

Analysis of random Boolean networks using the average sensitivity

Steffen Schober* and Martin Bossert

Institute of Telecommunications and Applied Information Theory, Ulm University
Albert-Einstein-Allee 43, 89081 Ulm, Germany

February 17, 2013

Abstract

In this work we consider random Boolean networks that provide a general model for *genetic regulatory networks*. We extend the analysis of James Lynch who was able to proof Kauffman's conjecture that in the *ordered phase* of random networks, the number of *ineffective* and *freezing* gates is large, where as in the *disordered phase* their number is small. Lynch proved the conjecture only for networks with connectivity two and non-uniform probabilities for the Boolean functions. We show how to apply the proof to networks with arbitrary connectivity K and to random networks with *biased* Boolean functions. It turns out that in these cases Lynch's parameter λ is equivalent to the expectation of *average sensitivity* of the Boolean functions used to construct the network. Hence we can apply a known theorem for the expectation of the average sensitivity. In order to prove the results for networks with biased functions, we deduct the expectation of the average sensitivity when only functions with specific connectivity and specific bias are chosen at random.

Keywords: Random Boolean networks, phase transition, average sensitivity

PACS numbers: 02.10.Eb, 05.45.+b, 87.10.+e

1 Introduction

In 1969 Stuart Kauffman started to study random Boolean networks as simple models of genetic regulatory networks [1]. Random Boolean networks that consists of a set of Boolean *gates* that are capable of storing a single Boolean value. At discrete time steps these gates store a new value according to an initially chosen random Boolean function, which receives its inputs from random chosen gates. We will give a more formal definition later. Kauffman made numerical

*Corresponding author. E-Mail: Steffen.Schober@uni-ulm.de

studies of random networks, where the functions are chosen from the set of all Boolean functions with K arguments (the so called *NK-Networks*). He recognised that if $K \leq 2$, the random networks exhibit a remarkable form of ordered behaviour: The limit cycles are small, the number of *ineffective gates*, which are gates that can be perturbed without changing the asymptotic behaviour, and the number of *freezing gates* that stop changing their state is large. In contrast if $K \geq 3$, the networks do not exhibit this kind of ordered behaviour (see [1, 2]). The first analytical proof for this *phase transition* was given by Derrida and Pomeau (see [3]) by studying the evolution of the Hamming distance of random chosen initial states by means of so called *annealed approximation*. The first proof for the number of freezing and ineffective gates was given by James Lynch (see [4], although slightly weaker results appeared earlier [5, 6]). Depending on a parameter λ , that depends on the probabilities of the Boolean functions, he showed that if $\lambda \leq 1$ almost all gates are ineffective and freezing, otherwise not. Although his analysis is very general, until now it was only applied to networks with connectivity 2 and non-uniform probabilities for the Boolean function: if the probability of choosing a constant function is larger or equal the probability of choosing a non-constant non-canalizing function (namely the XOR- or the inverted XOR-function), λ is less or equal to one. But it turns out that in some cases λ is equal to the expectation of the average sensitivity. Therefore we will first study the average sensitivity in Section 3. Afterwards it will be shown in Section 4 how to use the results from the previous section to apply Lynch's analysis to classical *NK-Networks* and *biased* random Boolean networks¹. But first we will give some basic definition used throughout the paper in Section 2.

2 Basic Definitions

In the following $\mathbb{F}_2 = \{0, 1\}$ denotes the Galois field of two elements, where addition, denoted by \oplus , is defined modulo 2. The set of vectors of length K over \mathbb{F}_2 will be denoted by \mathbb{F}_2^K . If \mathbf{x} is a vector from \mathbb{F}_2^K , its i th component will be denoted by x_i . With $\mathbf{u}^{(i)} \in \mathbb{F}_2^K$ we will denote the *unit vector* which has all components zero except component i which is one. The Hamming weight of $\mathbf{x} \in \mathbb{F}_2^K$ is defined as

$$w_H(\mathbf{x}) = |\{i \mid x_i \neq 0, i = 1, \dots, K\}|$$

and the Hamming distance of $\mathbf{x}, \mathbf{y} \in \mathbb{F}_2^K$ as

$$d_H(\mathbf{x}, \mathbf{y}) = w_H(\mathbf{x} \oplus \mathbf{y}).$$

A Boolean function is a mapping $f : \mathbb{F}_2^K \rightarrow \mathbb{F}_2$. A function f may be represented by its *truth table* \mathbf{t}_f , that is, a vector in $\mathbb{F}_2^{2^K}$, where each component of the truth table gives the value of f for one of the 2^K possible arguments. To fix an order on the components of the truth table, suppose that its i th component equals the value of the corresponding function, given the binary representation (to K bits) of i as an argument.

¹a definition will be given later

3 Average Sensitivity

In this section we will focus on the *average sensitivity*. The average sensitivity is a known complexity measure for Boolean functions, see for example [7]². It was already used to study Boolean and random Boolean networks for example in [8, 9].

Definition 1. Let f denote a Boolean function $\mathbb{F}_2^K \rightarrow \mathbb{F}_2$ and $\mathbf{u}^{(i)}$ a unit vector.

1. The sensitivity $s_f(\mathbf{w})$ is defined as:

$$s_f(\mathbf{w}) = \left| \left\{ i \mid f(\mathbf{w}) \neq f(\mathbf{w} \oplus \mathbf{u}^{(i)}), i = 1, \dots, K \right\} \right|.$$

2. The average sensitivity s_f is defined as the average of $s_f(\mathbf{w})$ over all $\mathbf{w} \in \mathbb{F}_2^K$:

$$s_f = 2^{-K} \sum_{\mathbf{w} \in \mathbb{F}_2^K} s_f(\mathbf{w})$$

Now consider the random variable $F_K : \Omega \rightarrow \mathcal{F}_K$, where \mathcal{F}_K denotes the set of all 2^{2^K} Boolean functions with K arguments. The probability measure is given by $P(F_K = f) = \frac{1}{2^{2^K}}$. The expected value of the average sensitivity of this random variable is denoted by $\mathbb{E}_{F_K}(s_f)$, and is given by

$$\mathbb{E}_{F_K}(s_f) = \sum_f P(F_K = f) s_f$$

The expected value was already derived in [10], and is given by:

Theorem 1 (Bernasconi [10]).

Let the random variable F_K be defined as above, then

$$\mathbb{E}_{F_K}(s_f) = \sum_f P(F_K = f) s_f = \frac{K}{2}.$$

We will now concentrate on biased Boolean functions. The bias of a Boolean function $f : \mathbb{F}_2^K \rightarrow \mathbb{F}_2$ is defined as the number of 1 in the functions truth table divided by 2^K . To define the bias of a random Boolean function two definitions are possible. First we can assume that the truth tables of the Boolean functions are produced by independent Bernoulli trials with probability p for a one (This should be called *mean* bias, used for example in [3, 8]). Therefore consider the random variable $F_{K,p}$. The probability of choosing a function f is given by

$$P(F_{K,p} = f) = p^{\text{wh}(\mathbf{t}_f)} (1-p)^{2^K - \text{wh}(\mathbf{t}_f)}$$

For $p = 1/2$ this is equivalent to the definition of F_K .

²here it is called *critical complexity*

As a second possibility, we can only choose functions which have bias p whereas to all other functions we assign probability 0 (we will call this *fixed* bias). Therefore consider the random variables $F_{K,p}^{\text{fixed}} : \Omega \rightarrow \mathcal{F}_K$. Denote the truth table of a function f by \mathbf{t}_f . Further denote the set of all Boolean functions f with K arguments and $w_H(\mathbf{t}_f) = p2^K$ with $\mathcal{F}_{K,p}$. The probability for a certain function chosen according $F_{K,p}^{\text{fixed}}$ is given by

$$P(F_{K,p}^{\text{fixed}} = f) = \begin{cases} \frac{1}{|\mathcal{F}_{K,p}|} & \text{if } f \in \mathcal{F}_{K,p} \\ 0 & \text{if } f \notin \mathcal{F}_{K,p} \end{cases}$$

Both definitions ensure that the expectation to get a one is equal to p if the input of a function is chosen at random (with respect to uniform distribution). But it will turn out that these two different methods of creating biased Boolean functions, have a major impact on the average sensitivity.

The expectation of the average sensitivity of $F_{K,p}$ was derived in [8]:

Theorem 2 ([8]). *Let the random variable $F_{K,p}$ be defined as above:*

$$\mathbb{E}_{F_{K,p}}(s_f) = 2Kp(1-p)$$

For the random variable $F_{K,p}^{\text{fixed}}$ we will now proof the following theorem:

Theorem 3. *Let the random variable $F_{K,p}^{\text{fixed}}$ be defined as above:*

$$\mathbb{E}_{F_{K,p}^{\text{fixed}}}(s_f) = \frac{2^{K+1}Kp(1-p)}{(2^K - 1)}.$$

Proof. To find $\mathbb{E}_{F_{K,p}^{\text{fixed}}}(s_f)$ we will first consider the random variable $F_{K,t} : \Omega \rightarrow \mathcal{F}_K$ where $t \in \{0, 1, \dots, 2^K\}$ and the probability of a function is given by

$$P(F_{K,t} = f) = \begin{cases} \frac{1}{\binom{2^K}{t}} & \text{if } w_H(\mathbf{t}_f) = t \\ 0 & \text{else} \end{cases}.$$

Consider the Boolean functions as functions into \mathbb{R} by identifying $0, 1 \in \mathbb{F}_2$ with $0, 1 \in \mathbb{R}$. Then we get for the function f :

$$\begin{aligned} s_f &= 2^{-K} \sum_{\mathbf{w} \in \mathbb{F}_2^K} \left| \left\{ i \mid f(\mathbf{w}) \neq f(\mathbf{u}^{(i)} \oplus \mathbf{w}), i = 1, \dots, K \right\} \right| \\ &= 2^{-K} \sum_{\mathbf{w} \in \mathbb{F}_2^K} \sum_{i=1}^K (f(\mathbf{w}) - f(\mathbf{w} \oplus \mathbf{u}^{(i)}))^2 \\ &= 2^{-K} \sum_{\mathbf{w} \in \mathbb{F}_2^K} \sum_{i=1}^K (f(\mathbf{w}) + f(\mathbf{w} \oplus \mathbf{u}^{(i)}) - 2f(\mathbf{w})f(\mathbf{w} \oplus \mathbf{u}^{(i)})). \end{aligned}$$

where $\mathbf{u}^{(i)}$ again denotes the unit vector with i th component set to 1. Hence by the linearity of the expectation

$$\begin{aligned} \mathbb{E}_{F_{K,t}}(s_f) = 2^{-K} \sum_{\mathbf{w} \in \mathbb{F}_2^K} \sum_{i=1}^K & \left(\mathbb{E}_{F_{K,t}}(f(\mathbf{w})) + \mathbb{E}_{F_{K,t}}(f(\mathbf{w} \oplus \mathbf{u}^{(i)})) \right. \\ & \left. - 2\mathbb{E}_{F_{K,t}}(f(\mathbf{w})f(\mathbf{w} \oplus \mathbf{u}^{(i)})) \right). \end{aligned} \quad (1)$$

Now we form a matrix with the truth tables of all functions with Hamming weight t as column vectors:

$$M = \left(\mathbf{c}^{(1)}, \mathbf{c}^{(2)}, \dots, \mathbf{c}^{(\binom{2^K}{t})} \right) \text{ where } \mathbf{c}^{(i)} \in \mathbb{F}_2^{2^K}$$

M has exactly $\binom{2^K}{t}$ columns and 2^K rows. Each entry $M_{i,j}$ in the i th row and j th column equals the value of function f_j given the binary representation of i as input.

Hence $\mathbb{E}_{F_{K,t}}(f(\mathbf{w}))$ is determined by the number of 1 in the row associated with \mathbf{w} divided by the length of the row. Consider an arbitrary row i . This row has a one at position j if the corresponding column $\mathbf{c}^{(j)}$ has a one at position i . But there are $\binom{2^K-1}{t-1}$ column vectors with a 1 at position i . It follows:

$$\forall \mathbf{w} \in \mathbb{F}_2^K : \quad \mathbb{E}_{F_{K,t}}(f(\mathbf{w})) = \frac{\binom{2^K-1}{t-1}}{\binom{2^K}{t}} = \frac{t}{2^K}. \quad (2)$$

As this holds for all \mathbf{w} , we have

$$\forall \mathbf{w}, \mathbf{u}^{(i)} \in \mathbb{F}_2^K : \quad \mathbb{E}_{F_{K,t}}(f(\mathbf{w} \oplus \mathbf{u}^{(i)})) = \frac{t}{2^K}. \quad (3)$$

To find an expression for $\mathbb{E}_{F_{K,p}^{\text{fixed}}}(f(\mathbf{w})f(\mathbf{w} \oplus \mathbf{u}^{(i)}))$ we consider two arbitrary rows l, m ($l \neq m$). Define the following sum:

$$\gamma_{l,m} = \sum_{i=1}^{\binom{K}{t}} M_{l,i} M_{m,i}.$$

Obviously $M_{l,i} M_{m,i} = 1$ only if we have a 1 in both rows at position i . This means for the column vectors $\mathbf{c}^{(i)}$ of M , we have $\mathbf{c}_l^{(i)} = \mathbf{c}_m^{(i)} = 1$. But there are exactly $\binom{2^K-2}{t-2}$ such column vectors in M . Therefore we have

$$\forall l, m, l \neq m : \gamma_{l,m} = \binom{2^K-2}{t-2}.$$

As $\mathbf{w} \neq \mathbf{w} \oplus \mathbf{u}^{(i)}$ for all $\mathbf{w}, \mathbf{u}^{(i)}$ it follows:

$$\mathbb{E}_{F_{K,t}}(f(\mathbf{w})f(\mathbf{w} \oplus \mathbf{u}^{(i)})) = \frac{\binom{2^K-2}{t-2}}{\binom{2^K}{t}} = \frac{t(t-1)}{2^K(2^K-1)}. \quad (4)$$

Hence substituting Equations (2), (3) and (4) into Equation (1) leads to

$$\mathbb{E}_{F_{K,t}}(s_f) = \frac{K(2^K - t)t}{2^{K-1}(2^K - 1)}.$$

Finally the claimed expression for $\mathbb{E}_{F_{K,p}^{\text{fixed}}}(s_f)$ can be obtained from the above equation by a substitution of $t: t \rightarrow p2^K$. \square

It should be noted, that the Theorems 1 and 2 can be proved using in a similar way. Also worth noting is the fact, that if the functions are chosen according $F_K, F_{K,p}^{\text{fixed}}$ or $F_{K,p}$ the expectation of the sensitivity of a fixed vector \mathbf{w} (namely the expectation of $s_f(\mathbf{w})$) is independent of \mathbf{w} (see Equation (1),(2), (3) and (4)). Hence the following lemma holds

Lemma 1. *If $F = F_K, F_{K,p}^{\text{fixed}}$ or $F_{K,p}$, then*

$$\forall \mathbf{w}, \mathbf{v} \in \mathbb{F}_2^K : \mathbb{E}_F(s_f(\mathbf{w})) = \mathbb{E}_F(s_f(\mathbf{v}))$$

Before proceeding to the next section, it should be noted, that using the same arguments as in the proof of Theorem 3, we can also prove the expectation of average sensitivity of order l , defined as

$$s^{(l)}(f) = 2^{-K} \sum_{\mathbf{w} \in \mathbb{F}_2^K} |\{\mathbf{x} \in \mathbb{F}_2^K \mid w_H(\mathbf{x}) = l \text{ and } f(\mathbf{w}) \neq f(\mathbf{w} \oplus \mathbf{x})\}|.$$

In this case, instead of summing up all unit vectors in Equation (1), we sum up all vectors of Hamming weight l . As the equations (2) and (4) hold for all $\mathbf{w} \in \mathbb{F}_2^K$ we conclude that

$$\mathbb{E}(s^{(l)}(F_{K,p}^{\text{fixed}})) = \binom{K}{l} \frac{2^{K+1}p(1-p)}{(2^K - 1)}$$

and by similar arguments

$$\mathbb{E}(s^{(l)}(F_{K,p})) = \binom{K}{l} 2p(1-p)$$

respectively

$$\mathbb{E}(s^{(l)}(F_K)) = \frac{1}{2} \binom{K}{l}.$$

4 Extending Lynch's analysis

As already mentioned James Lynch gave a very general analysis of randomly constructed Boolean networks (see [4]). Before stating his results we give a formal definition for Boolean networks A Boolean network \mathbf{B} is a 4-tuple

$(V, E, \tilde{F}, \mathbf{x})$ where $V = \{1, \dots, N\}$ is a set of natural numbers, E is a set of labeled edges on V , $\tilde{F} = \{f_1, \dots, f_N\}$ is a ordered set of Boolean functions such that for each $v \in V$ the number of arguments of f_v is the *in-degree* of v in E , these edges are labeled with $1, \dots, \text{in-degree}(v)$, and $\mathbf{x} = (x_1, \dots, x_N) \in \mathbb{F}_2^N$. Suppose that a vertex i has K_i in-edges from vertices $v_{i,1}, \dots, v_{i,K_i}$. For $\mathbf{y} \in \mathbb{F}_2^N$ we define

$$\mathbf{B}(\mathbf{y}) = (f_1(y_{v_{1,1}}, \dots, y_{v_{1,K_1}}), \dots, f_N(y_{v_{N,1}}, \dots, y_{v_{N,K_N}})).$$

The state of \mathbf{B} at time 0 is called the *initial state* \mathbf{x} , so we define $\mathbf{B}^0(\mathbf{x}) = \mathbf{x}$. For time $t \geq 1$ the state is inductively defined as $\mathbf{B}^t(\mathbf{x}) = \mathbf{B}(\mathbf{B}^{t-1}(\mathbf{x}))$. Hence we can interpret V as set of gates, E and \tilde{F} describes their functional dependence and \mathbf{x} is the networks initial state.

Assume some ordering f_1, f_2, \dots on the set of all Boolean functions \mathcal{F} , where each function f_i depends on K_i arguments. Further a random variable $F : \Omega \rightarrow \mathcal{F}$ with probabilities $p_i = P(F = f_i)$ such that $\sum_{i=1}^{\infty} p_i = 1$ and $\sum_{i=1}^{\infty} p_i K_i^2 < \infty$. Now a random Boolean network consisting of N gates is constructed as follows: For each gate a Boolean function is chosen independently, where the probability of choosing f_i is given by p_i . Suppose a function f was chosen that has K arguments, these arguments are chosen at random from all $\binom{N}{K}$ equally likely possibilities. At last an initial state is chosen at random from the set on all equally likely states. If the Boolean functions are chosen according to our previously defined random variable F_K we will call this networks *NK-Networks* with connectivity K . If the functions are chosen according to $F_{K,p}^{\text{fixed}}$ or $F_{K,p}$ we will call this networks *biased random Boolean networks* with connectivity K and fixed bias p respectively mean bias p .

Let us now state Lynch's results. His analysis depends on a parameter $\mathbb{R} \ni \lambda \geq 0$ depending only on the functions and their probabilities. We will define λ later in Definition 3. First we have to state Lynch's definition of *freezing* and *ineffective* gates:

Definition 2 (Lynch [4] Definition 1 Item 2 and 5).

Let $\mathbf{x} \in \mathbb{F}_2^N$ and $v \in V$.

1. Gate v freezes to $\mathbf{y} \in \mathbb{F}_2^N$ in t steps on input \mathbf{x} if $\mathbf{B}_v^{t'}(\mathbf{x}) = \mathbf{y}$ for all $t' \geq t$.
2. Let $\mathbf{u}^{(i)} \in \mathbb{F}_2^n$.
A gate v is t -ineffective at input $\mathbf{x} \in \mathbb{F}_2^K$ if $\mathbf{B}^t(\mathbf{x}) = \mathbf{B}^t(\mathbf{x} \oplus \mathbf{u}^{(v)})$.

Now we will state the main result.

Theorem 4 (Lynch [4] Theorem 4 and 6).

Let α, β be positive constants satisfying $2\alpha \log \delta + 2\beta < 1$ and $\alpha \log \delta < \beta$ where $\delta = \mathbb{E}(K_i)$.

1. There is a constant r such that for all $\mathbf{x} \in \mathbb{F}_2^N$

$$\lim_{n \rightarrow \infty} P(v \text{ is ineffective in } \alpha \log N \text{ steps}) = r$$

When $\lambda \leq 1$, $r = 1$ and when $\lambda > 1$, $r < 1$.

2. There is a constant r such that for all $\mathbf{x} \in \mathbb{F}_2^N$

$$\lim_{n \rightarrow \infty} P(v \text{ is freezing in } \alpha \log N \text{ steps}) = r$$

When $\lambda \leq 1$, $r = 1$ and when $\lambda > 1$, $r < 1$.³

The above theorem shows that if $\lambda \leq 1$ almost all gates are freezing and ineffective and otherwise not. The next corollary gives us more information what happens if $\lambda > 1$:

Corollary 1 (Lynch [4] Corollary 3 and Corollary 6). *Let $\lambda > 1$. For almost all random Boolean networks*

1. *if gate v is not $\alpha \log N$ -ineffective, there is a positive constant W such that for $t \leq \alpha \log N$, the number of gates affected by v at time t is asymptotic to $W\lambda^t$,*
2. *if gate v is not freezing in $\alpha \log N$ steps, there is a positive constant W such that for $t \leq \alpha \log N$, the number of gates that affect v at time t is asymptotic to $W\lambda^t$.*

Now we will state the definition of λ for Boolean networks:

Definition 3 (Lynch [4], Definition 4). *Let f be a Boolean function of K arguments. For $i \in \{1, \dots, K\}$, we say that argument i directly affects f on input $\mathbf{w} \in \mathbb{F}_2^K$ if $f(\mathbf{w}) \neq f(\mathbf{w} \oplus \mathbf{u}^{(i)})$. Now put $\gamma(f, \mathbf{w})$ as the number of i 's that directly affect f on input \mathbf{w} . Given a constant $a \in [0, 1]$, we define*

$$\lambda = \sum_{i=1}^{\infty} p_i \sum_{\mathbf{w} \in \mathbb{F}_2^{K_i}} \gamma(f_i, \mathbf{w}) a^{\text{wh}(\mathbf{w})} (1-a)^{K_i - \text{wh}(\mathbf{w})}.$$

Obviously $\gamma(f, \mathbf{w})$ is identical to $s_f(\mathbf{w})$ which will be used instead in the further discussion. The constant a is the probability that a random gate is one (at infinite time) given that all gates at time 0 have probability 0.5 of being one. (see [4, Definiton 2]). Assume that we choose the functions according a random variable F which should be either F_K , $F_{K,p}^{\text{fixed}}$ or $F_{K,p}$. The functions are chosen out the set \mathcal{F}_K , we denote a function's probability with p_f . It follows that

$$\lambda = \sum_{\mathbf{w} \in \mathbb{F}_2^K} a^{\text{wh}(\mathbf{w})} (1-a)^{K - \text{wh}(\mathbf{w})} \sum_f p_f s_f(\mathbf{w}) \quad (5)$$

$$= \sum_{\mathbf{w} \in \mathbb{F}_2^K} a^{\text{wh}(\mathbf{w})} (1-a)^{K - \text{wh}(\mathbf{w})} \mathbb{E}(s_F(\mathbf{w})) \quad (6)$$

$$= \mathbb{E}(s_F(\mathbf{w})) \sum_{i=0}^K \binom{K}{i} a^i (1-a)^{K-i} \quad (7)$$

$$= \mathbb{E}(s_F(\mathbf{w})) = \mathbb{E}_F(s_f) \quad (8)$$

³Please note that we here state a slightly weaker result than in the original analysis.

$\mathbb{E}(s_F(\mathbf{w}))$ denotes the expectation of the sensitivity for a fixed \mathbf{w} , Equation (7) follows from Lemma 1. Therefore, together with Theorem 1 and Theorem 3 we proved the following:

Theorem 5 (Biased random Boolean networks). *For random Boolean networks, if*

1. *the functions are chosen according random variable $F_{K,p}$, it follows that*

$$\lambda = 2Kp(1 - p),$$

2. *the functions are chosen according random variable $F_{K,p}^{\text{fixed}}$, it follows that*

$$\lambda = \frac{2^{K+1}Kp(1 - p)}{2^K - 1}.$$

As a special case of the above theorem we get (or by using Theorem 1)

Theorem 6 (NK -Networks). *In random Boolean networks, where the functions are chosen according to the random variable F_K*

$$\lambda = \frac{K}{2}.$$

5 Discussion

The results about NK -Networks are consistent with experimental results. In fact if $K \leq 2$ almost all networks almost all gates are freezing and almost all gates are ineffective and otherwise not (see [2]).

Obviously, the border between the ordered and disordered phase is given by $\lambda = 1$. The resulting phase diagram for biased random Boolean networks, where the functions are chosen according to $F_{K,p}^{\text{fixed}}$ and $F_{K,p}$ is shown in Figure 1. It is interesting to note that if the functions are chosen with fixed bias, then also Boolean networks with connectivity $K = 2$ can become unstable. This conclusion can be drawn from Lynch's original result already. As mentioned in the introduction, he showed for $K = 2$, that $\lambda > 1$ if the probability of choosing a non-constant non-canalizing function, namely the XOR or the inverted XOR function, is larger than the probability of choosing a constant function. For example if the bias is 0.5, the probability of choosing a constant function is zero, whereas both XOR and inverted XOR function have probability greater zero, hence $\lambda > 1$.

It is interesting to compare our results with previous results obtained first by Derrida and Pomeau using the so called *annealed approximation* (see [3]). In their *annealed model* the functions and connections are chosen at random at each time step. Considering two instances of the same annealed network starting in two randomly chosen initial states $\mathbf{s}_1(0), \mathbf{s}_2(0)$ they show that

$$\lim_{N \rightarrow \infty} \lim_{t \rightarrow \infty} \frac{d_H(\mathbf{s}_1(t), \mathbf{s}_2(t))}{N} = c$$

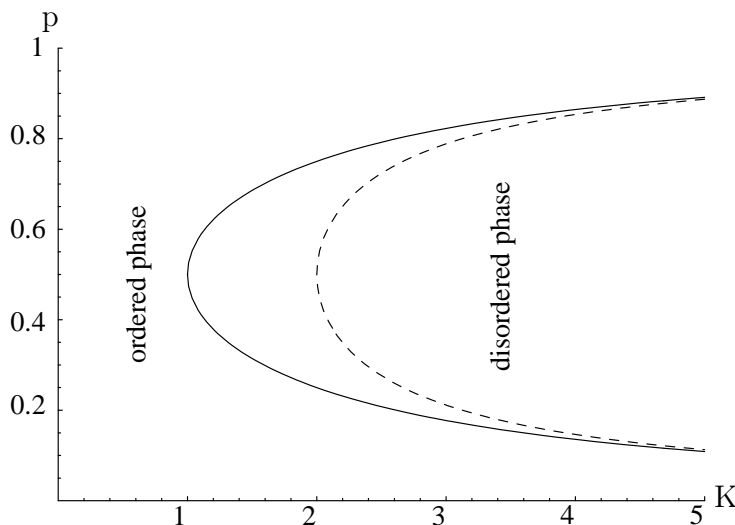


Figure 1: Phase diagram for biased random networks: Functions chosen according $F_{K,p}$ (dashed) and $F_{K,p}^{\text{fixed}}$ (solid)

where $c = 1$ if

$$2Kp(1-p) \leq 1$$

and $c \leq 1$ otherwise. It is remarkable that the two models behave similar, but it is unclear whether this holds in general.

6 Acknowledgement

We would like to thank our colleges Georg Schmidt and Stephan Stiglmayr for proofreading and Uwe Schoening for useful hints.

References

- [1] S. Kauffman, Metabolic stability and epigenesis in randomly constructed nets, *Journal of Theoretical Biology* 22 (1969) 437–467.
- [2] S. Kauffman, The large scale structure and dynamics of genetic control circuits: an ensemble approach, *Journal of Theoretical Biology* 44 (1974) 167–190.
- [3] B. Derrida, Y. Pomeau, Random networks of automata - a simple annealed approximation, *Europhysics Letters* 2 (1986) 45–49.
- [4] J. F. Lynch, Dynamics of random boolean networks, in: *Conference on Mathematical Biology and Dynamical Systems*, University of Texas at Tyler, 2005.

- [5] J. F. Lynch, On the threshold of chaos in random boolean cellular automata, *Random Structures and Algorithms* (1995) 236–260.
- [6] J. F. Lynch, Critical points for random boolean networks, *Physica D: Non-linear Phenomena* 172 (1-4) (2002) 49–64.
- [7] I. Wegener, *The Complexity of Boolean Functions*, Wiley-Teubner Series in Computer Science, John Wiley, B.G. Teubner, 1987.
- [8] I. Shmulevich, S. A. Kauffman, Activities and sensitivities in boolean network models, *Physical Review Letters* 93 (4).
- [9] S. Kauffman, C. Peterson, B. Samuelsson, C. Troeln, Genetic networks with canalyzing boolean rules are always stable, *Proceedings of the National Academy of Science* 101 (49).
- [10] A. Bernasconi, *Mathematical techniques for the analysis of boolean functions*, Ph.D. thesis, Dipartimento di Informatica, Universita di Pisa (March 1998).