

## Stability of a model food web

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We investigate numerically the stability of a model food web, introduced by Nunes Amaral and Meyer [Phys. Rev. Lett. **82**, 652 (1999)]. The model describes a system of species located in niches at several levels. Upper level species are predated on those from a lower level. We show that the model web is more stable when it is larger, although the number of niches is more important than the number of levels. The food web is self-organizing itself, trying to reach a certain degree of complexity, i.e., number of species and links among them. If the system cannot achieve this state, it will go extinct. We demonstrate that the average number of links per species and the reduced number of species depend in the same way on the number of niches. We also determine how the stability of the food web depends on another parameter of the model, the killing probability. Despite keeping the ratio of the creation and killing probabilities constant, increasing the latter reduces significantly the stability of the model food web. We show that connectance dependence on the number of niches has a power-type character, which agrees with the field data, and that it decreases with the number of species also as a power-type function.

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### I. INTRODUCTION

Food webs (FWs) are systems of many species interacting with each other in a given way and forming a complex system [1]. Such structures are very interesting from a theoretical point of view and also from a practical one since many habitats are *de facto* FWs. It is therefore natural that they have been studied by biologists since a long time (see e.g., [2]). Recently physicists also got interested in FWs treated as complex systems of interacting particles [3–7]. Theoretical models developed by them present different levels of sophistication and resemblance to either present day or paleontological biological data. Some of them are dealing with fixed number of species and/or interactions among them [4,8], while others allow for changes in these characteristics. Also the range of problems studied is rather vast—distribution of extinct species (avalanches) [3,9–11], unification of macroevolution and microevolution [7], models in a network changing dynamically in time [12,13], and cost of resources transfer in food webs [14–16]. Applicability of critical phenomena concepts to FWs in general and the niche model [17] in particular has been also discussed [18]. Interesting reviews of models used and discussed by physicists in population dynamics are given in [6,19].

There is, however, one important aspect which received attention by biologists [20] but, to the best of our knowledge, has not been considered by physicists. It is the relation between FW complexity and its stability. Early papers by ecologists [21] suggested that stability increases with complexity. The reasoning was that it is easier for a new species to invade a habitat which has been already destroyed by men (low diversity) than to invade a tropical forest. However later May [22] and then Pimm and Lawton [23], using mathematical models, claimed that the opposite is true—complex sys-

tems could not be stable. At the same time field studies seemed to confirm the earlier statement. Since that time several attempts, based generally on mean-field approach and differential equations (see, e.g., the review by McCann [20]), have been proposed to solve this paradox. In particular Kondoh [24] suggested that complex FW systems could be stable due to their dynamic, not static, architecture, which may correspond to adaptation of species (like food preferences) to changing conditions within the FW.

In order to see how the stability-complexity relation will look in an agent-based (Monte Carlo) FW model, we took the well-known Amaral-Meyer (AM) model [3]. It has been already intensively studied [9–11], without however an in-depth analysis of its stability. There are several reasons for choosing this model for such investigations. It shows good agreement with the biological data [3,11]; it has dynamic structure, with both number of species and number of links among them changing in time. Finally, it is simple and therefore allows for clear identifications of the results. We assume here, like in the original AM model, that the species characteristics do not depend neither on density of species nor on time.

### II. MODEL

The AM model consists of  $L$  levels, each containing  $N$  niches, which could be either occupied by a species or empty. Each species at level  $l$  ( $l=0, 1, \dots, L$ ) preys on species occupying the level  $l-1$  except for species at the bottom level. The bottom level (producers) could be plants, microbes, bacteria, etc. They are autotrophs; using detritus (dead plant or animal matter) they produce energy used by others. On the next levels there are consumers, feeding on producers. They are heterotrophs—could not make their own food. Finally on the highest level are secondary consumers, sometimes called also top predators, who are feeding on consumers. We assume here that consumers, due to their cognitive constraints, foraging strategy or other limitations, could

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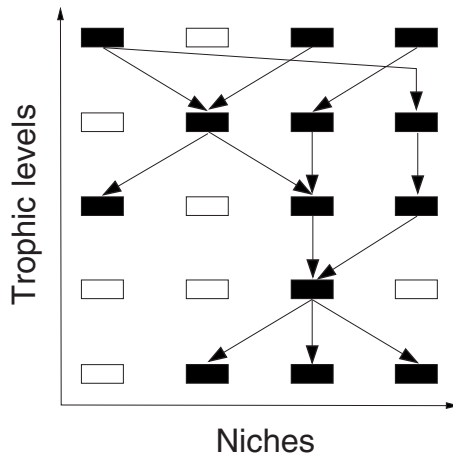


FIG. 1. An example of a food web in the AM model with  $L=5$  levels and  $N=4$  niches. Black rectangles stand for occupied niches. Interaction between species (niches) are represented by the arrows.

not switch from one type of prey to another. Hence if all the prey of a given predator vanishes, the predator must also disappear. Therefore, apart from the bottom level (primary producers, prey only) and the top level (top predators) every species may be prey and predator at the same time. Each predator has up to  $k$  links (parameter of the model) to randomly chosen species at the adjacent lower level. Dynamics of the FW is generated by two simple processes, killing and creation. In each time step, every species at the bottom level is removed with probability  $p$  (killing probability, next parameter of the model) and the respective links to predators in the level 1 are cut. A predator which lost all its links in this way is likewise eliminated and links to species from the level 2 which predate on it are removed. This process may propagate up to the top level, creating an avalanche. The size of the avalanche is determined by the total number of species affected by removing an occupied niche at the bottom level. As far as creation is concerned, each remaining species produces, with probability  $\mu$  (another parameter), a species which could be, with equal probability, put on an empty niche either at the same level, one level below or one level above. The new species receives links to randomly chosen sites at the adjacent lower level. An example of a FW in the AM model is shown in Fig. 1.

The model has therefore the following parameters: number of levels  $L$ , number of niches  $N$ , maximum number of links per species  $k$ , killing probability  $p$ , and creation probability  $\mu$ . As in previous papers [3,9–11] we assume here that  $p=2\mu$ . It has been shown in those papers that the model has critical features, namely, the distribution of the avalanches sizes follows a power law.

In this paper we shall investigate the relation between FW stability and its complexity. Although intuitively clear, both notions are not defined in ecology in an unequivocal way. Complexity is generally associated with connectance,  $C$ , defined as [25,26]

$$C = \frac{W}{S^2}, \quad (1)$$

where  $W$  is the actual number of links (feeding connections) in the network and  $S$  is the species richness, i.e., the number of species in the FW. It should be mentioned however that this is the most widely used but not the only definition of connectance. For some authors [26] complexity is just connectance, for others [27] it is the product of connectance and the number of species, and for still others [24] it is composed of two factors—high species richness and dense trophic links—or sometimes [25] even three ( $S$ ,  $C$ , and link density) factors. Here we take the simplest definition that complexity is identical with connectance.

Definition of stability in biological systems also creates a problem. It is of course a rather obvious notion if a FW is modeled by a set of differential equations, but otherwise, as stated in [28], operational measures are not very precise. Stability is often related to cascading extinctions which result in the disappearance of all species in a given FW [29]. McCann [20] gave a detailed discussion of FW stability together with presentation of several definitions and their limitations. In all real life and model FWs fluctuations in the number of species at different trophic levels are observed. Therefore general stability, related to the tendency of the system to go away from extremely low or extremely high densities, seems natural to be adopted. In theoretical models a measure of stability is needed and here, like in [24] the probability that at the end of simulations the investigated FW will contain some species, defines our index of stability or survival chance. We are aware that such a definition depends to some extent on the simulation details—maximum time of simulations and the number of runs. After some checking we have decided that the maximum simulation time taken by us [ $2 \times 10^6$  Monte Carlo steps (MCSs)] is satisfactory and stretching simulation time, even by an order of magnitude, will produce results almost identical with those presented in this paper. Similarly for the statistics determining the survival chance, differences between averaging over 200 (used here) and 300 runs are negligible. On the other hand scatter of the extinction times is huge and taking 10 or 200 runs does not improve the situation in any way. Therefore the plots presenting average extinction times should be taken *cum grano salis*.

In our previous paper [11] we have investigated the effect of changing  $N$  on the stability of a FW with a fixed value of  $L=7$ , showing that an increase in  $N$  stabilizes the FW. However, the role of  $L$  has not been discussed, neither the relation between stability and complexity. These problems are addressed in the present paper. When writing about population dynamics the term *viability* is customarily used to describe survival success. In FW literature more often *stability* is employed.

Intrinsic characteristics of the investigated FWs, emerging in time and useful in understanding its features, are connectance  $C$ , number of species  $S$  in the FW, and the density of links  $\lambda$  per species. To be able to compare results coming from FWs of different sizes, we shall also use another quantity—the reduced number of species  $\rho$ . The definitions are as follows [25,26]:

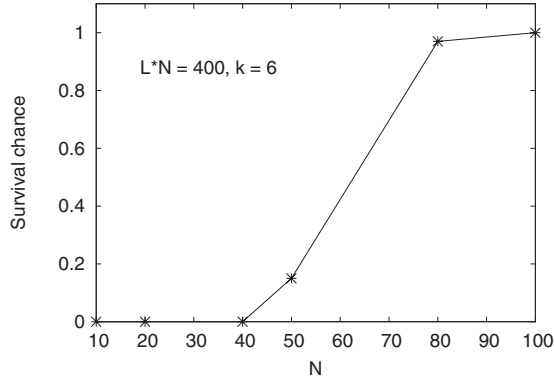


FIG. 2. Survival chance versus number of available niches  $N$  at each level for the case of constant total number of niches, i.e.,  $N \cdot L = 400$ . FWs with small values of  $N$  are more vulnerable.

$$\begin{aligned}
 S &= \left\langle \left\langle \sum_{j,l} a^l(j;t) \right\rangle_{\Delta t} \right\rangle_r, \\
 C &= S^{-2} \left\langle \left\langle \sum_{l,j,i} C^l(i,j;t) \right\rangle_{\Delta t} \right\rangle_r, \\
 \lambda &= S^{-1} \left\langle \left\langle \sum_{l,j,i} C^l(i,j;t) \right\rangle_{\Delta t} \right\rangle_r, \\
 \rho &= \frac{S}{NL}, \quad (2)
 \end{aligned}$$

where  $C^l(i,j;t)$  is the element of the connection matrix, with values 0 or 1, between species  $i$  at level  $l$  and species  $j$  at level  $l-1$  at time  $t$ .  $a^l(j;t) = 1$  if at time  $t$  the niche  $j$  at level  $l$  is occupied and is equal to zero if it is empty. Brackets  $\langle \dots \rangle_{\Delta t}$  denote averaging over a time period  $\Delta t$ , which we took equal to  $2 \times 10^4$  MCSs after rejecting the first  $2 \times 10^4$  MCSs, except for very small FWs, which got extinct sooner.  $\langle \dots \rangle_r$  means averaging over runs. At the beginning of simulations the FW was empty and we filled up half, randomly chosen niches at the bottom level. Upper levels were then consecutively populated and appropriate links were created, according to the general rules. In general we have performed simulations until  $2 \times 10^6$  MCSs and averaged over 100 independent runs.

### III. RESULTS

In order to see how the size of the system influences the stability, we have studied first a FW of a fixed total number of available niches and we took  $N \cdot L = 400$ . Field data often refer to similar sizes of FWs [1,17]. We fix the maximum number of links at  $k=6$  and take killing probability  $p=0.01$ , as in the original AM model. Survival chance and the average extinction time as functions of simulation time, measured in Monte Carlo steps, are shown in Figs. 2 and 3.

As could be seen from Fig. 2, among FWs with a constant total number of niches,  $L \cdot N = \text{const}$ , the bigger the number of niches  $N$  at every level is, the more stable a given food web is. For  $N \leq 40$  ( $L \geq 10$ ) the food webs have no chance to

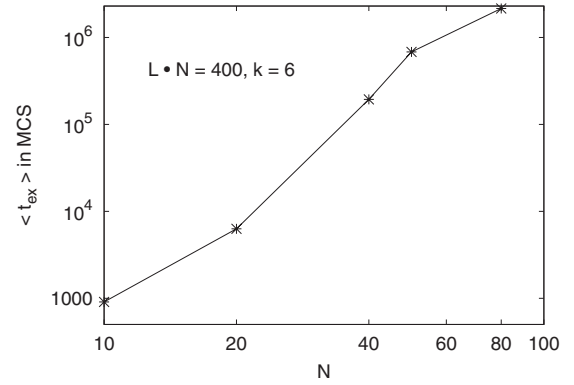


FIG. 3. Average extinction time as a function of  $N$  for the case of constant total number of niches, i.e.,  $N \cdot L = 400$ . Log-log scale. FWs with bigger number of niches  $N$  have longer life expectancy.

exist. This agrees with the field data [1,17], where observed FWs had only few trophic levels but contained many species.

Similar conclusions could be drawn from the results for the average extinction times as a function of  $N$ . FWs with a big number of trophic levels, each of which contains only a few niches, have very short life expectancy and die out after several thousands of Monte Carlo steps. The average extinction time increases then with  $N$ . Thus again, if  $L \cdot N = \text{const}$ , FWs with bigger values of  $N$  (less trophic levels  $L$ ) seem to be more stable. However, one should handle the data in Fig. 3 with caution. As mentioned above, all the results were averaged over 100 independent runs and although the data for the average extinction time offer some insight in the stability of FWs and are consistent with our findings on the survival chance shown in Fig. 2, it should be noted that the extinction times of a given food web were scattered very much within each series of runs.

Let us focus now on FWs with a constant number of trophic levels  $L$ . We shall concentrate our attention on the case  $L=3$ , which corresponds to a class of FWs most often studied by biologists [1,2], and vary  $N$  and  $k$  to get more insight into the stability issue.

As shown in Fig. 4, FWs containing a small number of niches at each trophic level (less than 40) are not stable at all. They die out very quickly with probability 1. Then there is a narrow transition region for  $40 < N < 60$ , in which a food web has a nonvanishing (but less than 1) chance to survive. For  $N > 60$  all food webs studied by us are stable and survive until the end of simulations. Changing the maximum number of links  $k$  between the species helps only a little in the transition region: increasing  $k$  leads to stable food webs at slightly smaller values of  $N$ .

After showing that the number of niches,  $N$ , is more important for the stability of a FW than the number of levels  $L$ , let us consider now the case of  $L=3$  and investigate the dependence of the earlier introduced quantities— $C, S, \rho, \lambda$  on  $N$  and the maximum number of links,  $k$ , a predator may have. In Fig. 5 on the left panel we present reduced number of species,  $\rho$ , as a function of  $N$  for  $k=6, 8$ , and  $12$ . As could be expected, with increasing  $N$  the reduced number of species grows; hence the FW moves away from potentially dangerous low density regime. Similarly, allowing for more

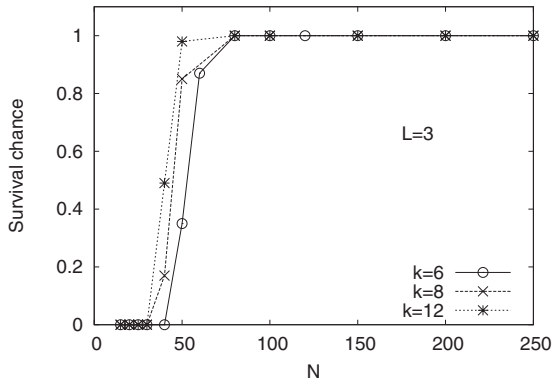


FIG. 4. Survival chance versus number of available niches,  $N$ , at each level for the case of constant number of trophic levels  $L=3$  and several values of the maximum value,  $k$ , of links per predator. Larger values have positive effect on stability.

links increases  $\rho$ , which again agrees with experimental observation that stability is increased by addition of trophic interactions [30]. The dependence of the average number of links  $\lambda$  has a similar dependence. It is interesting however to note that the growth of  $\rho$  and  $\lambda$  saturates at a certain level and for  $N > 100$  the growth is quite slow. This may suggest that there exists an optimal reduced number of species and average density of links. Further increase in  $\rho$  and/or  $\lambda$  will not improve the stability and therefore is not realized. Such a situation may be called self-regulation or self-organization of a FW. There exists therefore an optimal degree of complexity which allows the FW to exist. If a FW cannot reach those values, it remains in a vulnerable state and most probably will vanish. Saturation of the average link density with increasing the number of niches and relatively weak dependence of the “asymptotic” values of  $\lambda$  on the maximum value of  $k$  may be an argument in favor of the statement [31,32] that there exists an upper limit to the link density [33]. It is also interesting that by shifting the data for  $\rho$  one arrives at nearly overlapping, except for very small systems, curves for  $\rho$  and  $\lambda$  (see Fig. 6). Figure 7 shows, on a doubly logarithmic scale, the plot of the connectance  $C$  [Eq. (2)] versus size  $N$  of the FW. The dependence has a power-type character,

$$C \propto N^{-1}, \quad (3)$$

irrespective of the value of  $k$ . To see whether the power-type dependence found by us agrees qualitatively with field data,

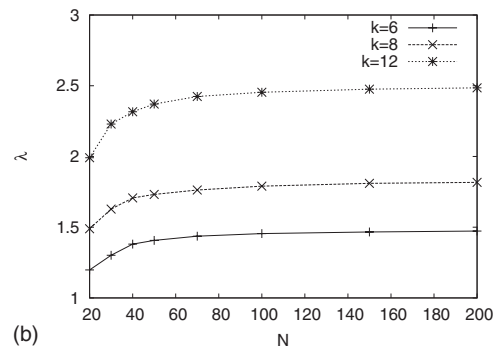
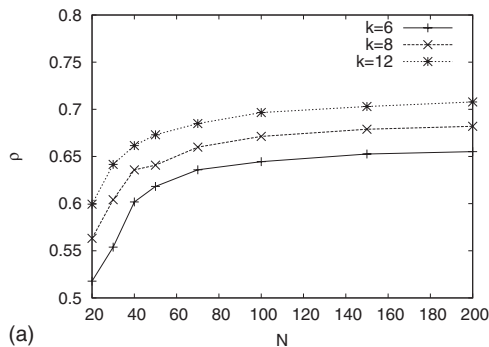


FIG. 5. Left panel: reduced number of species in the FW versus number of niches  $N$ . Right panel: average number of links per species also as a function of  $N$ . In both cases number of levels  $L=3$ . After initial increase, later on the dependence on  $N$  is rather weak.

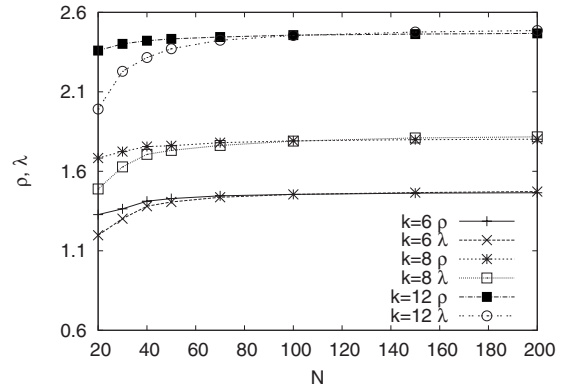


FIG. 6. Comparison of the dependence of reduced number of species  $\rho$  and number of links per species  $\lambda$  for  $L=3$ . Data for  $\rho$  are shifted upward for better comparison.

we took from Table I of Ref. [26] data for FWs characterized by the number of links per species ( $L/SW$  in their notation) of about 4. This roughly corresponds to our parameter  $k=4$ , which also measures the number of links a species could have. As seen from Fig. 7 field data also show power-type behavior with the same exponent.

Connectance could also be related to the number of species  $S$ . Guill and Drossel [25] investigated in detail the niche model introduced earlier by Williams and Martinez [17] and have found that for systems not larger than 150 species the relation has the form

$$C \propto S^{-\alpha}, \quad (4)$$

with  $\alpha=0.88$ , which, in turn, gives a very weak dependence of  $\lambda$  on  $S$ ,

$$\lambda \propto S^{0.12}. \quad (5)$$

Our estimations of  $\alpha$  (see Fig. 8), not restricted in the size of the FW, give similar value of  $\alpha$ , namely,  $\alpha=0.91$ , irrespective of the value of  $k$ . Hence, the dependence of  $\lambda$  on  $S$  is even weaker. Close resemblance of the two results coming from different models may suggest that the relation between  $C$  and  $S$  is an important characteristic of a FW.

For FWs with more than just three levels, we have obtained nearly identical results as reported above for  $L=3$ . In particular for  $L=6$  the exponent  $\alpha$  is estimated as 0.9.



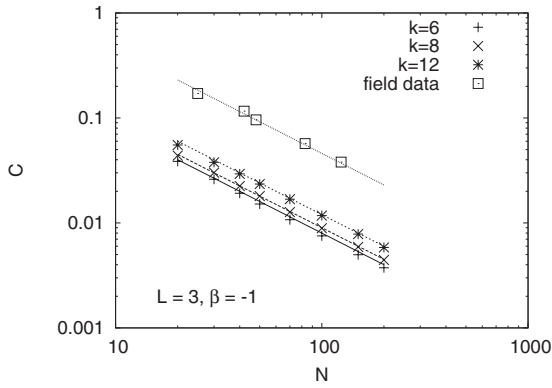


FIG. 7. Dependence of the connectance on  $N$ . Doubly logarithmic scale. The exponent is equal to  $-1$ . Field data are for Ythan Estuary 1 and 2, St. Marks Seagrass, St. Martin Island, and Bridge Brook Lake and are taken from Ref. [26].

We turn now to change one more parameter playing an important role in determining the behavior of a FW, namely, the killing probability,  $p$ , of species from the lowest level. It has been shown before [3,10,11] that for the properties investigated in those papers, i.e., distribution of avalanches, pyramidlike structure of FWs, etc., the parameter  $p$  does not play an essential role. As in the original AM paper and the later ones [3,10,11], we keep the creation probability two times larger than the killing probability.

Figures 9 and 10 show the average survival chance and the average extinction time as functions of  $p$  for  $L=8$  and  $N=50$  and several values of  $k$ . Again, the extinction times are very noisy. Averaging over even 1000 runs does not help and therefore the lines show trends rather than values of  $t_{ex}$ . On the other hand the survival chance does not change very much if we average over, say, 20 instead of 100 runs. Increasing the killing probability destabilizes a FW rather fast, despite the fact that we are augmenting creation probability at the same time. If we kill too many species at the bottom level there are simply not enough resources at that level to support the FW pyramid. In other words, big scale extinction avalanches [3,9,11] happen too often and the system becomes unstable. Increasing the maximum number of links,  $k$ , helps us to maintain FW in an alive state, although, as seen from Fig. 11, where the average extinction times are shifted

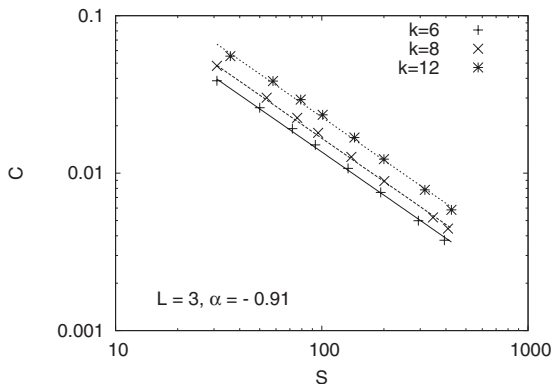


FIG. 8. Connectance versus number of species on a doubly logarithmic scale.

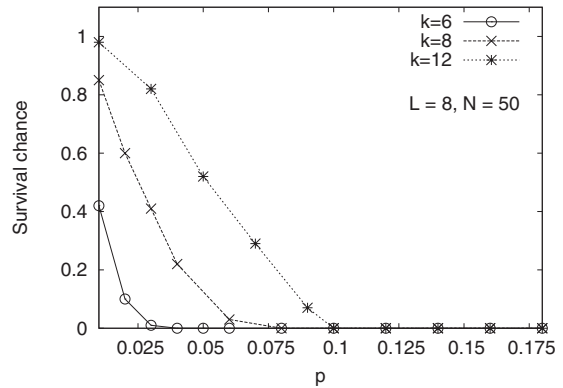


FIG. 9. Survival chance versus killing probability  $p$  for  $L=8$  and  $N=50$  and several values of  $k$ . Regardless of the value of  $k$ , no FW is stable for  $p$  larger than 0.1.

along the horizontal axis, the character of extinctions remains the same. Increasing the number of available niches,  $N$ , would make the system more stable, as we have seen from Fig. 4. For a smaller number of levels, say  $L=4$ , the dependencies will look almost exactly the same. The average number of links  $\lambda$  shows (see Fig. 12) that increasing  $p$  leads not only to smaller survival chances and faster extinction, but it also reduces the complexity (if measured by  $\lambda$ ) of the FW. Those with more levels are more complex in the sense of average species having more links to its prey. It comes from a different distribution of links in FW with  $L=4$  and with  $L=8$ , as shown in Fig. 13. We see that in FWs with higher vertical structure there are more multiconnected species than in those with fewer levels. For stable FWs this distribution of links depends only very weakly on the number of niches  $N$ , as shown in Fig. 14. The number of surviving species fluctuates. For  $L=8$  and  $N=100$  the values range from about 150 to 700, independently of the value of  $k$ . For twice smaller FWs, i.e., for  $N=50$ , the number of surviving species is also two times smaller.

Let us go back now to the case of a fixed total number of niches,  $L \cdot N=400$ . One of the measures characterizing a FW is the length of food “trees” forming the web [11,17,34]. In our paper, the trees are defined as follows: each predator at the top level is the root of a new tree. Starting from the root

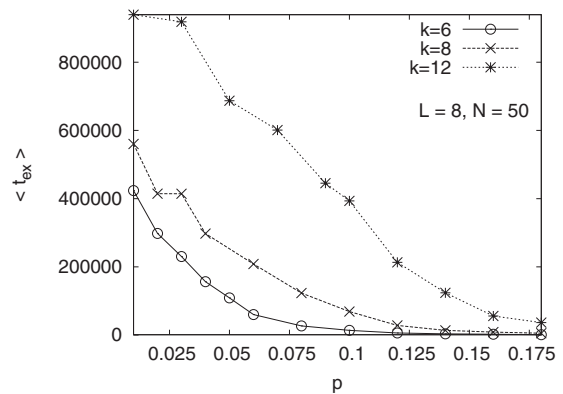


FIG. 10. Average extinction time versus killing probability  $p$  for  $L=8$  and  $N=50$  and several values of  $k$ .

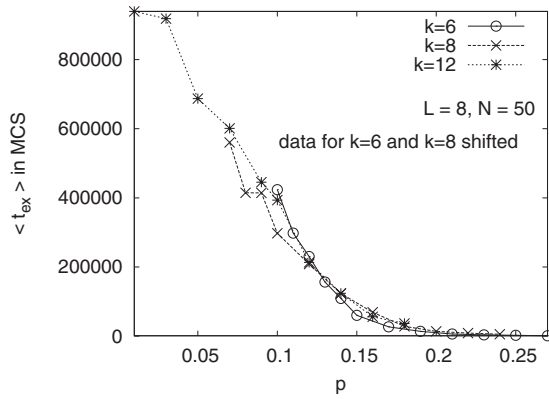


FIG. 11. Average extinction time versus killing probability  $p$  for  $L=8$  and  $N=50$  and several values of  $k$ , where the data for smaller values of  $k$  have been shifted. It follows that the process of disappearing of a FW goes along the same steps for various values of  $k$ , although it happens at different times.

we go along its links to the lower level and mark all species the root is feeding on. Then we check links to find their prey species and so on. Since different predators do not really compete for food in the AM model, 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. In Fig. 15, food tree distributions at time step  $T=1.5 \times 10^6$  MCSs of three stable food webs are shown. We see that the FWs have different structures. If a food web is “wide” but “short” (big  $N$ , small  $L$ ), there are more small trees than the large ones. Increasing the value of  $L$  results in increasing the size of the largest tree. At the same time the number of small trees decreases. Note that the more big trees are in a FW (i.e., more species are omnivorous), the less is the probability that killing one species at the bottom level will start an avalanche, which could endanger the existence of the whole FW. Thus, the slope of the tree distribution in a food web could be used as a measure of its stability: FWs characterized by small slopes are more stable.

IV. CONCLUSIONS

We have investigated stability of a FW within the AM model [3] with respect to changes of its size ( $L, N$ ), maxi-

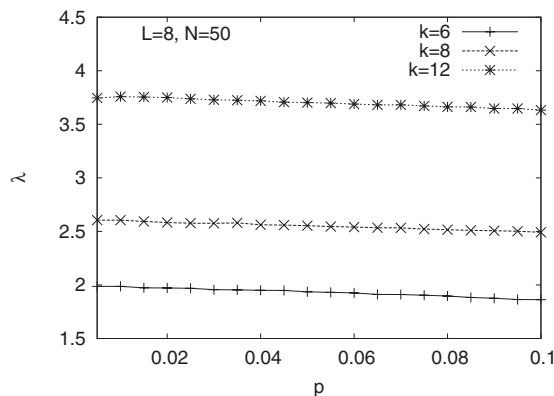


FIG. 12. Average number of links per species,  $\lambda$ , versus killing probability  $p$  for the same system as shown in Fig. 11.

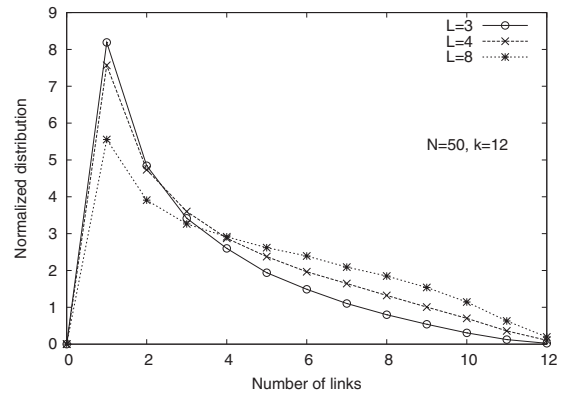


FIG. 13. Distribution of number of links per species normalized by the number of levels  $L$ . FWs with few levels tend to have a more skewed distribution—many predators have just one link and few are multilinked. This tendency is reversed when the number of trophic levels is growing.

imum number of links ( $k$ ), and killing probability ( $p$ ). We have introduced the following quantities characterizing a FW—its connectivity  $C$ , average number of links per species  $\lambda$ , which separately, or together with  $C$ , could correspond to complexity of the FW, the average number of species  $S$ , and corresponding to it reduced number of species  $\rho$ , i.e., the actual number of species divided by maximum possible number of species. These quantities may be used as a measure of the diversity of the FW. The model studied by us has a dynamic architecture, the number of occupied niches, i.e., number of species, and a number of connections between them are changing in time. Therefore the suggestion made by Kondoh [24] that dynamic systems increase their stability is supported by our findings. We have also shown that reduced number of species and link density behave in the same way when the number of niches increases; they grow rather rapidly in the transition region from an unstable to a stable FW and stay almost constant once the stability is reached. This implies that the model FW self-organizes itself, keeping only a number of niches sufficient for survival and connections among them. The values depend, but not strongly, on the

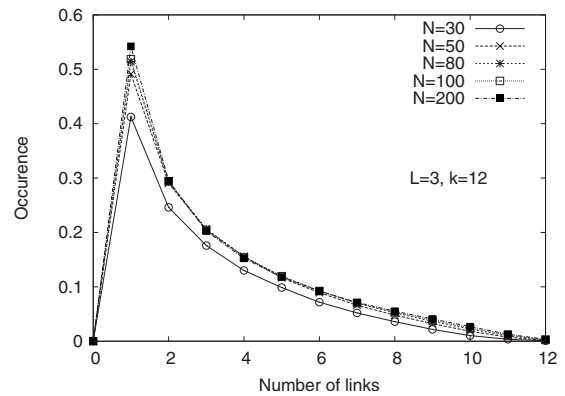


FIG. 14. Normalized by the number of levels  $L$ , distribution of number of links per species for several values of the number of available niches,  $N$ , in one level. For small  $N$  food webs are unstable. Once stability is reached, the distribution does not change greatly.

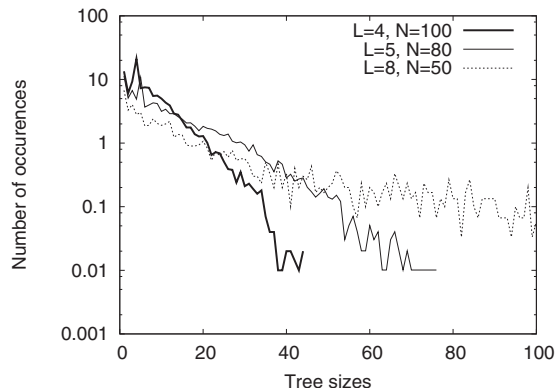


FIG. 15. Distribution of food trees at time  $T=1.5 \times 10^6$  MCS for three different food webs (semilogarithmic scale). The maximal size of a tree increases with  $L$ .

parameters of the model— $k$  and  $N$ . The process is independent of the initial number of occupied lowest level niches. We have also demonstrated that the number of species at the same trophic level is more important for the stability of FWs than the number of those levels, which may explain why most of the experimentally studied FWs have relatively few levels. We have also shown that the connectance, which is one of the parameters used by biologists [17,26] to measure complexity of a FW, declines in a power-type way with increasing number of niches. This agrees, up to the value of the exponent, with the field data taken for FW with similar values of the average number of links [26]. We have obtained, using a different model of a FW, nearly identical results for the relation between connectance and the number of species as Guill and Drossel [25]. According to one of the definitions

of biodiversity [35], it is the variability among living organisms and ecological complexes. Therefore our reduced number of species could be used as a measure of biodiversity, like it has been done in [33]. We have demonstrated that both the average number of links per species and reduced number of species behave in a similar way, growing with the number of trophic levels. This also agrees with biological data [1,2,17]. Although stable systems, like those with  $N=100$  or more, may seem larger than the ones observed in nature [1,17], only a fraction of niches is occupied in a stable model of a FW, which brings the number of living species in such a FW close to the experimental data. If we keep the product  $n \cdot L \cdot k$  constant, stability is ensured if the number of niches and links is increased at the cost of reducing the number of levels. Such relations are valid for not too large killing probability  $p$ . Increasing its value, say above  $p=0.1$ , reduces drastically the differences between particular cases. Finally, we have found a connection between the slope of the food tree distribution of a FW and its stability: the steeper the slope the more vulnerable the FW.

One should however remember that in the construction of the AM model one assumption is not very realistic. A species (predator) could feed on any species from the level below. In reality predating range is restricted by, e.g., spatial distances or geographic obstacles. In this respect the niche model [17,18] is more realistic.

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