Mass extinction in a dynamical system of evolution with variable dimension

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Introducing the effect of extinction into the so-called replicator equations in mathematical biology, we construct a general model where the diversity of species, i.e., the dimension of the equation, is a time-dependent variable. The system shows very different behavior from the original replicator equation, and leads to mass extinction when the system initially has high diversity. The present theory can serve as a mathematical foundation for the paleontologic theory for mass extinction. This extinction dynamics is a prototype of dynamical systems where the variable dimension is inevitable. [S1063-651X(99)06707-0]

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INTRODUCTION

Mathematical biological models of evolution [1–6] have been a recent object of study in relation to complex systems [7], in which the techniques of statistical physics play a powerful role. In particular, the problem of the extinction of a species in an ecosystem [8] has been discussed within the framework of physics [2–4,9]. On the other hand, the mechanism of mass extinction has been a classical and controversial problem studied by a number of researchers in paleontology [10–12] and evolutionary biology [13]. The conclusions based on the results of these studies can be divided into two categories, one emphasizing exogenous shocks (*bad luck*) [10,14–16] and the other, endogenous causes (*bad genes*) [4,17]. By combining both views, a mathematical model of mass extinction has been proposed [18], which is highly phenomenological. In this paper, we not only combine the views of the bad luck effect and the bad gene effect in extinction, but also construct a model of mass extinction starting from a traditional mathematical biological equation, which describes the dynamics of populations of interacting species.

This model reflects the former view (the bad luck effect), e.g., the situation where several biotas, which have been separated from each other for a long time, are suddenly integrated into a larger ecological network by some exogenous shock (*biotic fusion*) [19,20]. (One example of this kind of large-scale extinction, caused by such biotic fusion, can be seen in a comparison of the number of families of land mammals in North America and South America before, during, and after the formation of the Panama land bridge between the two continents in the Pleistocene epoch about two million years ago [21].) We assume that the interaction coefficients for this produced ecosystem can be written in the form of a random matrix [22–24]. Meanwhile, following the latter view (the bad gene effect), we adopt the concept of an *extinction threshold*, which we introduce into the replicator equations [1] of the population dynamics. We refer to these large dimensional replicator equations with random interspecies interactions and the extinction threshold as *extinction dynamics*.

The extensive numerical simulations show that the behavior of the extinction dynamics is quite different from the behavior by the original replicator equations without an extinction threshold. First, the nature of phase space of the extinction dynamics is clarified, which can be characterized by a small number of parameters. That is to say, a distribution of a basin size of each attractor is characterized by a *power law*. Moreover, the dependence of the results on the parameters suggests that the original replicator equations without the extinction threshold should also follow the same law. Therefore, extinction dynamics can be a powerful tool for investigating the complex behavior of the original replicator equations because extinction dynamics has rather simple attractors, while the original replicator equations often have complex attractors, such as chaos or *heteroclinic cycles*.

We also find several significant features that characterize mass extinction. Defining the *diversity* as the number of existing species, we first find that final value of this quantity is largely independent of its initial value. Second, we find that mass extinction does not occur immediately after an environmental change, but begins after a number of *induction times* [25]. The dependence of this time development of the diversity, *the extinction curve*, on the parameters is extensively studied. The time evolution of other important variables is also studied, which are *average fitness* and *distribution of the interspecies interaction coefficients*.

MODEL

Replicator equations with random interspecies interactions

First, let us consider the following ordinary differential equations called the *replicator equations* (RE) [1],

$$\frac{dx_i(t)}{dt} = x_i(t)\left(\sum_{j=1}^{N_I} a_{ij}x_j(t) - \sum_{j,k=1}^{N_I} a_{jk}x_j(t)x_k(t) \right) \quad (1)$$

on an N_I dimensional simplex

$$\sum_{i=1}^{N_I} x_i(t) = 1 \quad [0 \le x_i(t) \le 1]. \quad (2)$$

The replicator equations have become well-established models in many fields [1], including sociobiology, studies of the prebiotic evolution of macromolecules, mathematical ecology, population genetics, game theory, and even economics. In particular, N_I dimensional RE is equivalent to the $N_I - 1$ dimensional general Lotka-Volterra equation [1], the analysis of which is one of the main subjects of mathematical biology. The variable x_i denotes the *population density* of species i. N_I denotes the initial number of species, that is, the initial value of diversity. The (i,j)th element of the matrix $A = (a_{ij})$ determines the effect of species j on the change rate of species i. Here we use $a_{ii} = -1$ for intraspecies interaction coefficients, and we assign the interspecies interaction coefficients $a_{ij}(i \neq j)$ as time-independent Gaussian random numbers with mean 0 and variance v. In general, this random asymmetric interaction matrix drives this system into a nonequilibrium state.

The assumptions we make for these asymmetric random interactions are based on the hypothesis that a biotic fusion reorganizes species relationships in a random fashion [20]. This kind of ecosystem with random interaction can be produced, for example, by a reduction in a habitat area, which paleontologists have asserted to be a trigger for mass extinction [12]. Because the reduction in a habitat area may confine many biologically isolated species to a narrow area, it drives them into competition and, eventually, brings about biotic fusion. In this sense, a large-scale biotic fusion of many biotas can occur as well as a fusion of two biotas [20]. Moreover, even a biotic fusion of only two biotas (as the formation of the Panama land bridge) may change the interaction a_{ij} even if both ith and jth species belong in a same biota, and the two-biota fusion may yield a random a_{ij} because, for example, the biotic fusion may changes the preference of predation for each species (e.g., ith species in North America may prefer kth species in South America than jth species in North America).

Here we note that, for example, for marine animals, the biotic fusion can take place not only by a decline in sea level, which causes habitat area reduction, but also by an increase in the sea level, which causes a connection of sea areas separated from each other for a long time. Therefore, the biotic fusion hypothesis here can be an explanation for the question of why a number of mass extinctions take place because of both the decline or the increase in the sea level. One of the purposes of the present study is to show that any large-scale biotic fusion and any subsequent random interspecies interactions may play a role in the bad luck effect for mass extinction.

Several pioneering studies of such a random interaction model have been carried out using the theory of random systems. However, these studies have dealt with limited cases, such as the local stability condition for a linear version of RE [23], the replica variational theory for RE with symmetric random interactions, which ensures equilibrium states [2], and the dynamic mean field theory for noise-driven RE with asymmetric interactions [3] only in the parameter region, where the asymmetry is weak and the system is ensured to approach a fixed point. On the other hand, the global behavior of RE with fully asymmetric random interaction is hardly treated analytically, because the equations are highly nonlinear and the dynamics often show not only convergence

to a fixed point, but also complex behavior, such as *heteroclinic orbits* [26,27] or *chaos* [28,29], even at low dimension ($N_I \geqslant 4$).

It is useful to transform the variable $x_i(t)$ to $y_i(t) \equiv \log(x_i(t))$ and to deal with the replicator equations, in the form of difference equations by the simple Euler method, as

$$y_i(t+1) = y_i(t) + \Delta t (f_i(t) - \bar{f}), \qquad (3)$$

$$f_i(t) = \sum_j a_{ij} e^{y_j(t)}, \qquad (4)$$

$$\bar{f}(t) = \sum_i e^{y_i(t)} f_i(t), \qquad (5)$$

where Δt is a small constant for the discretization, and is used as the unit of time in the following simulations and figures. $f_i(t)$ and $\bar{f}(t)$ denote the fitness of ith species and average fitness over all species, respectively. The transformation is effective, in particular, for numerical calculations because some of $x_i(t)$'s often take a very small value, which may cause underflow. Hereafter, we use Eqs. (3)–(5) in the numerical calculations.

The extinction dynamics

We should note here that extinction is not well defined in the RE model with large N_I and random interactions because such a model generally has heteroclinic orbits. When a heteroclinic orbit approaches a *saddle*, where some species are extinct, the population densities exponentially approach zero. However, they never actually reach zero because the orbit is bound in the *interior* of the simplex (2). In the vicinity of the saddle, the values for these population densities are too small to cause underflow by naive numerical calculations. Nevertheless, some of these populations eventually begin to revive, causing the orbit to leave for another saddle. This transition among saddles continues cyclically or chaotically. The exponential approach of population to zero and its revival to the order $O(1)$ play a significant role in heteroclinic orbits. However, in the real world, such a small population density cannot be sustained. In this sense, heteroclinic orbits have never been believed to be biologically significant.

Considering the above problem, we introduce the parameter δ to the dynamics [Eqs. (1)–(2)] to represent the extinction threshold; at each discrete time step, the population density $x_k (= \exp(y_k))$ is set to zero if this quantity becomes less than δ. The population densities of the surviving species $\{x_i\}$ $(i \neq k)$ are then renormalized to satisfy $\Sigma_{i \neq k} x_i = 1$. This renormalization implies that the niche of an extinct species is divided among the survivors. The diversity decreases through the above process, and we denote its value by N. The introduction of δ is also nothing but a finite size effect on RE, because δ coincides with a minimum unit of reproduction for each species, and its reciprocal $1/\delta$ corresponds to the permissible population size of an ecosystem.

It must be noted here that the present model belongs to a class of systems for which the dimension is a time-dependent variable. Since this time-dependence is inevitable not only in population dynamics [30,31], but in many other fields as

well, such a highly nonlinear model has never been systematically analyzed.

Whenever there is a given set of parameters A, δ and an initial diversity $N_I \equiv N(t=0)$, the initial state $\{x_i(0)\}$ evolves until a steady state is achieved. Extinction never occurs in this steady state, and there remains a stable subecosystem with a comparatively small number of surviving species (*core species*) N_F ($\leq N_I$). Although almost all orbits converge to an equilibrium point in this state, we also find periodic orbits. Chaotic orbits are very rare. Heteroclinic orbits are never achieved because the existence of the finite δ prohibits any orbit from approaching a saddle. Such stability is always achieved by any finite δ. This is a new type of destruction of a high dimensional attractor, which is, in general, called *crises* in the theory of chaos [32]. Therefore, let us refer to this kind of dynamics as *extinction dynamics* (ED). By a series of extensive numerical simulations, we investigate the features of ED, especially the dependence of ED on three parameters: N_I, v, and δ.

From the point of view of random system theory, it is important to observe typical behavior for ED by executing *random average* of quantities over samples of a random matrix A. Hereafter, we will, in general, write this average as $\langle \ldots \rangle_A$.

RESULTS

The basin-size distribution

The first results of this paper concern the basin-size distribution for ED with a large number of basins of attraction. Here, we identify each ''attractor'' only by the composition of core species, not by its trajectory. In other words, even if several isolated attractors coexist in a system of core species, we do not discriminate between these attractors and we regard them to be in one basin of ''attraction.'' The reason for this is that, in ED, such coexistence is rare, and this classification of basins of attraction also agrees with the classification of subecosystems created by ED.

In order to obtain the basin-size distribution, we (a) iterate ED starting from a sufficient number of random initial states in a system with the same parameters and the same random matrix A, (b) count basin size S_j as the number of initial states that converge to jth attractor, and (c) make a rank-size distribution $S(n)$ by sorting $\{S_j\}$'s, where the natural number n denotes the rank of each basin, and can reach the total number M of attractors found in the simulation. For example, an attractor with rank $n=1$ indicates that it has the largest basin size $S(1)$, while another attractor with rank M means that it has the smallest basin size $S(M)$. Therefore, in general, the rank-size distribution $S(n)$ is a nonincreasing function of n. Moreover, the above process is iterated for a sufficient number of random matrices A with the same v, and we finally obtain a basin-size distribution $\langle S(n) \rangle_A$ for a parameter set. $\langle S(n) \rangle_A$'s for various parameter sets are shown in Fig. 1.

It is clear that the basin-size distribution $\langle S(n) \rangle_A$ characteristically follows a power law. Moreover, each exponent of the power depends only on N_I, neither on δ nor v. This exclusive dependence on N_I can be understood intuitively because the number of combinations of core species (the number of attractors) depends only on N_I. Therefore, a
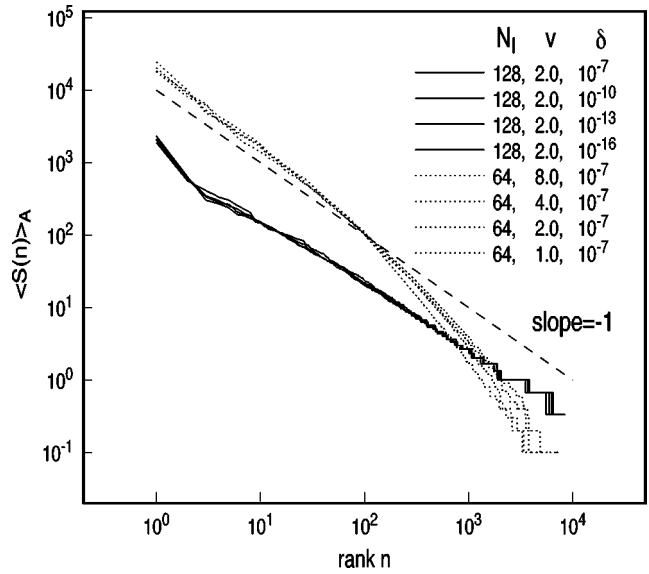

FIG. 1. Basin-size distributions $\langle S(n) \rangle_A$ (vertical axis) as a function of rank n (horizontal axis) for (a) $N_I=64$, sampled from 100 000 initial states and averaged over ten samples of A and (b) $N_I=128$ from 20 000 initial states and three samples of A.

larger N_I provides a larger number of attractors and hence, a smaller exponent. On the other hand, the independence of δ strongly suggests that the basin-size distribution of the original RE (ED in the limit $\delta \rightarrow 0$) also follows the power law. This conjecture is relevant to the hierarchical coexistence of an infinite number of attractors in RE [33]. The power law of a rank-size relationship with an exponent near unity is often referred to as Zipf's law [34] in linguistics and other diverse fields [35].

The extinction curves

Figure 2 shows the second result of this paper: average diversity as a function of time, $\langle N(t) \rangle_A$ (*the extinction*
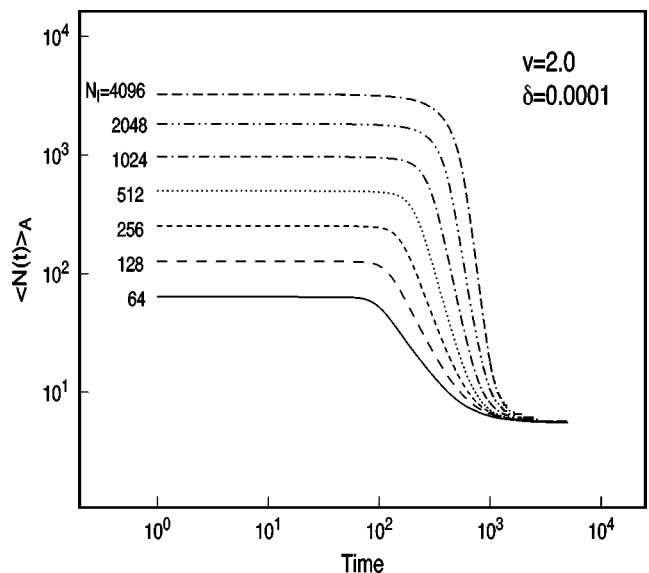

FIG. 2. Extinction curves [average diversity $\langle N(t) \rangle_A$ vs time t] for various values of N_I with $\delta=0.0001$ and $v=2.0$. Each curve represents an average taken over 1000 samples of A.
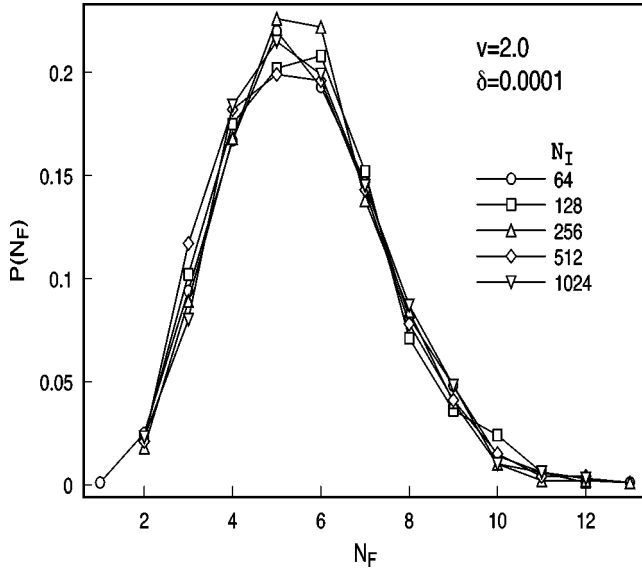
FIG. 3. Distribution $P(N_F)$ of the final diversity N_F of core species for several values of N_I. The distribution was obtained using 1000 samples of random matrices A (1000 runs of extinction dynamics).

FIG. 4. (a) Extinction curves [average diversity $\langle N(t) \rangle_A$ vs time t] for various values of v with $N_I = 64$ and $\delta = 0.0001$, averaged over 1000 samples of A. (b) The average diversity of the core species $\langle N_F \rangle_A$ is shown as a function of v.

curve). Two significant characteristics can be observed from this figure. The first is that the average final diversity $\langle N_F \rangle_A$ is independent on N_I. This result implies that no matter how large the diversity of initial species, the average diversity of species in the final state is small by comparison. That is $N_F \ll N_I$. In other words, when a large random ecosystem emerges as a result of a biotic fusion, a mass extinction of "size" $N_I - \langle N_F \rangle_A$ will occur. Second, the avalanche of mass extinction begins after some *induction time* [25] t_I, and ends in each case at nearly the same time $t_R \sim 10^3 (\geqslant t_I)$. As N_I becomes larger, t_I also becomes larger and approaches t_R. Therefore, for a sufficiently large N_I, the extinction curve shows a sharp drop at t_I. Such an abrupt mass extinction occurring on a short time scale is highly relevant to the notion of *punctuated equilibria* [36].

The induction time and the abrupt drop in diversity at a large N_I is explained by the small rate of change for each x_i at $t = 0$, and a faster than exponential decay of x_i for extinct species. At time $t = 0$, the absolute value of the fitness $f_i(0) \equiv \Sigma_{j=1}^{N_I} a_{ij} x_j(0)$ [the first term in the parentheses of the right-hand side of the equation (1)] for each species i is of estimated order $O(\sqrt{v/N_I})$ by a simple calculation. The absolute value of the average fitness $\bar{f}(0) \equiv \Sigma_{i=1}^{N_I} f_i(0) x_i(0)$ (the second term in the parentheses) has the same order. Therefore, as N_I becomes larger, the absolute value of the change rate $f_i - \bar{f}$ at $t = 0$ becomes smaller in proportion to $1/\sqrt{N_I}$, which makes the induction time larger because a smaller change rate makes populations change more slowly. However, the rapid decay eventually drives populations into extinction around the induction time. Therefore, almost all species, except for core species, are expected to become extinct synchronously in the limit of large N_I.

It should also be noted here not only that the average diversity $\langle N_F \rangle_A$ of a core species is independent of N_I but also that the distribution $P(N_F)$ of N_F itself does not depend on N_I, as shown in Fig. 3.
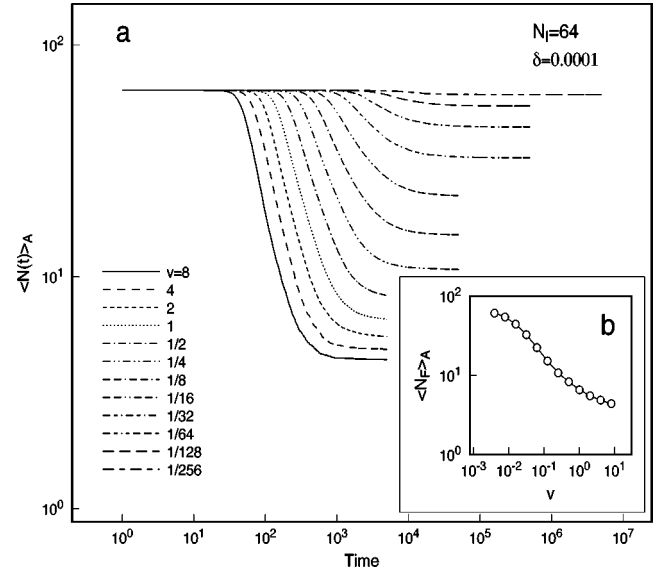
Figure 4 concerns the variation of extinction curves with v. As v becomes larger, the induction time t_I becomes shorter [Fig. 4(a)], and $\langle N_F \rangle_A$ becomes smaller [Fig. 4(b)]. Consequently, when the order of the interspecies interaction coefficients becomes large compared to the absolute value of the intraspecies ones ($\{a_{ii} = -1\}$), the avalanche of mass extinction begins earlier, and a smaller diversity of species survives. The extinction curves for several values of δ are also shown in Fig. 5. It should be noted that the final diversity $\langle N_F \rangle_A$ is independent from δ. This means that, no matter how small δ is, extinctions are inevitable in ED. This inevitability is consistent with the fact that no extinction occurs in RE without the extinction threshold ($\delta = 0$). In fact, the simulation and the analytical estimation equally show
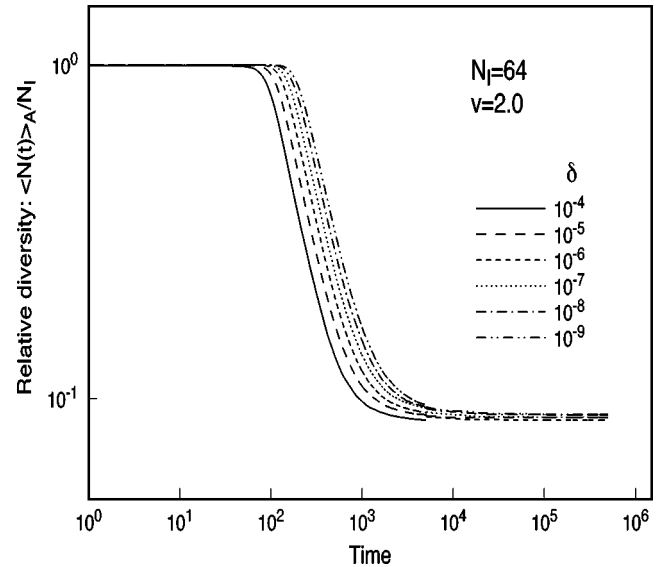

FIG. 5. Extinction curves [average diversity $\langle N(t) \rangle_A$ vs time t] for various values of δ with $N_I = 64$ and $v = 2.0$, averaged over 1000 samples of A.
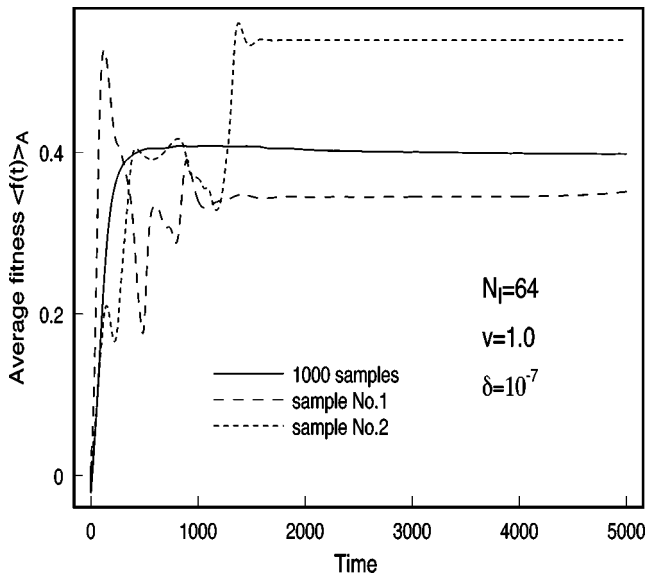
FIG. 6. Time development of average fitness $\bar{f}(t)$ over 1000 samples of A with $N_I = 64$, $v = 2.0$, and $\delta = 10^{-7}$ (solid line). Each dotted line represents one sample. The fitness $\bar{f}$ goes up and down and, in general, the final value is not the highest.
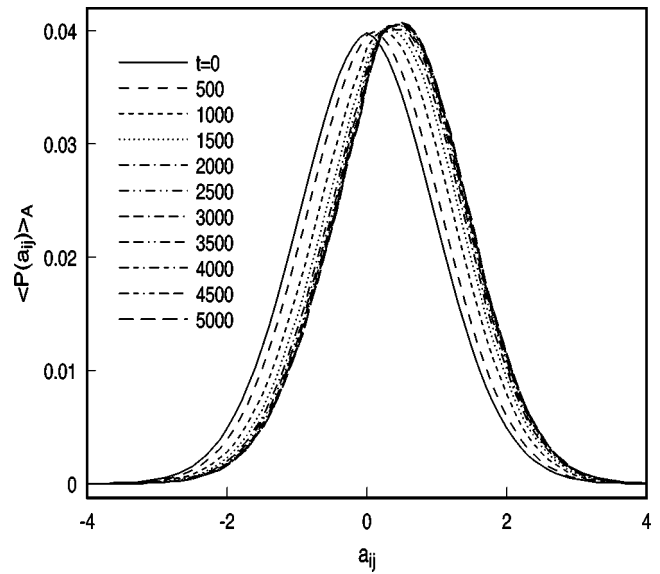

FIG. 7. Time development of the distribution $\langle P(a_{ij}) \rangle_A$ of elements $\{a_{ij}\}$ of interaction matrices averaged over 2000 samples. $N_I = 64$, $v = 2.0$, and $\delta = 10^{-7}$.

$t_I \sim -\log(\delta)$, and t_I diverges to infinity in the limit $\delta \to 0$, that is, no extinction occurs in finite time. From Figs. 2, 4, and 5, we can conclude that $\langle N_F \rangle_A$ depends only on v, but not on N_I nor δ, which is in contrast with the parameter dependence of $\langle S(n) \rangle_A$ only on N_I.

The average fitness and the nature of the shrink matrix

Here we discuss the time development of average fitness $\bar{f}$ through extinction dynamics, as depicted in Fig. 6. It should be noted that the average fitness takes on positive values, except during the short period at the beginning. This reminds us that the average fitness is a nondecreasing function if the interaction matrix is ensured to be symmetric, as in the equation of selection in population genetics. The final value for the average fitness $\bar{f} \sim 0.4$ is higher than what would be expected for a randomly generated ecosystem with the same diversity ($N_F \sim 8$). Thus, more stable ecosystems are self-organized by ED. We also observe that $\langle \bar{f}(t) \rangle_A$ does not show a monotonic increase and reaches a maximum value at a time near t_I. This, in general, suggests that the average fitness shoots up in response to the avalanche of extinction of low-fitness species around the induction time and settles down to a final value via competition among core species.

The time development for the distribution of elements of interaction matrices via extinction dynamics is depicted in Fig. 7. The average of a_{ij} shifts to a positive value, which means that the interaction matrix of the subecosystem becomes cooperative via extinction dynamics. This also contributes to an increase in average fitness. It should be noted that the distribution continuously holds its Gaussian distribution shape. Therefore, the interspecies interaction coefficients of core species are still random, and various types of relationships among core species are realized by ED. The time development of $\langle a_{ij} \rangle_A$ is also shown in Fig. 8.

DISCUSSION

In this paper, we have ignored any effects of immigrants or invaders, which increase the diversity, and we have focused on global biotic fusion where no species ever comes from the outside. Moreover, we did not consider any mutants, because the avalanche of mass extinction occurs so quickly that no significant evolution of mutants can occur. By neglecting these effects, the nature of extinction on a rather short time scale was exclusively clarified. However, by introducing the effect of increasing diversity (the process of *speciation*) [37], we can study the nature of ED on a much larger time scale. In fact, an analysis of the interesting prob-
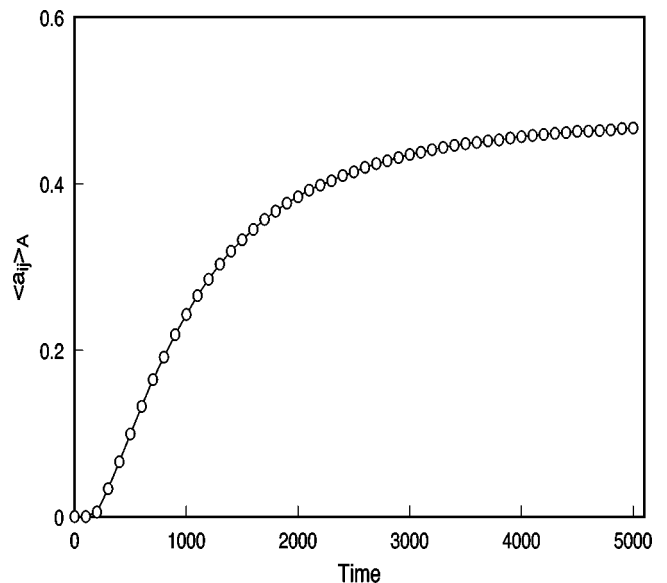

FIG. 8. Time development of the average $\langle a_{ij} \rangle_A$ of elements a_{ij} of interaction matrices averaged over 2000 samples. $N_I = 64$, $v = 2.0$, and $\delta = 10^{-7}$.

lem of whether ED shows *self-organized criticality* [4,9] is in progress.

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[1] J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems* (Cambridge University Press, Cambridge, 1988)

[2] S. Diederich and M. Opper, Phys. Rev. A **39**, 4333 (1989).

[3] M. Opper and S. Diederich, Phys. Rev. Lett. **69**, 1616 (1992).

[4] P. Bak and K. Sneppen, Phys. Rev. Lett. **71**, 4083 (1993).

[5] H. Flyvbjerg, K. Sneppen, and P. Bak, Phys. Rev. Lett. **71**, 4087 (1993).

[6] J. de Boer, B. Derrida, H. Flyvbjerg, A. D. Jackson, and T. Wettig, Phys. Rev. Lett. **73**, 906 (1994).

[7] M. Mezard, G. Parisi, and M. A. Virasoro, *Spin Glass Theory and Beyond* (World Scientific, Singapore, 1987).

[8] B. W. Roberts and M. E. J. Newman, J. Theor. Biol. **180**, 39 (1996).

[9] P. Bak, K. Chen, and M. Creutz, Nature (London) **342**, 780 (1989).

[10] A. Hallam, in *Causes of Evolution*, edited by R. M. Ross and W. D. Allmon (University of Chicago Press, Chicago, 1990).

[11] D. M. Raup, *Extinction: Bad Genes or Bad Luck?* (W. W. Norton, New York, 1991).

[12] A. Hallam, *An Outline of Phanerozoic Biogeography* (Oxford University Press, Oxford, 1994).

[13] J. Maynard Smith, Philos. Trans. R. Soc. London, Ser. B **325**, 242 (1989).

[14] L. W. Alvarez, W. Alvarez, F. Asara, and H. V. Michel, Science **208**, 1095 (1980).

[15] M. F. Coffin and O. Eldholm, Sci. Am. (Int. Ed.) **269**, 26 (1993).

[16] S. B. Hedges, P. H. Parker, C. G. Sibley, and S. Kumar, Nature (London) **381**, 226 (1996).

[17] L. Van Valen, Evol. Theor. **1**, 1 (1973).

[18] M. E. Newman and B. W. Roberts, Proc. R. Soc. London, Ser. B **260**, 31 (1995).

[19] G. J. Vermeij, Science **253**, 1099 (1991).

[20] M. E. Gilpin, Proc. Natl. Acad. Sci. USA **91**, 3252 (1994).

[21] R. M. May, Sci. Am. **239**, 119 (1978).

[22] M. R. Gardner and W. R. Ashby, Nature (London) **228**, 784 (1970).

[23] R. M. May, Nature (London) **238**, 413 (1972).

[24] A. Roberts, Nature (London) **251**, 607 (1974).

[25] N. Saitô, N. Ooyama, Y. Aizawa, and H. Hirooka, Prog. Theor. Phys. Suppl. **45**, 209 (1970).

[26] R. M. May and W. J. Leonard, SIAM (Soc. Ind. Appl. Math.) J. Appl. Math. **29**, 243 (1975).

[27] T. Chawanya, Prog. Theor. Phys. **94**, 163 (1995).

[28] M. E. Gilpin, Am. Nat. **113**, 306 (1979).

[29] A. Arneodo, P. Coullet, and C. Tresser, Phys. Lett. A **79**, 259 (1980).

[30] K. Tregonning and A. Roberts, Nature (London) **281**, 563 (1979).

[31] L. R. Ginzburg, H. R. Akçakaya, and J. Kim, J. Theor. Biol. **133**, 513 (1988).

[32] E. Ott, *Chaos in Dynamical Systems* (Cambridge University Press, Cambridge, 1993).

[33] T. Chawanya, Prog. Theor. Phys. **95**, 679 (1996).

[34] G. K. Zipf, *Human Behavior and the Principle of Least Effect* (Addison-Wesley, Reading, MA, 1945).

[35] I. Kanter and D. A. Kessler, Phys. Rev. Lett. **74**, 4559 (1995).

[36] S. J. Gould and N. Eldredge, Nature (London) **366**, 223 (1993).

[37] K. Tokita and A. Yasutomi, OUCMT Report No. 1999-7.