

Evolution as a self-organized critical phenomenon

(macroevolution/punctuated equilibrium/self-organization/criticality)

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ABSTRACT We present a simple mathematical model of biological macroevolution. The model describes an ecology of adapting, interacting species. The environment of any given species is affected by other evolving species; hence, it is not constant in time. The ecology as a whole evolves to a “self-organized critical” state where periods of stasis alternate with avalanches of causally connected evolutionary changes. This characteristic behavior of natural history, known as “punctuated equilibrium,” thus finds a theoretical explanation as a self-organized critical phenomenon. The evolutionary behavior of single species is intermittent. Also, large bursts of apparently simultaneous evolutionary activity require no external cause. Extinctions of all sizes, including mass extinctions, may be a simple consequence of ecosystem dynamics. Our results are compared with data from the fossil record.

There is a good deal of evidence that biological evolution is not gradual, but episodic, with long periods of stasis interrupted by bursts of rapid activity. This intermittent pattern has been observed for the evolution of single species, as represented by their morphology (Fig. 1A). It has also been observed across taxa. In particular, Raup, Sepkoski, and Boyajian (2–6) have found a similar pattern in the fossil records for the distribution of extinction events (Figs. 2A and 3A). Gould and Eldredge (7) have coined the term punctuated equilibrium to describe the intermittent behavior of the evolution of single species (see ref. 8 for a review and documentation of the phenomenon). We shall use the term to describe intermittency in general.

Punctuated equilibrium is sometimes presented as a theory of the observed intermittency. We view it as a phenomenological principle describing certain empirical features of the fossil record. The fundamental cause of evolutionary change is explained by Darwin’s theory (9) which locates it to natural selection operating by struggle among individual organisms for reproductive success. Darwin’s theory may thus be thought of as the “atomic theory” for evolution. However, there is no theory deriving the consequences of Darwin’s principles for macroevolution. This is the challenge to which we are responding.

By studying the stratigraphic records of 19,897 fossil genera, Raup, Sepkoski, and Boyajian (2–6) found that not only do extinction events occur in bursts within families, but different genera often show the same extinction profile. It appears that the evolution of different families “marches to the same drummer.” Some extinction events are regional (10), and the largest events are global. It has therefore been suggested that extinction events are caused by external forces, such as changing sea levels (11), worldwide climatic pulses (12), or meteorites (13). We do not question that such events can cause and have caused extinctions. But we demonstrate here—within a model—that large catastrophic extinctions can occur as the

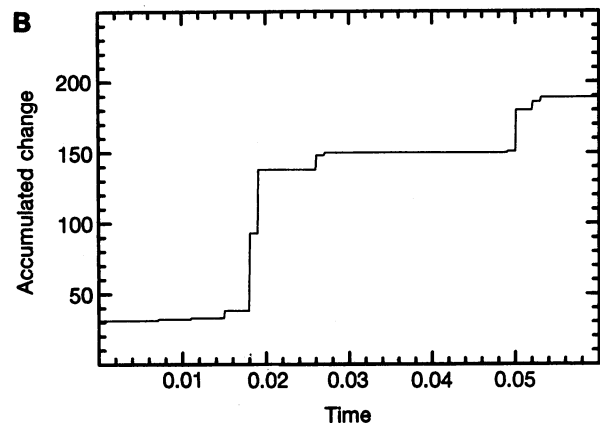
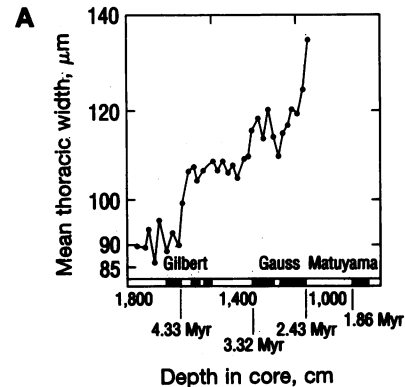


FIG. 1. (A) Time series for the variation of the morphology of a single species. The figure shows the increase in thoracic width of the Antarctic radiolarian *Pseudocubus vema* over 2.5 million years (Myr) according to Kellogg (1). (B) Model prediction for time series for change of single species morphology, estimated as its accumulated mutational activity.

natural consequence of the internal dynamics of biology, with no explicit need for external triggering mechanisms.

Indeed, large dynamical systems have a tendency to evolve or self-organize into a “critical” nonequilibrium state characterized by bursts or avalanches of dynamical activity of all sizes (14–17). This behavior is known as self-organized criticality, and below we discuss how such behavior may appear in an ecology driven by Darwinian evolution.

The present article is not the first one theorizing that the intermittency of biological evolution might be caused by self-organized critical behavior. In particular, Kauffman and Johnsen (18) studied elaborate models, the so-called “NKC-models,” for coevolving species operating at the edge of

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criticality, with periods of stasis interrupted by coevolutionary avalanches. It was argued that the ecology as a whole was "most fit" at the critical point. However, these models do not self-organize; some external tuning of the system, "divine intervention," was needed to obtain critical behavior (19, 20).

This article is organized in the following way: in the next section we present our model. The subsequent section describes the characteristics of an ecology that has evolved to the self-organized, critical state. The predictions of the model are compared with observations. Our final section contains discussion and conclusions.

The Model

Our investigation starts at the level of species. We consider the microevolution acting up to this level as being decoupled from the macroevolution that we wish to understand. This decoupling, of course, is not a claim of falseness or irrelevance of microscopic mechanisms. It is an assumption that divides the problem into more manageable parts.

The basic picture that we have in mind is the evolutionary fitness landscape envisioned by Wright in his seminal work, the shifting balance theory of evolution, reviewed in ref. 21. The properties of a population are modified by means of mutation and differential selection toward higher fitness. Random mutations allow individuals to cross barriers of lower fitness and move to other maxima and initiate a population at or near this new maximum.

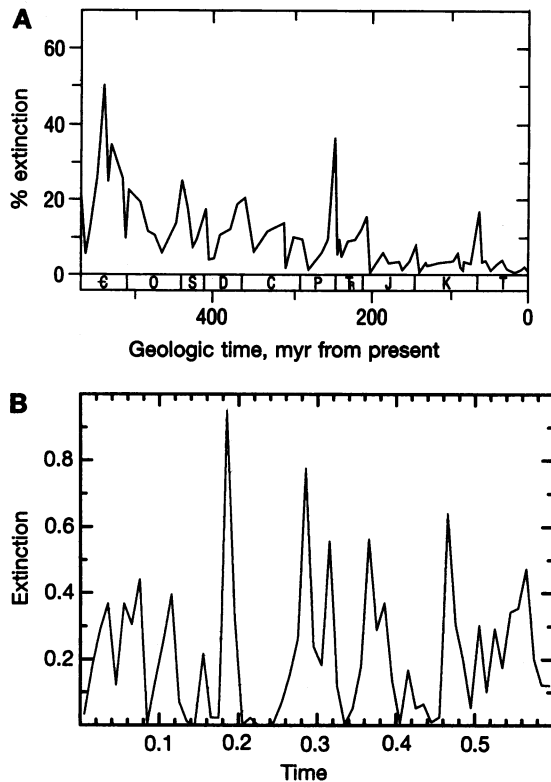


FIG. 2. (A) Temporal evolution of extinctions recorded over the last 600 million years (Myr) as given by Sepkoski (6). The ordinate shows estimates of the percentage of families that went extinct within intervals of approximately 5 Myr. (B) Temporal evolution of the "mutation" activity of species recorded in a one-dimensional model ecology with 200 "species" and a mutation rate parameter $T = 0.01$. Rectangular blocks along x-axis represent approximate lengths of individual geologic periods. C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; TR, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary.

For simplicity, we define a species as a group of individuals with genetic codes in the vicinity of the same fitness peak. The basic evolutionary step in our theory is the transformation of one species to a similar, more fit species. We call this step a "mutation" of the species, following Gould and Eldredge (8). The detailed mechanisms making this step possible are not our concern: we refer to the work of others for its motivation. For instance, the diffusion of a species from one state to another has been described by Lande (22) and by Newman *et al.* (23). The mechanism is mutation and differential selection of the fitter variant, causing the whole population to evolve to this variant. Fig. 4 shows how this step may take place in a laboratory experiment.

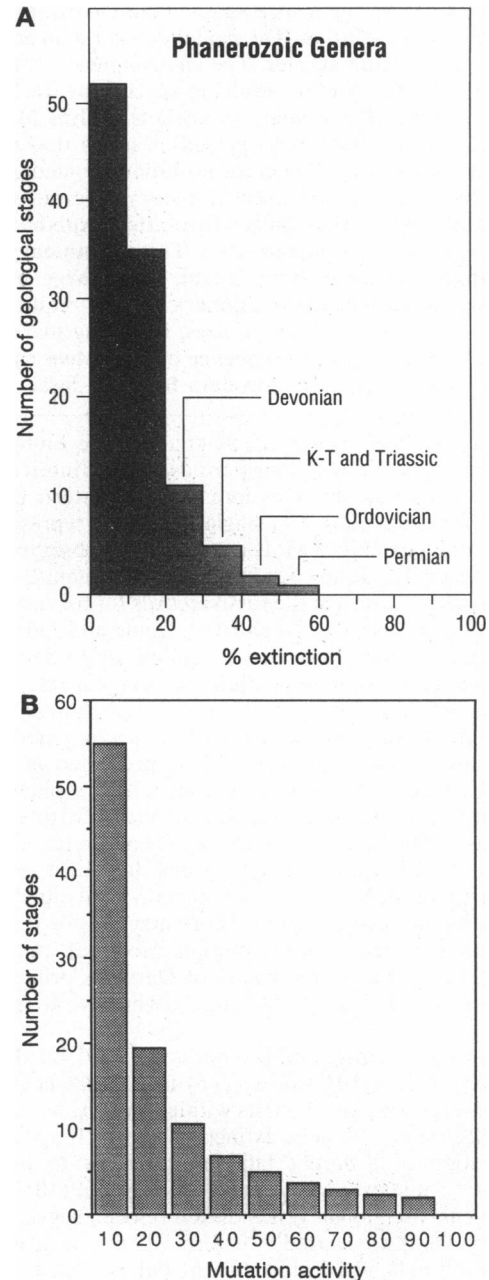


FIG. 3. (A) Histogram of extinction events from Fig. 1A as shown by Raup (3). The extinctions are binned in 106 intervals of approximately 5 million years each. The distribution is highly skewed, with 52 of the intervals having less than 10 percent extinction, and a few large extinction events with up to 60 percent extinction. K-T, Cretaceous-Tertiary. (B) Histogram of mutation activity as predicted by the random neighbor version of our model.

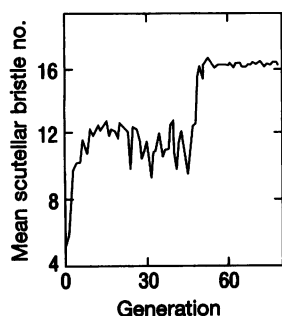


FIG. 4. “Punctuation” in mean scutellar bristle number in female *Drosophila melanogaster*, as observed in the laboratory by MacBean *et al.* (24), as simplified by Parsons (25). The number of bristles jumps to a “fitter” value in response to selective pressure.

In principle, the “fitness” landscape for a given species can be expressed as a function of its genetic code (18, 26) and also of the genes of certain other species on which it depends. However, we ascend another step in the level of abstraction: we assume that the fitness landscape is sufficiently rough that escape of a species from one local fitness maximum to another results in the replacement of one effective barrier toward further evolution with another effective barrier. In general the value of the new barrier may depend on the old barrier. We find that the predictions of our model remain essentially independent of such correlations. Since it has no bearing on our results, we assume that the new barriers are uncorrelated with the old ones. The insensitivity of the large-scale behavior to the details of the local, small-scale dynamical mechanisms is a general feature of all critical systems. It is this robustness that allows us to choose the simplest model for our investigations. With this, we have done away with many details of any specific model and obtained generality and mathematical simplicity in return. Our choice between what to leave in and what to leave out of the simplified model is an expression of what we consider quintessential mechanisms of evolution.

The probability of jumping from one state to a better one is $p = e^{-B/T}$, where B is a random number expressing the barrier—i.e., the number of mutations separating the two states—and T is an effective mutation parameter defining the timescale of mutations. Notice that although the typical time between jumps from one state to another is large—i.e., $1/p$ is small—the jump itself is very fast (22). It is a generic property of rugged fitness landscapes that low fitness is related to low barriers and high fitness to high barriers. A species with high fitness is unlikely to evolve to even higher fitness, as its barrier is high, whereas a species with low fitness has an easy time doing this. Thus, the barrier of stability, B , can be thought of as a measure of fitness.

All of the above describes the evolution of a single species in a given landscape. However, according to Van Valen (27) and as also pointed out by Kauffman and Johnsen (18), the fitness landscape experienced by one species depends on other species in the ecology; it is a “rubber” landscape, changing with the physical properties of other species and therefore with their genes. The interacting species can, for instance, be consecutive links in a food chain. As the fitness of one species improves, the fitness of its neighbors is affected, typically making some of them likely to evolve. Thus, species coevolve.

The model assumes that fitnesses of these neighbors take new values, either directly as a consequence of the different environment or because they quickly move to a new local fitness maximum, with a new, and by assumption random, barrier value B toward further evolution. In the course of doing this, however, they may have induced other species to a fast evolution to new local fitness maxima with new random barrier values toward further evolution. We assume that the interac-

tions between species are sufficiently weak or dilute to allow this primary chain reaction of coevolution to die out fast. Thus, in such a brief chain reaction, only a finite number of species, say K on the average, are affected, and we choose a timescale in our model in which the primary chain reaction is represented by a single step.

For the sole purpose of simplifying the bookkeeping of the network of interactions among species, let us assume first that the network forms a simple chain. We may then think of species as being positioned on a straight line, each species interacting with its two nearest neighbors on the line. Initially, we choose random values of B between 0 and 1 for the barriers toward further evolution experienced by the species. The choice of initial condition does not affect the outcome of evolution in this model. In the limit where the mutation parameter T is low, the next species to mutate is always the one with the lowest barrier—i.e., the next species to succumb is the least fit, as envisioned by Darwin.

Thus, the dynamics are as follows: The species i with the lowest barrier is assigned a new random value of B between 0 and 1. The two neighbors on the line are also assigned new random numbers between 0 and 1. Thus, even if any of these neighbors had a high fitness before, this property is likely to be lost. In the next step, the species which now has the lowest fitness mutates, affecting the fitness of its neighbors, and so on.

The actual rate of evolution varies enormously with the value of the minimum barrier representing the next species likely to mutate spontaneously. As the system evolves it turns out that no species with barrier values significantly above a certain self-organized threshold, B_c (equal to 0.667 in the case considered here, see Fig. 5), will ever mutate spontaneously. Species evolve only when their environment has changed sufficiently to lower their barriers (28, 29). No highly improbable events are required in evolution. Instead, the improbable is made probable by changes in the environment; the rubber landscape of a species coevolving with other species is modified by them to allow successive small but rapid evolutionary steps.

Life in the Self-Organized Critical State

As evolution proceeds, the ecology organizes itself into a state where further evolution takes place as avalanches of hectic coevolutionary activity or “punctuations” in the language of Gould and Eldredge. An avalanche may be defined rigorously as the total activity during a period where at least one species has a barrier below the critical threshold B_c . During an avalanche, there are several species with relatively low fitness.

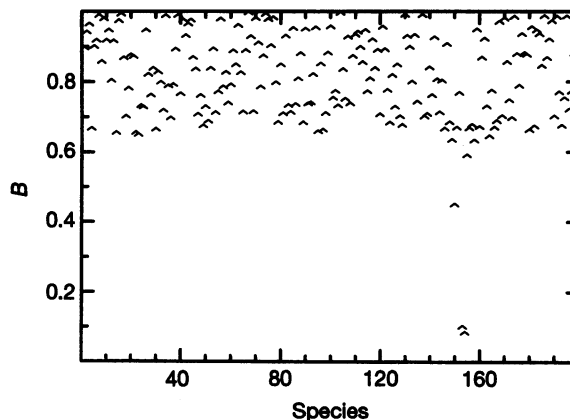


FIG. 5. Illustration of the “food-chain” version of our model. A snapshot of the barrier values for the different species is shown. Most barriers are above the critical value $B_c = 0.667$. The species with fitnesses below the threshold participate in an avalanche. In the next step, the species with the lowest barrier, here number $i = 154$, will mutate.

Between avalanches, in periods of stasis, the fitnesses of all species are above the threshold, so nature appears to be in balance.

The magnitude or size of an avalanche or punctuation is defined as the total number of successful evolutionary moves constituting the avalanche. If one plots a histogram of the number of avalanches of a given size s , one finds that the size distribution is a power law, $N(s) = s^{-\tau}$ with the exponent $\tau = 1.1$ (30). This power-law distribution indicates that the system is in a critical state, the terminology being borrowed from theoretical physics. Avalanches of all sizes occur, including large catastrophic ones. Power laws have the unique feature of scale invariance—i.e., if the argument is changed by a factor a , the function is still a power law with a prefactor $a^{-\tau}$. In our model, the catastrophic events occur due to a collective behavior of the interacting and competing species, each of which is trying to gain maximum fitness in its landscape. The model says nothing about the actual nature of the interaction leading to extinction of a specific species. It could be the result of falling prey to other species, starvation from changes in habitat or competition from other species, or epidemics; in short, the usual fates of the weak.

The important point is that in this model there is no need for external causes, such as climatic changes, to explain the observed pattern of extinction events, even when these cut across functional, physiological, and ecological lines. In particular, no external cataclysmic impact is necessary to generate large events in evolution. Extinction events as big as the late Permian event, with an estimated 60% of the genera becoming extinct (2), or the late Cretaceous event, which provided an opening for the early Tertiary evolutionary radiation of mammals, occur as endogenous events of evolution in its normal mode in our model.

Returning to our artificial lattice arrangement of the network of interactions between species, the exponent of the power law depends on the dimension of the lattice (28–30). On a two-dimensional lattice the exponent is 1.27 . . . , in higher dimensions it is yet higher, but the exponent does not exceed 3/2, and actually has that value for all lattice dimensions larger than four. If the network of interactions is chosen to be random—a choice that may resemble reality more than any lattice network—the exponent can be calculated analytically to be exactly 3/2 (29), and a number of other properties can be derived analytically as well (30).

Since the minimum barrier value fluctuates, the actual timescale represented by a single mutation in our computer simulation varies enormously. To represent the evolution on a real timescale, simulations have been performed at a low value of the mutation parameter, $T = 0.01$. At each time step, a given species with barrier B_i mutates with the probability $p = \exp(-B_i/T)$. When a species mutates, we assign both it and its two neighbors new random barrier values B between 0 and 1.

In Fig. 2 we compare the activity pattern of the model with the time series for the relative number of taxonomic families becoming extinct in consecutive intervals, as presented by Sepkoski (6). Note in both cases the intermittent behavior, with a few large peaks representing mass extinction events and many small peaks representing periods with smaller relative numbers of extinctions.

Fig. 3B shows the distribution of avalanche sizes for the version with random connections. Our numerical simulations and theoretical considerations (30) confine the value of the activity exponent τ to the narrow range between 1.1 and 1.5, whereas actual data for extinction events shown in Fig. 3A appear slightly steeper. But the data are too scanty to allow for a real quantitative test of the theory.

During an avalanche, individual species may undergo many mutations, such that their properties or “morphologies” can change significantly, even if the effect of individual mutations is small. Thus, on a timescale that is large compared with that of the avalanche, evolution sometimes appears to take place in

terms of saltations. Fig. 1B shows the accumulated number of mutations for a single species versus time in the model. The number of mutations might be seen as a measure of the change in morphology for that particular species. The evolution shows punctuated equilibrium behavior, as also seen for example in the data of Fig. 1A. For more data see also ref. 8 and references therein—e.g., the well-documented elephant lineages of refs. 31 and 32.

There is a close connection between the punctuations of evolution (and the periods of stasis) of the individual species (Fig. 1) and the global intensity of evolutionary activity (see Fig. 6). They are two sides of the same coin: the self-organized critical state.

The most interesting feature of evolution is, paradoxically, the existence of periods of stasis. During such periods, species in an ecology seem to be in balance. Fig. 7 shows a histogram of the lifetimes of genera based on data on 17,505 genera tabulated by Sepkoski, as presented by Raup and Sepkoski (2). The distribution varies smoothly from very many genera with short life spans to few genera with long life spans, up to several hundred million years. The number of genera N , with a lifetime t can be fitted quite well to a power law, $N(t) \propto 1/t^\alpha$, with $\alpha \approx 2$. For our model we find a power law with an exponent $\alpha = 1.1$. If the evolutionary activity, as measured in terms of the number of extinctions, is measured for an extended period, there will in general be several smaller and larger avalanches taking place during that period. One can prove mathematically that the distribution of activity in such intervals will converge towards a Pareto–Levy distribution function in the limit where there are many avalanches. This Pareto–Levy distribution preserves the power-law tail from the large events. This contrasts the situation where one has many small events, and the distribution converges to a Gaussian one.

In Fig. 2B, we have coarse grained the timescale of an ecology of 200 species evolving over a total of 2^{14} steps in 60 equal time intervals. The large fluctuations seen in the distribution of individual avalanches remain. The Pareto–Levy distribution is not a power law for small events. To extend the power law downwards, it is important to coarse grain over small intervals. Thus, it would be nice to see the histogram of fossil extinctions measured on a finer timescale, such as a million years.

Discussion and Conclusions

For the present model to have any chance of representing evolution in nature, it is important that the properties we have focused on are robust and fundamentally unchanged by essentially any modification of the model that leaves its defining

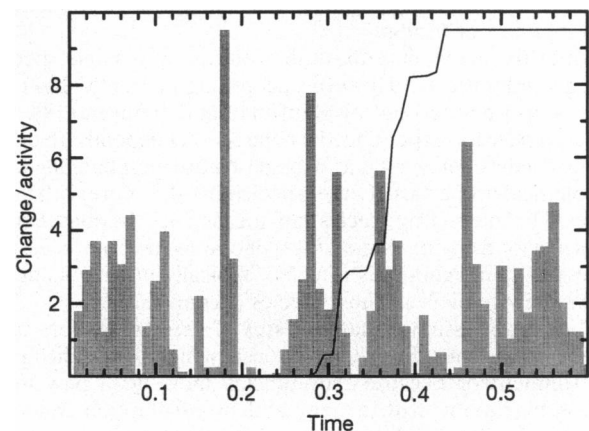


FIG. 6. Model predicted time series of global extinctions together with the evolution of a single, randomly chosen, species. The bursts of rapid variation take place during periods of large biological activity.

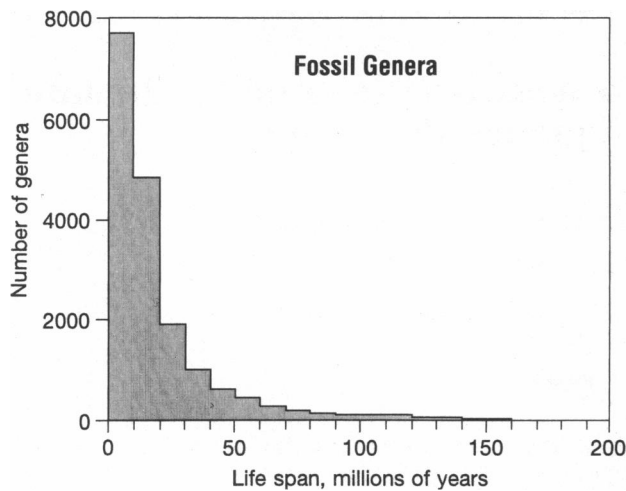


FIG. 7. Lifetime distribution for genera as recorded by Sepkoski, Raup, and Boyajian (2–6). The distribution can be well fitted by a power law $N(t) \propto 1/t^2$.

elements unchanged. We have simulated many versions of the model with many different representations of the interactions between species. In all cases, we found punctuated equilibrium with exponents depending only on the dimension of the lattice.

Our results demonstrate the advantage of simple “toy” models over more complicated and supposedly more realistic models. Not only are the toy models numerically tractable, but they are also exactly mathematically solvable in some respects. For the random neighbor model described in ref. 29, one can explicitly prove that it self-organizes to the critical state and find a number of properties of that state (29, 33). For the general model, the mechanism for self-organized criticality has been identified by Paczuski *et al.* (30). Having completed the present study, one could in principle return to the more elaborate representations of the landscape for the single species, for instance the spin-glass model (26) or the NKC model (18). On the basis of our observation of robustness, we conjecture that our conclusions, including the specific values of the exponents, will remain unaltered.

One important observation from this study is that Darwinian evolution acting on the level of the individual does not converge toward a state where every species is maximally fit—i.e., a state in which all barrier values B are maximal. In a noninteractive ecology, this would eventually happen, but the timescale would be enormous since one would have to wait for the occurrence of states with very high B values and, therefore, very low transition rates. The ecology discussed here evolves relatively fast to the globally correlated critical state, and once it has arrived there, it keeps evolving forever, alternating between periods of stasis and intermittent spikes of coevolutionary activity of all sizes. According to this scenario, life in its normal state is synonymous with volatility, not with stability and fitness. Darwin’s principle does not translate directly to the whole ecosystem, which does not evolve toward higher fitness or stability. The critical state is not “a nice place to be,” contrary to what Kauffman and Johnsen suggested. As the least-fit species mutates to improve its fitness, other species find their fitnesses reduced and soon mutate too, possibly triggering changes throughout the ecology, as we have seen. As the fitness of any species is no more durable than the state of

the species with which it interacts, all species experience a “Red Queen” effect: they are forced to keep evolving towards higher fitness just to maintain their fitness.

Can any of this be studied in the laboratory? One possibility is to study the dynamics of a limited ecology of very simple species on the molecular level (34, 35) to identify the interplay between local punctuations at the level of single species and the evolution of the ecology as a whole.

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