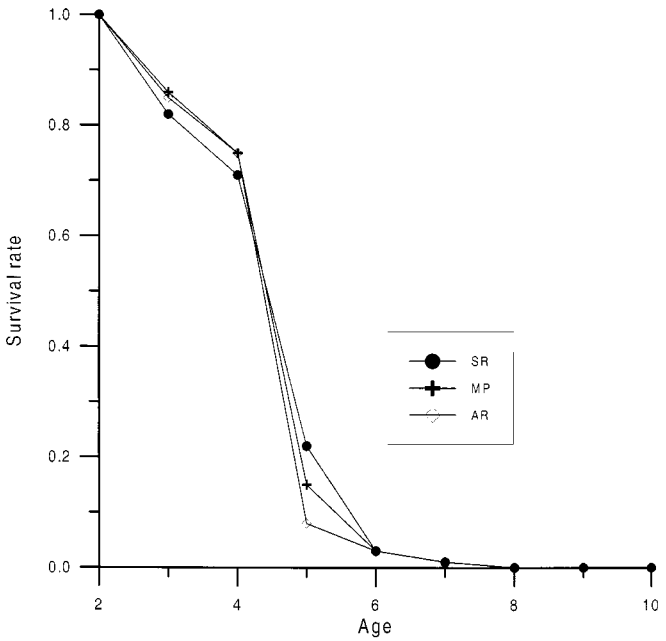

Fig. 5. Survival rate after 800 MCS *versus* age.

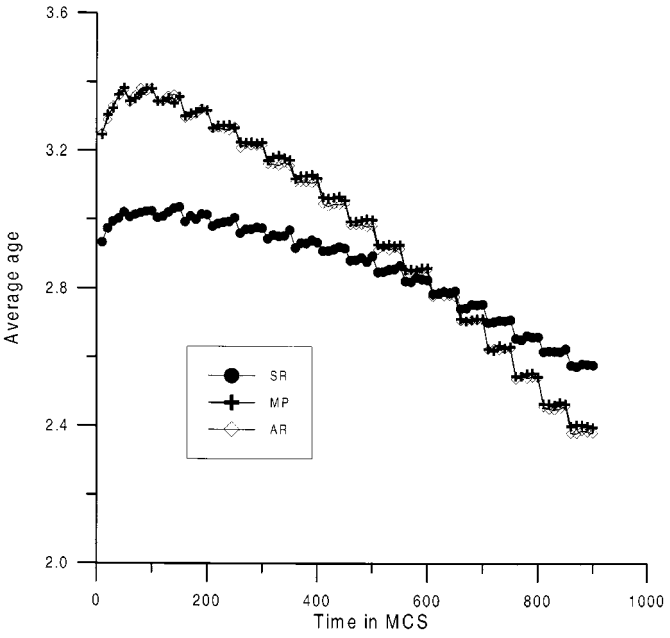

Fig. 4. Average age *versus* time.

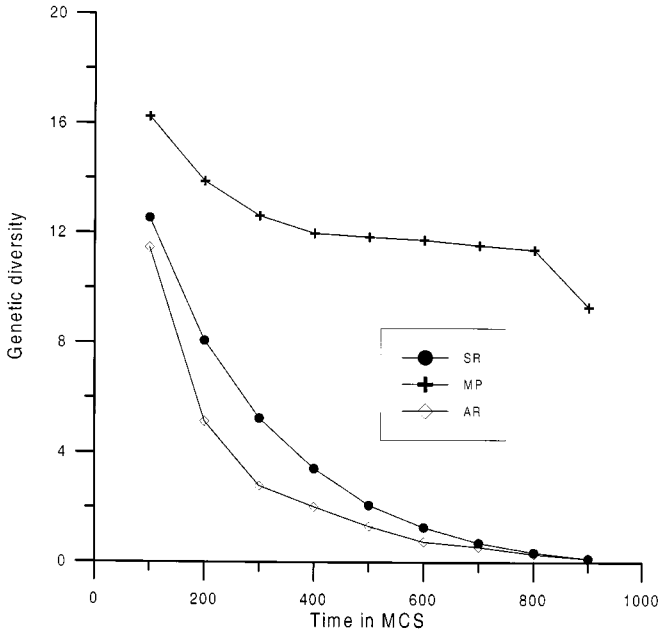

Fig. 6. Genetic diversity *versus* time.

SR, gives better ones than AR. The character of the curves does not change substantially neither with time nor with changing mutation rate. Increasing M leads to a much better survival rate for SR (Fig. 7).

Genetic diversity is by far the largest for MP, then comes SR and finally AR. In each case the value of the genetic diversity is diminishing with time and it becomes close to zero for 900 MCS. Such, unrealistic in nature, homogeneization of the population is due to a short genotype – only 20 loci. Genetic diversity increases, as it should, with increasing N and p. The fact that the genetic diversity features are not clearly seen *e.g.* in the adaptation is due to the fact that the latter is coming from the phenotypes and the former from the genotypes.

For the evolution of a population the vital question is its chances of survival in a given environment. Table 1 shows the percentage of extinct populations after 900 MCS (*i.e.* 90% changes in the optimal phenotype) in a series of 100 runs. Populations with higher mutation rates and birth rates become extinct less frequently. Increasing birth rate is clearly more effective.

For populations with low mutations and birth rates the MP is the most efficient; for average values of the parameters there is no preference. When the mutation rate

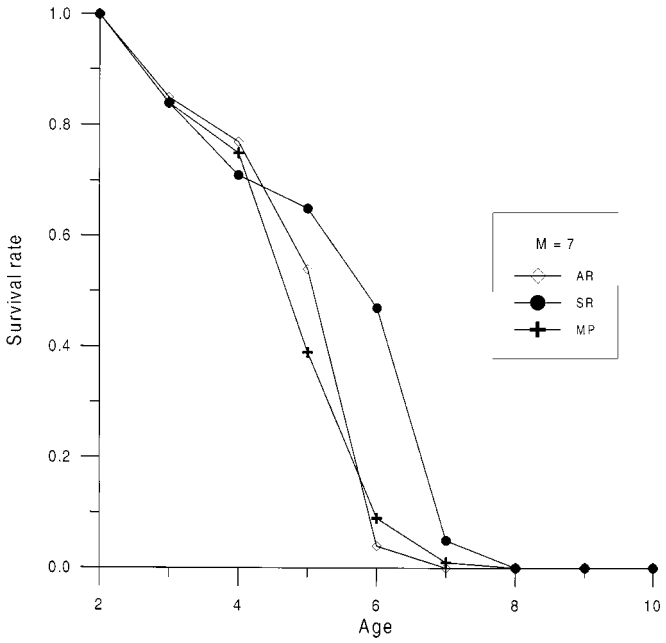

Fig. 7. Survival rate, after 800 MCS, *versus* age for the case of $M = 7$. The values of the remaining parameters and notation are the same as in Figure 1.

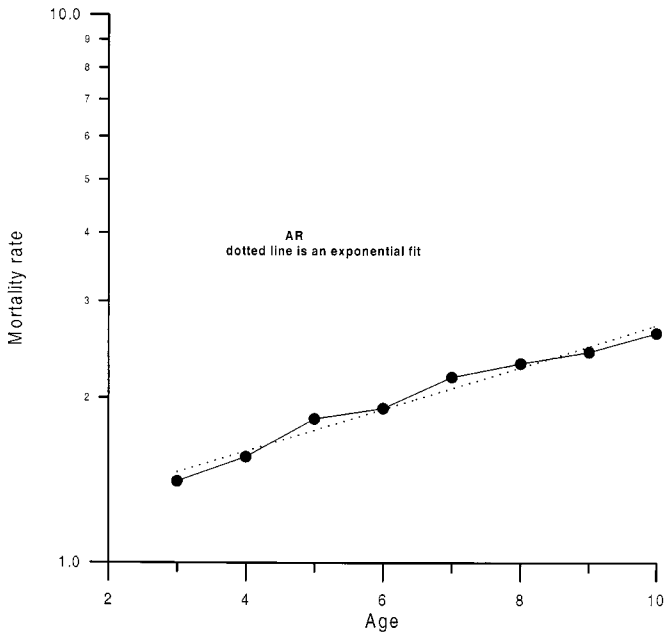

Fig. 8. Mortality rate *versus* age for the AR population. Data taken after 2 changes of the environment. Values of the parameters as in Figure 1.

Table 1. Percentage of extinct populations after 900 MCS. The optimal phenotype has been changed in 90%.

probability of mutation	maximum No. of offspring			type of reprod.
	4	5	7	
	40	24	8	AR
0.0005	47	17	7	MP
	49	13	0	SR
	39	15	5	AR
0.001	35	16	7	MP
	28	16	0	SR
	15	1	0	AR
0.005	14	3	1	MP
	18	2	0	SR

is high and the birth rate is low, again MP is the preferred one. Finally if the birth rate is high then SR gives the best survival chances. The mortality rate defined [3] as the ratio of the number $\mathcal{N}(w)$ of individuals having, at a given moment, age w, to the number of individuals having age $w+1$, is known [3] to have in nature the exponential form (*Gompertz law*). This is indeed what we have found in our simulations (see Fig. 8). Since however in our model the individuals live a rather short life, there are just a few (8 at most) points in the mortality rate *versus* age curve. Therefore its functional form can be deduced only approximately. Another quantity of interest is the age distribution – $\mathcal{N}(w)$ *versus* age dependence. It is decreasing with age and it is best fitted by a third order polynomial. Age distribution and mortality rate have, as far as we can deduce from the restricted data, the same pattern for the three reproduction scenarios.

4 Conclusions

On the basis of the introduced earlier model [9,10] we have shown that out of the three considered reproduction schemes – asexual (for haploid organisms), meiotic parthenogenesis and sexual (both for diploid organisms), in general SR is the most favorable. It gives the best adaptation to the changing environment, best survival rates and, what may be the most important, less populations following SR become extinct. In a very demanding habitat also SR leads to the highest population size. This preference of the SR disappears if the physiological birth rate of the population is low. Then the MP is the most efficient. In our simulations the populations with different reproduction schemes were not evolving together, hence there was no effect of direct competition. However all three evolution processes started from the same conditions, like initial number of individuals, distribution of the genotypes and habitat requirements.

Our results go in the same direction as the earlier findings of Stauffer, S. Moss de Oliveira and Bernardes [4,6–8]. Their work is, in general, based on the Penna model [5], which apart from a formal similarity with ours, is quite different. In both models an individual's genotype is represented by a computer word containing a string of 1 and 0. In the Penna model however each "locus" represents a time interval in the individual's life and a 0 or 1 determines whether during that period the "health" of the individual deteriorates (1) or remains the same (0). If an individual acquires a certain number of diseases (1's) – it dies. Mutations, which are only harmful, change a 0 into a 1. In our model mutations are also only bad, but with respect to the actual optimal phenotype. Since the changes brought by mutations are inherited by the progeny, when

the optimal phenotype is changed later on, they might, and often do, turn out to be beneficial. Since in our model there are no males and females, only the reproduction may follow a sexual pattern, the mutation rate is the same for all members of the population and it does not change in time. Also the survival of an individual is calculated here in a different way than in the Penna model.

The present work, using a different model, supports the above mentioned earlier claims that SR by keeping more diversified populations gives them better chance to survive cataclysms. We have also shown under which conditions such preference of the SR is valid.

One should however take the presented here and elsewhere (*e.g.* [3,6]) evidence of the advantages of the SR *cum grano salis*. In all those models every member of the sexually reproducing population was able to breed, which is clearly not the case in nature.

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