

**Critical Boolean networks with scale-free in-degree distribution**

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We investigate analytically and numerically the dynamical properties of critical Boolean networks with power-law in-degree distributions and for two choices of update functions. When the exponent of the in-degree distribution is larger than 3, we obtain results equivalent to those obtained for networks with fixed in-degree, e.g., the number of the nonfrozen nodes scales as  $N^{2/3}$  with the system size  $N$ . When the exponent of the distribution is between 2 and 3, the number of the nonfrozen nodes increases as  $N^x$ , with  $x$  being between 0 and  $2/3$  and depending on the exponent and on the cutoff of the in-degree distribution. These and ensuing results explain various findings obtained earlier by computer simulations.

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Complex dynamical systems, where a large number of units interact in a nontrivial way, are often modeled as networks. The units from which these networks are built can show various types of intrinsic dynamics, including oscillations. Whenever the dynamics can be reduced to only two possible states per node, a Boolean network is obtained. Kauffman was the first to use random Boolean networks (RBNs) to model the dynamics of genetic and protein networks [1,2]. Although Boolean models represent a strong simplification of the far more complex reality, there exist several examples where the modeling of a cellular network by Boolean variables captures correctly the essential dynamics of the system [3,4].

RBNs are directed graphs where each node  $i$  has a Boolean value  $\sigma_i \in \{0, 1\}$  and an update function  $f_i$  which determines the new value in the next time step as function of the state of those nodes that have a link to node  $i$ . Links and functions are assigned at random, given certain constraints concerning the number of inputs per node or the set of functions. The update can be performed in different ways. We consider here the usual case of synchronous update. After some time, the dynamics reaches an attractor, i.e., a periodic sequence of states. Depending on the parameters of the network, the dynamics is either in the *frozen* phase, in the *chaotic* phase, or at the critical point between the two. In the frozen phase, all apart from a small number of nodes assume a constant value on the attractors, i.e., they are frozen. When the state of a node is changed, on average less than one node will be changed in the next time step and the size of a perturbation decreases with time. In the chaotic phase, a nonvanishing proportion of nodes keeps changing their state even after a long time. The size of a perturbation increases with time, since a change in the state of one node will lead on an average to a change of the state of more than one node in the next time step. Most studies of RBNs have focused on the critical point, which is at the boundary between these two phases, and where a perturbation of one node propagates on an average to one other node. These studies deal mainly with the (mean) number and size of attractors, motivated by Kauffman's original claim that biological networks are poised at the critical point, and that attractors can be equated with cell types. Despite of the long time since the introduction of the model, a full analytical understanding of critical RBNs was obtained only recently [5–7].

A key concept at understanding the dynamics of critical RBNs is the classification of the nodes according to their dynamical behavior on attractors into frozen, nonfrozen, and relevant nodes [8]. Relevant nodes are those nodes that determine the attractors, while the other nonfrozen nodes are slaved to the dynamics of the relevant nodes; changing their state does not change the attractor. A stochastic process that gradually determines the frozen core starting from the nodes that have a constant function was used in [6,9] to prove that the number of nonfrozen nodes in critical RBN scales as  $N^{2/3}$ , and the number of relevant nodes as  $N^{1/3}$ , with  $N$  being the number of nodes in the network. In the limit of large network size, scaling functions for the number of nonfrozen and relevant nodes were calculated analytically. These results are independent of the number of inputs per node and of the particular choice of the set of update functions.

All studies mentioned so far assign  $k$  inputs to each node, while the number of outputs is Poisson distributed, since incoming links are connected at random to a node where they originate. However, biological networks are known to have a broad degree distribution, which is often well described by a power law (see [10] and references therein). For this reason, several recent studies were devoted to Boolean dynamics on scale-free networks. The majority of these studies use a scale-free in-degree distribution and a Poissonian out-degree distribution, but other implementations can also be found. Observations made in computer simulations are that attractors are shorter and frozen nodes are more numerous in critical scale-free networks compared to RBNs with a fixed number of inputs, given the same total number of links and of nodes [11,12], and that attractors are sensitive to perturbations of highly connected nodes, but not of sparsely connected nodes [13,12]. These and other [14,15] simulation results are merely stated and are not embedded into an analytical framework. Analytical results obtained so far are limited to calculating the phase diagram using the annealed approximation [13,16,17]; only the work by Lee and Rieger [18] went further by calculating the asymptotic Hamming distance in the chaotic phase and extrapolating the results to the critical point by using a finite-size scaling ansatz in combination with the calculation of the size distribution of perturbed clusters.

In this paper, we will present an analytical calculation for RBNs with scale-free input distributions at the critical point,

obtaining scaling laws for the number of nonfrozen and relevant nodes. Our results, which are confirmed by a numerical evaluation, explain the above-mentioned findings of computer simulations and convey a clear understanding of the properties of attractors in these systems.

We consider critical networks that have an in-degree distribution  $P(k)$  that follows a power law,  $P(k)=Ak^{-\gamma}$  for  $k>1$ . The normalization constant  $A$  depends on the minimum and the maximum in-degrees. We fixed the minimum in-degree to 2; the maximum in-degree depends on the network size and the chosen implementation of the model (see below). We consider only the case  $\gamma>2$ , where such a normalization is possible. In the case  $2<\gamma<3$ , the second moment of the degree distribution diverges and it has been argued in [18] that this should change the dynamical properties. The out-degree distribution is Poissonian with a mean  $\langle k \rangle = \sum_k k P(k)$ , since the input connections are chosen at random from all nodes, just as for RBNs with fixed  $k$ .

We investigated two ways of creating the input distribution. First, we assigned to each node  $i$  a number  $k_i$  of inputs that was drawn from the distribution  $P(k)$ , not allowing values  $k_i$  larger than  $N$  or smaller than 2. The total number of links and the largest value of  $k_i$  differ in this case between different networks. Second, we fixed the number of nodes with  $k$  inputs exactly at the value  $NP(k)$  (rounded to the nearest integer), which gives a distribution  $P(k)$  that has a cutoff at  $k_{\max} \sim N^{1/\gamma}$ . In part of the above-mentioned studies, networks with scale-free in-degree distributions were generated using a constraint that does not allow multiple connections between the same nodes or using a preferential-attachment algorithm, however, all these are known to create correlations between the degree of neighboring nodes [19], which in turn can affect the dynamics on these networks [20]. In order to avoid such complications, we connect the incoming links at random to any node without imposing any constraints.

We also investigated several ways of assigning the Boolean functions to the nodes. First, we chose biased functions with a parameter  $p$ , assigning to each of the  $2^{k_i}$  input configurations the output 1 with a probability  $p$  and the output 0 with a probability  $1-p$ . The value of  $p$  was chosen such that the network is critical, i.e., that  $p=1/\langle k \rangle$  [13]. The main results did not depend on whether we chose the exact mean (which can be different for each network) or the theoretical mean  $\sum_k k P(k)$ . The second way of assigning the Boolean functions is to take only constant and reversible functions. There are two constant functions, which fix the value of a node to either 0 or 1, irrespective of its input values. For each value of  $k$ , there are 2 reversible functions, which are defined by the condition that changing the value of one input always changes the output. A node with a reversible function becomes frozen only if all of its inputs are frozen. Such a network is critical if the total number of nodes equals the total number of inputs to nodes with reversible functions. Links to nodes with constant functions have no effect and can be omitted, so that the total number of links becomes identical to the total number of nodes.

For pedagogical reasons, we will present in the following our analytical calculations in the form appropriate for the second, simpler case of only frozen and reversible functions.

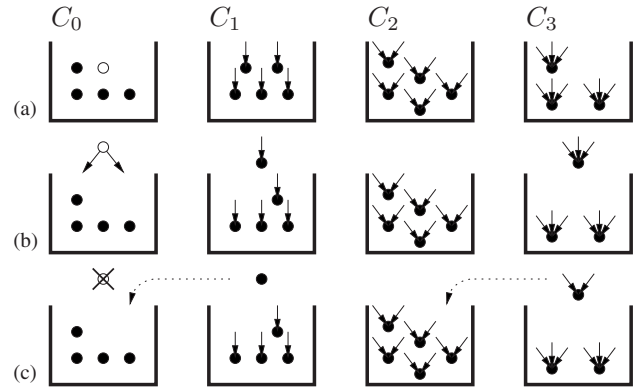


FIG. 1. Illustration of the stochastic process used to determine the frozen core. (a) Nodes are placed in containers according to the number of inputs of which we do not yet already know for sure that they are frozen. A node  $\circ$  from container  $C_0$  is chosen in order to determine its effect on the other nodes. (b) This node becomes an input to a node in container  $k$  with probability  $k/N$ . In this example, it becomes the input to 2 nodes. (c) The frozen links are removed, the two nodes are moved to the neighboring containers, and node  $\circ$  is removed from the system.

The generalization to other cases is straightforward. At the end of the calculations, we will outline how our calculations can be modified to apply to the first case. In fact, from the way in which the results follow from the calculations, it is evident that our results are valid for other choices of the set of update functions, as long as the set used for a node with  $k$  inputs becomes identical to the set used for a node with  $k-1$  inputs when a randomly chosen input is frozen and as long as the parameters are such that the network is critical.

We adjusted the method proposed in [6] in order to determine the size of the frozen core of critical networks with scale-free input distributions. The frozen core is determined starting from the nodes with constant functions and determining stepwise all those nodes that become frozen as a consequence of their inputs becoming frozen. The main idea of our method is to not specify the network in advance, but to choose the connections within the network while determining the frozen core. To this purpose, we place all  $N$  nodes of the network into “containers”  $C_k$  according to the number  $k$  of inputs, as shown in Fig. 1. As mentioned above, inputs to nodes with constant functions are omitted and these nodes are therefore put into container  $C_0$ . The largest container index is  $k_{\max}=N$  or  $k_{\max} \sim N^{1/\gamma}$ , depending on the method chosen for creating the input distribution. The contents of the containers change with time, since we remove stepwise all those inputs of which we know that come from a frozen node. The “time” we are defining here is not the real time for the dynamics of the system, but it counts the steps of the stochastic process that we use to determine the frozen core. During one time step, we choose one node from the container  $C_0$  and determine to which nodes this node is an input. Since the inputs are picked at random, the chosen node is connected to each input with probability  $1/N$ . These inputs are removed and the corresponding nodes moved from container  $C_k$  to container  $C_{k-1}$  (or to a lower container, when more than one connection is made to the same node, or pos-

sibly to container 0 in the more general case where update functions are included that can become frozen with only part of their inputs frozen). At the end of the time step, we remove the chosen node from the system and the number  $N$  of nodes in the system is reduced by 1. Thus, at each time  $t$ , the number  $|C_k|$  of nodes in container  $C_k$  is the number of nodes that have  $k$  inputs that have not yet become frozen during the process. In container  $C_0$  are those nodes of which we know already that are frozen, but we have not yet determined to which other nodes they are an input. We denote from now on the total number of nodes in the system by  $N_{\text{ini}}$ , which is identical to  $N(t=0)$ . The number  $N_{\text{ini}} - N(t)$  of nodes has been removed from the system. They are those nodes for which we have already determined that they are frozen and to which other nodes they are an input.

The process ends when there are no nodes left in container  $C_0$  or when all nodes are in container  $C_0$ . In the latter case, the entire network freezes and the dynamics of the system runs to the same fixed point for all initial conditions. In the first case, there is a set of nonfrozen nodes. In order to determine the topology of the nonfrozen part of the network, one can then fix the connections that have not yet been determined by connecting the remaining inputs at random to the remaining nodes.

Before showing the results of our computer simulations of this process obtained for an ensemble of many networks, let us first perform an analytical calculation in order to predict the mean number of nodes remaining in the different containers at the end. We begin by evaluating the mean number of nodes in container  $C_k$  at the moment where only the fraction  $\epsilon = N/N_{\text{ini}}$  nodes are left in the system. At this moment, container  $C_k$  contains all nodes that had initially  $l \geq k$  inputs and where  $l - k$  inputs have already become frozen. The probability that an input has not yet become frozen is identical to  $\epsilon$ , since only the proportion  $\epsilon$  of nodes have not yet been removed and since an input is connected to every node with the same probability. Since container  $C_l$  contained initially  $\propto N_{\text{ini}} l^{-\gamma}$  nodes, we have

$$|C_k| \propto N_{\text{ini}} \sum_{l=k}^{k_{\text{max}}} l^{-\gamma} \epsilon^k (1-\epsilon)^{l-k} \binom{l}{k}. \quad (1)$$

For small  $\epsilon$ , nodes in container  $C_k$  originated in containers  $C_l$  with  $l \geq k$  and we can therefore set  $l - k \approx l$ . Replacing the sum with an integral, using  $e^{-x} \approx (1-x)$  and  $\binom{l}{k} \approx l^k$ , we obtain the approximate expression

$$|C_k| \propto N_{\text{ini}} \epsilon^k \int_k^{k_{\text{max}}} l^{k-\gamma} e^{-l\epsilon} dl \quad (2)$$

When evaluating this integral, we have to consider three possible cases:

(i) The integral is independent of the cutoff because  $k < \gamma - 1$ . In this case we obtain

$$|C_k| \sim N_{\text{ini}} \epsilon^k. \quad (3)$$

(ii)  $k > \gamma - 1$  and  $\epsilon^{-1} < k_{\text{max}}$ . In this case the exponential function determines the cutoff to the integral and we obtain

$$|C_k| \sim N_{\text{ini}} \epsilon^{\gamma-1}. \quad (4)$$

(iii)  $k > \gamma - 1$  and  $\epsilon^{-1} > k_{\text{max}}$ . In this case  $k_{\text{max}}$  determines the cutoff to the integral and we obtain

$$|C_k| \sim N_{\text{ini}} \epsilon^k k_{\text{max}}^{k-\gamma+1}. \quad (5)$$

The stochastic process ends when no nodes are left in container  $C_0$ . On an average, the number of nodes in container  $C_0$  is identical to the number of nonfrozen inputs minus the number of nonfrozen nodes, since the network is critical. If we neglect stochastic fluctuations during the process, the number of nodes in container  $C_0$  becomes zero at the same time when the number of nodes in container  $C_k$  with  $k > 1$  becomes zero, i.e., when  $\epsilon = 0$ . However, stochastic fluctuations will terminate the process earlier at the moment where the fluctuations of the number of frozen nodes become of the same order as the expected number of frozen nodes. The variance of the number of frozen nodes is evaluated as follows. The probability that a given input has not yet become frozen at the moment where  $N$  nodes are left in the system is  $\epsilon$ . When  $\epsilon$  is small, the number of nonfrozen inputs is Poisson distributed, with the variance being identical to the mean, which is proportional to  $N_{\text{ini}} \epsilon$ . For small  $\epsilon$ , the vast majority of nonfrozen inputs is found in container  $C_1$ . Now a node in container  $C_1$  would be in container  $C_0$  had its remaining input also become frozen during the process and it follows that the variance of the number of frozen nodes is also of the order  $N_{\text{ini}} \epsilon$ . The typical fluctuations in the number of frozen nodes are therefore of the order  $\sqrt{N_{\text{ini}} \epsilon} = \sqrt{N}$ . Equating this number with the expected number of nodes in  $C_0$ , which in turn is of the same order as the expected number of nodes in  $C_2$ , we obtain the following condition for the end of the stochastic process, where  $N$  is identical to the number of nonfrozen nodes,  $N_{\text{nf}}$ :

$$|C_2| \sim \sqrt{N_{\text{nf}}} = \sqrt{N_{\text{ini}}} \epsilon. \quad (6)$$

Depending on the value of  $\gamma$  and on the dependence of  $k_{\text{max}}$  on  $N_{\text{ini}}$ , the number of nonfrozen nodes scales in a different way with  $N_{\text{ini}}$ .

For  $\gamma > 3$ , the first of the three above cases applies to  $|C_2|$ , and solving condition (6) for  $N_{\text{nf}}$ , we obtain

$$N_{\text{nf}} \sim N_{\text{ini}}^{2/3} \quad (7)$$

at the end of the stochastic process. This is the same result as for a RBN with fixed  $k$ . Whenever the input distribution  $P(k)$  has a finite second moment, the number of nonfrozen nodes scales as  $N_{\text{ini}}^{2/3}$  and the number of nonfrozen nodes with two nonfrozen inputs scales as  $N_{\text{ini}}^{1/3}$ . The number of nonfrozen nodes with more than two nonfrozen inputs depends on whether  $k < \gamma - 1$ , but it is in any case much smaller than the number of nonfrozen nodes with two nonfrozen inputs and we do not evaluate it here further.

When  $2 < \gamma < 3$  and when  $k_{\text{max}} \propto N_{\text{ini}}$ , the second case applies and we obtain using Eq. (4)

$$N_{\text{nf}} \sim N_{\text{ini}}^{(2\gamma-4)/(2\gamma-3)}. \quad (8)$$

For  $\gamma = 3$ , the exponent is  $2/3$ ,  $N_{\text{nf}} \sim N_{\text{ini}}^{2/3}$ , and it decreases to 0 as  $\gamma$  approaches 2.

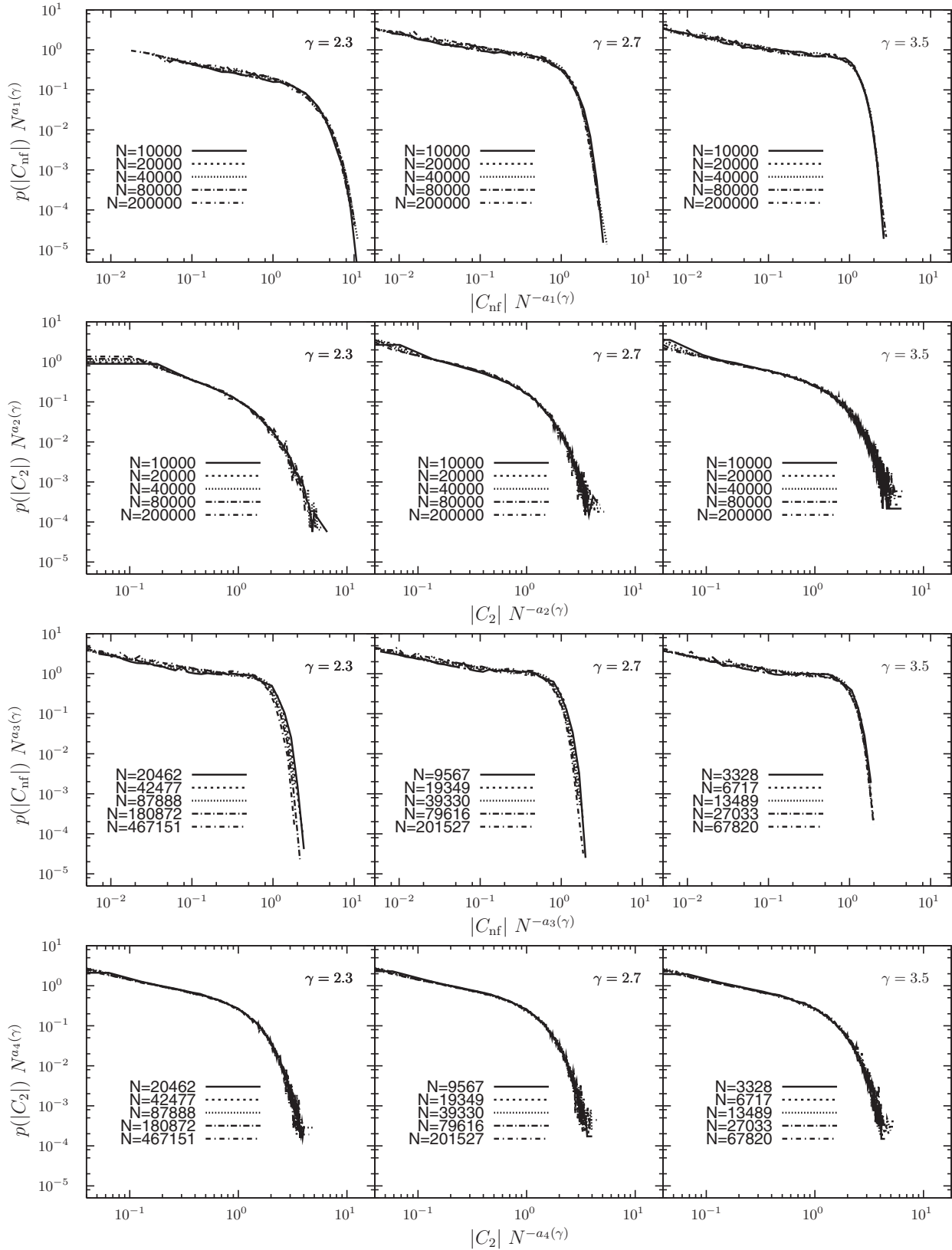


FIG. 2. Scaling collapse for the total number of nonfrozen nodes (first and third line) and for the number of nodes with two nonfrozen inputs (second and fourth line), for three different values of  $\gamma$  and for the two different ways of choosing the input distributions,  $k_{\max} \sim N$  (first two lines) and  $k_{\max} \propto N^{1/\gamma}$  (last two lines). The function  $a_i(\gamma)$  are the appropriate exponents obtained from Eqs. (8) and (9), i.e.,  $a_1(\gamma) = (2\gamma - 4) / (2\gamma - 3)$ ,  $a_2(\gamma) = a_1(\gamma) / 2$ ,  $a_3(\gamma) = 2\gamma / (\gamma + 6)$ ,  $a_4(\gamma) = a_3(\gamma) / 2$ . Each data set is generated by averaging over  $10^5$  realizations.



When  $2 < \gamma < 3$  and when  $k_{\max} \propto N_{\text{ini}}^{1/\gamma}$  (which is the case when the input distribution is fixed), the third case applies and we obtain

$$N_{\text{nf}} \sim N_{\text{ini}}^{2\gamma/(\gamma+6)}. \quad (9)$$

These results, Eqs. (6)–(9), are also valid for other distributions of Boolean functions which are tuned to the critical point as long as the set used for a node with  $k$  inputs becomes identical to the set of functions (including their weights) used for a node with  $k-1$  inputs when a randomly chosen input is frozen. For instance, when biased Boolean functions are chosen, there is a probability  $p_f^k = p^{2^k} + (1-p)^{2^k}$  that a node with  $l > k$  inputs becomes frozen when  $l-k$  inputs are frozen. Therefore the expression (2) for  $|C_k|$  obtains an additional factor  $1-p_f^k$ . This factor is never close to 0 and therefore does not change the scaling behavior of the integral.

Our computer simulations confirm all these analytical considerations. We performed simulations for both cases described above, with biased functions, and with only constant and reversible functions. Since the curves look similar in both cases and since the quality of the data collapse is equally good in both cases, we show in Fig. 2 only the results obtained for the case of constant and reversible functions, for both ways of choosing the input distributions. The excellent quality of the data collapses, which are based on the power laws predicted by the theory, confirms our analytical calculations.

Our results have a variety of implications. First, they show that many properties obtained for critical networks with a fixed number of inputs apply also to networks with a scale-free in-degree distribution once the frozen nodes have been removed. In particular, the number of nonfrozen nodes with more than one nonfrozen input scales as the square root of the number of nonfrozen nodes. Only the dependence of the number of nonfrozen nodes on the total number of nodes

is changed when  $\gamma \in (2, 3)$ . We can therefore take over the results obtained in [6] based on these properties of the nonfrozen nodes. It follows in particular that the number of relevant nodes in networks with a scale-free input distribution scales as the square root of the number of nonfrozen nodes and that the number of relevant components is of the order of  $\log N_{\text{ini}}$ , with all but a limited number of relevant components being simple loops. It therefore follows again that the mean number and length of attractors diverge faster than any power law with the network size. This explains the finding in [13] that the state-space structure of critical RBNs with fixed  $k$  and with a power-law input distribution is similar. Second, the number of nonfrozen nodes decreases with decreasing  $\gamma \in (2, 3)$  because the exponent becomes smaller. This explains why several authors have seen more frozen nodes and shorter attractors in scale-free networks compared to standard RBNs. Third, the set of nonfrozen and relevant nodes is dominated by nodes with many inputs. This is due to the fact that each input has the same probability of surviving the stochastic process until the end. The average number of inputs of a node that has a surviving link is proportional to  $\int k^2 N(k) dk$ , which is dominated by  $k_{\max}$  for  $\gamma \in (2, 3)$ . When a relevant node is perturbed, the attractor is changed with a large probability. However, when a frozen node is changed, the attractor changes with a probability that vanishes in the limit  $N \rightarrow \infty$ . This explains the findings in [13, 12] that attractors respond sensitively mainly to perturbations of highly connected nodes. Fourth, our results disagree with the finite-size arguments in [18], which predict that the number of nonfrozen nodes scales as  $N_{\text{ini}}^{(\gamma-1)/\gamma}$ . This is in our view due to the fact that an infinite (sustained) perturbation has properties that are fundamentally different from those of finite perturbations, in which case arguments based on finite-size scaling do not work.

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- [1] S. A. Kauffman, *J. Theor. Biol.* **22**, 437 (1969).  
 [2] S. Kauffman, *Nature (London)* **224**, 177 (1969).  
 [3] S. Bornholdt, *Science* **310**, 449 (2005).  
 [4] R. Albert and H. G. Othmer, *J. Theor. Biol.* **223**, 1 (2003).  
 [5] B. Samuelsson and C. Troein, *Phys. Rev. Lett.* **90**, 098701 (2003).  
 [6] V. Kaufman, T. Mihaljev, and B. Drossel, *Phys. Rev. E* **72**, 046124 (2005).  
 [7] B. Drossel, in *Reviews of Nonlinear Dynamics and Complexity*, edited by H.-G. Schuster (Wiley, New York, 2008), Vol. 1, pp. 69–110, ISBN 978-3-527-40729-3.  
 [8] U. Bastolla and G. Parisi, *Physica D* **115**, 219 (1998).  
 [9] T. Mihaljev and B. Drossel, *Phys. Rev. E* **74**, 046101 (2006).  
 [10] R. Albert, *J. Cell Sci.* **118**, 4947 (2005).  
 [11] J. J. Fox and C. C. Hill, *Chaos* **11**, 809 (2001).  
 [12] S.-i. Kinoshita, K. Iguchi, H. Yamada, Y. Tokuyama, M. Tokuyama, I. Oppenheim, and H. Nishiyama, *AIP Conf. Proc.* **982**, 768 (2008).  
 [13] M. Aldana, *Physica D* **185**, 45 (2003).  
 [14] A. Castro e Silva, J. Kamphorst Leal da Silva, and J. F. F. Mendes, *Phys. Rev. E* **70**, 066140 (2004).  
 [15] R. Serra, M. Villani, and L. Agostini, *Physica A* **339**, 665 (2004).  
 [16] M. Aldana and P. Cluzel, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 8710 (2003).  
 [17] P. Fronczak, A. Fronczak, and J. A. Holyst, *Phys. Rev. E* **77**, 036119 (2008).  
 [18] D.-S. Lee and H. Rieger, *J. Phys. A* **41**, 415001 (2008).  
 [19] S. Weber and M. Porto, *Phys. Rev. E* **76**, 046111 (2007).  
 [20] S. Weber, M.-T. Hütt, and M. Porto, *Europhys. Lett.* **82**, 28003 (2008).