Extinction dynamics of Lotka-Volterra ecosystems on evolving networks

F. Coppex,[1] M. Droz,[1] and A. Lipowski[1,2]

[1]*Department of Physics, University of Geneva, CH 1211 Geneva 4, Switzerland*
[2]*Faculty of Physics, A. Mickiewicz University, 61-614 Poznań, Poland*
(Received 19 December 2003; published 1 June 2004)

We study a model of a multispecies ecosystem described by Lotka-Volterra-like equations. Interactions among species form a network whose evolution is determined by the dynamics of the model. Numerical simulations show power-law distribution of intervals between extinctions, but only for ecosystems with sufficient variability of species and with networks of connectivity above certain threshold that is very close to the percolation threshold of the network. The effect of slow environmental changes on extinction dynamics, degree distribution of the network of interspecies interactions, and some emergent properties of our model are also examined.

I. INTRODUCTION

Lotka-Volterra models of interacting species have a well established role in population ecology [1]. Being inspired by an oscillatory behavior in some prey-predator systems, they are typically used to model populations on a time scale shorter than the lifetime of the describing species. It means that long-term properties of ecosystems (macroevolution) are usually not captured within such an approach. On the other hand, models used to describe macroevolution very often use the dynamics that operates at the level of species rather than individuals. Such coarse-grained models usually refer to the notion of fitness of a species that is not commonly accepted [2].

Recently, there has been some attempts to study macroevolution using models equipped with dynamics that operates at the level of individuals [3–5]. Taking into account that Lotka-Volterra models are relatively successful in describing many aspects of population dynamics it would be desirable to apply such an approach also to macroevolution. Some time ago Abramson introduced a discrete version of Lotka-Volterrra ecosystem [6] and studied certain characteristics of extinctions. His model is an example of a one-dimensional food chain with $M(\sim 100)$ trophic levels and a single species occupying a given trophic level. Since in realistic food webs $M \sim 4-6$ with typically many species belonging to a given trophic level [7,8], these are highly nonrealistic assumptions. Nevertheless, extinction dynamics in Abramson's model shows some features that are characteristic to Earth's biosystem.

In the present paper we introduce a Lotka-Volterra model that describes a simplified ecosystem of N species of predators and one species of preys. Our model can be thus considered as a simple food web model with only two trophic levels. Competition between predator species is described by a certain network [9] of interactions whose evolution is coupled with dynamics of the model. Namely, when a certain species becomes extinct (i.e., its density falls below a certain threshold) it is replaced by new species with a newly created set of interactions with some of existing species. Despite obvious simplifications the model exhibits some properties that are typical to more complicated ecosystems, such as, for example, power-law distributions of intervals between extinctions. Within our model we can also examine how robust this power-law distribution is. We find that under certain conditions, such as, for example, very sparse interactions between species or too strong a dominance of a small group of species, these power-law characteristics disappear and the model is driven into a regime where extinctions have exponential distributions or where there are no extinctions and the ecosystem enters a steady state. In our opinion, such regimes might be relevant when a restricted (either in space or time) evolution of an ecosystem or its part is studied. Interestingly, a threshold value of connectivity that separates power-law extinctions and steady state is very close to the percolation threshold of the random network of interspecies interactions.

According to a large class of statistical physics models of biological evolution, avalanches of extinctions do not require external factors to trigger them, but might be a natural consequence of the dynamics of an ecosystem. As a result, these external factors, such as, e.g., climate changes, solar activity, or the impact of a big meteorite, are very often neglected in such studies [10]. But such factors certainly affect the ecosystem and there is a good evidence of it [11]. Let us emphasize that even the basic mechanism that triggers avalanches of extinctions is not known and is a subject of an intensive multidisciplinary debate [12].

One possibility to take external factor(s) into account in our model is to modify a growth rate of prey. Since dynamics of the model is nonlinear, such a change might have more dramatic consequences than merely a change of densities of species. And indeed we noticed that dynamics of extinctions is strongly dependent on the growth rate. It turns out that in our model abundance of preys leads to a larger frequency of extinctions, and in periods of hunger there are less extinctions. This is clearly due to nonlinearity of the dynamics. A larger growth rate increases the density of preys that in turn increases densities of predators. With increased densities, dynamics becomes more competitive and extinctions become more frequent. Such a periodically modulated growth rate leaves some traces also in the probability distribution of extinctions. It might be interesting to notice that paleontologi-

cal data also show some traces of periodic events, but their proper understanding is still missing [11,13]

During evolution some species are favored and selected at the expense of less fortunate ones. Evolution constantly searches for the best solutions that resemble an optimization process. For example, a large size of organisms of a given species might be an advantage in some situations, but might cause some problems in other situations. What might be Nature's solution to this problem? Will it be middle-size species or rather two groups of species sitting at the extremes of conflicting requirements? In our opinion, this aspect of evolution is also often omitted in models of macroevolution. Within our model we looked at such emergent properties of species selected by evolution. It turns out that depending on some dynamical details, our model can reproduce both types of solutions of such an optimization problem.

In Sec. II we introduce our model and briefly describe the numerical method we used. Obtained results are presented in Sec. III. In Sec. IV we summarize our results and suggest some further extensions of our work.

II. MODEL AND NUMERICAL CALCULATIONS

We study a Lotka-Volterra ecosystem that consists of N species of predators with densities $\rho_i (i=1,2,\ldots,N)$ who are all feeding on one species of preys with density ρ_0. We assume that each predator species i is characterized by a parameter $k_i (0 < k_i < 1)$ that enters evolution equations of the model through death and growth terms

$$\dot{\rho}_0 = g(t)\rho_0(1-\rho_0) - \frac{\rho_0}{N}\sum_{i=1}^{N} f(k_i)\rho_i, \qquad (1a)$$

$$\dot{\rho}_i = -d(k_i)\rho_i(1-\rho_0) + f(k_i)\rho_i\rho_0 \left(1 - \frac{k_i\rho_i + \sum_j' k_j\rho_j}{k_i + \sum_j' k_j}\right), \qquad (1b)$$

where $i=1,2,\ldots,N$. In our model we assume that species interact mainly through environmental capacity terms [the last term in Eq. (1b)]. Namely, the growth rate of a given species i is reduced not only due to its density but also due to weighted (with the factor k) densities of a group of randomly selected neighboring species. In Eq. (1b) summation over these neighboring species is denoted by (Σ'). Approximately, we might interpret the coefficient k_i as the size of organisms of ith species — the bigger they are the bigger their role in the environmental capacity term. We also assume that the growth rate of preys is corrected by the environmental capacity term and due to external factors might be a slowly varying function of time $[g(t)]$. In principle, external factors might also affect other terms of model (1), but for simplicity we restrict its influence only to the growth rate of preys. Functions $d(k)$ and $f(k)$ reflect the k dependence of death and growth of our species. Explicit form of functions $g(t)$, $f(k)$, and $d(k)$ will be given later.

Differential equations (1) are solved using the Runge-Kutta fourth-order method. Multispecies Lotka-Volterra ecosystems were subject to intensive studies since the pioneering work of May [14]. It is known that such systems might evolve toward the steady state with positive densities. However, in some cases, in the steady state the density of some species might be zero. Each time a density of a certain species in model (1) drops below a threshold value which we fix as $\varepsilon = -10^{-7}$ we consider such a species as extinct [15]. Such a species is then replaced by a new species with a randomly assigned density [from the interval $(0,1)$], the coefficient $k(0 < k < 1)$ that is randomly drawn from the distribution $p(k)$, and a new set of neighbors (all links of the "old" species are removed). With such rules the model rather describes N niches, and we assume that a time to create a species which will occupy a niche is relatively short compared to the typical lifetime of a species.

We assume that a newly created species makes z links with randomly selected neighbors. Links are not directional so a newly created species will also enter the evolution equation of species it is neighboring. If the extinct species would be chosen randomly the network of interactions would have been a random graph. However, it is the dynamics (1) that determines which species are extinct. Thus, extinct species are not selected randomly and the resulting network is in general not a random graph.

III. RESULTS

In the following we describe numerical results obtained for some particular cases of model (1).

A. Intervals between extinctions

Various paleontological data suggest that dynamics of extinctions has some power-law distributions of sizes or durations [11]. In our model we measured time intervals t between successive extinctions. In these calculations we used a constant growth term of preys $g(t) \equiv 1$. We examined two cases: (i) model I, $f(k_i) \equiv 1$, $d(k_i) \equiv 1$ and (ii) model II, $f(k_i) = k_i$, $d(k_i) \equiv 1$. Unless specified otherwise we select k_i randomly with a homogeneous distribution on the interval $(0,1)$ $[p(k) = 1]$. Our results are shown in Fig. 1. In the simplest case, model I with $z = 4$ and $k_i \equiv 1$ [i.e., all species during the evolution have identical $k_i (=1)$] we obtain exponentially decaying distribution of intervals between extinctions $P(t)$. Such a decay is also seen for model I $(z=4)$ with linear distribution of k_i namely $p(k) = 2k$. We expect that such a behavior appears when a distribution of k_i in the ecosystem is relatively narrow and shifted toward unity. Such an effect might be due to the small width of distribution $p(k)$ (i.e., a distribution from which we draw k_i) or might be dynamically generated as in model II. In this case even though k_i are chosen from a homogeneous distribution, the dynamics favors large k_i species (due to their larger growth rate) and they dominate the ecosystem. When the distribution of k_i in the ecosystem is more uniform [model I with $p(k) = 1$] our simulations suggest that $P(t)$ decays as a power law. Let us notice, however, that a power-law behavior is seen only on
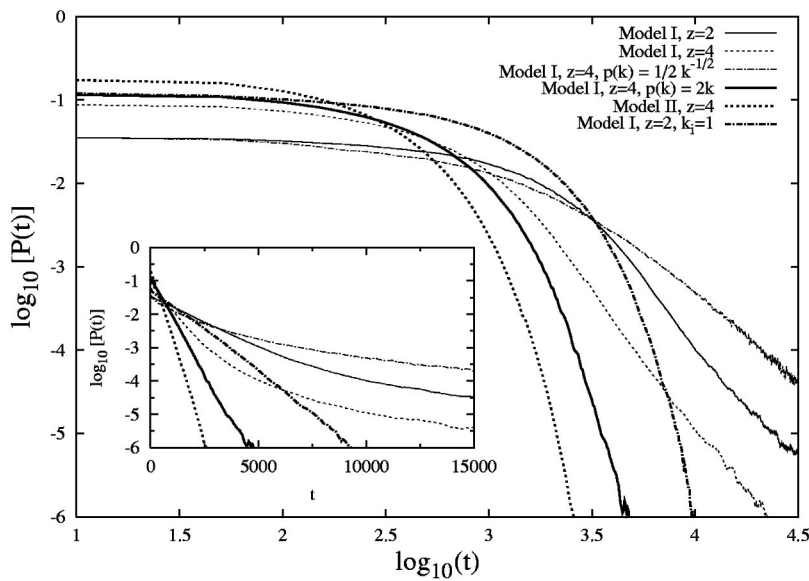
FIG. 1. Probability distribution of intervals between successive extinctions $P(t)$ calculated for some particular cases of model (1) for $N=100$. The inset shows the same data but plotted on a linear logarithmic scale.

approximately one decade and we cannot exclude that on a larger time scale a different (perhaps exponential) behavior appears as was already observed in some other macroevolutionary models [3]. Let us also notice that for model I with $p(k)=k^{-1/2}/2$ the power-law distribution $P(t)$ seems to decay as t^{-2}, i.e., with the exponent consistent with some paleontological data [11] as well as with predictions of some other models [4]. However, one has to recognize that the error bars on experimental data are rather large and that a non-power-law behavior cannot be excluded.

Note that a power-law decay of $P(t)$ is seen only for sufficiently large z. When z is too small, we observed that the ecosystem enters the steady state where all ρ_i are positive and there are no extinctions. This is probably due to the fact that the competition among predators is too weak (or rather too sparse). To examine the transition between these-two regimes in more detail we measured the averaged time between extinctions τ and the results are seen in Fig. 2. One can see that τ diverges around $z \sim 1.8$ [16]. Such a value of the threshold parameter suggests that this transition might be related to the percolation transition in our network of interspecies interactions. To examine such a possibility we measured the average size of the largest cluster of connected links in the network R (normalized by the number of species N) and the results are shown in Fig. 2. Vanishing of this quantity locates the percolation transition [17]. One can see that the percolation transition takes place at a larger value, namely around $z \sim 2.0$. Our results suggest that these two transitions take place at different values of z. However, the analysis of finite size effects especially in the estimation of τ is rather difficult and we cannot exclude that these two transitions actually overlap, as might be suggested by their proximity. Such a result would show that the dynamical regime of an ecosystem (i.e., steady state or active with power-law distribution of extinctions) is determined by the geometrical structure of its interactions.

B. Effect of a modulated growth rate

Now we examine the role of a modulated in time growth rate of preys. Such a modulation is supposed to mimic the

influence of an external factor like a change of a climate. One of the questions that one can ask in this context is how such a change affects the extinction dynamics. We studied model I with $p(k)=1$ and $d(k_i)\equiv 1$. The growth rate of preys we chose as $g(t)=1+A\sin(2\pi t/T)$, where A and T are parameters. A typical behavior in the case of model I with such a growth rate is shown in Fig. 3. One can see that increased growth rate increases the density of preys ρ_0 that increases the density of predators. However, it increases also the frequency of extinctions. Such a behavior, namely the increased extinction rate during abundance of food, might at first sight look as counterintuitive. This effect is related to the form of environmental capacity terms in the growth rate in Eq. (1b), namely $1-(k_i\rho_i+\Sigma'_j k_j\rho_j)/(k_i+\Sigma'_j k_j)$. Such a term certainly has a larger variability for increased density of predators ρ_i, and for some species (depending on the distribution of links, coefficients k_i, and densities) it causes faster extinction. Let us also notice that since the period of modulation T is quite large, there is no retardation effect between density of preys
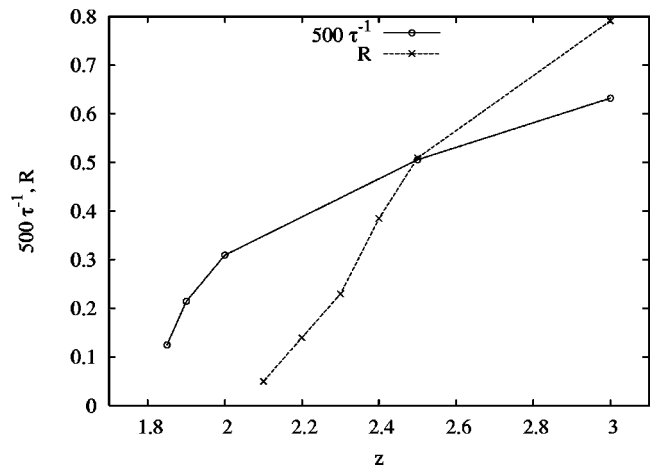

FIG. 2. The inverse average time between extinctions τ^{-1} and the percolation probability R as a function of z. Plotted results are based on calculations for $N=100$, 200, 300, and 400 and extrapolation $N \rightarrow \infty$.
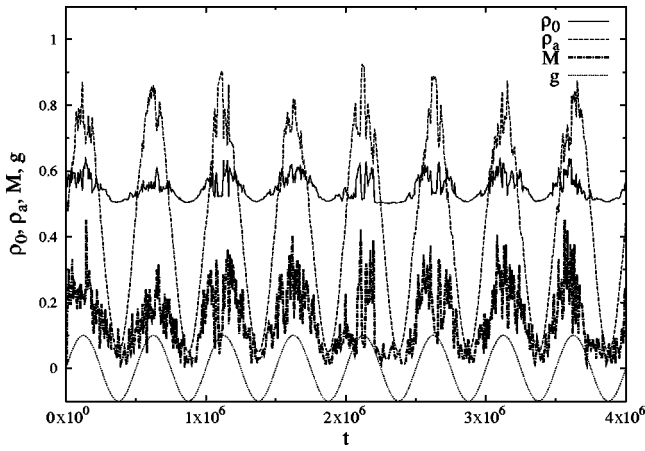
FIG. 3. A time evolution of the density of preys ρ_0, average density of predators $\rho_a - (1/N)\Sigma_{i=1}^{N}$, and the number of extinctions M (divided by 20) in the time interval $\Delta t = 10^3$ for the model I with $N=100$ and $z=4$. A rescaled modulated growth rate $[g(t)-1]/10 = 0.09 \sin(2\pi t/T)\,(T=10^5)$ is also shown.

and predators. We observed such retardation for smaller values of $T(\sim 1000)$.

Modulated growth rate of preys affects also the probability distribution of intervals between extinctions $P(t)$ as shown in Fig. 4. One can see that the period of modulation T is imprinted in $P(t)$. Let us notice that certain paleontological data do show some signs of periodicity but its origin still remains unclear [11,13].

It is known that slowly changing ecosystems sometimes undergo catastrophic shifts [18]. As a result, the ecosystem switches to a contrasting alternative stable state. It would be interesting to examine whether multispecies ecosystems, as described by our model (1), might also exist in such alternative states. If so, one can ask whether, for example, structure of the network of interspecies interactions or extinction dynamics are the same in such states.

C. Emergent properties of species

It might be interesting to ask what are the characteristics of species that are preferred by the evolution in our ecosys-
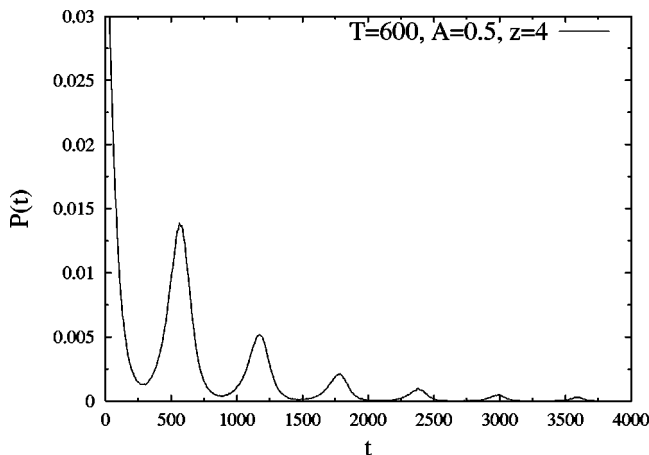

FIG. 4. Probability distribution of intervals between successive extinctions $P(t)$ calculated for model I with modulated growth rate ($N=100$).
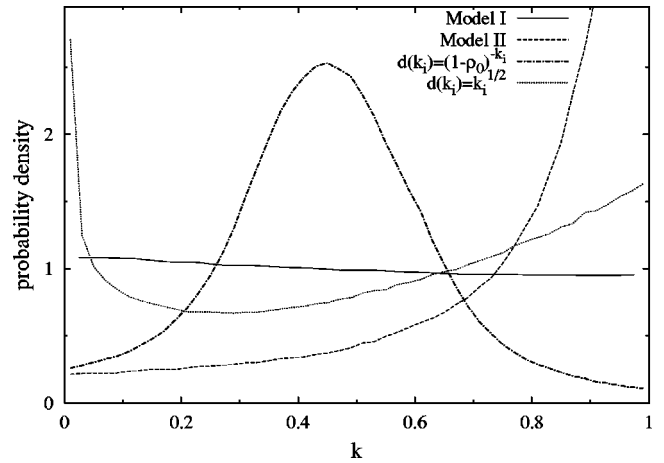

FIG. 5. Distribution of k_i in the steady state of some particular cases of model (1) (see text).

tem. Since species are characterized only by the number k_i it is equivalent to calculating the distribution of k_i in the steady state of model (1). Of course, due to selection this distribution in general will be different than the distribution $p(k)$, i.e., the distribution from which we draw k_i of a newly created species. Some of our results are shown in Fig. 5 [all results for $g(t) \equiv 1, z=4, N=100$].

In the case of model I $[f(k_i) \equiv 1, d(k_i) \equiv 1]$ with homogeneous initial distribution of k_i $[p(k)=1]$ one can see that the steady state distribution is also approximately homogeneous (with a slight bias favoring small-k species). We checked that model I shows this behavior also for other distributions $p(k)$ (what you put is what you get). Different behavior appears for model II $[f(k_i)=k_i, d(k_i) \equiv 1]$. In this case the growth rate factor $f(k_i)$ of the i-th species is proportional to k_i, which certainly prefers species with large k_i. The numerical results for homogeneous distribution $p(k)=1$ confirm such a behavior (Fig. 5). We observed a similar strong preference of large k_i species also for model II with other distributions $p(k)$.

We also examined the selection pattern in the presence of some competing effects. To compensate a strong preference toward large-k species we made simulations for our model with $f(k_i)=k_i$, $d(k_i)=\sqrt{k_i}$, and $p(k)=1$. Such a term reduces the death rate of small-k species. Our results show (Fig. 5) that in this case distribution of k_i has two maxima at the extremities of the interval (0,1). On the other hand, with the same model but for $d(k_i)=(1-\rho_0)^{-k_i}$ (which also reduces the death rate of small-k species) we obtain a distribution with a single maximum around $k=0.45$. It would be desirable to understand the origin of the qualitative difference between these two cases.

Actually, there is yet another property of our species that is subjected to evolutionary selection, namely the number of links l_i (degree) of a given species. Although at the beginning each species acquires z links this number changes during the evolution because some links of a given species might be created or removed due to creation or extinction of another species. And since it is the dynamics of our model and not the random process that determines which species are removed, one can expect that the degree distribution might be
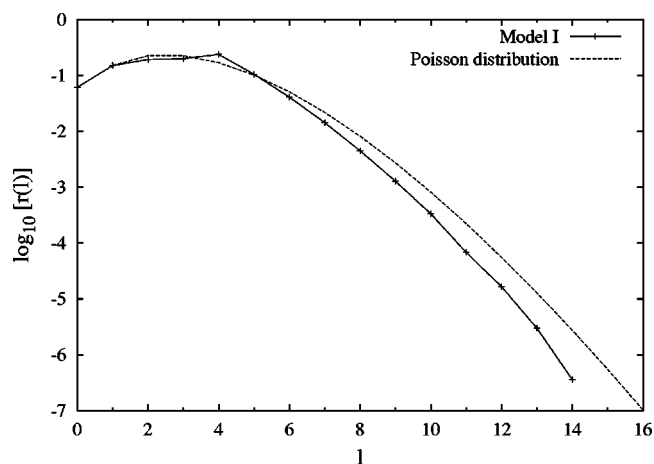
FIG. 6. Probability distribution $r(l)$ of sites with a given connectivity l for model I with $z=4$ and $N=100$ compared with the corresponding Poissonian distribution ($\langle l_i \rangle = 2.98$).

different from the Poissonian distribution that is characteristic for random graphs (see [19] for a precise definition of random graphs).

To check statistical properties of the network of interactions in our model we calculated the degree distribution. Our results for model I with $z=4$ and $N=100$ are shown in Fig. 6. Let us notice that although each species has z links at the beginning it does not mean that the average number of links connected to a given site $\langle l_i \rangle$ equals z since the dynamics of the model might preferentially remove sites of certain connectivity. And indeed, numerical calculations show that in this case $\langle l_i \rangle = 2.98 < z = 4$, i.e., dynamics preferentially removes sites of larger connectivity. For comparison with the random graph we also plot the Poissonian distribution $r(l) = e^{-\langle l_i \rangle} \langle l_i \rangle^l / l!$, where $\langle l_i \rangle = 2.98$. It should be emphasized that the distribution might be approximately fitted using a Poisson distribution, for example with $\langle l_i \rangle = 2.65$. However, it is then not a physically relevant distribution since the average connectivity $\langle l_i \rangle = 2.65$ differs from the value $\langle l_i \rangle = 2.98$ obtained from the simulations. In this sense the distribution is not Poissonian. One can see that for large connectivity the degree distribution decays faster than the Poissonian distribution. This result confirms that dynamics of the model preferentially removes highly connected species. Such sites are probably more susceptible to fluctuations in the system due to extinctions and creation of new species. On the other hand, poorly connected species are more likely to arrive at a relatively stable state. Similar results concerning the degree distribution were obtained in some other cases of our model.

IV. CONCLUSIONS

In the present paper we studied extinction dynamics of a Lotka-Volterra model of a two-level food web. In our model N species of predators feed on a single species of preys. Competition between predators, which is specified by a certain network of interactions, leads to their extinction and replacement by new species. The distribution of intervals between successive extinctions in some cases has power-law tails and thus resembles the extinction pattern of the real ecosystem. However, when the network of interactions between predators is too sparse the ecosystem enters the steady state. We have shown that such a change of behavior might be related to a percolation transition of the network. We also examined an influence of external factors on the evolution of the ecosystem. More specifically, we studied the evolution of our model in a case when the growth rate of preys is changing periodically in time. It turns out that such a modulation substantially changes the frequency of extinctions. Counterintuitively, periods with abundance of preys have a higher frequency of extinctions than periods with lesser amount of preys. Moreover, we examined some properties of species that are preferentially selected by the dynamics of our model. Under some conditions preferred species are a compromise to the conflicting dynamics. Under some other conditions, preferred species form two antagonistic (with respect to the conflicting rules) groups. We also examined the degree distribution of the network of interactions between species. It turns out that the dynamics of the model has a slight preference to remove species of higher connectivity. As a result degree distribution shows some deviation from Poissonian distribution that is characteristic to random graphs.

It would be desirable to examine some extensions of our model. For example one can introduce additional trophic levels or other forms of interspecies interactions. One can also examine a variable number of species that would allow us to create new species using a certain mutation mechanism rather than assuming that they appear as soon as a niche becomes empty. Another possibility that is outside the scope of the majority of macroevolutionary models would be to make further study of the emergent properties of species. For example, one can imagine that a group of species in the ecosystem is well adapted and essentially not subjected to evolutionary changes. On the other hand, there is a group of "newcomers" where evolutionary changes are much more frequent. How are evolution and properties of newcomers influenced by the properties of well-adapted species? Such problems might be easily approached within our model. Selection of a certain group of species (with a given value of k, for example) can be considered as a selection of a certain strategy. One can examine models of this kind where species have multicomponent parameters $[k=(k^a, k^b, \dots)]$. Consequently, one can study evolutionary selection of more complicated traits, strategies, or behaviors. Such an approach would provide an interesting link with certain evolutionary aspects of game theory [20].

[1] J. D. Murray, *Mathematical Biology* (Springer, Berlin, 1989); J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems* (Cambridge University Press, Cambridge, 1988).

[2] P. Bak and K. Sneppen, Phys. Rev. Lett. **71**, 4083 (1993); B. Drossel, Adv. Phys. **50**, 209 (2001).

[3] D. Chowdhury, D. Stauffer, and A. Kunwar, Phys. Rev. Lett. **90**, 068101 (2003).

[4] P. A. Rikvold and R. K. P. Zia, Phys. Rev. E **68**, 031913 (2003).

[5] M. Hall, K. Christensen, S. A. di Collobiano, and H. J. Jensen, Phys. Rev. E **66**, 011904 (2002).

[6] G. Abramson, Phys. Rev. E **55**, 785 (1997).

[7] B. Drossel and A. J. McKane, *Handbook of Graphs and Networks: From the Genome to the Internet*, edited by S. Bornholdt and H. G. Schuster (Wiley-VCM, Berlin, 2002), e-print: nlin.AO/0202034; D. Chowdhury and D. Stauffer, e-print q-bio.PE/0311002.

[8] C. Quince, P. G. Higgs, and A. J. McKane, in *Biological Evolution and Statistical Physics*, edited by M. Lässig and A. Vallerian (Springer-Verlag, Berlin, 2002).

[9] R. Albert and A. -L. Barabási, Rev. Mod. Phys. **74**, 47 (2002).

[10] One of the few macroevolutionary models that takes into account external factors was studied by Roberts and Newman [B. W. Roberts and M. E. J. Newman, J. Theor. Biol. **180**, 39 (1996)]. This model, however, is a variant of the Bak-Sneppen model with dynamics operating at the level of species.

[11] M. E. J. Newman and R. G. O. Palmer, e-print adap-org/9908002.

[12] M. E. J. Newmann and R. G. Palmer, *Modelling Extinction* (Oxford University Press, New York, 2003).

[13] D. M. Raup and J. J. Sepkoski, Proc. Natl. Acad. Sci. U.S.A. **81**, 801 (1984).

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

[15] Statistical properties of extinctions that we study in this paper are not affected by the precise value of the ε as soon as it has a small value ($\varepsilon \ll 1$).

[16] For noninteger z (i.e., the number of links of newly created species) we used the following procedure: with probability $z - [z]$ we created $[z]+1$ links and with probability $1+[z]-z$ we created $[z]$ links. On average such a recipe produces z links.

[17] D. Stauffer and A. Aharony, *Introduction to Percolation Theory* (Taylor & Francis, London, 1982).

[18] M. Scheffer, S. Carpenter, J. A. Foley, C. Folks, and B. Walker, Nature (London) **413**, 591 (2001).

[19] B. Bollobás, *Random Graphs*, 2nd ed. (Cambridge University Press, Cambridge, 2001).

[20] R. Axelrod, *The Evolution of Cooperation* (Basic Books, New York, 1984); J. Maynard Smith, *Evolution and the Theory of Games* (Cambridge University Press, Cambridge, 1982).