

## Diversity and extinction in a lattice model of a population with fluctuating environment

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I study a lattice stochastic model of a mutating population sensitive to the influence of a fluctuating environment. The dynamics of the population stressed by linear and periodic disturbances is investigated. In agreement with previous studies of nonspatial models, I find a critical rate of change in the environmental variable beyond which the population becomes extinct, and I show explicitly that the presence of space in the model can affect the critical rate. Further, I study the diversity defined as the total number of different cell types present in the lattice as a function of intensity and frequency of the environmental disturbance. If the disturbance becomes fast and intense the population becomes extinct. Interestingly, I find that for moderate stresses the diversity increases with the intensity and frequency of disturbance. The transition between large diversity and extinction is sharp, implying that the populations with high diversity are generally the ones closest to the extinction threshold. When subjected to colored noise of increasing intensity the system grows in diversity but at the same time is more likely to become extinct. [S1063-651X(99)04111-2]

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### I. INTRODUCTION

In recent years much effort has been devoted to the study of spatial dynamics in biological systems. Present work in theoretical ecology and population biology has renewed the interest in the role of spatial patterns in ecological communities [1]. In addition to problems in ecology and conservation biology, spatial effects in model populations have attracted attention also in the field of complex systems. Examples include scaling theory and pattern formation, the species-area relation, fractal distribution of species, and chaos [1,2].

It is well known that the abundance of populations in nature is sensitive to fluctuations of the external environment. Nonspatial mathematical models and computer simulations have been used to study the fluctuations of population abundances responding to the environmental changes [3]. Most of the studies have concentrated on the short scale of some generations (ecological time), a time span in which natural selection hardly can be considered a force at play.

Fewer investigations have addressed the case in which the genotype and phenotype of individuals in the population can change in time via mutations and stabilizing selection induced by the effect a fluctuating environment. One reason is that (with the exception of microorganisms) most of the living populations cannot be studied experimentally for the long time scales necessary to observe mutation and natural selection. The possibility of an evolutionary change is thus more of interest in a paleobiological perspective. It is possible that environmental fluctuations had a major role in the evolution and extinction of populations, being possibly as important as interspecific competition [4].

Several authors [5–8] have considered nonspatial mathematical models for evolution and extinction in fluctuating environments. In Ref. [6] individuals of a finite population are subject to a stabilizing selection whose intensity depends

on the difference between the quantitative value of a given phenotype and an optimal value that fluctuates in time (the maladaptation directly affects the carrying capacity). In the presence of directional selection the phenotypic variable lags behind the environmental variable. If the lag becomes too large for individuals to efficiently replace the next generation, the species becomes extinct. Spatial models including dispersal have also been considered [9] in an analysis of the limits to dispersal and adaptation of a spatial population.

A related problem that has attracted attention is the maintenance of diversity in a community affected by environmental fluctuations. Theoretical arguments and field data suggest that diversity is larger at intermediate levels of disturbance. It has been argued that very little disturbance will result in a dominance of few species or subspecies, while a wildly changing environment determines the extinction of most of the types, irrespective of their level of adaptation [10]. On the much larger time scale of evolutionary time, it has been suggested [11] that speciation rates might be enhanced in populations living in disturbed environments.

In the present paper I examine the dynamics of a stochastic cellular automaton subject to an external fluctuating environment. Following the introductory discussion, I focus in particular on three aspects. First, by using a lattice model, space is explicitly taken into account as well as competition for space and dispersal. Second, the possibility of mutations among the cells of the lattice and the spread of the new cell type are directly included in the model. Third, I study the role of environmental fluctuations imposed externally. The explicit presence of space in the model introduces a new time scale, namely the spread time of a new cell type originating from a mutation. In general this may play a role in the dynamics of extinction and the diversity of the population. I investigate the extinction limit, analyzing the relation with nonspatial models and the role of environmental disturbance. The paper will then focus on the maintenance of diversity under environmental fluctuations and the relationship with the extinction risk.

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## II. MODEL

The fitness of living organisms depends critically on abiotic factors like temperature, moisture, or chemical composition of the environment [12]. In general the rate of biological processes follows an optimum response curve as a function of the value of the external factor, which is bell shaped. This implies an optimal performance for some intermediate value of the external variable and a poor response for extreme values. Other than the peak value, the optimum response curve is characterized by a width that is large for tolerant species and small for nontolerant ones.

In the present model a mutating population is distributed on a square lattice of coordinates  $(x,y)$  with at most one individual per site. A function  $E_{ext}(t)$  independent of the lattice site is assigned externally as a function of time according to a deterministic or stochastic law. This function represents an external abiotic factor affecting the fitness of the population, such as temperature, moisture, or chemical composition, as mentioned above. A function  $E_t(x,y)$  that depends on the position in the lattice represents the value of the best performance for the individual hosted in the cell of coordinates  $(x,y)$ . This quantity (which can also be called the phenotypic variable) changes with time due to mutations, diffusion to neighboring cells, or death. For our purposes a selection among the cell types is introduced, privileging the survival and growth of the types having a value of  $E_t(x,y)$  close to the external disturbance  $E_{ext}(t)$ . Let us examine all the possible processes in order.

(i) *Mutation.* Each mutation, occurring with probability  $\mu$  per lattice site and unit time, creates a new type of cell that is distinct from the others only by the index  $E_t(x,y)$ . If a mutation occurs at the lattice site  $(x,y)$  then  $E_t(x,y)$  changes as

$$E_{t+\delta t}(x,y) = E_t(x,y) + r, \quad (1)$$

where  $r$  is a random positive or negative number with Gaussian distribution of variance  $\sigma_\mu$ . The mutation rate is independent of the value of the phenotypic variable  $E_t(x,y)$  in the cell.

(ii) *Death.* The cells of the lattice are sensitive to the fluctuating field  $E_{ext}(t)$ . The probability of extinction  $\epsilon$  of the cell  $(x,y)$  is calculated as

$$\epsilon = \epsilon_0 (1 - e^{-\xi}) \delta t, \quad (2)$$

where

$$\xi = |E_{ext}(t) - E_t(x,y)|/s \quad (3)$$

is a parameter characterizing the deviation from the best condition,  $s$  gives the sensitivity of the cell type to the environmental variable,  $\epsilon_0$  specifies the extinction probability of the worst fit (for which  $\xi \rightarrow \infty$ ), and  $\delta t$  is the time step. Evidently this functional form for  $\epsilon$  favors the survival of types having  $|E_t(x,y) - E_{ext}(t)| \ll s$ .

(iii) *Dispersal.* The spreading of a type around neighboring cells and spatial competition between different types are introduced. Let an empty cell be surrounded by individuals of some type  $j$ . The probability per unit time that an empty square becomes occupied by a cell of type  $j$  is calculated as

$$P_d = 1 - \exp(-\gamma), \quad (4)$$

with

$$\gamma = gn_j^*(1 + \xi_j)^{-1}, \quad (5)$$

where  $g$  is a dispersal rate,  $n_j^*$  is the number of cells occupied by the type  $j$  and surrounding the empty site, and  $\xi_j$  refers to type  $j$ . If more types  $j_1, j_2, \dots$  surround an empty square, the one with lowest  $\xi_j$  (best fitness) is given privilege. If a square is already filled, it can be reoccupied by a new type only if among the neighboring cells there is one with a smaller  $\xi$ .

The time is discrete and the updating of each cell is synchronous. This kind of procedure is justified considering that for stochastic models like the present one there is practically no difference between synchronous and asynchronous updating, where only one cell is modified at each step [13]. After one process has taken place (for example, the death of some of the cells) the vector  $X(x,y)$  and  $E_t(x,y)$  representing the occupancy of each cell and the optimal value, respectively, are updated simultaneously so that the next process can occur sequentially. During one time step all processes (mutation, death, dispersal) have occurred once with proper fixed order.

A spatially explicit model of competing species similar to the one described in this work has been used, for example, in Refs. [13,14]. Their model, however, does not consider the role of environmental fluctuations, which is one of the major points addressed by the present paper.

## III. RESULTS

I first examine the dynamics of the model for some imposed disturbances. As a first application a linear disturbance of the form  $E_{ext}(t) = E_{ext}(0)(1 - \beta t)$  will be considered, where  $\beta$  characterizes the rate of environmental change. After the calculation has started with only one cell type filling the lattice, the number of coexisting types increases to a steady value. Figure 1 shows the optimal value  $\langle E_t \rangle$  averaged over all the cells of the lattice as a function of time. The various lines correspond to different values of the rate  $\beta$ . When  $\beta$  is small compared to a critical value  $\beta_c = \sigma_\mu \mu r(g)$  where  $r(g)$  is a function of the dispersal rate (to be discussed later) the population can follow efficiently the changing environment, adapting to the external field  $E_{ext}(t)$ . Increasing  $\beta$  to values larger than  $\beta_c$  causes the population to become extinct with certainty. Note that when  $\beta \sim \beta_c$  the population becomes less effective in following the environmental change, a consequence of the decrease in the average fitness.

The existence of a critical rate before extinction has been predicted theoretically in a series of studies. In Refs. [6,7] it was shown that the optimum lags with respect to the environmental variable. Figure 1 also shows that for  $\beta < \beta_{max}$  the rate in the change of the optimal value is close to the rate  $\beta$  of the environmental change. With increasing  $\beta$  the curves accumulate around the curve  $\beta \approx \beta_c$ . In this situation the rate of change in the optimal value becomes fixated to  $\beta_c$ .

Figure 2 shows  $\langle E_t \rangle$  as a function of time for a fixed  $\beta$  and varying  $g$ . The important role played by spatial effects is evident in the fact that populations with a high dispersal rate can follow more efficiently the environmental changes.

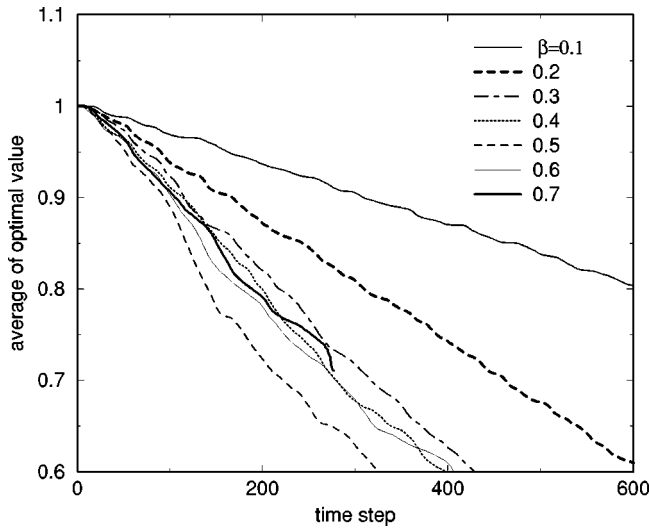


FIG. 1. Average value of the optimum calculated as  $\sum x_i [E_{opt,i} / E_{ext}(0)] / \sum x_i$  where  $x_i$  is the abundance of the type  $i$ ,  $E_{opt,i}$  its optimal value, and  $E_{ext}(0)$  the value of  $E_{ext}$  at  $t=0$ . The environmental variable changes linearly according to the expression  $E_{ext}(t) = E_{ext}(0)(1 - \beta t)$  with different rates  $\beta$ . The population subjected to the largest rate ( $\beta=0.7$ ) becomes extinct at a time step  $\sim 280$ . In the simulations the following values of the parameters are used:  $\mu_0 = 10^{-3}$ ,  $g = 0.5$ ,  $\delta t = 1/300$ ,  $\epsilon_0 = 0.9$ ,  $\sigma_\mu / s = 0.011$ , and  $S = 900$ .

Lynch, Gabriel, and Wood [15] have considered a nonspatial model for a microbial (nonsexual) population. When subject to a linear change, the maximum rate before extinction is found to be proportional to  $\mu r'^{1/2}$ , where  $r'$  in their model represents the rate of increase of the population at the optimum. Due to the intrinsic nonlinearities in the present model, I have investigated the relation  $\beta_c = \mu \sigma_\mu r(g)$  empirically from the output of the numerical program rather than analytically. Some results are shown in Fig. 3. Populations with large dispersal rate are less subject to the extinction risk. The

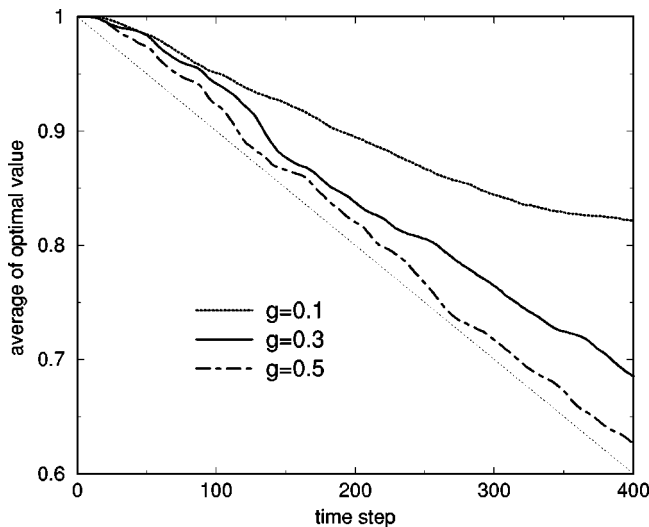


FIG. 2. Average value of the optimum phenotype of the population with fixed  $\beta=0.3$  (see caption of Fig. 1) and different dispersal rates  $g$ . The rest of the input parameters are the same as in Fig. 1.

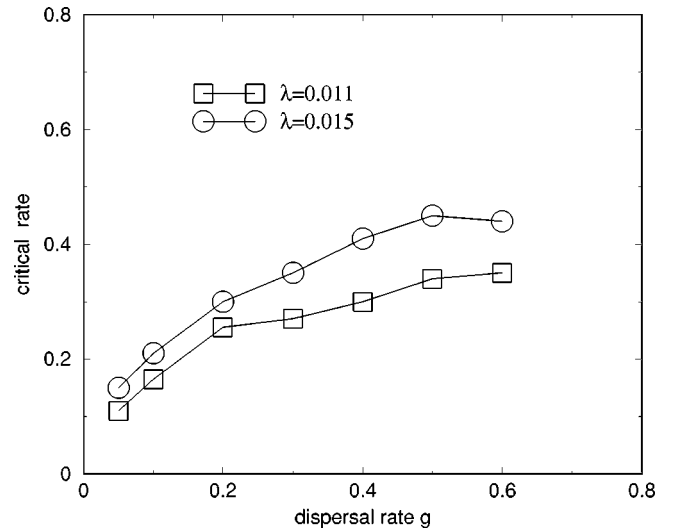


FIG. 3. Critical velocity of the environmental change  $\beta$  leading to the extinction threshold as a function of the dispersal rate  $g$  for a linear change of the disturbance. The rest of the input parameters are the same as in Fig. 1. Two different values of  $\lambda = \sigma_\mu / s$  are considered.

figure additionally shows that the proportionality of  $\beta_c$  with  $\sigma_\mu$  is also approximately respected.

I then considered a periodically changing disturbance of the simple form

$$E_{ext}(t) = E_0 + \Gamma \sin(\Omega t), \tag{6}$$

where  $\Gamma$  is the amplitude of the disturbance and  $\Omega$  the frequency. Periodic disturbances can be due to seasonal cycles or orbital-forced oscillations [4,15]. Figure 4 shows the average optimal value  $\langle E_t \rangle$  as a function of time. In agreement with Ref. [15] a time lag between the external disturbance  $E_{ext}(t)$  and  $\langle E_t \rangle$  determines a phase difference between the

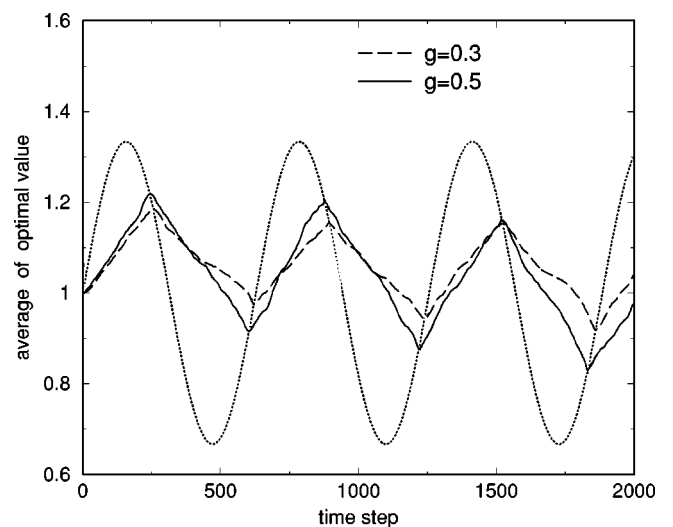


FIG. 4. Average value of the optimum phenotype when the population is subjected to periodic disturbance (indicated with a dotted line). Two different values of the dispersal rate are considered. The rest of the input parameters are the same as in Fig. 1.

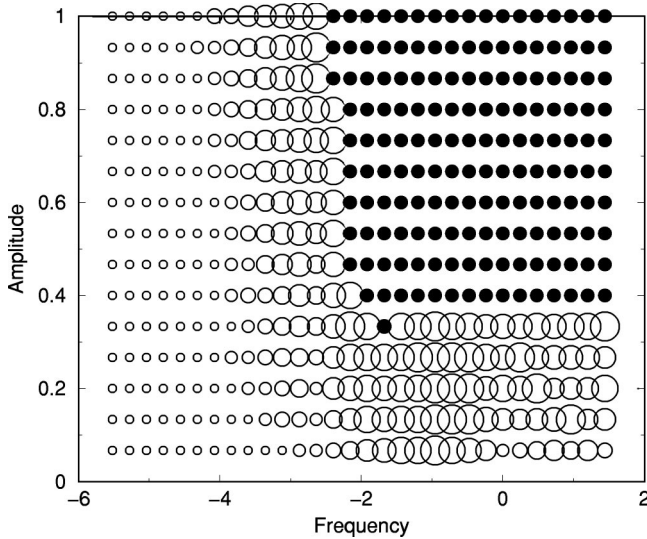


FIG. 5. Average number of cell types when the population is subjected to a periodic disturbance  $E_{ext}(t) = E_{ext}(0) + \Gamma \sin(\Omega t)$  is shown on a two-dimensional plane where the abscissa and ordinate are the frequency  $\Omega$  and the amplitude  $\Delta E/s$  of the disturbance. The area of the circle is proportional to the average number of cell types. Black dots denote the cases in which the whole population has become extinct before the simulation was completed. For each point the calculation lasted 1500 time steps. The parameters are the following:  $S = 900$ ,  $g = 0.2$ ,  $\mu = 10^{-3}$ , and  $\epsilon_0 = 0.9$ .

two curves. The role of space is again emphasized by changing the dispersal rate  $g$ . Note that larger dispersal rates result in a faster adaptation.

In the following I examine the maintenance of diversity, defined in the model as the number of different cell types present on the lattice. To study the diversity with imposed periodic disturbance, numerical calculations were performed within a range of different frequencies and amplitudes. For each run the average number of cell types present in the lattice during a simulation was calculated.

In Fig. 5 the axes represent the frequency and amplitude of the disturbance. The average number of cell types present in the lattice is proportional to the area of the circles. At low frequencies and small amplitudes few cell types are present on the lattice. A favorable mutation spreads in the lattice with a time of the order  $\tau \approx gS^{1/2}$  where  $S$  is the area of the lattice (times are in units of one time step and lengths in units of one lattice spacing). In this area of the graph, characterized by  $\Omega\tau \ll 1$ , a favorable mutation can spread before the external conditions have changed sensitively. Therefore, the optimal value is always close to  $E_{ext}(t)$  and the population is dominated by few well-fitted types.

At higher frequencies and small amplitudes the population tends to maintain higher diversity (bottom right in the graph). This feature can be understood recalling that a cell type can spread if on the average it is better fitted than neighboring types, and tends to retreat in the opposite case. If  $\Omega^{-1}$  becomes of the order or larger than  $\tau$  a cell type experiences cycles of good adaptation and maladaptation before it has time to retreat completely (in the bad period of the cycle) or to spread extensively (during the good conditions). This effect tends to conserve all the types whose optimal value falls around the average of the disturbance  $E_0$ . The range of the

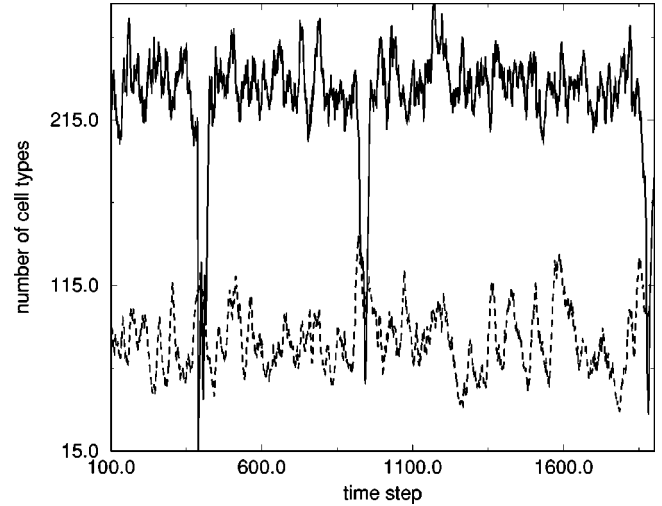


FIG. 6. Total number of types as a function of time for a disturbance  $E_{ext}(t)$  changing as a correlated (brown) noise of variance  $\sigma_E$ . The continuous line refers to a very disturbed environment ( $\sigma_E/s = 2.4 \times 10^{-3}$ ) while the dashed line refers to a weakly disturbed one ( $\sigma_E/s = 7.5 \times 10^{-4}$ ). Each simulation has been obtained perturbing 30 different systems. Diversity and extinction probability are larger for the strongly disturbed system. The input for all the calculations is the same time series.

optimal values that remain frozen is proportional to the sensitivity parameter  $s$  (the amplitude is reported as a ratio to sensitivity  $s$  in the graph).

At intermediate frequencies and high amplitudes a relatively great diversity is present as well. This can be interpreted as due to the effect of opportunistic cell types, whose chance of survival would be small if the environment were constant due to the predominant competition of the best-fitted type. The changing environment, preventing any type from becoming the best fitted, favors the coexistence and growth of several types.

Finally, at large amplitudes and frequencies the population is not able to follow efficiently the changing conditions and becomes extinct. This region is shown by dark circles in the graph. The balance between extinction and high diversity is quite sharp, as evident from the fact that in the graph the extinction region is completely surrounded by areas where the diversity is high. A population located at the boundary with the extinction region experiences on the average a large diversity, but at the same time is more subject to random sudden extinctions.

In addition to the number of cell types one can study the variance in the phenotypic variable. I found a trend similar to the one presented in Fig. 5, namely the region of extinction is surrounded by regions where the variance is large.

Real fluctuations of the environment and the biotic response can be more complex than linear or sinusoidal; in some cases they resemble more closely colored noise with a reddened spectrum [3,16]. This noise is characterized by fluctuations whose frequency decreases with the intensity according to a power law [16,17]. Figure 6 shows a simulation using a correlated brown noise with two different values of the variance  $\sigma_E$ . To gain better statistics I have considered 30 different populations. The average number of cell types is found to be larger for the case of strong disturbance (high



variance). The extinction probability also increases with the intensity of the disturbance. In fact, in the case of large environmental variance several populations became extinct simultaneously three times during the simulation (in correspondence with these events the number of cell types has plummeted in Fig. 6).

The results for correlated noise show that a large diversity is associated with strong levels of disturbance, but on the other hand strong disturbances may lead the population to a sudden extinction. It was shown in Fig. 5 that in the case of periodic disturbances, the extinction region is close to the area of large diversity. The results reported in Fig. 6 evidently parallel the ones for periodic disturbances.

#### IV. CONCLUSIONS

To investigate the robustness of the model I considered several different values of the input parameters and studied some variants of the program. In general, an increase of the mutation rate causes the extinction region to shrink, while an increase of the spread rate determines an opposite behavior. Increasing the total time of the calculation can produce a different shape of the plot in Fig. 5, but the qualitative features, which are the ones addressed by the present study, do not change. A possible dependence of the mutation rate  $\mu$  on the state of maladaptation has also been investigated taking  $\mu$  in the form  $\mu \rightarrow \mu \exp(-\xi)$ . This also does not produce qualitative differences with respect to what is shown.

Concluding, the effect of environmental fluctuations on a simple lattice model of a population has been considered. In the case of linear variations of the environmental variable I have found a critical rate beyond which the population cannot keep pace with the environmental change. The situation is more complex for periodic disturbances. If the period of the disturbance becomes comparable to the spreading time of cell types on the grid, essentially all cell types whose optimal value falls in the range spanned by the environmental vari-

able will possibly be maintained. Strong variations of the environment can keep a larger diversity in the system, but on the other hand they also trigger more frequently an extinction of the population.

It is possible to speculate on the main consequence of the model, the maintenance of high diversity at intermediate levels of disturbance. The “intermediate disturbance hypothesis” in its modern formulation has been recently examined in a series of studies [11]. In essence the hypothesis states that habitats with little or very strong disturbance are both poor in species, the former because of the dominance of a few of the most competitive species and the latter because the frequent extinctions deplete the diversity. The present model lends weight in a natural way to the hypothesis of a maximum diversity at intermediate disturbances.

The model I have described obviously presents several limitations. A first simplification is the absence of interbreeding among different cell types. Second, the response of populations to a changing environment is likely to be a very complex process in nature, implying the opening of adaptive space whenever a species becomes extinct, creating empty patches and so on. In addition, it can be expected that the death of several individuals following a strong environmental stress determines the isolation of subpopulations where phenotypic changes are believed to proceed faster. The fact that in the present model a higher diversity is found without founder effect following the isolation of subpopulations might be of interest for the modeling of sympatric speciation induced by environmental stress. Finally, I have considered only one single trait related to only one external variable. It is possible that more complete models will allow for a direct comparison with living and fossil populations.

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