

Conditions for Adaptation of an Evolving Population

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We propose a model to study the adaptation of an evolving population to a given environment. Using the Monte Carlo simulations we find how much the phenotypes of individuals of the population and those required by the environment may differ for the population to grow. We show that survival chances are greater if the number of the phenotype's features is smaller. In the case when a part of the population may colonize an empty niche, we show that there is a minimum value of the similarity of the two environments in order that such a colonization may succeed. We also show that the two populations differentiate with time. [S0031-9007(96)00054-3]

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The similarity, at least at a formal level, between some evolution processes and statistical physics methods has led to a growing interest of physicists in biological problems [1–5]. Some of them have been investigating the problem of speciation and constructed simple models showing interesting features, such as the condition for species formation within sympatric and geographic speciation. By necessity, all physical models are simple and deal only with a part of the biological aspects considered to be important. Problems of various types of speciation, e.g., requiring or not geographical barriers and adaptation, were intensively discussed by biologists in [6–8].

In this paper we present a new model, more appropriate to the case of geographic speciation. Again, many essential features are neglected. We are looking for answers to the following two questions: Under what conditions can a population survive in a given environment (more precisely, to what kind of an environment a population can adapt)? If the population may also migrate to another, initially empty, space—what are the necessary similarities between the two environments, in order that the population can develop in both regions?

The first (one region) problem may correspond to the situation when a certain area, previously empty, becomes populated by different species. The founders are a genetically random population. This also can be regarded as the first step in the peripatric speciation proposed by Mayr [8]. The second problem may be related to filling up of an ecological niche by a population adapted to a previous environment. Because of the limitations of our model (see below), we do not consider full speciation but rather adaptation processes which are the first stage of speciation processes [8]. We use the Monte Carlo technique.

The model.—The habitat for the investigated population is, as usual in the Monte Carlo simulations, represented by a two-dimensional ($L \times L$) square lattice with hard boundary conditions. The population consists of M individuals. No more than one individual may occupy a lattice site.

Each individual is characterized by its genome, i.e., a sequence of genes. The respective allele may be either dominant (A) or recessive (a). Here we consider diploidal organisms, hence the genotype of an individual sitting at the site i can be written as a sequence of 0's (aa), 1's ($Aa = aA$), and 2's (AA):

$$G_i = \{G_i^1, G_i^2, \dots, G_i^N\}, \quad G_i^\alpha = 0, 1, 2, \quad (1)$$

where N is the size of the genome.

We assume that the phenotype F of an individual, i.e., a set of its features, simply follows from its genotype. The relation between the two is far from being simple or well understood; e.g., in different environments the same genotype may manifest itself as different phenotypes and vice versa. In our simple model we neglect those complications. We assume that if $G_i^\alpha = 1$ or 2 then $F_i^\alpha = 1$ or, i.e., if $G_i^\alpha = 0$, then $F_i^\alpha = 0$. Hence

$$F_i = \{F_i^1, F_i^2, \dots, F_i^N\}, \quad F_i^\alpha = 0, 1. \quad (2)$$

Let us define the phenotype size as the number of phenotype features N . To produce an offspring two parents are needed, each contributing one allele, in such a way that particular features are inherited independently. After producing an offspring the parents die. An individual can become a parent provided it moved into a new location (see below).

The environment is characterized by a certain “ideal phenotype” \hat{F} . The survival probability p_i for an individual i during the time interval $(t, t + \Delta t)$ is defined by the similarity of its phenotype to the ideal one \hat{F} :

$$p_i(t) = N^{-1} \sum_{\alpha=1}^N F_i^\alpha(t) \wedge F^\alpha, \quad (3)$$

where \wedge denotes the common part of the two F 's. Hence, the ideal phenotype may be regarded as corresponding to an individual characterized by $p_i = 1$. We also define the average adaptation of the population at time t to the environment as

$$A(t) = M^{-1} \sum_{j=1}^M p_j(t). \quad (4)$$

A number of important factors, such as selection rules for breeding, mutation, genetic drift, Malthusian factor, etc., have been omitted here in order to keep the number of external parameters minimal.

Simulation.—The simulation algorithm consists of initially putting M individuals on the lattice. The genotypes of the individuals are random sequences of 0's, 1's, and 2's. Then in one time step we choose randomly an individual i ; from Eq. (3) we calculate its survival probability. We choose randomly an adjacent site to move an individual. Only if the site is empty is the move realized, and the mating partner is selected randomly from nearest neighbors. The condition that only the individual which moved can mate is equivalent in our model to all other acts necessary in life to breed. This activity is required here only from one partner. The parents produce x offsprings which are located in random empty places (if there are no such places the simulation stops) or in a given way on the lattice. The parents then die.

The simulations were run for the lattice $L = 30$, concentration of the founders $c = ML^{-2} = 0.2$, number of offspring $x = 3$. The averaging was over at least 20 and in some cases 100 samples. For the considered model and a given phenotype, we have found that populations with $c < 0.2$ died out rather fast, i.e., after $t \approx 500$ we got $c = 0$. The choice of $x = 2$ also led to extinction of the population, while for $x = 4$ and absence in the model of the factor relating death and fertility processes, the population overcrowds ($c = 1$) soon.

It should be noted that in an initial distribution of the phenotypes there will be twice as many 1's as 0's, since the genotypes of the initial population are random. The initial adaptation of the random population can be obtained from (4) as

$$A(0) = \frac{1}{3}(1 + m), \quad (5)$$

where $m \in [0, 1]$ is the relative number of 1's in the ideal phenotype \hat{F} . A population survived if, after the simulation time $t = 2 \times 10^4$ steps, we had $c > 0$.

Single region.—Let us consider a single environmental system, characterized by its ideal phenotype (pattern) \hat{F} , with a population initially having random sequences of genotypes (random population). Simulations lead us to the following observations.

Because of the way a phenotype is constructed from a genotype, the chance for a population to survive grows with the number of 1's in the pattern [see Eq. (5)].

The survival of the random population depends also on the size N of the phenotype. The chance of survival grows as N decreases.

For a fixed size of the phenotype and a defined pattern, there is a critical value of the initial adaptation given by a critical value m_c of the number of 1's in the pattern. Below this value all populations die out, and above it the ratio of surviving populations grows rapidly. m_c , as well as the rate of the surviving populations, increases with

increasing N . For $N > 10$ we observe a steplike increase in the number of surviving populations, similar to the curves known from phase transitions. Figure 1 illustrates the above observations. Although m_c increases with N , it never attains unity. Let us denote by m_{50} the relative number of 1's in the pattern necessary for at least 50% of the random populations to survive. As seen in Fig. 2, m_{50} initially increases with N quite fast, then asymptotically goes to a value ≈ 0.8 .

We may also define, in analogy to the general investigation of the birth and death processes [9], the probability of birth, λ , and of death, μ , in a unit time:

$$\mu(t) = 1 - A(t), \quad \lambda(t) = KA(t)c(1 - c). \quad (6)$$

From simulations we have found that $K = 3.26$. The simulation curves coincide with those following from Eq. (6). They are smooth and symmetric with respect to $c = 0.5$. Their shape does not depend on the structure of the ideal phenotype \hat{F} .

We define the similarity of the phenotypes of two individuals i and j as

$$\text{sim}^f(i, j; t) = N^{-1} \sum_{\alpha=1}^N F_i^\alpha(t) \wedge F_j^\alpha(t). \quad (7)$$

This is analogous to the "spin glass order parameter" $q^{\alpha\beta}$ introduced in this context by Derida and Higgs [2]. We may use sim^f to check the changes in the phenotypes of the population. As can be seen in Fig. 3(a) the phenotypes of the population become more and more homogeneous. After some 3×10^4 steps, about 90% of the population shows total similarity ($\text{sim}^f = 1$).

We can repeat the same kind of estimations for the genotypes, defining the measure of their likeness analogously as in (7). Time development of sim^g is shown in Fig. 3(b). The behavior is different from that in Fig. 3(a)—because of hereditary rules the shape of the genetic similarity distribution does not change significantly, although the mean value of sim^g increases with time. This increase is rather fast at the beginning and

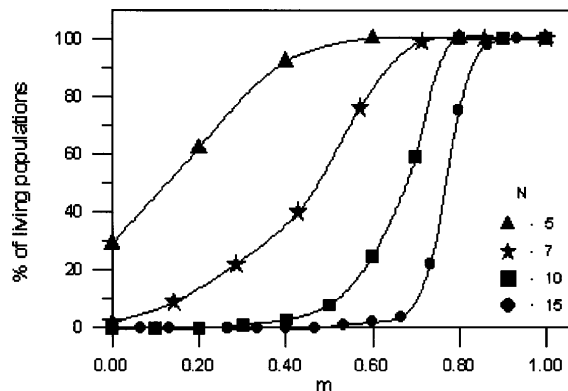


FIG. 1. The relation between m , i.e., the relative number of 1's in the pattern, and percentage of the surviving populations for different sizes N of the phenotype.

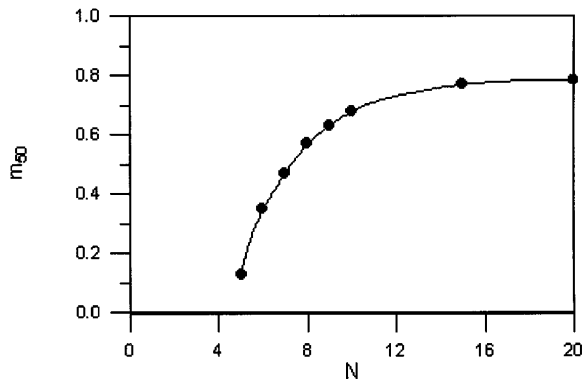


FIG. 2. The relation between m_{50} , i.e., the relative number of 1's in the pattern necessary for at least 50% of the populations to survive, and size N of the ideal phenotype.

then an asymptotic one. Even at much later moments the scatter of genotypes is quite large. These results agree with the observation in biology [10]—identical-looking individuals can contain different genotypes, since part of the genetic variety is masked by dominance.

We have found that the adaptation as well as concentration of the surviving population are characterized by a fast initial growth and then an asymptotic one. The adaptation is quite high— $A(t > 10^3) > 0.9$.

Another factor which influences, for a given pattern and its size, the survival of a population is the way the offspring are located. Since we consider only the case of each pair of parents giving birth to 3 descendants,

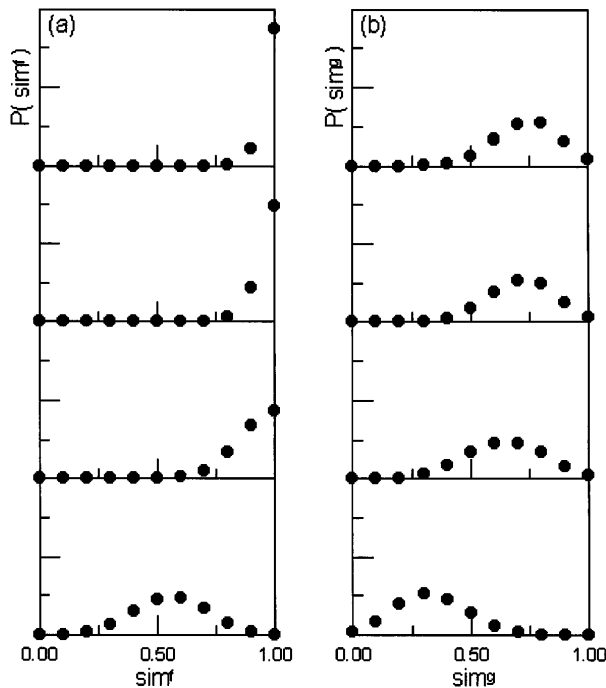


FIG. 3. The similarity distribution for phenotype (a) and for genotype (b). The earliest is at the bottom, and subsequent curves (moving upwards) are at intervals of 10^4 time steps.

we simulated two classes—in the first one, two of the offspring were put in the places of the parents and only the third one randomly; in the second case all three were located at random positions. We have found that the former way strongly increases the survival chances when the initial population is put in a cluster.

Finally, we should mention that even in such a simple model as ours, the role of the genotype is important. For the same initial distribution of phenotypes the population of homozygotes grows much faster and, lacking the malthusian factor, dies out of suffocation.

Two regions.—In order to answer the second question formulated earlier, let us consider two regions characterized by two ideal phenotypes (patterns) \hat{F}_I and \hat{F}_{II} . As before, initial random population is located in one of them, say, the first one. We want to know under what conditions this population can colonize the second region. We define, as in (7), the measure of similarity of the phenotypes of the two patterns

$$\text{sim}(I, II) = N^{-1} \sum_{\alpha=1}^N \hat{F}_I^\alpha \wedge \hat{F}_{II}^\alpha. \quad (8)$$

In Fig. 4 we present the change in concentration [Fig. 4(a)] and adaptation [Fig. 4(b)] of the population in the second region as a function of time. The curves are parametrized by $\text{sim}(I, II)$. For example, if $\hat{F}_I = 1111111000$ and $\hat{F}_{II} = 1111111111$, then $\text{sim}(I, II) = 0.7$.

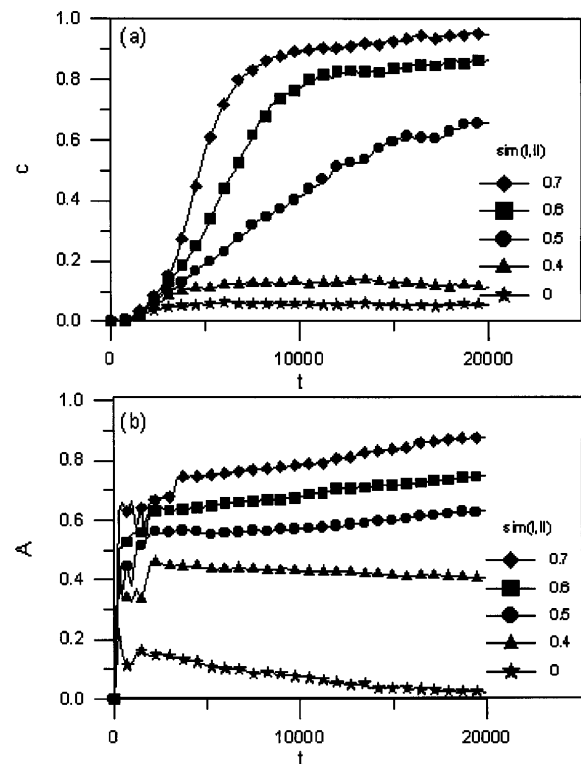


FIG. 4. The change in the concentration (a) and in the adaptation (b) of the population in the second region as a function of time.

It is evident from Fig. 4 that there is a critical value $\text{sim}_c(\text{I, II}) = 0.5$, below which a population which developed in I from an initial random one has no chance of populating the second region. This critical value does not depend on the size N of the phenotype, but it depends on the ratio of the length of the border between the two regions and the size of the first one. With the increase of this ratio, the critical value slightly decreases.

If $\text{sim}(\text{I, II}) \geq \text{sim}_c(\text{I, II})$ we can describe the growth of the population in the region II by the Verhulst-Pearl-Reed equation [11]

$$\frac{dc}{dt} = rc(1 - c), \quad (9)$$

where r is the growth rate. r increases with the increase of $\text{sim}(\text{I, II})$. The simulation results agree well with those coming from Eq. (9).

In Fig. 5 we show the increase with time of the number of offspring born in region II depending on the origin of their parents. Clearly the natives form the bulk of the population. The fast initial growth and subsequent stabilization follows from Eq. (6), i.e., $\lambda \rightarrow 0$ for $c \rightarrow 1$. The role of immigrants in colonization of region II is marginal. The influence of the population in II on the population in I is negligible also.

We have also investigated the time evolution of the similarity of individuals belonging to different regions. It turns out that the phenotypes in the two regions become more and more different. Each one is adapting to its pattern. We have hence a differentiation of the initial population. However, since the patterns have to be similar, the populations are never totally different; i.e., their similarity never goes to zero.

In conclusion, we have presented a simple model allowing the investigation of the conditions necessary for a population to grow in a given environment and colonize

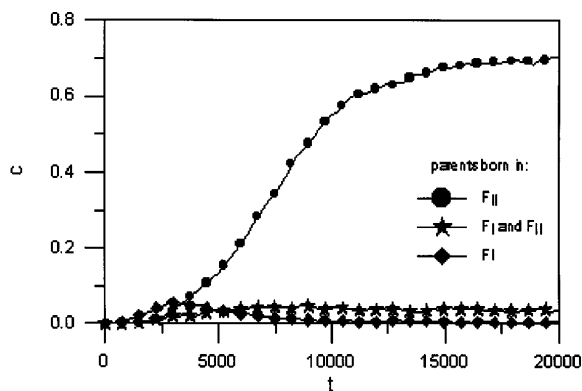


FIG. 5. The change in the concentration of the population in the second environment as a function of time, depending on the origin of parents.

a new, empty niche. We have shown that, within the limits set by our model, a random population must have an initial adaptation larger than a certain critical value in order to grow in a region with an ideal phenotype \hat{F} . The condition is related to the structure of \hat{F} . When the condition is met, we expect a very fast colonization of the region, i.e., an “explosion” of the population, such as the ones predicted, due to other reasons, in Bak’s model [3,4]. This adaptation of the average phenotype in the population to the pattern of the environment is just one of the sides of the natural selection. The population has a better chance of survival if the ideal phenotype is small and contains more 1’s. Moreover, if the population grows, the adaptation increases asymptotically to a value close to 1.

In the case of two regions we have a process of populating an ecological niche characterized by a pattern different from that of the main (first) region. We have found that there exists a certain minimum similarity between patterns in both regions in order that a population which adapted to the first one can successfully colonize the second one. With increasing time, the two populations will have different phenotypes, although never totally different. Since we did not introduce any rules for mating, both populations can still interbreed, and we do not define a new species in the second region. Instead, we have found under what conditions a part of the population can migrate and populate a different habitat.

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