

Dynamics of coevolutionary processes

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Two different models for biological evolution that exhibit critical self-organization and punctuated equilibrium are studied with a view to numerically compare two possible types of adaptive dynamics: A species can evolve towards states of increasingly better adaptive abilities via the simple, original Darwinian scenario (evolution in a stationary environment) or in the recently conceived coevolutionary fashion. A numerical study of these two types of adaptive dynamics is performed, within the framework of two distinct mathematical models of evolution. [S1063-651X(98)02205-3]

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I. INTRODUCTION

In recent years there has been great activity in the study of physical models able to mimic biological evolutionary processes. As a consequence, much light has been shed on diverse features of the rich Darwinian landscape. Of course, intriguing problems still await elucidation. Among them we single out here the following one. It is generally accepted that the traditional view of Darwinian evolution, according to which the most fit of random mutants are selected, faces a major problem [1–7]: *It is much too slow to account for real evolution.* Bak has lucidly described the difficulty [1]: If, for the sake of argument, we imagine the outer world frozen (for a while) and try to construct from scratch an equally fit species by recourse to *engineering techniques rather than by evolution*, we will be forced to accept that eons are needed. By starting at a random configuration one certainly will reach a wrong and much less fit maximum. It would be necessary to systematically go through all configurations, involving exponentially large times. Shapiro [8] and Hoyle and Wickramasinghe [9] have developed similar argumentative lines.

Coevolution, as an alternative to simple evolution in a fixed environment, has been proposed as a way out of this dilemma. The dynamical script for such a process reads as follows: Individual species adapt in slow fashion to a changing environment without ever climbing high fitness barriers, which allows for a fast evolutionary process [1]. Quoting Bak's words [1], "What the individual sees as his superior fitness may better be characterized as a self-consistent integration into a complex system. Biology constructed the solution to the fitness problem together with the problem itself. It is much simpler to construct a complicated crossword puzzle by a coevolutionary process than to solve it by trial and error."

In order to fix the terminology we will agree to reserve

the word "evolution" to describe the traditional Darwinian point of view: Species "adapt" to a fixed environment, to which the remaining species, of course, "contribute." "Coevolution," instead, refers to a dynamical process in which all species simultaneously "evolve," that is, a single species must adapt to a changing environment in a self-consistent fashion.

Some recent results indicate that the latter adaptive mechanism yields better results than the former in some evolutionary scenarios [10,11]. However, *a test of this assertion within the context of physical models (coevolutionary dynamical systems) remains to be performed.* Remedying this situation constitutes the leitmotif of the present effort, where we tackle the evolution vs coevolution competition (the investigation of which should motivate any worker in the field) in *numerical terms*, by studying the different dynamics within the framework of two different models: (i) the celebrated *NKC* (the accepted terminology) models of Kauffman and Johnsen [12,13], which have proved to be of great utility in explaining many evolutionary features of the terrestrial ecosystem (for example, radiation and stasis as generic properties, the Cambrian explosion, Permian quiescence, and rederivation of Von Baer's laws) [12,14], and (ii) recently a more general model of biological evolution [15,16] that exhibits robust critical behavior with punctuated equilibrium [17] without external tuning. Interesting "realistic" features of this model include the prediction of power laws governing the extinction distribution curves [18] and its ability to reproduce Sepkosky's evolutionary activity curves [19] and lifetime species distribution curve [19,20] constructed on the basis of fossil records.

We intend to provide some answers concerning the coevolution vs evolution question by comparing fitnesses resulting from different dynamics (i.e., coevolutionary vs evolutionary ones) as applied within the framework of a given model, in the two cases enumerated above. "Fitness" is a relative concept and can be meaningfully applied only within a given ecology. Thus the mean fitness of some species in a given ecology (read here, a given model) can be compared with its mean fitness in the same model (but with a different evolutionary dynamics). We perform this kind of comparison here within the framework of the two models referred to above. [Indeed, we compare *different dynamics* (coevolutionary and evolutionary), not *different ecologies*.] Once the fitness land-

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scape is defined (for instance, by giving the N , K , and C values in the case of the Kauffman models), the model's statistical nature is fixed (as, for example, the number of local maxima and their distribution, see [12]). Given the landscape, different adaptive strategies (and diverse dynamics) become possible (e.g., different mutation rates and genetic material exchange among individuals) in order to attain either a global maximum or a "good" local one. The effectiveness of recombination, for instance, depends in subtle ways upon the ruggedness of the adaptive landscape (see Chap. 2 of [12]). It is then obligatory to compare strategies for fixed values of the above parameters, i.e., for a given type of surface, and such will be our philosophy in studying evolution vs coevolution. Fitness is a landscape-related concept. Comparisons are to be made for the same surface. It should be remarked that, within the present context "more fit" does not mean "more complex." We are not discussing complex evolution here. The "complexity" of our "organisms" remains approximately constant in our model insofar as the number of "genes" behaves in such a manner. A terminological point merits some discussion. We know that the coevolutionary picture is not incompatible with Darwin's theory since the species are still evolving by random mutations and selection of the fitter variants, but in a variable landscape. The coevolutionary picture, however, may have some consequences at the macroevolutionary level, such as punctuated equilibrium, that Darwin apparently was not aware of. We shall differentiate between "simple" evolution, or the original Darwinian mechanism, and coevolution, or the neo-Darwinian one.

II. THE NKC MODEL

In Kauffman and Johnsen's NKC models [12,13] each species is represented by an N -site chain. The state of each site (or gene) may adopt one of two possible values: zero or one. The degree to which a species is adapted to the environment is numerically measured by the so-called fitness (F) variable. The larger the F value, the better our species is adapted to its environment. For the k th species F_k is obtained by summing over the site contributions. The site contribution, in turn, depends on (i) the state of other (K , say) genes of the k th chain and (ii) the states of *other* species' genes (amounting to C genes, say). The fitness contribution of each site, for each of the 2^{K+C+1} combinations of states of itself, on the one hand, and each of the $K+C$ other sites influencing it, on the other, is assigned at random at the moment of switching on the simulation process. At this moment, the $K+C$ sites that are to influence any particular site are randomly chosen as well. This choice is not modified, afterward, during the course of the simulation process. In it we shall deal with M species (a number that remains fixed).

The evolutive process proceeds as follows. We start from a random initial configuration (i.e., the N_i initial site states, $i=1, \dots, M$, are randomly chosen). In *each* of a (long) series of time steps a particular species (the j th, say) and one of its associated sites are both randomly selected. This site state is modified and the (new) F_j value is computed. If, as a consequence of this modification, F_j grows, this change in the site state is retained. Otherwise, it is discarded and the site state is returned to its previous condition.

Consider now single-species (again the j th one, say) evolution. The site states of the remaining $M-1$ ones are "frozen." In these circumstances the evolutive process may be visualized in terms of an "adaptive walk" on a rugged "fitness landscape" (on the vertices of an N -dimensional Boolean hypercube). This adaptive walk stops if the species gets trapped at a local maximum. Kauffman shows [4] that the ruggedness of the fitness landscape grows with K (in the geneticist's parlance, K measures the richness of epistatic interactions among the components of the system). For $K=2$ the structure of the fitness landscape is such that the F_j mean value $\langle F_j \rangle$, evaluated over a large number of distinct simulation runs, is maximized.

In a coevolutive system (i.e., all species simultaneously evolve), we need to consider the fact that both the fitness and the fitness landscape of each species become functions of what happens with the *other* species (by virtue of the C couplings). Thus, because of the couplings, an adaptive move by one species projects onto the fitness landscapes of the other species and alters those fitness landscapes more or less profoundly. Over time, each species jockeys uphill on its own landscape and thereby deforms the landscapes of its ecological neighbors. Any such move by one species may increase or decrease the fitness of each neighbor on the latter's landscape and alter the uphill adaptive walks accessible to that neighbor.

It is interesting to mention that [12] in the coevolutive scenario, the average value of $\langle F_j \rangle$ over the M different species $\langle \langle F \rangle \rangle$ becomes a maximum for some K value (let us call it K^0) that depends upon M , N , and C . For $K=K^0$ the system evolves at the "edge of chaos," that is, for $K > K^0$ the ecosystem behaves as a quasioordered system (i.e., most species freeze over and just a few undergo significant alterations). On the other hand, for $K < K^0$ most species exhibit variations during the evolution process, with some frozen islands. The edge of chaos corresponds to that situation for which a frozen component percolates across and covers the ecosystem. It has been analytically shown, for the special instance $K=N-1$ [5], that under some conditions a phase transition takes place from a frozen to a chaotic phase.

III. FERNÁNDEZ, PLASTINO, AND DIAMBRA'S MODEL

We consider now the Fernández-Plastino-Diambra (FPD) model of Ref. [15]. We deal with M distinct, interacting biological species, each of which is represented by a vector in \mathcal{R}^N . The components V_α^i of \vec{V}^i represent different phenotypic features (α, β, \dots) that are to be affected and modified by the evolutive process. The degree to which the i th species is "adapted" to the environment is represented by a quantity F_i , to be called its fitness:

$$F_i = \sum_j^M \sum_{\alpha, \beta}^N g_{\alpha\beta}^{ij} V_\alpha^i V_\beta^j + \sum_\gamma^N V_\gamma^i A_\gamma^i, \quad i=1, \dots, M, \quad (1)$$

where the hypermatrix $g_{\alpha\beta}^{ij}$ provides the details of the inter-species interaction and the second summand on the right-hand side is an "environmental" one (see below). We assume $g_{\alpha\beta}^{ij} = -g_{\beta\alpha}^{ji}$. This is a reasonable assumption because if the α feature of the species i gives it a competitive edge

against the β feature of the j species, the latter gives it, of course, a competitive disadvantage against the former (symbiosis is excluded). The A_γ^i matrix mimics the environmental influence (such as climate and geography) over the γ feature of the i th species.

Of course, the components of \vec{V}^i must necessarily exhibit some degree of correlation, as genes are simultaneously involved in several phenotypic features. We represent this correlation by recourse to mappings between a set of $k+1$ real parameters and each of these components, i.e.,

$$f_\beta: a_0^i, \dots, a_k^i \rightarrow V_\beta^i, \quad (2)$$

that is,

$$V_\beta^i = f_\beta(a_0^i, \dots, a_k^i), \quad (3)$$

with f_β an arbitrary function. The set a_0^i, \dots, a_k^i defines in fact the i species. As a result of biological mutations, these parameters are allowed to vary with time.

The components of V denote different phenotypic features of the species that this vector represents. These features are correlated, via the a 's, in the manner just described. Genetic changes, here mimicked by modifications in the a values, drive the evolutive process. The correlations just mentioned constitute an essential aspect of the model. Without them, a given species might (eventually) attain, after a series of appropriate mutations, *any* phenotypic feature whatsoever. This does not happen in nature. Changes in the a 's are to be understood as reflecting uncorrelated genetic modifications (changes in one or more bases in one or more genes), while changes in the V 's represent the concomitant phenotypic modifications that, to a greater or lesser extent, will be mutually correlated.

The system evolves in the following fashion. We start with an arbitrary initial configuration (the a_i 's are randomly chosen within $[-1, 1]$) and, in each of a series of time steps, mutation effects are mimicked by slightly modifying the a_i 's for the l th species. Both the selection of l and the nature of the changes are random. The condition $|\vec{V}^i| = 1$ is enforced so as to avoid unrestricted growth (with time) of $|\vec{V}^i|$.

A particular mutation (change in a given a) is "accepted" if it increases the corresponding fitness (as a consequence of such a mutation F_i grows). The a change is retained in this case. Otherwise it is discarded and the a_i 's end up with their previous values.

Extensive numerical studies suggest that such a system never reaches an equilibrium situation, which could be guessed from the skew symmetry of g^{ij} [21]. The number of species M is kept constant for the sake of simplicity.

Also for the sake of simplicity we choose, as in [15] (i) our hypermatrix in the form

$$g_{\alpha\beta}^{ij} = k_{ij} \delta_{\alpha\beta} \quad (4)$$

and (ii) $A_\gamma^i = 0$. Thus Eq. (1) reduces to

$$F_i = \sum_{j=1}^M k_{ij} \vec{V}^i \cdot \vec{V}^j, \quad i = 1, \dots, M, \quad (5)$$

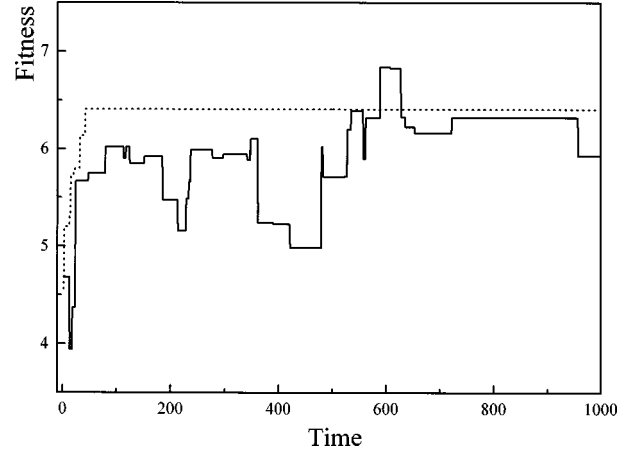


FIG. 1. A typical example of single-species, NKC fitness evolution (vertical axis, arbitrary units). The full line corresponds to coevolutive results, the dashed line to a simple Darwinian scenario. In both cases $M=20$, $N=10$, $K=4$, and $C=3$.

where $k_{ij} = -k_{ji}$. A given percentage of the k_{ij} 's is set equal to zero. The remaining k_{ij} 's are randomly chosen within $[-1, 1]$ (for $i < j$). These values are kept constant throughout. We call C the fraction of nonvanishing k_{ij} 's. These simplifications notwithstanding, a complex enough dynamics ensues that can account for important details of fossil records. As polynomials are the basis of any reasonable function space, the "correlation functions" discussed above can be chosen in a simple and general fashion as k -degree polynomials [cf. Eq. (3)]

$$f_\beta = \sum_{n=0}^k a_n x^n, \quad x = \beta/N, \quad (6)$$

so that

$$V_\beta^i = \sum_{n=0}^k a_n^i (\beta/N)^n.$$

IV. COMPARATIVE DYNAMICS

A. NKC model

We present here our main results, beginning with those obtained with reference to NKC models. We compare evolutive vs coevolutive dynamics within a constant scenario, that is, for identical values of M , N , K , and C (remember that we compare different adaptive dynamics, *not* different ecologies).

The typical temporal evolution of F for a single species is depicted in Fig. 1. We take $M=20$, $N=10$, $K=4$, and $C=3$. In the coevolutive scenario F starts increasing rapidly and then stabilizes itself, with oscillations around some fixed value. After 30 000 generations no deviations from this pattern are appreciated, i.e., equilibrium is not reached. Figure 1 also displays, for the sake of comparison (identical values of M , N , K , and C), the single-species fitness F of a given species in a Darwinian evolutionary scenario ($M-1$ species frozen). Equilibrium is rapidly reached.

These results can be better understood with reference to Fig. 2, a fitness versus K plot. Here we study the coevolu-

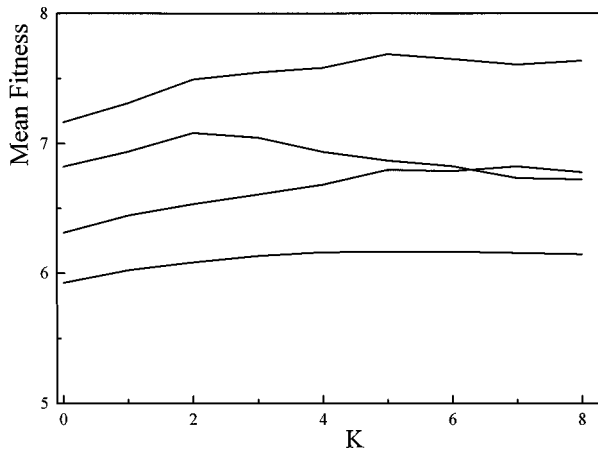


FIG. 2. Average equilibrium fitness versus K (arbitrary units). The curves, from top to bottom, correspond, respectively, to *a*, the Darwinian scenario, with the maximum number of mutations per generation (MMs) equal to 4; *b*, the same as *a* but with the MMs equal to unity. *c*, the same as *b* but for a coevolutionary scenario; and *d*, the same as *c* but with the MMs equal to 4.

tionary mean fitness $\langle\langle F \rangle\rangle$ and the Darwinian mean $\langle F \rangle$. The average over distinct simulations is taken by running 30 of them in coevolutionary scenarios (averaging over all coevolving species) and 100 in Darwinian evolutionary ones (30 000 time steps have been taken in the oscillatory regime of the former in order to compute mean values).

Features already described by Kauffman are also present in Fig. 2. The Darwinian mutant variant $\langle F \rangle$ exhibits a peak at $K=2$. On the other hand, the coevolutionary $\langle\langle F \rangle\rangle$ peak is attained at some C -dependent K^0 , where it is supposed that the system evolves at the edge of chaos: For $K > K^0$ the evolutionary process is a ‘‘poor’’ one, as the system is mostly frozen, for $K < K^0$ the system behaves in a rather chaotic fashion, which diminishes its adaptive capacities.

Assume now that species evolve by changing the states of up to n sites in each time step, the actual number being randomly determined. An important point to be mentioned with regard to the simulations reported in Fig. 2 is that *the fitness level reached by the coevolutionary system is smaller than the one found in the Darwinian process*. This difference is rather small for systems that evolve in such a fashion that only one gene is allowed to vary in each step (species ‘‘explore’’ variations in just one of the sites per step), but grows when we allow for larger n values. This is seen in Fig. 2 for $n=4$ situations, a better simulation of biological ‘‘reality.’’ The F value of species evolving in a frozen environment augments because the larger exploration step allows for escape from the trapping by some local maxima that shorter exploration steps would not be able to evade. The coevolutionary F , instead, does not necessarily benefit from larger exploration steps. The environment also changes rapidly and an accelerated ‘‘red queen’’ effect obtains [6].

Deviations with respect to the F mean value are rather insensitive to the value of K . In the coevolutionary scenario the standard deviation varies between 1.5×10^{-2} and 3×10^{-2} . In the Darwinian scenario variations between 7×10^{-2} and 9.5×10^{-2} are encountered.

The average time needed to reach a stable evolutionary plateau is plotted in Fig. 3. In the simple Darwinian case, the

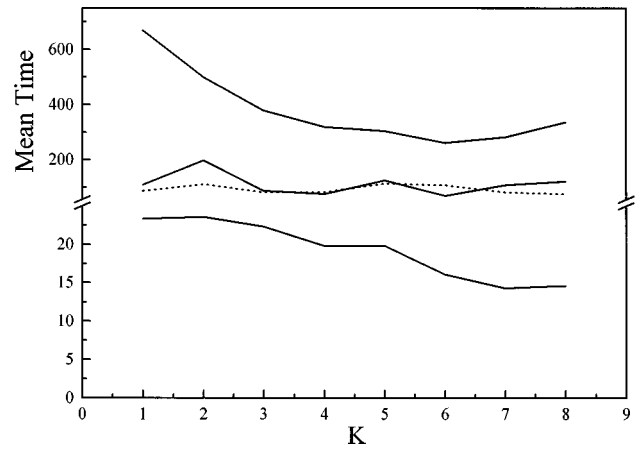


FIG. 3. Relevant ‘‘evolution times’’ versus K (arbitrary units). Top curve, average time (see the text) for a coevolutionary system; middle curves, minimum evolutionary time required (see the text) for coevolutionary stability (full line) and maximum Darwinian time needed to attain a stable adaptive plateau (dotted line) (they are of the same order of magnitude); lower curve, Darwinian average time.

average time is an average taken over all species. In the coevolutionary case, the average time is the time needed to reach, for the first time, that F_{mean} value corresponding to a given value of K . As suggested by Fig. 1, the former average time is smaller than the latter. Additionally, we display in Fig. 3 the *maximum* time needed to reach a stable evolutionary plateau (Darwin scenario) and compare it to the minimum time required to attain a stable situation (albeit with oscillations) in the coevolutionary case. The conclusions reached above with reference to the average time still apply. These results do not change if we modify (singly or jointly) C , M , and/or N .

B. FPD model

We consider now the FPD model [9,10]. Single-species fitness is the subject of Figs. 4 and 5, where time evolution is studied ($M=17$, $N=7$, $C=0.5$, and $K=5$ in both figures). Figure 4 corresponds to an arbitrary species coevolving with

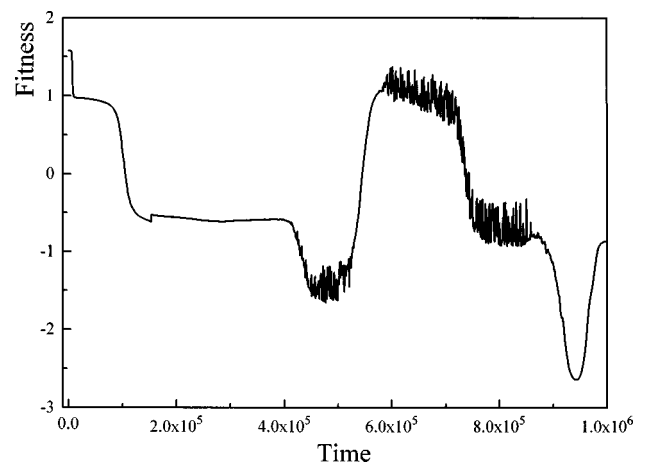


FIG. 4. Typical coevolutionary single-species fitness versus time (arbitrary units) for the FPD model ($M=17$, $N=7$, $C=0.5$, and $K=5$).

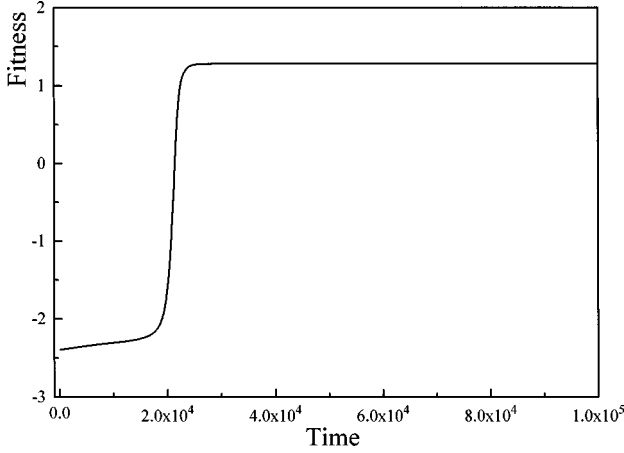


FIG. 5. Typical FPD Darwinian single-species fitness versus time (arbitrary units). Note that the scale here is different from that of Fig. 4.

the remaining ones, while Fig. 5 depicts Darwinian evolution in a frozen environment (the remaining species do not evolve). Strong fitness oscillations are appreciated in the coevolutionary case, while, in the Darwinian scenario, the single species fitness grows swiftly and monotonically, reaching a maximal plateau.

The time-average fitness in the coevolutionary situation vanishes [cf. Eq. (5); in summing over i , the antisymmetric nature of the k_{ij} enforces this result independently of the C , M , or N values). In the Darwinian instance, the time-average fitness is estimated as follows. The single-species fitness is given by

$$\begin{aligned} F_i &= \sum_{j \neq i} k_{ij} \vec{V}^i \vec{V}^j = \sum_{j, \alpha} k_{ij} V_\alpha^i V_\alpha^j = \sum_{\alpha} V_\alpha^i \sum_{j \neq i} k_{ij} V_\alpha^j \\ &= \sum_{\alpha} V_\alpha^i W_\alpha^i, \end{aligned} \quad (7)$$

with

$$W_\alpha^i \equiv \sum_{j \neq i} k_{ij} V_\alpha^j. \quad (8)$$

As just one species evolves here, the species subindex i can be disregarded without loss of generality. Thus

$$F = \sum_{\alpha} V_\alpha W_\alpha = |\vec{V}| |\vec{W}| \cos \theta, \quad (9)$$

where θ is the angle between the vectors \vec{V} and \vec{W} . In a given simulation run F reaches a maximum and then remains constant. If the correlation among the components of \vec{V} is small enough, the maximum obtains for $\cos \theta = 1$ (the vector \vec{V} becomes parallel to \vec{W}). In a more general instance $\cos \theta$ is smaller than unity. Thus we can adopt the approximation (remember that $|\vec{V}| = 1$)

$$F_{\max} = |\vec{W}|. \quad (10)$$

One averages over all possible simulation runs. In order to estimate the value of $\langle |\vec{W}| \rangle$ we employ the result

$$|\vec{W}|^2 = \sum_{\alpha} W_\alpha^2 \quad (11)$$

and proceed to work in a mean-field fashion with

$$\langle |\vec{W}| \rangle^2 \approx \langle |\vec{W}|^2 \rangle, \quad (12)$$

so that

$$\langle F_{\max} \rangle \approx \sqrt{\langle |\vec{W}|^2 \rangle}. \quad (13)$$

This approach entails an error of the order of a standard deviation (for any quantity x we have $\sigma_x^2 = \langle x^2 \rangle - \langle x \rangle^2$). Now, with the notation $k_j \equiv k_{ij}$ (see above the comment on the species subindex i) we have

$$W_\alpha^2 = \sum_j \sum_l k_j V_\alpha^j k_l V_\alpha^l, \quad (14)$$

so that, as no correlation exists between the k 's and the V 's,

$$\langle W_\alpha^2 \rangle = \sum_j \sum_l \langle k_j k_l \rangle \langle V_\alpha^j V_\alpha^l \rangle. \quad (15)$$

Notice that the k_j themselves are uncorrelated (they are randomly chosen in $[-1, 1]$), so that

$$\langle k_j k_l \rangle = \langle k_j^2 \rangle \delta_{jl}. \quad (16)$$

Summing up, we have

$$\langle W_\alpha^2 \rangle = \sum_j \langle k_j^2 \rangle \langle V_\alpha^j{}^2 \rangle, \quad (17)$$

where $\langle k_j^2 \rangle = 1/3$ and $\langle V_\alpha^j{}^2 \rangle \approx 1/3$ (the last equality holds if the correlation among the V 's is small enough that the V_α^j 's themselves could have been randomly chosen in $[-1, 1]$). Replacement of these results in Eq. (13) yields

$$\langle F_{\max} \rangle \approx \sqrt{\sum_{\alpha, j} \frac{1}{9}} = \sqrt{\frac{CMN}{9}}. \quad (18)$$

We see that, independently of C , M , or N , the Darwinian average fitness is better (of a superior quality) than the corresponding coevolutionary quantity.

In Sec. IV A we have discussed average and minimum times. In this respect, the situation here is of an instructive character indeed: The coevolutionary average fitness *vanishes* and the individual (coevolutionary, single-species) fitness wildly oscillates around zero (see Fig. 4). On the other hand, in the simple Darwinian stage the fitness swiftly increases monotonically until saturation is reached.

V. TIMING AND TIMES

In thinking about evolution, one confronts the question of how hard it may have been to “find” a particular structure or property. Such problems appear most trying when the structure or property in question requires the concerted action of a

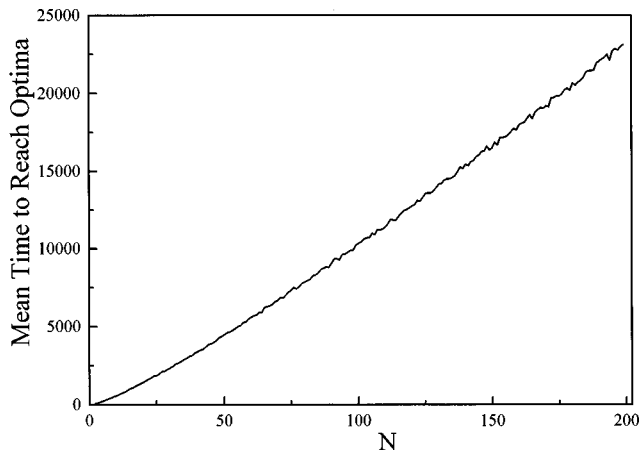


FIG. 6. Average number of steps required to reach maximum fitness in the NKC model as a function of the chain length N (for $K=0$ and $A=20$). Each point is obtained by averaging the results of 1000 simulation runs. It is clearly seen that the required number of steps tends to increase more slowly than N^2 .

large number of constituents. If we explore the different possibilities via random trials, the time needed to find such a structure increases exponentially with the number of genes (or amino acids) that the task demands. As a corollary, evolutionary times much longer than the age of the Universe would be required even for a “humble” bacteria. Let us give the name of *plausibility argument* to the previous statement, often used in rebuttals of orthodox evolution in the manner of Darwin. For more detailed examples of the plausibility argument see Refs. [8] and [9].

In the light of the present calculations, serious doubts are cast over such a line of reasoning. For the sake of argument, let us consider a very simple scenario within the framework of the NKC model: Our “fitness surface” (or fitness landscape) exhibits just one maximum and we are concerned with an organism that needs several steps to approach this maximum. This is the $K=0$ case. For each gene an optimal state exists (zero or one), independently of the state of the remaining genes, and we can assume, without loss of generality, that the maximum fitness obtains when all sites are in state 1. Initially, our organism occupies a given (randomly determined) position on the fitness surface and we aim to get it transported to the “best” site. According to our rules, we randomly select one site and modify it if its state is 0 (otherwise, we do nothing). This process is repeated over and over. How many steps (S) are required (in average) to attain maximum fitness? Actually, $S \ll 2^N$ (the number of distinct chains). The mean number of trials required to reach a particular site (and thus be sure that it will be assigned a 1) is N and we must repeat this procedure N times (in order to reach all sites). Thus $S \leq N^2$. The problem with the plausibility argument is that it ignores the fact that each time a beneficial mutation is retained the number of remaining configurations to be explored steadily decreases and with it the exploration time.

Of course, if instead of just 2, the number of states per gene is 20 (the number of amino acids), the argument continues to hold. The upper bound for the number of steps is now AN^2 , with A the number of states per site. Figure 6 depicts the (average) results of a series (indeed, 1000 for

each point) of simulation runs in the $A=20$ case. A slower rate of growth than in the AN^2 case is appreciated. For surfaces of a more complex shape, the presence of multiple maxima allows, of course, for an even smaller S value.

Thus, in order to refute the plausibility argument one does not need to appeal to the clever coevolution arguments in the manner of Bak [1] or to principles of self-organization, in the manner of Kauffman [12] (i.e., using the argument that many properties of organisms may be probably emergent collective properties of their constituents). This is a correct argument, but not the only solution to the problem of “adequate” temporal lapses.

VI. CONCLUSIONS

We have attempted to show that the plausibility argument needs careful re-examination, as it ignores the fact that, as it evolves, an organism retains favorable mutations, which considerably reduce the “accessible configuration space.” In other words, “memory” constitutes an important evolutive feature that the plausibility argument disregards and memory accelerates the evolutive process.

In turn, the coevolutive argument [10] asserts that in coevolution, each species dynamically deforms the fitness landscapes being traversed by the other species in such a way that both can continue to climb uphill without getting stuck on local maxima. When they do get stuck, the maxima get turned into minima (due to coupling among landscapes), which can be climbed out of by simple Darwinian means. Thus coupled species evolving by Darwinian means can bootstrap each other up the evolutionary ladder far more efficiently than they can climb it alone. By competing with one another, coupled species improve one another at increased rates [4].

In analyzing the coevolutive argument we should ask ourselves what the guarantee is that a species in a local maximum will continue climbing uphill and reach a better maximum. Our NKC results show that precisely the opposite situation takes place. At this point, some important and intriguing results that tend to support the coevolutive argument deserve mention and discussion [10,11]. For instance, Hillis [11] considers the problem of designing fast and efficient chips for the hardware implementation of common computational tasks, such as sorting numbers. To this end, the connections among circuits of the sorting network are coded and one lets the resulting system evolve, evaluating the string fitness according to (i) the number of circuit elements, (ii) the connections required (the fewer the better), and (iii) its “sorting” performance (with respect to a quantity of *fixed* test numbers). This would mimic Darwinian evolution. Coevolution here would entail letting the test numbers (to be sorted) themselves evolve in such a fashion that the *test number fitness* is regarded as higher the lower the performance of the sorting network in sorting the test numbers. Hillis found that this coevolution between the sorting networks and the sorting problems led more rapidly to better solutions than had been achieved by the evolution of sorting networks alone. Obviously, this result is at variance with *ours*.

However, the biological evolutive dynamics is quite different from that found in optimization problems. The biological evolutionary dynamics strongly depends on the shape

of the adaptive landscape [22]. In particular, the family of *NKC* landscapes exhibits ultrametricity features and a high degree of similitude to the energy surfaces of spin glasses [23–26]. In addition to its interpretation as a model of genetic interactions in a multigene system, the Kauffman *NK* model has been used to study adaptive somatic evolution in the immune response [27]. In other words, this model can probably be counted among the ones that most closely resemble biological reality.

On the other hand, landscapes arising by solving engineering problems are quite different from biological ones. In the former the “genotype-phenotype” mapping is of a relatively simple character. Parameters of the engineering problem to be optimized are coded in the genotype in more or less straightforward fashion (for instance, circuit connections), while in a biological scenario the phenotype arises from the genotype as a final result of the morphogenesis process and the mapping is anything but straightforward, morphogenesis being a very complex phenomenon that produces a phenotype as both the temporal and spatial consequences of the structural and catalytic properties of proteins, encoded in time and space by the genome and acting in concert with both nonprotein materials and physical and chemical forces, to yield the resulting organism.

Another crucial difference between engineering and biological “outputs” is worth mentioning in this connection. The coding required in the former is so (relatively) “trivial” that, in the case one uses genetic algorithms as evolutive

ones, it permits two individuals *placed far apart on the landscape* to generate a new one by recourse to crossover, that is, to interchange parts of their respective “strings” (Hillis example). In biology this is evidently an impossibility (think of cats and dogs, for example). The search for new and better individuals is of an exclusive *local* nature. Regarded in this light, the results of Ref. [11] appear to be less impressive than at first sight.

No one can deny, of course, that the terrestrial ecosystem undergoes *coevolution* processes as a (quite complex) dynamical system. Our calculations in two model scenarios indicate, however, that *coevolution does not constitute the crucial dynamical factor* that accelerates evolution but rather that the ecosystem evolves notwithstanding the fact that *coevolution may actually “retard” things*. In a coevolutionary system, organisms can keep evolving forever since the peaks may disappear because of the variations of the other species. Thus the species can keep climbing (and may be becoming more complex) without necessarily becoming more fit. Indeed, the mechanism has been called the red queen effect, referring to the red queen and Alice who kept running without getting anywhere.

Simple Darwinian evolution is quite efficient by itself. In some sense, then, one may imagine that for “successful” species, the whole ecosystem can be regarded as a sort of quasistationary mean field, so that they can advantageously exploit the original Darwinian mechanism so as to evolve rapidly.

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