On the number of attractors in random Boolean networks

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The evaluation of the number of attractors in Kauffman networks by Samuelsson and Troein is generalized to critical networks with one input per node and to networks with two inputs per node and different probability distributions for update functions. A connection is made between the terms occurring in the calculation and between the more graphic concepts of frozen, nonfrozen and relevant nodes, and relevant components. Based on this understanding, a phenomenological argument is given that reproduces the dependence of the attractor numbers on system size.

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1. INTRODUCTION

Boolean networks are often used as generic models for the dynamics of complex systems of interacting entities, such as social and economic networks, neural networks, and gene or protein interaction networks [1]. The simplest and most widely studied of these models was introduced in 1969 by Kauffman [2] as a model for gene regulation. The system consists of \( N \) nodes, each of which receives input from \( K \) randomly chosen other nodes. The network is updated synchronously, the state of a node at time step \( t \) being a Boolean function of the states of the \( K \) input nodes at the previous time step, \( t-1 \). The Boolean updating functions are randomly assigned to every node in the network, and together with the connectivity pattern they define the realization of the network. For any initial condition, the network eventually settles on a periodic attractor. Thus the number and the lengths of the attractors are important features of the networks. Of special interest are critical networks, which lie at the boundary between a frozen phase and a chaotic phase [3, 4]. In the frozen phase, a perturbation at one node propagates during one time step on an average to less than one node, and the attractor lengths remain finite in the limit \( N \to \infty \). In the chaotic phase, the difference between two almost identical states increases exponentially fast, because a perturbation propagates on an average to more than one node during one time step [5]. Based on computer simulations, the mean attractor number of critical \( K = 2 \) Kauffman networks with a constant probability distribution for the 16 possible updating functions was once believed to scale as \( \sqrt{N} \) [2]. With increasing computer power, a faster increase was seen (linear in [6], “faster than linear” in [7], stretched exponential in [8, 9]). Then, in a beautiful analytical study, Samuelsson and Troein [10] have proven that the number of attractors grows indeed faster than any power law with the network size \( N \). A proof that the number and length of attractors of critical \( K = 1 \) networks increases faster than any power law was published some time later [11]. These two proofs, although they apply to closely related systems, are conceptually different. The latter derives structural properties of the relevant part of the networks, and obtains from there a lower bound for the number of attractors. In contrast, in [10] the mean number of attractors is obtained by a direct calculation that uses the saddle-point approximation, and which yields no graphic understanding of how the attractor numbers arise.

It is the purpose of the present article to show how the attractor numbers arise in terms of the relevant parts of the networks. To this aim, the method chosen by Samuelsson and Troein is in the next section applied to the critical \( K = 1 \) networks, for which an intuitive understanding already exists. The dependence of attractor numbers on system size \( N \) can indeed be reproduced by phenomenological arguments based on this understanding. In section 3, it is shown that these networks are similar in many respects to critical \( K = 2 \) networks, of which a more general class than usual will be defined. Applying the calculation to this more general class leads eventually to a phenomenological argument that reproduces the dependence of attractor numbers on system size.

2. CRITICAL NETWORKS WITH ONE INPUT PER NODE

Let us first consider critical networks with connectivity \( K = 1 \). A random network with one input per node is critical if among the four possible Boolean functions only the two nonfrozen ones, “copy” and “invert”, are chosen. In [12] and [11], exact results for the topology of \( k = 1 \) networks are derived. The network consists of the order of \( \ln(N) \) unconnected components, each of which contains a loop of relevant nodes, and trees rooted in these loops. Relevant nodes are defined as those nodes whose state is not constant and that control at least one relevant element [9]. They determine the attractors of the system. The number of loops of size \( l \) is Poisson distributed with a mean \( 1/l \), if \( l \) is smaller than a cutoff size \( L_c \). The cutoff loop size scales as \( L_c \sim \sqrt{N} \) [11, 12].

Following the calculation by Samuelsson and Troein [10], we calculate in the following the mean number of attractors of length \( L \). More precisely, we calculate the mean number of cycles in state space. While an attractor is always a cycle in state space, the reverse is not neces-
sarily true, since an attractor must be accompanied by a shrinking state space volume. However, for the networks discussed in this paper, cycles are almost always attractors, since the dynamics on the trees rooted in the loops is being slaved to the dynamics on the loops, and therefore the initial states of the trees will be forgotten. For every network that contains trees, the number of initial states that leads to a given cycle is larger than the period of the cycle, and the cycles are attractors.

Let \( \langle C_L \rangle_N \) denote the mean number of cycles in state space of length \( L \), averaged over the ensemble of networks of size \( N \). On a cycle of length \( L \), the state of each node goes through a sequence of 1s and 0s of period \( L \). Let us number the 2\(^{L-1} \) possible sequences of period \( L \) of the state of a node by the index \( j \), ranging from 0 to \( m - 1 = 2^{L-1} - 1 \), with sequence 0 being the constant one. Following Samuelsson and Troein, we consider two functions and a proportion \( 1 \equiv \delta_x \equiv \delta_x(j) \) of the expression

\[
\sum_{j} x_j \ln \left( \frac{x_{\phi(j)}}{x_j} \right) = \sum_{j \in \rho_h^L} \left( \frac{z_h}{|\rho_h^L|} + \delta x_j \right) \ln \left( \frac{1 + \frac{|\rho_h^L|}{z_h} \delta x_{\phi(j)}}{1 + \frac{|\rho_h^L|}{z_h} \delta x_j} \right)
\]

\[
\simeq \frac{|\rho_h^L|}{z_h} \sum_{j \in \rho_h^L} (\delta x_{\phi(j)} - \delta x_j)
\]

\[
= -\frac{1}{2} \frac{|\rho_h^L|}{z_h} \sum_{j \in \rho_h^L} (\delta x_{\phi(j)} - \delta x_j)^2
\]

(3)

and

\[
\prod_{i \in \rho_h^L} (x_i)^{-1/2} \simeq \left( \frac{z_h}{|\rho_h^L|} \right)^{-|\rho_h^L|/2}.
\]

In the limit \( N \to \infty \), the terms containing \( (\delta x_j)^2 \) vanish in the limit and the saddle-point integration gives contributions only from values \( \delta x_j \) of the order of \( 1/\sqrt{N} \).

The integral over the \( \delta x_j \) can be performed by using the variables \( (\delta x_{\phi(j)} - \delta x_j) \), leading to

\[
\langle C_L \rangle_N \simeq \frac{1}{L} \left( \frac{N}{2\pi} \right)^{m-1} \prod_h \int \frac{dz_h}{|\rho_h^L|} \left[ \frac{2z_h}{|\rho_h^L| N} \right]^{1/2} \int \frac{dz_h}{\sqrt{z_h}}.
\]

(4)

Integration space is given by the condition \( \sum_h z_h = 1 \) (with all \( z_h > 0 \)).

Let us now interpret the \( N \)-dependence in this result. To this purpose, we derive the number of attractors of
length \( L \) from the known topological properties of \( K = 1 \) networks. As mentioned above, the network consists of the order of \( \ln N \) components, each of which contains a loop and trees rooted in the loops. The cutoff in loop size is \( l_c \approx \sqrt{N} \). The expected number of states on a loop of a randomly chosen size \( l \) that belong to a cycle of length \( L \) is

\[
\sum_h \frac{1}{|\rho_h^L|} |\rho_h^L| = H_L, \tag{5}
\]

the first factor being the probability that \( l \) is a multiple of \(|\rho_h^L|\), and the second factor being the number of states in the set number \( h \). As mentioned above, the number \( n_l \) of loops of size \( l \) is Poisson distributed with a mean \( 1/l \), leading to

\[
(C_L)_N \approx \sum_{(n_l) \leq l} \prod_{l \leq l} \left( \frac{e^{-1/l} \left( \frac{1}{l} \right)^{n_l}}{n_l!} H_L^{n_l} \right) = \sum_{(n_l) \leq l} \prod_{l \leq l} \left( \frac{e^{-1/l} \left( \frac{H_L}{l} \right)^{n_l}}{n_l!} \right) \approx \prod_{l \leq l} e^{(H_L - 1)/l} = e^{(H_L - 1)/l} \ln d/l \approx e^{(H_L - 1) \ln \sqrt{N}} = N^{(H_L - 1)/2}. \tag{6}
\]

The mean number of attractors of length \( L \) scales as the number of relevant nodes, \( \sqrt{N} \) (which is proportional to the number of nodes in the largest loop), to the power \( H_L - 1 \). We will see below that an equivalent statement can be made for the \( K = 2 \) critical networks. In order to obtain also the \( L \)-dependent prefactor in Eq. (4), the full probability distribution of the number of loops of a size of the order of \( l_c \) would have to be taken into account in calculation (6), instead of simply integrating up to \( l_c \).

Let us conclude this section by discussing the implications of the fact that we do not discriminate between sequences that can be transformed into each other by exchanging 1s and 0s. The numbers and the periods of the attractors are determined by the loops in the network. We call a loop “even” if it contains an even number of “invert” functions, and “odd” if it contains an odd number of “invert” functions. The state of an even loop of size \( l \) is the same after \( l \) updates, while the state of an odd loop of size \( l \) is inverted after \( l \) updates. If \( l \) is a prime number, the period of a cycle on an odd loop is \( 2l \), with the second half of the cycle being obtained from the first half by exchanging 0s and 1s. However, our rules defined above (and in [10]) classify this as a cycle of period \( l \), since assigning only the first half of a sequence to the nodes on the loop, makes a contribution to Eq. (1) if \( l \) is a multiple of \( L \). Furthermore, exchanging the 1s and 0s on a component does not lead to a new cycle according to our calculation, but in reality this doubles the number of cycles.

Repeating calculation (6) for a system with only “copy” functions and by discriminating sequences that can be transformed into each other by exchanging 1s and 0s, the result remains the same, but with \( H_L \) now counting the true number of invariant sets.

For a system that contains also “invert” functions, the calculation becomes more complicated, since the mean number of states of a loop belonging to a cycle of length \( L \) is no longer given by Eq. (5). Let \( H_L \) again count the number of true invariant sets. The probability that a loop has a given cycle is now \( 1/2|\rho_h^L| \) if the second half of the cycle is not obtained from the first half by exchanging 1s and 0s. Otherwise, the probability is \( 3/2|\rho_h^L| \). The mean number of states on a loop that belong to a cycle of length \( L \) is therefore \( H_L/2 \) for odd \( L \) and \( H_L/2 + H_L/2 \) for even \( L \), and these two expressions replace the \( H_L \) in the exponent in (6) for odd and even \( L \) respectively.

### 3. A GENERAL CLASS OF CRITICAL \( K = 2 \) NETWORKS

Now, let us consider \( K = 2 \) networks, where each node has 2 randomly chosen inputs. The 16 possible update functions are shown in table I.

| \( \text{In} \) | \( \mathcal{F} \) | \( C_1 \) | \( C_2 \) | \( \mathcal{R} \) |
|-------|-------|-------|-------|-------|
| 00    | 1     | 0     | 1     | 1     |
| 01    | 0     | 1     | 0     | 1     |
| 10    | 1     | 0     | 0     | 1     |
| 11    | 1     | 1     | 1     | 1     |

Table I: The 16 update functions for nodes with 2 inputs. The first column lists the 4 possible states of the two inputs, the other columns represent one update function each, falling into four classes.

The update functions fall into four classes [5]. In the first class, denoted by \( \mathcal{F} \), are the frozen functions, where the output is fixed irrespectively of the input. The class \( C_1 \) contains those functions that depend only on one of the two inputs, but not on the other one. The class \( C_2 \) contains the remaining canalyzing functions, where one state of each input fixes the output. The class \( \mathcal{R} \) contains the two reversible update functions, where the output is changed whenever one of the inputs is changed. Critical networks are those where a change in one node propagates to one other node on an average. A change propagates with probability \( 1/2 \) to a node that has a canalyzing update function \( C_1 \) or \( C_2 \), with probability zero to a node that has a frozen update function, and with probability 1 to a node that has a reversible update function. Consequently, if the frozen and reversible update functions are chosen with equal probability, the network is critical. Usually, only those models are considered where all 16 update functions receive equal weight. We now consider the larger set of models where the frozen and reversible update functions are chosen with equal probability, and where the remaining probability is divided between the
$C_1$ and $C_2$ functions. Those networks that contain only $C_1$ functions are different from the remaining ones. Since all nodes respond only to one input, the link to the second input can be cut, and we are left with a critical $K = 1$ network, which was discussed in the previous section. We shall see below that all the other models, where the weight of the $C_1$ functions is smaller than 1, fall into the same class, where the number of attractors is given by the expression derived in [10] and reproduced below.

For all these critical $K = 2$ networks, the mean number of attractors of length $L$ is given by the expression [10]

$$
\langle C_L \rangle_N = \frac{1}{L} \sum_{n} \left( \begin{array}{c} N \\ n \end{array} \right) \prod_{j} \left( \sum_{l_{i,k}} \frac{n_i n_k}{N^2} (P_L)_{i,k}^j \right)^{n_{j}},
$$

with $(P_L)_{i,k}^j$ being the probability that a node that has the input sequences $l_i$ and $k$ generates the output sequence $j$. This expression is the obvious generalization of Eq. (1) to two inputs per node. Using again Stirling’s formula and replacing the sum with an integral, this leads to the generalization of Eq. (2), see [10]

$$
\langle C_L \rangle_N \simeq \frac{1}{L} \frac{N}{2\pi} \int dx \ e^{-N \sum_{i,j} x_i \ln \left( \frac{1}{2} \sum_{j,k} x_j x_k (P_L)_{j,k}^i \right)} \prod_{i} \sqrt{x_i}.
$$

For a network with only $C_1$ functions, this reduces immediately to Eq. (1). The exponent has its maximum at zero, and this value is reached only if [10]

$$
x_i = \sum_{j,k} x_j x_k (P_L)_{j,k}^i \text{ for all } i .
$$

This condition is satisfied for $x_0 = 1$. For a network with only $C_1$ functions, it is more generally satisfied for $x_{\phi(i)} = x_i$ (for all $i$). For all other critical networks, there exists only the maximum at $x_0 = 1$. This is shown as follows: Eq. (9) can be transformed into

$$
\sum_{i>0} x_i = \sum_{i>0} x_0^2 (P_L)_{00}^i + 2 \sum_{i,j>0} x_0 x_j (P_L)_{0j}^i + \sum_{i,k,j>0} x_j x_k (P_L)_{jk}^i,
$$

$$
1 - x_0 = 2 x_0 \sum_{j>0} \frac{1}{2} x_j + \sum_{j,k,j>0} x_j x_k (P_L)_{jk}^j \leq x_0 (1 - x_0) + (1 - x_0)^2 = 1 - x_0.
$$

Here, we have used $(P_L)_{00}^j = 0$ for $j > 0$ and $\sum_{j>0} (P_L)_{0j}^0 = 1/2$ for all considered models. The inequality becomes an equality only if $x_0 = 1$, or if $\sum_{i,k,j>0} x_j x_k (P_L)_{jk}^i = (1 - x_0)^2$. The latter condition is satisfied if and only if all $(P_L)_{jk}^j$ with $j, k > 0$ and $x_j, x_k > 0$ vanish. They cannot vanish if there are frozen update functions. They do vanish if there are only $C_1$ update functions. It remains to be shown that they cannot vanish for a system containing $C_2$ functions, but no

frozen functions. Assume $x_i > 0$. Since a node with two input sequences $i$ has nonconstant output sequences (one of which we denote by $ii$) with a positive probability, there occurs a term $x_i x_{\phi(i)} (P_L)_{ii}^j$. Now, the sequences $i$ and $ii$ taken together, have only 2 out of the 4 possible combinations of 2 bits. However, among the $C_2$ functions there are functions that yield a constant output if the input is $i$ and $ii$. Therefore even in a $C_2$ network, not all $(P_L)_{jk}^j$ with $j, k > 0$ and $x_j x_k > 0$ vanish. We thus have shown that all considered critical $K = 2$ networks satisfy (9) only at $x_0 = 1$. For large $N$, only small values $x_j$ (for $j > 0$) contribute to the integral in (8), and a Taylor expansion in the $x_j$ (for $j > 0$) gives [10]

$$
\langle C_L \rangle_N \simeq \frac{1}{L} \frac{N}{2\pi} \int dx \ e^{N f(x)}
$$

with

$$
f(x) \simeq \sum_{i>0} x_i \ln \frac{x_{\phi(i)}}{x_i} + \sum_{i>0} x_i x \cdot A_{i}^j x
$$

$$
\simeq \frac{1}{2} \sum_{i>0} x_i (x \cdot A_{i}^j x)^2
$$

where $(A_{i}^j)_{jk} = (P_L)_{jk}^j - 1/2 (\delta_{j\phi(i)} + \delta_{k\phi(i)})$. For a $C_1$ network, the matrix $(A_{i}^j)_{jk}$ vanishes, and we obtain again (2). The maximum of $f(x)$ is obtained when $x_{\phi(i)} = x_i$ for all $i$. At this maximum, the first and second term vanish, and the third term is of the form $N x^3$. Consequently, only values $x_i$ (with $i > 0$) up to the order $N^{-1/3}$ contribute to $\langle C_L \rangle_N$. This means that the proportion of nodes that are not frozen on an attractor is of the order $N^{-1/3}$, and the total number of nonfrozen nodes is of the order $N^{2/3}$. This is in contrast to the critical $K = 1$ network, where a nonvanishing proportion of nodes is nonfrozen. Changing the variables again to $z_h = \sum_{i \in \phi^{h}_L} x_i$, and $\delta x_i = x_i - z_h/|\rho^{h}_L|$, the integration over the $\delta x_i$ gives now

$$
\langle C_L \rangle_N \simeq \frac{1}{L} \frac{N}{2\pi} \prod_{h>0} \int \frac{dz_h}{|\rho^{h}_L| z_h} \ e^{-\sum_{h>0} N (z_h)^2 / 2 |\rho^{h}_L|^2 z_h}
$$

with $(B_{L}^h)_{jk} = (P_L^h)_{jk} - 1/2 (\delta_{j\phi} + \delta_{k\phi})$, and with $(P_L^h)_{jk}$ being the probability that the output sequence belongs to set $h$ if the input sequences belong to the sets $j$ and $k$. Introducing a new variable $y_h = z_h N^{1/3}$, we obtain an additional factor $N^{-2/3(N^{1/3})/6}$, and the mean number of cycles of length $L$ becomes [10]

$$
\langle C_L \rangle_N \simeq \frac{1}{L} \frac{N^{2/3}}{(2\pi)^{2/3}} \prod_{h>0} \int \frac{dy_h}{|\rho^{h}_L| y_h} \ e^{-\sum_{h>0} (y_h)^2 / 4 |\rho^{h}_L|^2 y_h}
$$

While integration space for the $z_h$ was restricted by the condition $\sum_{h} z_h = 1 - x_0$, there is no constraint for the $y_h$. 
With the understanding gained from the $K = 1$ critical networks, we can interpret the calculation as follows. The difference between $K = 1$ and $K = 2$ critical networks comes from the fact that in the $K = 2$ networks only the fraction $N^{-1/3}$ of nodes is nonfrozen. This modifies the exponent of $N$ in the final result, and this leads to the different form of the $z_h$ integration. Both types of networks have in common that the main contribution to the integral comes from the neighborhood of the subspace satisfying $x_{\phi(i)} = x_i$ for all $i$. This means that the majority of nonfrozen nodes receive input from one nonfrozen node, the other input being frozen. The nonfrozen part of a $K = 2$ critical network resembles therefore a $K = 1$ critical network. The proportion of nonfrozen nodes receiving input from two nonfrozen nodes, cannot be larger than of the order $N^{-1/3}$, since the $\delta x_i$ are of the order $N^{-1/3}$. Thus, the nonfrozen part of a $K = 2$ critical network differs from a $K = 1$ critical network by a proportion $N^{-1/3}$ of nonfrozen nodes having two nonfrozen inputs. Apparently, this difference does not affect the scaling of $\langle C_L \rangle_N$ with $N$, but only the $L$-dependent prefactor. If the number of relevant nodes scales as $N^{1/3}$ (as is numerically found in [7]), the law

$$\langle C_L \rangle_N \sim N^{(H_L - 1)/3}$$

means that the mean number of attractors of length $L$ scales as the number of relevant nodes, $N^{1/3}$ (which is proportional to the number of nodes in the largest component), to the power $H_L - 1$. It can be obtained by a phenomenological argument similar to the one used in the previous section. Assume there are $N^{1/3}$ relevant nodes arranged in $\sim \ln N$ components, with the number of components of size $l$ being Poisson distributed with a mean $1/l$. Since at most the proportion $N^{-1/3}$ of nonfrozen nodes have two nonfrozen inputs, only a finite number of relevant nodes have two nonfrozen inputs, and all relevant components apart from a finite number are cycles without additional links, just as for the $K = 1$ critical network. The mean number of states on a component of size $l$ that belong to a cycle of length $L$ is therefore in the limit of large $N$

$$\sum_k \frac{1}{|\rho_L^h|} |\rho_L^h| = H_L,$$

just as for the $K = 1$ critical network. If the number $n_l$ of relevant components of size $l < l_c \sim N^{1/3}$ is Poisson distributed with a mean $1/l$, we obtain

$$\langle C_L \rangle_N \sim \sum_{(n_l)_{l \leq l_c}} \prod_{l \leq l_c} \left( e^{-1/l} \left( \frac{1}{l} \right)^{n_l} H_L^{n_l} \right)$$

$$\sim e^{(H_L - 1) \ln N^{1/3}} = N^{(H_L - 1)/3}. \quad (15)$$

4. CONCLUSIONS

In this paper, we have considered the mean number of attractors of length $L$ for critical $K = 1$ and $K = 2$ networks. We have applied the method by Samuelsson and Troein [10] and have interpreted the results in terms of the topological properties of the nonfrozen part of the network. For the $K = 1$ networks, the dependence of the number of attractors of length $L$ on the system size $N$, $\langle C_L \rangle_N \sim N^{(H_L - 1)/2}$ could be understood as resulting from the network containing the order of $N^{1/2}$ relevant nodes arranged in $\sim \ln N$ components, with the number of components of size $l$ being Poisson distributed with a mean $1/l$. The nonrelevant nodes sit in trees rooted in the loops.

Then, we could show that all $K = 2$ critical networks can be treated by the same calculation. Only for networks consisting only of $C_1$ functions, the step from Eq. (13) to Eq. (14) cannot be made, since the matrix $(B^h_L)_{jk}$ vanishes in this case. $C_1$-networks are in fact $K = 1$ critical networks, and Eq. (13) is identical to Eq. (4) in this case. All the other $K = 2$ networks show the same dependence of attractor numbers on system size, with only the $L$-dependent prefactor being different (because the matrix $(B^h_L)_{jk}$ is different for a different choice of weights for the update functions). We saw that only the proportion $N^{-1/3}$ of nodes is nonfrozen, and that almost all nonfrozen nodes depend only on one nonfrozen input. The nonfrozen part of critical $K = 2$ networks resembles strongly a $K = 1$ critical network, and by analogy to the $K = 1$ critical network we concluded that the scaling with $N$ of the number of attractors of length $L$ in $K = 2$ critical Boolean networks can be understood as resulting from the network being composed of the order of $N^{1/3}$ relevant nodes arranged in $\sim \ln N$ components, with the number of components of size $l$ being Poisson distributed with a mean $1/l$. Only the proportion $N^{-1/3}$ of all nodes is not frozen, and those nonfrozen nodes that are not relevant sit in trees rooted in relevant components.

The calculation indicates that there are several quantities that show a scaling with $N$. Among these are the number of nonfrozen nodes, the number of relevant nodes, and the number of nonfrozen nodes with two nonfrozen inputs. Evaluating these scaling properties to more detail could be the next step in understanding Kauffman networks.

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