RISK OF POPULATION EXTINCTION FROM PERIODIC AND ABRUPT
CHANGES OF ENVIRONMENT

Andrzej Pekalski∗
Institute of Theoretical Physics, University of Wroclaw,
pl. M. Borna 9, 50-203 Wroclaw, Poland

Marcel Ausloos†
GRAPES@SUPRATECS B5a Sart Tilman, B-4000, LIEGE, Euroland

A simulation model of a population having internal (genetic) structure is presented. The population is subject to selection pressure coming from the environment which is the same in the whole system but changes in time. Reproduction has a sexual character with recombination and mutation. Two cases are considered - oscillatory changes of the environment and abrupt ones (catastrophes). We show how the survival chance of a population depends on maximum allowed size of the population, the length of the genotypes characterising individuals, selection pressure and the characteristics of the "climate" changes, either their period of oscillations or the scale of the abrupt shift.

I. INTRODUCTION

Estimation of the extinction risk for a population is, obviously, an important issue. It has been addressed in many papers, either by biologists (see e.g. [1]-[4]) or physicists ([7] -[13]). Several aspects have been considered – most often it was the problem of changing environment, like advancing ice-age [10, 15] and the question was – will the population adapt, or migrate? The effect of stochastic changes and random catastrophes on the population’s fate has been studied, via mean-field type analysis, by Lande [1]. Roberts and Newman [5] studied an extension of the Bak and Sneppen model [6], taking into account both bad genes and bad luck, represented by a catastrophe. In most of the papers describing population dynamics the genetic structure of the population has not been considered. Individuals were characterized by their continuous trait, represented by a real number \( z \in [0,1] \), see e.g. [13, 16]. Although in many cases such simplified approach is quite satisfactory, it cannot describe, for example, the influence of the genetic structure on the survival probability. In more refined models, individuals are characterized only be their genotypes which are subject to random mutations. Individual-based model of evolution has been recently proposed by Rikvold and Zia [17]. They used a fixed in time and random interaction matrix characterizing species and their phenotypes. The latter could be changed by random mutations. The model exhibits punctuated equilibrium – short periods with many changes in the genome space, separated by long periods of stassis.

In this paper we study how the survival chance of a population depends on such factors as type of the environmental changes (oscillatory or abrupt), length of the genotype characterising individuals and selection pressure. We shall use Monte Carlo (MC) simulations of a discrete time model.

II. MODEL

In our model a population is, at time \( t \), composed of \( N(t) \) individuals, which have no spatial location and are described by their age, which is increasing after each time step (see below) and their genotypes. A genotype consists of a double string (the organisms are diploidal) of \( L \) sites (loci) equal either zero or one. From a genotype a phenotype (single string) is constructed by taking at each site the product of the two values on both strings of the genotype. Hence the phenotype is also composed of a zeros and ones [18]. For \( L = 5 \) the process could be illustrated as follows:

| Genotype | Phenotype |
|----------|-----------|
| 0 1 1 0 1 | 0 0 1 0 0 |

*Electronic address: apekal@ift.uni.wroc.pl
†Electronic address: Marcel.Ausloos@ulg.ac.be
As can be seen, 0 is the dominant and 1 is the recessive allele. The population lives in a habitat which is characterized by an optimum $\Theta(t)$, which is, like the phenotype, a single string of 0’s and 1’s of length $L$. The agreement between the optimum and an individual $i$ phenotype $f_i$ determines its fitness $\varphi_i$

$$\varphi_i = \frac{1}{L} \sum_{i=1}^{L} [1 - \text{XOR}(f_i, \Theta(t))].$$

(1)

where XOR is the exclusive OR, equal 1 if either $f_i$ or $\Theta$ is equal 1, but not both. Therefore an individual having a phenotype equal to the optimum has the maximum probability of survival. This probability, $p_i$, is calculated from

$$p_i = \exp \left( -s \cdot \frac{w_i}{\varphi_i} \right),$$

(2)

where $s$ is the selection pressure which may describe how demanding is the environment. The larger is $s$, the more demanding is the habitat. An individual with a given fitness is less likely to survive when the selection pressure is high, since its survival probability is smaller, than when the selection pressure $s$ is small. $w_i$ is the age of the individual $i$. Initial values of the age and genotypes are random.

Our MC simulations follow the steps given below.

1. Pick the first available individual from a list,
2. Its fitness is calculated from eq.(1), then probability of survival, $p_i$ from eq.(2).
3. A random number, $r_i \in [0,1]$ is taken from a uniform distribution. If $r_i > p_i$ then the individual is removed from the system and the program goes back to 1.
4. If the individual survived, the next one is taken from the list as a partner for reproduction, and its survival probability is checked, like for the individual $i$. If it did not survived, again the program returns to 1,
5. The pair gives birth to up to 4 offspring. That value has been chosen since for a smaller one, say 2, the populations will soon die out, and larger values, like 6, will not change the results in any significant way. Each of the offspring is born if a random number $r \in [0,1]$ is smaller than the Verhulst factor

$$\pi = 1 - \frac{N(t)}{K},$$

where $K$ is the maximum number of individuals the habitat could support (carrying capacity). Therefore the Verhulst factor could be regarded as an yet another factor, apart from the selection pressure, limiting the growth of a population. The difference between the two is that the Verhulst factor acts only on offspring, which are either born or not. Because of the Verhulst factor the number of litter at a given birth could be any integer number between 0 and 4,
6. Each progeny receives its genotype via recombination and mutation. The two strings of the first parent’s genotype are cut at a random position and then glued across. From the two one string (a gamete) is chosen randomly and in one position the allele is changed (mutated) to the opposite. The chosen gamete will be one of the two chromosomes of the genotype of the offspring. The second chromosome is obtained from the second parent, following the same steps. From the genotype the phenotype is constructed in the way described above. Since the place of cutting the strings, mutated locus and the choice of the gametes, are random, each offspring coming from the same parents may have a different genotype,
7. After coming to the end of the list of individuals, the list is updated and shuffled. The time step as well as the age of the individuals is increased by one. The reason to include age is to get rid of perfectly fit individuals who otherwise would live forever in a constant environment.

A population in which a partner is chosen freely from all members of the population is called panmictic.

We shall consider below two cases. In each of them initially the optimum will be a string of zeros. Since zero is the dominant allele, this corresponds to a ”friendly” climate (three combinations of alleles in a genotype yield a zero in the phenotype, while only one combination gives 1). All 1’s in the optimum mark the most ”harsh” climate. In the first of the cases the optimum will change periodically, with a period denoted by $t_{ch}$, while in the second case it will change just once, after the system reached a stationary state. The degree of changes in this case will be measured by the number $b$ of zeros in the optimum switched from 0 to 1’s.
Our model has the following control parameters: maximum size of the system $K$, length of the genotypes $L$, selection pressure $s$ and either period of changes $t_{ch}$ or the number of bits $b$ changed in the optimum.

Typically we have run the simulations till 10 kMCS and averaged over 50 independent runs for larger systems and 500 for smaller ones. Time of extinction was determined as that moment when there was just one individual left in the population. Survival chance for a population was determined as the ratio of the number of runs in which a population survived to the end of simulations to the total number of runs.

III. RESULTS

A. Oscillations of the optimum

The behavior of populations in an oscillating environment has been recently studied by mean-field analysis and simulations in [13], where however no genetic structure has been considered and the populations were living on a lattice.

In our model the optimum was changed with periods of $t_{ch} = 20, 30, 50, 70, 100$ and 150 time units (MCS). In Figure 1 we show the time evolution of the concentration, average age and average fitness for fast ($t_{ch} = 50$) and slow ($t_{ch} = 150$ MCS) changes. As can be seen, the populations go extinct much sooner for faster changes of the optimum, what have been also found in [13][16]. Average fitness oscillates following the optimum but diminishes rather fast, indicating that populations could not adapt to the changing conditions. Relatively stable concentration is maintained due to a large number of offspring, which shows up in decreasing average age. Population enters into a critical region when the number of individuals is so low that a chance to meet a partner and to breed is smaller than the average survival probability. Progeny is not born, the average age jumps up and the fitness continues to drop. Since the average age is about 1.7, even a fast change of the optimum, like $t_{ch} = 20$, corresponds to about 15 generations, while $t_{ch} = 150$ is about 100 generations. In our model the generations are overlapping, meaning that parents do not die after giving birth to offspring. We have found out that a population could either adapt to the changing conditions, or go extinct. Since however the optimum does not change in space, we cannot have islands serving as a refuge for otherwise declining population, or the number of bits $b$ changed in the optimum.

Simple following of the optimum by the average phenotype may not be however a guarantee of survival for a population, as seen from Figure 2, where average Hamming distance [20] between the optimum and the phenotypes is shown. Following of the optimum by the average phenotype may not be however a guarantee of survival for a population, otherwise declining population, as has been found out in [19].

Average age is about 1.7, even a fast change of the optimum, like $t_{ch} = 20$, corresponds to about 15 generations, while $t_{ch} = 150$ is about 100 generations. In our model the generations are overlapping, meaning that parents do not die after giving birth to offspring. We have found out that a population could either adapt to the changing conditions, or go extinct. Since however the optimum does not change in space, we cannot have islands serving as a refuge for otherwise declining population, or the number of bits $b$ changed in the optimum.

The dependence of the average time of extinction, $<t_{ex}>$, on the period of changes, $t_{ch}$, is shown in Figure 3. As could be expected, there exists a minimum value of the selection for which all populations died out. For smaller selections some populations would survive. This threshold value of the selection will be henceforth denoted by $s_c$. The results shown below are for the threshold values equal $s_c = 0.16$ for $K = 2500$ and $K = 10000$ and for $s_c = 0.15$ for $K = 200$. We have observed here a well known fact [21][21] that small populations are more vulnerable and a weaker selection pressure drives them to extinction.

As seen, average extinction time increases linearly with $t_{ch}$ and the slope is practically independent of the maximum size of the population.

For selections stronger than $s_c$ we observe also linear dependence of $<t_{ex}>$ on $t_{ch}$, with the same slope, but lying lower than for $s_c$. Figure 4 shows how $<t_{ex}>$ depends on $t_{ch}$ when the length of the genotype changes. The maximum size of the system was $K = 2500$. Clearly, individuals with longer genotypes (more complex) are better off, live longer, than the ones with shorter genotypes. In each case we have observed a linear dependence of $<t_{ex}>$ on $t_{ch}$.

Average extinction time reduced by the product of the period of the changes and the length of the genotype is shown in Figure 5. While for fast changes we observe differences among various cases, for long-period oscillations the reduced $<t_{ex}>$ stabilizes at about 1.

To ensure that the most often used averaging over just 50 independent runs yields good statistics, we present in Figure 6 the values of $<t_{ex}>$ obtained in 50 runs for $L = 30$, $t_{ch} = 50$, $s = 0.16$ and several values of $K$. Apart from that, we have observed that the results do not change when we average over 50 independent runs for $L = 30$ and $t_{ch} = 50$. In such a case, we have used the same threshold values equal $s_c = 0.15$ for $K = 200$, $s_c = 0.16$ for $K = 2500$ and $K = 10000$. We have observed here a well known fact [21][21] that small populations are more vulnerable and a weaker selection pressure drives them to extinction.
FIG. 1: Time dependence of (a) concentration, (b) average age and (c) average fitness, when the optimum changes with periods $t_{ch} = 50$ MCS and $t_{ch} = 150$ MCS. Carrying capacity $K = 2500$, genotype length $L = 20$, selection pressure $s = 0.17$, average over 50 runs.

FIG. 2: Average Hamming distance between optimum and a phenotype in the case of population surviving and vanishing. $t_{ch} = 300$ MCS

FIG. 3: Average time to extinction $< t_{ex} >$ versus periods $t_{ch}$ of optimum oscillations for small ($K = 200$), medium ($K = 2500$) and large ($K = 10000$) carrying capacities. $L = 30$, $s = 0.16$, except for $K = 200$, where $s = 0.15$
FIG. 4: Average time to extinction $< t_{ex} >$ versus periods $t_{ch}$ of optimum oscillations for three values of the genotype length $L = 20, 30, 50$. Carrying capacity $K = 2500$, $s = 0.16$

FIG. 5: Reduced average time to extinction (see text) versus $t_{ch}$. Parameters’ values are the same as in Figure 4.

from very small populations ($K = 200$), all other systems show rather small scatter. Therefore in the following for $K = 200$ we took averages over 500 runs.

It should be noticed that the survival chance of a population depends very strongly on the selection pressure. There is a range of the selection pressure values within which some populations may die, while some may stay alive. Outside that range either all populations die or all stay alive. For example for $K = 2500$, $L = 50$, $t_{ch} = 50$ at $s = 0.14$ all populations survive, meaning that they were able to adapt (continuously) to the changing habitat. At $s = 0.15$ only 15% survive, and at $s = 0.16$ all die. Survival chance as a function of the selection pressure has a nearly step-like character. The threshold values of the selection, $s_c$, are equal 0.16 for $L = 50$ and $L = 30$, irrespective of the rate of changes $t_{ch}$ and $s_c = 0.15$ for $L = 20$. This means that populations of individuals with shorter genotypes are more vulnerable than those with longer ones. In general, the system always tries to follow the optimum. If the selection is too strong, then the distance between the average phenotype and the optimum is small, but many individuals are

FIG. 6: Distribution of the extinction times at 50 independent runs for different carrying capacity values $K$. $L = 30$, $s = 0.16$, $t_{ch} = 50$. 
FIG. 7: Time dependence of (a) concentration, (b) average age and (c) average fitness when the environment changed after 500 MCS. Two types of changes \( b = 50 \% \) and \( b = 75 \% \) (loci in the optimum changed). \( K = 2500, L = 20, s = 0.15 \)

FIG. 8: Survival chance versus number of changed loci in the optimum for short (\( L=20 \)), medium (\( L=30 \)) and long (\( L=50 \)) genotypes. Selection values are (a) \( s =0.18 \), (b) \( s = 0.20 \), (c) \( s = 0.22 \) and (d) \( s = 0.24 \). \( K = 2500 \).

killed and the killing rate may be too high for the population to survive. If the selection is weaker, the distance is larger, but less individuals are killed and the population survives.

B. Abrupt changes of the optimum

Let us present the time dependence of the concentration, average fitness and average age (Figure 7). The system shown is a medium size population (\( K = 2500 \)) with a short genotype (\( L = 20 \)). We let it evolve in a constant environment until 500 MCS when the population reached a stationary state, and then changed either half of the zeros in the optimum to ones, or 75 percent of zeros to ones. Afterwards the optimum remained constant, but with the new values. If a population survived the shock of the change, it will continue to exist, although with lower average fitness, and lower average age.

The survival chance of a population as a function of the number of changes in the optimum (Figure 8) clearly depends on the length of the genotype.
FIG. 9: The same data as in Figure 8 except that now the survival chance is plotted against the percentage of changed loci, not their absolute number.

FIG. 10: Survival chance versus the number of changed loci for three values of the carrying capacity – $K = 200$, $K = 500$ and $K = 2500$. $L = 30$, $s = 0.20$

If we however plot the survival chance against the relative change in the optimum, i.e. the percentage of changes, then, as seen from Figure 9, the differences between populations with genotypes of different length disappear. Rather strong dependence on the selection pressure has the same character as before.

Figure 10 shows that small populations ($K = 200$) have a lesser chance to survive medium or large scale catastrophes than bigger populations. This is clearly different from what we have found for periodic changes.

The threshold values of the selection, $s_c$, could be deduced from Figures 8 and 10 as the points where the curves touch the horizontal axis. Hence, e.g. $s_c = 0.17$ for $K = 2500$ in Figure 8.

IV. CONCLUSIONS

We have presented a model of population dynamics where two types of the habitat changes are possible – oscillatory ones (with different periods of the oscillations) and abrupt ones, which may be called catastrophes, when the scale of the catastrophe may vary.

As should be expected, selection pressure plays the crucial role in each case, but when the changes are oscillatory, a small increase in the value of the selection pressure shifts the population from the "all survive" into "all extinct" region. This effect is weaker when the environment changes abruptly. Since the habitat after a catastrophe remains unchanged, populations which survived it will not decay, while in a periodically changing habitat surviving initial oscillations is by no means a guarantee that a population will also survive next changes, which, at the beginning, are from a "better" to a "worse" climate. Populations characterized by longer genomes, presumably corresponding to more complex animals, live longer in the case of periodic changes and could sustain bigger catastrophes. Catastrophes are
more dangerous for small than for larger populations. Stochasticity plays a more important role in small populations. As recently shown by Shnerb e.a, life has a better chance on large habitats. The situation is however different when the optimum is oscillating. Here the size of the population, or more precisely, of the carrying capacity, seems to have only small influence on the fate of a population. If the selection pressure is strong enough in the oscillating optimum, a small population will become extinct, but this will happen most probably at the same time as for a large population. In the case of a catastrophe, small populations face a much bigger danger of being eliminated. If they however survive the catastrophe they may live on, without a risk of elimination.

The results obtained by us, although using different simplifications in construction of the models, agree with what has been found by Shnerb e.a and biologists that a population in conditions changing in time may either adapt and live well, or perish. Our finding that Hamming distance between the optimum and the phenotype (bad gene) is not sufficient to predict extinction, and some other, abiotic, factor influences the outcome, corroborates the statement by Roberts and Newman. The role of selection in the extinction probability has been, to the best of our knowledge, not studied by physicists, although its importance has been emphasized by biologists. Similarly, recombination, another very important factor in diversification of the genetic pool, is often neglected by physicists, apart from those dealing with the Penna model (see e.g.).

There are several extensions of our model which could provide interesting results and determine the model robustness, like changing the way a genotype is transcribed to a phenotype. Considering the model on a lattice could tell what is the role played by the topology of the system. More realistic would be a model with two sexes, where mating is possible only between individuals of the opposite sex. This should be done on a lattice, where the distance between the mates could play an important role. Another question left open in this paper is how important is the assumption that an individual could mate in each time step with a different partner. How the results would change if the partners will remain faithful to each other for all their lives?

Acknowledgment
We are grateful to the anonymous referees for their valuable and helpful remarks. MA admits some pertinent comments by P. Clippe. AP acknowledges the support of the COST10 STSM which permitted collaboration with MA on this project. Preliminary stages were also supported via a Santander grant. This work has been done within the framework of the UNESCO Chair of Interdisciplinary Studies at the University of Wroclaw.

[1] R. Lande, Am. Nat. 142, 911 (1993)
[2] M.L. Shaffer, BioScience, 31, 131 (1981)
[3] D. Goodman in M.E. Soulé ed. Viable Populations for Conservation, Cambridge Univ. Press, New York 1987
[4] R. Lande and S. Shannon, Evolution 50, 434 (1996)
[5] B. W. Roberts and M.E.J. Newman, J.Theor.Biol. 180, 39 (1996)
[6] P. Bak and K. Sneppen, Phys.Rev.Lett. 71, 4083 (1993)
[7] P.G. Higgs and B. Derrida, J.Phys. A 24, L985 (1991)
[8] N. Vanderwalle and M. Ausloos, J.Phys. A 29,309 (1996)
[9] A. La Barbera and B. Spagnolo, Physica A 314, 120 (2001)
[10] M. Droz and A. Pękalski, Phys. Rev. E 65, 051911 (2002)
[11] K. Pawlikowski and A. Pękalski, Physica A 342, 597 (2004)
[12] D. Chowdhury and D. Stauffer, Physica A 340, 685 (2004)
[13] I. Bena, M. Droz, J. Szwabiński and A. Pękalski, Phys.Rev E 76 011908 (2007)
[14] M. Hall, K. Christensen, S.A. di Collobiano and H.J. Jensen, Phys.Rev. E 66, 011904 (2002)
[15] C.M. Pease, R. Lande and J.J. Bull, Ecology 70, 1657 (1989)
[16] R. Bürger and M. Lynch, Evolution, 49, 151 (1995)
[17] P.A. Rikvold and R.K.P. Zia, Phys.Rev E 68, 031913 (2003)
[18] A. Fraser and D. Burnell, Computer Models in Genetics, McGraw-Hill, New York 1970
[19] N.M. Shnerb, E. Bettelheim, Y. Louzoun, O. Agaam and S. Solomon, Phys.Rev. E 63 021103 (2001)
[20] B. Drossel, Adv.Phys. 50, 209 (2001)
[21] N.M. Shnerb, Y. Louzoun, E. Bettelheim and S. Solomon, Proc.Nat.Ac.Sci. 97, 1022 (2000)
[22] J. Murray, Mathematical Biology, Springer, Berlin, Heidelberg, 1993
[23] M. Zawierta, P. Biecek, W. Waga and S. Cebrat Theory BioSci. 125 123 (2007)
[24] D. Stauffer, S. Moss de Oliveira, P.M.C. de Oliveira, J.S. Sa Martins, Biology, Sociology, Geology by Computational Physicists. Elsevier, Amsterdam 2006.
[25] K. Bokowska, M. Kula, S. Cebrat and D. Stauffer, Int. J. Mod. Phys. C. 18 1329 (2007).