Extinction risk and structure of a food web model

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We investigate in detail the model of a trophic web proposed by Amaral and Meyer [Phys. Rev. Lett. **82**, 652 (1999)]. We focus on small-size systems that are relevant for real biological food webs and for which the fluctuations play an important role. We show, using Monte Carlo simulations, that such webs can be nonviable, leading to extinction of all species in small and/or weakly coupled systems. Estimations of the extinction times and survival chances are also given. We show that before the extinction the fraction of highly connected species ("omnivores") is increasing. Viable food webs exhibit a pyramidal structure, where the density of occupied niches is higher at lower trophic levels, and moreover the occupations of adjacent levels are closely correlated. We also demonstrate that the distribution of the lengths of food chains has an exponential character and changes weakly with the parameters of the model. On the contrary, the distribution of avalanche sizes of the extinct species depends strongly on the connectedness of the web. For rather loosely connected systems, we recover the power-law type of behavior with the same exponent as found in earlier studies, while for densely connected webs the distribution is not of a power-law type.

PACS number(s): 87.10.−e, 05.40.−a, 05.45.−a, 05.70.Ln

I. INTRODUCTION

Food webs describe the resources and trophic relationships among species within an ecosystem. The first semi-quantitative descriptions of food webs were given by biologists at the end of the 19th century [1,2]. Later on prey-predator relationships between species were defined in terms of oriented graphs with hierarchical or layered structures [3]. The problem of describing such food webs was then taken over by mathematicians and physicists, and different modeling levels and types of models have been proposed.

A first group of models is constituted by the so-called *static models* in which the links between different species are assigned once and for all, according to different scenarios (random, scale-free, or small-world graphs [4,5], for example). Some properties of these food webs were analyzed and compared with available biological data, and the comparison usually turned out to be quite poor.

The second group of models contains the so-called *dynamic food web models*. The novelty consists in recognizing that the links between the species are generally not arbitrary and quenched, but emerge as the result of some intrinsic biological dynamics. There are then many possibilities for modeling the evolutionary dynamics [6]. The simplest one concerns two-layered systems with prey-predator Lotka-

Volterra type of dynamics (for a short review, see [7]). A very large body of work has been devoted to the study of population dynamics equations for more than two species [8,9]. In such cases, the links among the species can be modified according to the evolutionary dynamics. One important issue is the control of the robustness of such models when the complexity of the system is increased. Moreover, at a more refined level of description, the Lotka-Volterra mean-field dynamics can be replaced by individual-based models [10,11], taking into account the particularities of the interacting individuals and thus offering the possibility of including stochastic fluctuations. These dynamic food webs models allow therefore both the micro- and the macroevolution of an ecosystem to be treated on an equal footing [12,13].

The richness of the models mentioned above has its own drawbacks. Indeed, the number of control parameters defining the models is usually quite large; moreover, the dynamics is nonlinear. Thus, it is often impossible to get a global picture of the properties of the system. Accordingly, it is desirable to study some models that are as simple as possible, in order to clarify the relative importance of the various ingredients, while being able to capture the generic properties expected for food webs.

Several proposal have been made along this line in recent years (see, e.g., [14,15]). Williams and Martinez [16] introduced a very simple "niche" model, whose dynamics is controlled by two parameters, the species number and the connectivity. Predictions were made for several observable quantities such as the fractions of species at different levels, the vulnerability, and the degree of cannibalism. This model was reconsidered by Camacho *et al.* [17,18]. They showed that for large size and loosely connected food webs this

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model possesses some robust properties. Some characteristics such as the distributions of the number of prey and predators, or the number of trophic links, can be described by a scaling function depending only on one parameter, the connectivity. This universal behavior supports the idea that the methods of nonequilibrium statistical mechanics are well suited to approach food web problems. In 1999 Amaral and Meyer [19] proposed a "minimal" model whose numerical solution leads to a power-law distribution of extinction avalanche sizes, in good agreement with available data from the fossil record. It was shown later that this model is self-organized critical [20] and that the power law can be obtained analytically. Furthermore, taxonomic effects have been added to the model [21], but without significant effects.

In this work we are reconsidering the Amaral-Meyer (AM) model with the aim of investigating several of its properties which are relevant for real food webs and which have not been addressed in the previous work. The paper is organized as follows. In Sec. II, the model is described and several technical details concerning the Monte Carlo simulations, as well as the values of the control parameters, are given. Section III contains the main results. First, the dependence of the survival chance and of the average extinction time on the number of niches N and on the maximum number of feeding species k is studied. The problem of extinction due to stochastic effects is also discussed. Then the question of the pyramidal structure of the food web is approached. Time correlations between the occupied niches at different levels are investigated. The time evolution of the ratio of omnivores is also computed, for both viable and nonviable food webs. The distribution of food-tree sizes as a function of the values of N and k is found to exhibit different regimes. Finally, the problem of avalanches of species extinctions is reconsidered. In contradiction with previous results, it is found that strong deviations from simple power laws for the size distribution of these avalanches can be observed for large values of k. Some of our predictions are compared with real biological data and are found to be in good agreement. Conclusions are relegated to Sec. IV.

II. MODEL

A. Original AM model

The AM food web model consists of L trophic levels, each of them containing the same number N of niches, which can be either empty or occupied by a single species. Each species from level $l = 2, 3, \ldots, L$ feeds on at most k ($k \geq 1$) species that are randomly selected from the level below, ($l-1$) (see Fig. 1). Therefore a species from level l is a predator for some species at the level ($l-1$), and at the same time it may be a prey for species from the level ($l+1$) (except for the species on the top level L, which have no predators, and the species on the bottom level $l=1$ which have no prey).

The dynamics of the web is driven by the extinction and creation of species, as well as by the dynamically related evolution of the trophic links between the species. That is, at each time step [Monte Carlo step (MCS)], one starts by randomly removing species from the basal level 1, with a given extinction probability p. When a species goes extinct, all the
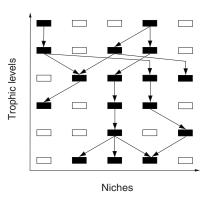

FIG. 1. Schematic representation of the AM food web model, for $L=6$ and $N=5$. The occupied niches are represented by the black rectangles and the interactions between species are depicted by the directed links.

links from it to species at the level 2 are removed. If as the result of these link removals a species at the level 2 loses all its prey from level 1, then it becomes extinct as well. This procedure of checking existing links and removal of species which lost all their food sources is then followed on each level up to the top level L. Hence an avalanche of extinctions of species can be generated.

Apart from extinctions, the AM model considers also the creation of species in free niches. Each species (which remains after the decimation procedure described above) at level l can repopulate, with a probability μ, an empty niche either at level l, ($l-1$), or ($l+1$). Newly created species receive at most k links, at random, to species from the adjacent lower level.

Extinction and creation of species are thus stochastic processes that differ from one realization of the food web to another, and one can address the question of the statistical properties of various characteristics of the system, like, for example, the size of the extinction avalanches, the extinction time (or, equivalently, the survival chance), the populations at all levels, the correlations between the different trophic levels, the density of the trophic links, etc. The dependence of these elements on the parameters of the model L, N, k, p, and μ is also an important aspect to be considered.

In this respect, the main result of the original paper [19] addressing the AM model was that the distribution of the sizes of the extinction avalanches can be fitted over about three decades by a power law with an exponent $a \approx -1.98$; this exponent was corrected to the value $a=-2$ in later work [20,21], which is supported by mean-field theoretical arguments. Moreover, it was argued that this power-law behavior is in agreement with available fossil data records. In Ref. [21] it has also been shown that the avalanche size distribution exhibits a maximum for small-size events, before developing the power-law behavior. However, most of the characteristics of the food web that were enumerated above were not addressed in the previous papers on the AM model and our work is therefore intended to fill this gap.

B. Reconsidering the model

We shall investigate here the AM model in more detail, by considering the canonical set of parameters used in [19],

namely, $L=7$ trophic layers, the extinction probability p $=0.01$, and the probability of creation $\mu=0.02$. We shall moreover investigate how the system characteristics depend on the number of niches N and on the highest possible number of links k that a predator may have. The results obtained will be compared to experimental data coming from investigations of some contemporary food webs [16,22,23]. Since the total size—i.e., the product of the number of layers and the mean number of occupied niches—of the experimentally observed food webs does not exceed 1000, we have decided to focus on N values that are smaller than the value of 1000 that was used in Refs. [19,21], and to work with $N \leq 100$, occasionally 200 and 500. As a consequence, the *role of fluctuations* in our systems becomes more important and many of the reported effects are clearly noise induced and/or noise affected, which actually makes them more relevant for real biological food webs. This choice of small N also allowed us to run the simulations for longer times than those considered in [19,21], which unveiled new aspects of the food web viability. In general, we performed simulations over $\sim 10^6$ MCS and the averaging was done over 100 runs (i.e., random realizations of the food web stochastic dynamics). In some cases, in order to check the viability of the system, we even went to $\sim 10^7$ MCS. Mean extinction times for the whole web were obtained by averaging over 500 runs.

III. RESULTS

A. Viability of the food web

A first result refers to the *viability* of the food web, i.e., to its capacity to survive in the long-time limit. The mechanisms leading to the collapse are connected with the stochastic nature of the extinction and proliferation events. Indeed, when the system is small, it may happen rather easily that at the lowest level, which is crucial for the survival of the web, only very few species survive. If, moreover, as is the case in the AM model, the values of both the creation and extinction probabilities are very low, then two scenarios are almost equally probable, namely, (i) either some empty niches at level 1 are repopulated and the web is, at least temporarily, safe, or (ii) existing species are all removed from this level, as illustrated in Fig. 2. This is the end of the food web, since without species at the basal level an avalanche containing all species is created and the web collapses. This *stochastic extinction* in small populations is a well-known effect in ecology [24].

By performing much longer simulations than in [19,21], we have found that small-size (e.g., $N=50$ or 70) and weakly coupled ($k=3-6$) systems are not viable and disappear in the long-time limit $t \approx 10^6$ MCS. Figure 3 illustrates how the chance that a web will survive to a given time t depends on N and k. The survival chance at time t is defined here as the ratio of the number of realizations (runs) for which the system was still existing at time t to the total number of trials.

The web of $N=100$ and $k=3$ turns out to be nonviable, too (out of 100 runs, none has survived to 10^7 MCS); however, increasing k to 4 stabilizes the system. The dependence of the mean extinction time on the number of niches N and on the maximum number of links k is illustrated in Fig. 4. It
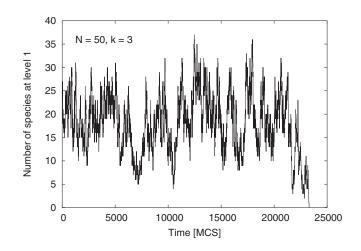

FIG. 2. Temporal evolution of the number of species on the basal level for $N=50$, $k=3$. Single run, exhibiting the complete extinction of the species on this level.

is obvious that an increase in k, i.e., the connectedness, stabilizes the web. Small, sparsely coupled webs cannot exist for a longer time.

B. Structure of the web

The next set of figures (see Fig. 5) illustrate the temporal evolution of the normalized populations at the different levels (i.e., the number of species at a given level divided by the total number of species in the web, at a given time). For the sake of clarity, only parts of the levels are shown. The AM model leads in a natural way to a *pyramidal form of the food web*, where the upper levels are less populated than the lower ones (see the upper panel of Fig. 5). This effect is less pronounced when the system is close to its collapse, as shown by the lower panel of Fig. 5. Comparison with Fig. 6 indicates that the pyramid effect almost disappears for systems with many niches (high N), and this is the reason it was not observed either in [19] or in [21] for which $N=1000$. Note
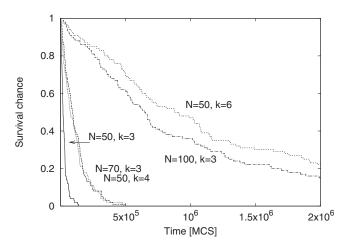

FIG. 3. Survival chance at time t for different values of N and k (evaluated from 100 runs). Increasing N and k increases the survival probability of the food web.
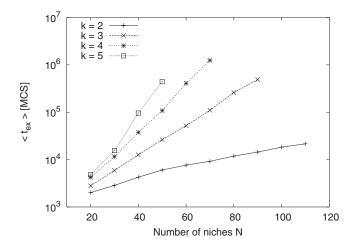
FIG. 4. Average extinction time of the whole food web as a function of the number of niches N for different values of k. The averages were performed over 500 runs. Small sparsely coupled webs cannot exist for a long time.

also that the pyramidal structure has been best observed by biologists in rather small food webs [22].

C. Correlations between trophic levels

As seen from both Figs. 5 and 6, the numbers of occupied niches at different levels are randomly oscillating in time. In order to check the *degree of correlation* of these oscillations, and whether there is some systematic time lag between them, we have calculated the correlation functions from the corresponding discrete-time series of the populations on the different levels, using the formula [25]

$$C_{ij}(t) = \mathcal{C}_i \begin{cases} \sum_{\tau=0}^{T-t} \delta N_i(\tau+t)\,\delta N_j(\tau) & \text{for } t \geq 0, \\ \sum_{\tau=0}^{T-|t|} \delta N_i(\tau)\,\delta N_j(\tau+|t|) & \text{for } t \leq 0. \end{cases} \quad (1)$$

Here $N_i(\tau)$ is the population of level $l=i$ at time τ (which is an integer number of MCSs) and $\delta N_i(\tau)$ is its fluctuation around the mean value,

$$\delta N_i(\tau) = N_i(\tau) - T^{-1} \sum_{\tau'=0}^{T} \delta N_i(\tau'); \quad (2)$$

t is the time lag (which can be positive or negative), and T is the total simulation time. The coefficient $\mathcal{C}_i$ was chosen such that the autocorrelation functions at zero lag are equal to 1,

$$\mathcal{C}_i = \left(\sum_{\tau=0}^{T} [\delta N_i(\tau)]^2 \right)^{-1}. \quad (3)$$

The results for $N=100$ and 200 are illustrated in Fig. 7.

We see that the time series at neighboring levels are highly correlated with each other at zero time lag. In other
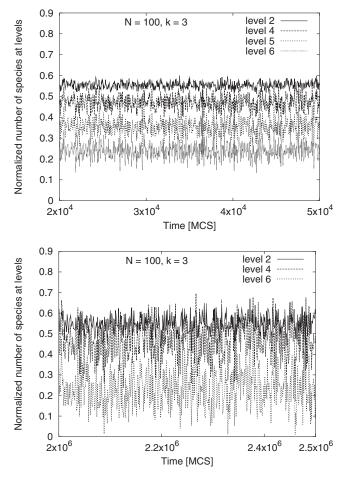

FIG. 5. Time dependence of the normalized populations of different levels for $N=100$, $k=3$. Upper panel: intermediate-time interval. Lower panel: long-time limit, just before the web collapse (data from single runs). Note the pyramidlike structure of the web (higher trophic levels less populated than the lower ones) and the increase of fluctuations before the web collapse.

words, species at a given level adjust immediately to the changes at the level below, which is a feature that could be expected in view of the constitutive dynamics of the model. The correlation of course decreases with increasing distance between the levels, but the peak at zero time lag remains. It should be noted that in the $N=100$ case (upper panel of Fig. 7), apart from the very narrow zero-lag correlation peak, there is also a rather broad structure centered around it. This structure is practically absent in the case of the larger system with $N=200$ (lower panel in Fig. 7) and is to be related to the long-time instability of the system with $N=100$ and $k=3$, and to the strong fluctuations that accompany its collapse.

D. Fraction of omnivores

Another biologically interesting feature is the *fraction of omnivores*, which are predators feeding on more than one prey [26]. Figure 8 shows the distribution of the number of links per predator for a nonviable (upper panel), and a viable (lower panel) system, at several times. The distribution remains virtually the same throughout the simulation time for a
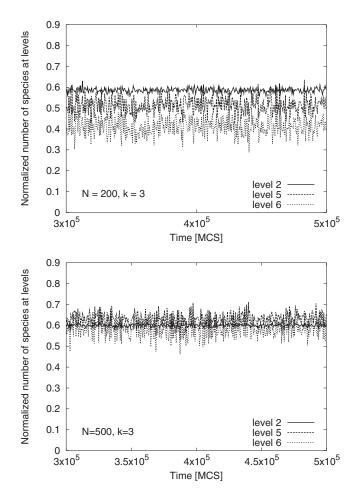
FIG. 6. Time dependence of the normalized populations of different levels for $k=3$. Upper panel: $N=200$. Lower panel: $N=500$ (data from single runs). The pyramid effect disappears for systems with many niches (high N).

FIG. 7. Cross correlations $C_{1,j}$ [see Eq. (1)] for $j=2,4,6$ (evaluated from single runs). Upper panel: $N=100$ and $k=3$. Lower panel: $N=200$ and $k=3$. The time series at neighboring levels are highly correlated with each other at zero time lag. The correlation decreases with increasing distance between the levels but the peak at zero time lag remains well pronounced.

viable web. However, for a nonviable one approaching extinction, the fraction of highly connected predators grows. In other words, close to the collapse, only predators feeding on many different kinds of prey will survive. In this sense, the presence of omnivores stabilizes the web, as documented experimentally in [26].

The average fraction of omnivores in a stationary state of the food web depends on the maximum value of links k, but it is rather insensitive to the number of niches N, as illustrated by the data in Table I. This feature also agrees with experimental results reported in [16].

In a stationary state of the web, the average number of links corresponding to different levels l has a similar type of profile; however, for high values of k we observe a maximum at intermediate levels, as illustrated in Fig. 9.

Food webs are also often characterized by the *length of the food chains* (or "trees") that form the web [16,22]. We define them in the following way. Each species with no predators is the root of a new tree. Starting from the root we go along its links to the lower level and mark all species the root is preying on. Then we check their links to find their prey species and so on. Since different predators do not really compete for food in the model (i.e., if they are linked to
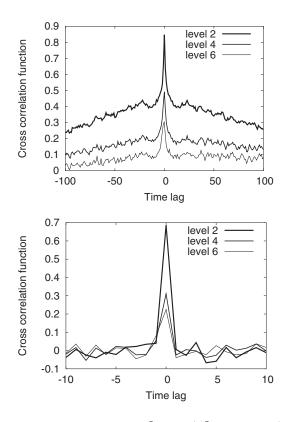
the same prey, they all get enough food), we can treat the partially overlapping trees as independent ones. The size of a tree is then simply the total number of species that belong to that tree.

As can be seen from Fig. 10, the food tree size distribution depends on the number of niches N in the system. The maximal tree size increases with N, as could be expected. Moreover, in a bigger system there is more space for trees of similar sizes and that is why the curves in Fig. 10 shift upward with increasing N. The linear dependence of the distribution of chain lengths on the semilogarithmic plot in Fig. 10 indicates an exponential decrease with increasing tree size.

The maximum number of links k between species also plays an important role on the food tree size distribution. The results for $N=100$ niches at two different time steps are displayed in Fig. 11. When k increases, small trees become less likely and bigger structures in the system are preferred instead. We can thus distinguish two regimes with different k dependence, namely, the regime of "small trees" (of size ≤ 10), whose number decreases with increasing k, while the number of "big trees" is an increasing function of k. Moreover, the maximal size of a food tree varies strongly with k. It is also interesting to note that for sufficiently large N there is a well-pronounced peak in the distribution of tree sizes at a size of 7, which is simply the number of trophic levels in the system.
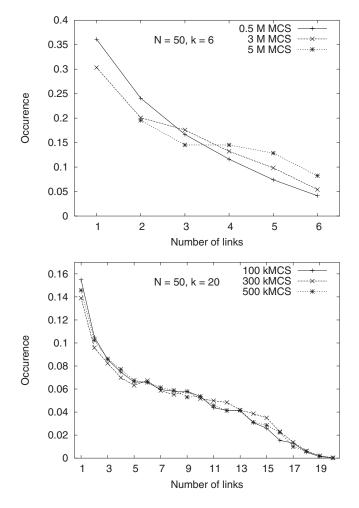
FIG. 8. Distribution of the number of links per predator for nonviable $k=6$ (upper plot), and viable $k=20$ (lower plot) systems, at different times. $N=50$ in both plots (evaluations from single runs). In viable webs the distribution remains essentially the same, while in nonviable ones the fraction of multiply connected niches grows with time.

Biologists [1,16] often describe food webs in terms of fractions of *basal, intermediate,* and *top* species. In this model these categories correspond to occupied niches at levels 1, 2–6, and 7, respectively. For viable systems the values we obtain for these fractions are not too sensitive to the values of N and are presented in Table II.

These results agree very well with biological data for a food web from Little Rock, Arkansas, USA; see [16] for further details.

TABLE I. Average fraction of omnivores in a stationary state of the web, for various k and N. The averages were taken over 100 runs.

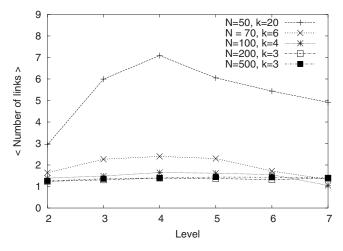|		k		
N	3	4	6	20
50	0.312	0.4185	0.6966	0.8543
100	0.2936	0.4944	0.6567	0.8648

FIG. 9. Number of links for different levels in a stationary state of the web, averaged over 100 runs. For small and highly connected systems the density of occupation of intermediate levels is the highest. For loosely connected large webs the distribution of densities is rather flat.

E. Avalanches of species extinctions

Finally, we analyzed the distribution of *avalanche sizes of species extinctions.* We observed the maximum in the distribution that was mentioned in [21], which becomes more pronounced with increasing number N of niches. For $k=3$, which was the value considered in [19,21], we recovered the known power-law behavior, extending over nearly three decades, with an exponent equal to $a=-2$, as calculated in [20,21]. This value does not seem to depend on N, and even for nonviable systems we got the same good fit to a power-law type of behavior, with the same exponent (see Figs. 12 and 13).

However, when the food web becomes highly connected (i.e., $k=6$ or larger) the deviations from the power-law behavior are very large, as illustrated in Figs. 13 and 14 for $k=20$. One may notice that for highly connected webs the fraction of larger avalanches increases, simply because the removal of a prey on which many predators feed is affecting more species.
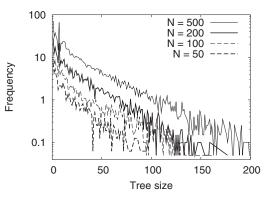

FIG. 10. Food tree size distribution at time $T=3\times10^5$ MCS as a function of the number of niches N ($k=6$, semilogarithmic scale, evaluation from 100 runs). The maximal tree size increases with N. Note that the curves shift upward with N, since in bigger systems there is more space for trees of similar sizes.
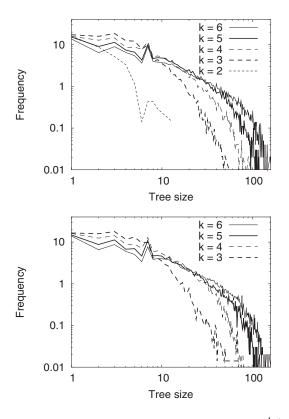
FIG. 11. Food tree size distribution at time $T=5\times10^4$ (upper plot) and 3×10^5 (lower plot) MCS as a function of the maximal number of links between species k ($N=100$, log-log scale, evaluation from 100 runs). There are two regimes with different k dependence: the number of "small trees" (of size ≤ 10) decreases with increasing k, while the number of "big trees" is an increasing function of k. The maximal size of a tree varies strongly with k.

Thus the power-law behavior, although widely present in large-N webs, is *not universal*, but is rather the result of a particular choice of the parameter values of the food web.

IV. CONCLUSIONS

We have presented a detailed discussion of several aspects of the AM model [19] of a food web that were neglected in previous studies. In particular, we concentrated on relatively small-sized systems and on the role the fluctuations can play in such systems, since this is the frame that is important in most real biological food webs. Several comparisons of the theoretical predictions with experimental data were also discussed.

Our simulations confirmed the observations of [21] concerning the distribution of avalanche sizes of species extinc-

TABLE II. Fraction of species at basal, intermediary, and top levels ($k=6$, averages over 100 runs).

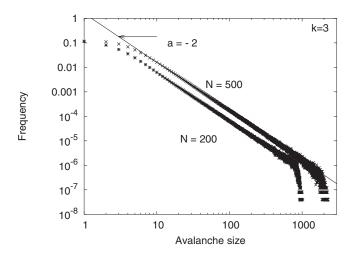| N	Basal	Intermediate	Top
100	0.16	0.79	0.05
200	0.10	0.80	0.10
500	0.12	0.79	0.09

FIG. 12. Distribution of avalanche sizes for $N=200$ and 500, for food webs with $k=3$ (estimated from 500 runs). The slopes are all identical and increasing the size of the web shifts the distribution to higher frequencies.

tions, the value of the power-law exponent $a=-2$, and the existence of a maximum depending on N. It is worth noting here that the same value $a=-2$ of the exponent of the distribution of extinction avalanches has also been found in two other different food web models, Refs. [27] and [28]. The last paper is a generalization of the Bak and Sneppen model [29], in which two factors determine the fate of a species—biotic ("bad genes") and abiotic ("bad luck").

For reference, we have kept the values of some of the model parameters (number of layers L, and probability of creation μ and of extinction p) the same as in the original AM model [19,21]. However the dependence of the system behavior on the number of niches N and on the maximum number of links per predator k turned out to be quite interesting. We have thus unveiled new features of the model not found in the earlier papers. A food web may collapse if it is too small and/or has not enough links between species. Sys-
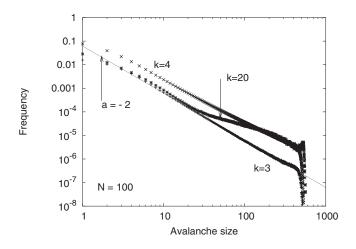

FIG. 13. Distribution of avalanches for $N=100$ and different k (estimated from 500 runs). For small values of k ($=3,4$) we observe the same slope as for large food webs (see Fig. 12). More highly connected webs do not exhibit a power-law-type distribution.
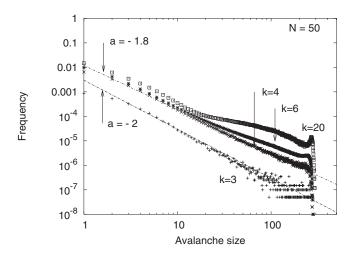
FIG. 14. Distribution of avalanches for $N=50$ and different k (estimated from 500 runs). The power-law-type dependence with the exponent $a=-2$ is observed only for $k=3$. For $k=4$ the distribution still has a power-law character, but with a different exponent. Further increase of k changes the type of behavior.

tems smaller than $N \approx 200$ show a pyramidlike structure, where the top levels are less populated than the bottom ones. The occupations of the levels are strongly correlated at zero time lag. When the web is close to a collapse, the fraction of highly connected predators (omnivores) significantly increases, which may lead sometimes to a (temporary) rescue

of the web. The distribution of the length of food trees has an exponential character and its type depends rather weakly on both N and k. Finally, the distribution of species extinctions shows an unexpected feature, contrary to the previously claimed universality of the power-law behavior; namely, that for large k values (i.e., highly connected webs) the distribution cannot be described any longer as a power law. It should also be noted that to some extent our investigations are complementary to those of Amaral and co-workers [18], where mostly large and loosely connected food webs have been studied.

Although several criticisms concerning the applicability of the AM model to biology have been raised [21,30], we have found that some theoretical results, such as the ratio of omnivores, the fraction of different-type (basal, middle, top) species, the food chain length, etc., are in very good agreement with experimental data [16,22,23] on food webs. The significance of this fact is a subject for further analysis.

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