# Persistence of Activity in Random Boolean Networks

Shirshendu Chatterjee and Rick Durrett \* Cornell University

December 20, 2008

#### Abstract

We consider a model for gene regulatory networks that is a modification of Kauffmann's (1969) random Boolean networks. There are three parameters: n = the number of nodes, r = the number of inputs to each node, and p = the expected fraction of 1's in the Boolean functions at each site. Following a standard practice in the physics literature, we use a threshold contact process on a random graph in which each node has in degree r to approximate its dynamics. We show that if  $r \ge 3$  and  $r \cdot 2p(1-p) > 1$ , then the threshold contact process persists for a long time, which corresponds to chaotic behavior of the Boolean network. Unfortunately, we are only able to prove the persistence time is  $\ge \exp(cn^{b(p)})$  with b(p) > 0 when  $r \cdot 2p(1-p) > 1$  and b(p) = 1 when  $(r-1) \cdot 2p(1-p) > 1$ .

Keywords: random graphs, threshold contact process, phase transition, random Boolean networks, gene regulatory networks

<sup>\*</sup>Both authors were partially supported by NSF grant 0704996 from the probability program at NSF.

## 1 Introduction

Random Boolean networks were originally developed by Kauffman (1969) as an abstraction of genetic regulatory networks. The idea is to identify generic properties and patterns of behavior for the model, then compare them with the behavior of real systems. Protein and RNA concentrations in networks are often modeled by systems of differential equations. However, in large networks the number of parameters such as decay rates, production rates and interaction strengths can become huge. Recent work by Albert and Othmer (2003) on the segment polarity network in *Drosophila melanogaster*, see also Chaves, Albert and Sontag (2005), has shown that Boolean networks can in some cases outperform differential equation models. Kauffman et al. (2003) used random Boolean networks to model the yeast transcriptional network, and Li et al (2004) have used this approach to model the yeast cell-cycle network.

In our random Boolean network model, the state of each node  $x \in V_n = \{1, 2, ..., n\}$  at time t = 0, 1, 2, ... is  $\eta_t(x) \in \{0, 1\}$ . Each node x has r input nodes  $y_1(x), ..., y_r(x)$  chosen randomly from the set of all nodes, and we draw oriented edges to each node from its input nodes. So the edge set is  $E_n = \{(y_i(x), x) : x \in V_n, 1 \le i \le r\}$ . Thus the underlying graph  $G_n$  is a random element chosen from the set of all directed graphs in which the in-degree of any vertex is equal to r. Once chosen the network remains fixed through time. The updating for node x is

$$\eta_{t+1}(x) = f_x(\eta_t(y_1(x)), \dots, \eta_t(y_r(x))),$$

where the values  $f_x(v)$ ,  $x \in V_n$ ,  $v \in \{0, 1\}^r$ , chosen at the beginning and then fixed for all time, are independent and = 1 with probability p.

A number of simulation studies have investigated the behavior of this model. See Kadanoff, Coppersmith, and Aldana (2002) for survey. Flyvberg and Kjaer (1988) have studied the degenerate case of r = 1 in detail. Derrida and Pommeau (1986) have shown that for  $r \geq 3$  there is a phase transition in the behavior of these networks between rapid convergence to a fixed point and exponentially long persistence of changes, and identified the phase transition curve to be given by the equation  $r \cdot 2p(1-p) = 1$ . The networks with parameters below the curve have behavior that is 'ordered' and those with parameters above the curve have 'chaotic' behavior. Since chaos is not healthy for a biological network, it should not be surprising that real biological networks avoid this phase. See Kauffman (1993), Shmulevich, Kauffman, and Aldana (2005), and Nykter et al. (2008).

To explain the intuition behind the result of Derrida and Pomeau (1986), we define another process  $\zeta_t(x)$  for  $t \ge 1$ . The idea is that  $\zeta_t(x) = 1$  if and only if  $\eta_t(x) \ne \eta_{t-1}(x)$ . Now if the state of at least one of the inputs  $y_1(x), \ldots, y_r(x)$  into node x has changed at time t, then the state of node x at time t+1 will be computed by looking at a different value of  $f_x$ . If we ignore the fact that we may have used this entry before, we get the dynamics of the threshold contact process

$$P(\zeta_{t+1}(x) = 1) = 2p(1-p)$$
 if  $\zeta_t(y_1(x)) + \dots + \zeta_t(y_r(x)) > 0$ 

and  $\zeta_{t+1}(x) = 0$  otherwise. Conditional on the state at time t, the decisions on the values of  $\zeta_{t+1}(x), x \in V_n$  are made independently.

We content ourselves to work with the threshold contact process since it gives an approximate sense of the original model and we can prove rigorous results about its behavior. To simplify notation and explore the full range of threshold contact processes we let q = 2p(1-p)and suppose  $0 \le q \le 1$ . As mentioned above, it is widely accepted that the condition for prolonged persistence of the threshold contact process is qr > 1. To explain this, we note that vertices in the graph have average out-degree r, so a value of 1 at a vertex will, on the average, produce qr 1's in the next generation.

To state our first result, we will rewrite the threshold contact process as a set valued process  $\xi_t = \{x : \zeta_t(x) = 1\}$ . We will refer to the vertices  $x \in \xi_t$  as occupied. Let  $\{\xi_t^1\}_{t\geq 0}$ be the threshold contact process starting from all occupied sites, and  $\rho$  be the survival probability of a branching process with offspring distribution  $p_r = q$  and  $p_0 = 1 - q$ . By branching process theory

$$\rho = 1 - \theta$$
, where  $\theta \in (0, 1)$  satisfies  $\theta = 1 - q + q\theta^r$ . (1.1)

**Theorem 1.** Suppose q(r-1) > 1 and let  $\delta > 0$ . There is a positive constant  $C(\delta)$  so that as  $n \to \infty$ 

$$\inf_{t \le \exp(C(\delta)n)} P\left(\frac{|\xi_t^1|}{n} \ge \rho - 2\delta\right) \to 1.$$

To prove this result, we will consider the dual coalescing branching process  $\xi_t$ . In this process if x is occupied at time t, then with probability q all of the sites  $y_1(x), \ldots, y_r(x)$  will be occupied at time t+1, and birth events from different sites are independent. Writing A and B for the initial sets of occupied sites in the two processes we have the duality relationship:

$$P(\xi_t^A \cap B \neq \emptyset) = P(\hat{\xi}_t^B \cap A \neq \emptyset), \quad t = 0, 1, 2, \dots$$
(1.2)

Taking  $A = \{1, 2, \dots, n\}$  and  $B = \{x\}$  this says

$$P(x \in \xi_t^1) = P(\hat{\xi}_t^{\{x\}} \neq \emptyset),$$

or the density of occupied sites in  $\xi_t^1$  is equal to the probability that  $\hat{\xi}^{\{x\}} - s$  survives until time t. Since over small distances our graph looks like a tree in which each vertex has r descendants, the last quantity  $\approx \rho$ .

From (1.2) it should be clear that we can prove Theorem 1 by studying the coalescing branching process. The key to this is an "isoperimetric inequality." Let  $\hat{G}_n$  be the graph obtained from our original graph  $G_n = (V_n, E_n)$  by reversing the edges. That is,  $\hat{G}_n = (V_n, \hat{E}_n)$ , where  $\hat{E}_n = \{(x, y) : (y, x) \in E_n\}$ . Given a set  $U \subset V_n$ , let

$$U^* = \{ y : x \to y \text{ for some } x \in U \}, \tag{1.3}$$

where  $x \to y$  means  $(x, y) \in \hat{E}_n$ . Note that  $U^*$  can contain vertices of U. The idea behind this definition is that if U is occupied at time t in the coalescing branching process, then the vertices in  $U^*$  may be occupied at time t + 1. **Theorem 2.** Let P(m,k) be the probability that there is a subset  $U \subset V_n$  with size |U| = m so that  $|U^*| \leq k$ . Given  $\eta > 0$  there is an  $\epsilon_0(\eta)$  so that for  $m \leq \epsilon_0 n$ 

$$P(m, (r-1-\eta)m) \le \exp(-\eta m \log(n/m)/2).$$

In words, the isoperimetric constant for small sets is r-1. It is this result that forces us to assume q(r-1) > 1 in Theorem 1. To see that Theorem 2 is sharp, define an undirected graph  $H_n$  on the vertex set  $V_n$  so that x and y are adjacent if and only if there is a z so that  $x \to z$ and  $y \to z$  in  $\hat{G}_n$ . The mean number of neighbors of a vertex in  $H_n$  is  $r^2 \ge 9$ , so standard arguments show that there is a c > 0 so that with probability tending to 1 as  $n \to \infty$  there is a connected component  $K_n$  of  $H_n$  with  $|K_n| \ge cn$ . If U is a connected subset of  $K_n$  with |U| = m then by building up U one vertex at a time we see that  $|U^*| \le 1 + (r-1)m$ .

Since the isoperimetric constant is  $\leq r - 1$ , it follows that when q(r - 1) < 1, there are bad sets A with  $|A| \leq n\epsilon$  so that  $E|\hat{\xi}_1^A| \leq |A|$ . Computations from the proof of Theorem 2 suggest that there are a large number of bad sets. We have no idea how to bound the amount of time spent in bad sets, so we have to take a different approach to show persistence when  $1/r < q \leq 1/(r-1)$ .

**Theorem 3.** Suppose qr > 1. If  $\delta_0$  is small enough, then for any  $0 < \delta < \delta_0$ , there are constants  $C(\delta) > 0$  and  $B(\delta) = (1/4 - 2\delta) \log(qr - \delta) / \log r$  so that as  $n \to \infty$ 

$$\inf_{t \le \exp(C(\delta) \cdot n^{B(\delta)})} P\left(\frac{|\xi_t^1|}{n} \ge \rho - 3\delta\right) \to 1.$$

To prove this, we will again investigate persistence of the dual. Let  $d_0(x, y)$  be the length of the shortest oriented path from x to y in  $\hat{G}_n$ , let

$$d(x, y) = \min_{z \in V_n} [d_0(x, z) + d_0(y, z)],$$

and for any subset A of vertices let

$$m(A, K) = \max_{S \subseteq A} \{ |S| : d(x, y) \ge K \text{ for } x, y \in S \}.$$
 (1.4)

Let  $R = \log n/\log r$  be the average value of d(1, y), let  $a = 1/4 - \delta$  and  $B = (a - \delta) \log(qr - \delta/\log r)$ . We will show that if  $m(\hat{\xi}_s^A, 2aR) < (\rho - 2\delta)n^B$ , then with high probability, we will later have  $m(\hat{\xi}_t^A, 2aR) \ge (\rho - 2\delta)n^B$ . To do this we first argue that when we first have  $m(\hat{\xi}_s^A, 2aR) < (\rho - 2\delta)n^B$ , there are at least  $(q - \delta)(\rho - 2\delta)n^B$  occupied sites so that the d distance between any two vertices is at least 2aR - 2. We run the dual process starting from these vertices until time aR - 2, so they are independent. With high probability at least one of these vertices, call it w, has  $n^B$  descendants. We run the dual processes starting from these  $n^B$  vertices for another aR units of time, and then pick one offspring from each of the duals which have survived till time aR to have a set that is suitably spread out and has size at least  $(\rho - 2\delta)n^B$ . It seems foolish to pick only one vertex w after the first step, but we do not know how to guarantee that the vertices are suitably separated after the second step if we pick more.

# 2 Proof of Theorem 1

We begin with the proof of the isoperimetric inequality, Theorem 2.

Proof of Theorem 2. Let P(m, k) be the probability that there is a set U of vertices in  $G_n$  of size m with  $|U^*| \leq k$ . Let p(m, k) be the probability that there is a set U with |U| = m and  $|U^*| = k$ . First we will estimate  $p(m, \ell)$  where  $\ell = (r - 1 - \eta)m$ .

$$p(m,\ell) = \sum_{\{(U,U'):|U|=m,|U'|=\ell\}} P(U^* = U') \le \sum_{\{(U,U'):|U|=m,|U'|=\ell\}} P(U^* \subset U')$$

According to the construction of  $G_n$ , the other end of each of the r|U| edges coming out of U is chosen at random from  $V_n$  so

$$P(U^* \subset U') = \left(\frac{|U'|}{n}\right)^{r|U|}$$

and hence

$$p(m,\ell) \le \binom{n}{m} \binom{n}{\ell} \left(\frac{\ell}{n}\right)^{rm}.$$
(2.1)

,

To bound the right-hand side, we use the trivial bound

$$\binom{n}{m} \le \frac{n^m}{m!} \le \left(\frac{ne}{m}\right)^m,\tag{2.2}$$

where the second inequality follows from  $e^m > m^m/m!$ . Using (2.2) in (2.1)

$$p(m,\ell) \le (ne/m)^m (ne/\ell)^\ell \left(\frac{\ell}{n}\right)^{rm}$$

Recalling  $\ell = (r - 1 - \eta)m$ , the last expression becomes

$$= e^{m(r-\eta)} (m/n)^{m[-1-(r-1-\eta)+r]} (r-1-\eta)^{-(r-1-\eta)m+rm}.$$

Letting  $c(\eta) = r - \eta + (1 + \eta) \log(r - 1 - \eta) \le C$  for  $\eta \in (0, r - 1)$ , we have

$$p(m, (r-1-\eta)m) \le \exp(-\eta m \log(n/m) + Cm).$$

Summing over integers  $k = (r - 1 - \eta')m$  with  $\eta' \ge \eta$ , and noting that there are fewer than rm terms in the sum, we have

$$P(m, (r-1-\eta)m) \le \exp(-\eta m \log(n/m) + C'm).$$

To clean up the result to the one given in Theorem 2, choose  $\epsilon_0$  such that  $\eta \log(1/\epsilon_0)/2 > C'$ . Hence for any  $m \leq \epsilon_0 n$ ,

$$\eta \log(n/m)/2 \ge \eta \log(1/\epsilon_0)/2 > C',$$

which gives the desired result.

To grow the cluster starting at a vertex x in  $\hat{G}_n$ , we add the neighbors in a breadth-first search. That is, we add all vertices y for which  $d_0(x, y) = j$  one at a time, before proceeding to the vertices at distance j + 1.

**Lemma 2.1.** Suppose  $0 < \delta < 1/2$ . Let  $A_x$  be the event that the cluster starting at x in  $\hat{G}_n$  does not intersect itself before reaching size  $n^{1/2-\delta}$ , and let  $A_{x,y}$  be the event that the clusters starting from x and y do not intersect before reaching size  $n^{1/2-\delta}$ . Then for all  $x, y \in V_n$ 

$$P(A_x^c), P(A_{x,y}^c) \le n^{-2\delta}.$$
 (2.3)

*Proof.* Let  $\delta' = 1/2 - \delta$ . While growing the cluster starting from x up to size  $n^{\delta'}$ , the probability of a self-intersection at any step is  $\leq n^{\delta'}/n$ , so

$$P(A_x) \ge \left(1 - n^{-(1-\delta')}\right)^{n^{\delta'}} \ge 1 - n^{2\delta'-1} = 1 - n^{-2\delta}.$$

The exact same reasoning applied to the cluster containing x intersecting the cluster of y grown to size  $n^{1/2-\delta}$ .

Lemma 2.1 shows that  $\hat{G}_n$  is locally tree-like. In the next lemma, we will use this to get a bound on the survival of the dual process for small times. Let  $\rho$  be the branching process survival probability defined in (1.1).

**Lemma 2.2.** If q > 1/r,  $\delta \in (0, qr - 1)$ ,  $\gamma = (20 \log r)^{-1}$ , and  $b = \gamma \log(qr - \delta)$  then for large n

$$P\left(\left|\hat{\xi}_{2\gamma\log n}^{\{x\}}\right| \ge n^b\right) \ge \rho - \delta.$$

*Proof.* Let  $A_x$  be the event that the cluster starting at x in  $\hat{G}_n$  does not intersect itself before reaching size  $n^{1/4}$ . On the event  $A_x$ , for  $t \leq 2\gamma \log n$ ,  $|\hat{\xi}_t^{\{x\}}| = Z_t$ , is a branching process with  $Z_0 = 1$  and offspring distribution  $p_0 = 1 - q$  and  $p_r = q$ . Since q > 1/r, this is a supercritical branching process. Let  $B_x$  be the event that the branching process survives. If we condition on  $B_x$ , then, using a large deviation results for branching processes from Athreya (1994),

$$P\left(\left|\frac{Z_{t+1}}{Z_t} - qr\right| > \delta \middle| B_x\right) \le e^{-c(\delta)t}$$
(2.4)

for large enough t. So if  $F_x = \{Z_{t+1} \ge (qr - \delta)Z_t \text{ for } \gamma \log n \le t < 2\gamma \log n\}$ , then

$$P(F_x^c|B_x) \le \sum_{t=\gamma \log n}^{(2\gamma \log n)-1} e^{-c(\delta)t} \le C_\delta n^{-c(\delta)\gamma}$$
(2.5)

for large enough *n*. On the event  $B_x \cap F_x$ ,  $Z_{2\gamma \log n} \ge (qr - \delta)^{\gamma \log n} = n^{\gamma \log(qr - \delta)}$ , since  $Z(\gamma \log n) \ge 1$ . Combining the error probabilities of (2.3) and (2.5)

$$P\left(\left|\hat{\xi}_{2\gamma\log n}^{\{x\}}\right| \ge n^{\gamma\log(qr-\delta)}\right) \ge P(B_x) - P(A_x^c) - P(F_x^c|B_x) \ge P(B_x) - \delta$$

for large enough n, as  $P(A_x) \ge 1 - n^{-1/2}$  by Lemma 2.1.

Lemma 2.2 shows that the dual process starting from one vertex will with probability  $\geq \rho - \delta$  survive until there are  $n^b$  particles. The next lemma will show that if the dual starts with  $n^b$  particles, then it can reach  $\epsilon n$  particle with high probability.

**Lemma 2.3.** If q(r-1) > 1, then there exists  $\epsilon_0 = \epsilon_0(q) > 0$  such that for any A with  $|A| = n^b$  the dual process  $\{\hat{\xi}_t^A\}_{t\geq 0}$  satisfies

$$P\left(\max_{t\leq\epsilon_0n-n^b}|\hat{\xi}_t^A|<\epsilon_0n\right)\leq\exp(-n^{b/4}).$$

Proof. Choose  $\eta > 0$  such that  $(q-\eta)(r-1-\eta) > 1$  and let  $\epsilon_0(\eta)$  be the constant in Theorem 2. Let  $\tau = \min\{t : |\hat{\xi}_t^A| \ge \epsilon_0 n\}$ . For  $t < \tau$ , let  $F_t = \{|\hat{\xi}_t^A| \ge |\hat{\xi}_{t-1}^A| + 1\}$ . Then for  $t \ge 0$   $P(F_{t+1}) \ge P(B_t \cap C_t)$ , where

$$B_t = \{ \text{at least } (q - \eta) | \hat{\xi}_t^A | \text{ particles of } \hat{\xi}_t^A \text{ give birth} \},\$$
  
$$C_t = \{ |U_t^*| \ge (r - 1 - \eta) | U_t | \}, \text{ where } U_t = \{ x \in \hat{\xi}_t^A : x \text{ gives birth} \}.$$

Using the binomial large deviations, see Lemma 2.3.3 on page 40 in Durrett (2007)

$$P(B_t) \ge 1 - \exp(-\gamma((q-\eta)/q)q|\hat{\xi}_t^A|), \qquad (2.6)$$

where  $\gamma(x) = x \log x - x + 1 > 0$  for  $x \neq 1$ . On  $G_t = \bigcap_{s=1}^t F_s$ ,  $|\hat{\xi}_t^A| \ge n^b$  and so

$$P(B_t|G_t) \ge 1 - \exp(-\gamma((q-\eta)/q)qn^b).$$

Since for  $t < \tau$ , we have  $|\hat{\xi}_t^A| < \epsilon_0 n$ , we can use Theorem 2 and the fact, that  $|U_t| \ge (q-\eta)n^b \ge n^b/(r-1)$  on  $G_t \cap B_t$ , to get

$$P(C_t|G_t \cap B_t) \ge 1 - \exp\left(-\frac{\eta}{2}\frac{n^b}{r-1}\log\frac{n(r-1)}{n^b}\right).$$

Combining these two bounds we get  $P(B_t \cap C_t | G_t) \ge 1 - \exp(-n^{b/2})$  for large n. Since  $\tau \le \epsilon_0 n - n^b$  on  $G_{\epsilon_0 n - n^b}$ ,

$$P\left(\tau > \epsilon_0 n - n^b\right) \le P(\bigcup_{t=1}^{\epsilon_n - n^b} F_t^c) \le (\epsilon_0 n - n^b) \exp(-n^{b/2}) \le \exp(-n^{b/4})$$

for large n and we get the result.

The next result shows that if there are  $\epsilon n$  particles at some time, then the dual survives for time  $\exp(cn)$ .

**Lemma 2.4.** If q(r-1) > 1, then there exists constants  $c, \epsilon_0 > 0$  such that for  $T = \exp(cn)$ and any A with  $|A| \ge \epsilon_0 n$ ,

$$P\left(\inf_{t\leq T} \left|\hat{\xi}_t^A\right| < \epsilon_0 n\right) \le 2\exp(-cn).$$

Proof. Choose  $\eta > 0$  so that  $(q - \eta)(r - 1 - \eta) > 1$ , and then choose  $\epsilon_0(\eta) > 0$  as in Theorem 2. For any A with  $|A| \ge \epsilon_0 n$ , let  $U'_t = \{x \in \hat{\xi}^A_t : x \text{ gives birth}\}$ . If  $|U'_t| \le \epsilon_0 n$ , then take  $U_t = U'_t$ . If  $|U'_t| > \epsilon_0 n$ , we have too many vertices to use Theorem 2, so we let  $U_t$  be the subset of  $U'_t$  consisting of the  $\epsilon_0 n$  vertices with smallest indices. Let

$$F_t = \{ |\hat{\xi}_t^A| \ge \epsilon_0 n \} \qquad G_t = \bigcap_{s=0}^t F_s$$
$$B_t = \{ \text{at least } (q - \eta) |\hat{\xi}_t^A| \text{ particles of } \hat{\xi}_t^A \text{ give birth} \}$$
$$C_t = \{ |U_t^*| \ge (r - 1 - \eta) |U_t| \}.$$

Now for  $t \ge 0$ ,  $F_{t+1} \cap G_t \supset B_t \cap C_t \cap G_t$ . Using our binomial large deviations result (2.6) again,  $P(B_t) \ge 1 - \exp(-\gamma((q-\eta)/q)q|\hat{\xi}_t^A|)$ . On the event  $F_t$ ,  $|\hat{\xi}_t^A| \ge \epsilon_0 n$ , and so  $P(B_t|G_t) \ge 1 - \exp(-\gamma((q-\eta)/q)q\epsilon_0 n)$ . Since  $|U_t| \le \epsilon_0 n$ , and on the event  $G_t \cap B_t$  $|U_t| \ge (q-\eta)\epsilon_0 n \ge \epsilon_0 n/(r-1)$ , using Theorem 2 we have

$$P(C_t|G_t \cap B_t) \ge 1 - \exp\left(-\frac{\eta}{2}\frac{\epsilon_0 n}{r-1}\log\frac{r-1}{\epsilon_0}\right)$$

Combining these two bounds  $P(F_{t+1}|G_t) \ge 1 - 2\exp(-2c(\eta)n)$ , where

$$c(\eta) = \frac{1}{2} \min\left\{\gamma\left(\frac{q-\eta}{q}\right)q\epsilon_0, \frac{\eta}{2}\frac{\epsilon_0}{r-1}\log\frac{r-1}{\epsilon_0}\right\}.$$

Hence for  $T = \exp(c(\eta)n)$ 

$$P\left(\inf_{t \le T} \left| \hat{\xi}_t^A \right| < \epsilon_0 n \right) \le P(\cup_{t=1}^T F_t^c) \le \sum_{t=0}^{T-1} P(F_{t+1}^c | G_t) \le 2 \exp(-c(\eta)n).$$

Lemma 2.4 confirms prolonged persistence for the dual. We will now give the

Proof of Theorem 1. Choose  $\delta \in (0, qr-1)$  and  $\gamma = (20 \log r)^{-1}$ . Define the random variables  $Y_x, 1 \leq x \leq n$ , as  $Y_x = 1$  if the dual process  $\{\hat{\xi}_t^{\{x\}}\}_{t\geq 0}$  starting at x satisfies  $|\hat{\xi}_{2\gamma \log n}^{\{x\}}| \geq n^b$  for  $b = \gamma \log(qr - \delta)$  and  $Y_x = 0$  otherwise. By Lemma 2.2, if n is large then  $EY_x \geq \rho - \delta$  for any x.

If we grow the cluster starting from x in a breadth-first search then all the vertices at distance  $\leq 2\gamma \log n$  from x are in the cluster of size  $n^{2\gamma \log r} \leq n^{1/10}$ . So if  $A_{x,z}$  is the event that the clusters of size  $n^{1/10}$  starting from x and z do not intersect, then

$$P(Y_x = 1, Y_z = 1) - P(Y_x = 1)P(Y_z = 1) \le P(A_{x,z}^c) \le n^{-4/5}$$

by Lemma 2.1. Using this bound,

var 
$$\left(\sum_{x=1}^{n} Y_x\right) \le n + n(n-1)n^{-4/5},$$

and Chebyshev's inequality shows that as  $n \to \infty$ 

$$P\left(\left|\sum_{x=1}^{n} (Y_x - EY_x)\right| \ge n\delta\right) \le \frac{n + n(n-1)n^{-4/5}}{n^2\delta^2} \to 0$$

Since  $EY_x \ge \rho - \delta$ , this implies

$$\lim_{n \to \infty} P\left(\sum_{x=1}^{n} Y_x \ge n(\rho - 2\delta)\right) = 1.$$
(2.7)

Choose  $\eta > 0$  so that  $(q - \eta)(r - 1 - \eta) > 0$ . Let  $\epsilon_0$  and  $c(\eta)$  be the constants in Lemma 2.4. Now if  $Y_x = 1$ , Lemma 2.2 shows that  $|\hat{\xi}_{T_1}^{\{x\}}| \ge n^b$  for  $T_1 = 2\gamma \log n$ . Combining the error probabilities of Lemmas 2.3 and 2.4, shows that within the next  $T_2 = \exp(c(\eta)n) + \epsilon_0 n - n^b$  units of time the dual process contains at least  $\epsilon_0 n$  many particles with probability  $\ge 1 - 2\exp(-n^{b/4})$  for large n.

Using the duality property of the threshold contact process we see that for any subset B of vertices

$$P(\xi_{T_1+T_2}^1 \supset B) = P\left(\hat{\xi}_{T_1+T_2}^{\{x\}} \neq \emptyset \; \forall x \in B\right)$$
  

$$\geq P\left(|\hat{\xi}_{T_1+T_2}^{\{x\}}| \geq \epsilon_0 n \; \forall x \in B\right)$$
  

$$\geq P(Y_x = 1 \; \forall x \in B) \cdot (1 - 2|B| \exp(-n^{b/4}))$$
  

$$\geq P(Y_x = 1 \; \forall x \in B) \cdot (1 - 2\exp(-n^{b/8})),$$

as  $|B| \leq n$ . Hence for  $T = T_1 + T_2$  using the attractiveness property of the threshold contact process and combining the last calculation with (2.7) we conclude that as  $n \to \infty$ 

$$\inf_{t \le T} P\left(\frac{|\xi_t^1|}{n} > \rho - 2\delta\right) = P\left(\frac{|\xi_T^1|}{n} > \rho - 2\delta\right)$$
$$\ge P\left(\xi_T^1 \supseteq \{x : Y_x = 1\}, \sum_{x=1}^n Y_x \ge n(\rho - 2\delta)\right) \to 1.$$

This completes the proof of Theorem 1.

### 3 Proof of Theorem 3

Recall the definition of m(A, K) given in (1.4). Let  $R = \log n / \log r$ ,  $a = (1/4 - \delta)$  and let  $\rho$  be the branching process survival probability defined in (1.1).

**Lemma 3.1.** If qr > 1 and  $\delta_0$  is small enough, then for any  $0 < \delta < \delta_0$  there are constants  $C(\delta) > 0$ ,  $B(\delta) = (1/4 - 2\delta) \log(qr - \delta) / \log r$  and a stopping time T satisfying

$$P\left(T < 2\exp\left(C(\delta)n^{B(\delta)}\right)\right) \le 3\exp\left(-C(\delta)n^{B(\delta)}\right)$$

such that for any A with  $m(A, 2aR) \ge (\rho - 2\delta)n^{B(\delta)}, \left|\hat{\xi}_T^A\right| \ge (\rho - 2\delta)n^{B(\delta)}.$ 

*Proof.* Let  $m_t = m(\hat{\xi}_t^A, 2aR)$ . We define the stopping times  $\sigma_i$  and  $\tau_i$  as follows.  $\sigma_0 = 0$ , and for  $i \ge 0$ 

$$\tau_{i+1} = \min\{t > \sigma_i : m_t < (\rho - 2\delta)n^B\},\\sigma_{i+1} = \min\{t > \tau_{i+1} : m_t \ge (\rho - 2\delta)n^B\}.$$

First we estimate the probability of the event  $E_i = \{m(\hat{\xi}_{\tau_i}^A, 2aR-2) \ge (q-\delta)(\rho-2\delta)n^B\}$ . Since  $\tau_i > \sigma_i$  for  $i \ge 1$ ,  $m_{\tau_i-1} \ge (\rho-2\delta)n^B$ , and hence there is a set S of size  $(\rho-2\delta)n^B$ such that any two vertices in S are 2aR apart. Using the binomial large deviation estimate (2.6), at least  $(q-\delta)(\rho-2\delta)n^B$  vertices of S will give birth at time  $\tau_i$  with probability  $\ge 1 - \exp(-\gamma((q-\delta)/q)q(\rho-2\delta)n^B)$ . If we choose one offspring from the vertices of Swhich give birth, then we have at least  $(q-\delta)(\rho-2\delta)n^B$  vertices at time  $\tau_i$  so that they are separated by distance 2aR - 2 from each other. So

$$P(E_i^c) \le \exp(-c_1(\delta)n^B), \tag{3.1}$$

where  $c_1(\delta) = \gamma((q - \delta)/q)q(\rho - 2\delta)$ .

On the event  $E_i$ ,  $\hat{\xi}^A_{\tau_i} \supseteq \zeta_i$  where  $|\zeta_i| \ge (q-\delta)(\rho-2\delta)n^B$  and all vertices of  $\zeta_i$  are distance 2aR-2 apart from each other.

Let  $A_x$  be the event that the cluster starting at x in  $\hat{G}_n$  does not intersect itself before reaching size  $n^{2a}$ . On the event  $A_x$ , as shown in Lemma 2.2,  $|\hat{\xi}_t^{\{x\}}| = Z_t^x$  for  $t \leq 2aR$ , where  $Z_t^x$  is a supercritical branching process with mean offspring number qr. Let  $B_x$  be the event of survival for  $Z_t^x$ ,  $P(B_x) = \rho > 0$  and  $F_x = \bigcap_{t=\delta R-2}^{aR-3} \{Z_{t+1}^x \geq (qr - \delta)Z_t^x\}$ . Using the error probability of (2.4)

$$P(F_x^c|B_x) \le \sum_{t=\delta R-2}^{aR-3} e^{-c'(\delta)t} \le C_{\delta} e^{-c'(\delta)\delta \log n/(\log r)} = C_{\delta} n^{-c'(\delta)\delta/(\log r)}$$

On the event  $B_x \cap F_x Z_{aR-2}^x \ge (qr - \delta)^{(a-\delta)R} = n^{(a-\delta)\log(qr-\delta)/\log r} = n^B$ . Hence for  $G_x = A_x \cap \{|\hat{\xi}_{aR-2}^{\{x\}}| \ge n^B\},$ 

$$P(G_x) \ge P(A_x \cap B_x \cap F_x) \ge P(B_x) - P(A_x^c) - P(F_x^c|B_x) \ge P(B_x) - \delta = \rho - \delta$$
(3.2)

for large enough n, as  $P(A_x) \ge 1 - n^{-4\delta}$  using Lemma 2.1.

Since each vertex of  $\zeta_i$  is 2aR - 2 apart from the other vertices of  $\zeta_i$ ,  $\hat{\xi}_t^{\zeta_i}$  is a disjoint union of  $\hat{\xi}_t^{\{x\}}$  over  $x \in \zeta_i$  for  $t \leq aR - 2$ . Let  $H_i$  be the event that there is at least one  $x \in \zeta_i$  for which  $G_x$  occurs. Then

$$P(H_i^c | E_i) \le (1 - \rho + \delta)^{|\zeta_i|} \le (1 - \rho + \delta)^{(q - \delta)(\rho - 2\delta)n^B} = \exp\left(-c_2(\delta)n^B\right), \quad (3.3)$$

where  $c_2(\delta) = (q - \delta)(\rho - 2\delta)\log(1/(1 - \rho + \delta)).$ 

If  $H_i \cap E_i$  occurs, choose any vertex  $w_i \in \zeta_i$  such that  $G_{w_i}$  occurs and let  $S_i = \hat{\xi}_{aR-2}^{\{w_i\}} = S_i$ . By the choice of  $w_i$ ,  $|S_i| \ge n^B$  and the clusters of size  $n^a$  starting from any two vertices of  $S_i$  do not intersect. So  $\hat{\xi}_t^{S_i}$  is a disjoint union of  $\hat{\xi}_t^{\{x\}}$  over  $x \in S_i$  for  $t \leq aR$ . Using (3.2)  $P(\hat{\xi}_{aR}^{\{x\}} \neq \emptyset) \geq \rho - \delta$ . We choose one vertex from  $\hat{\xi}_{aR}^{\{x\}}$  for each  $x \in S_i$  for which  $\hat{\xi}_{aR}^{\{x\}} \neq \emptyset$  to have a set  $W_i \subseteq \hat{\xi}_{aR}^{S_i}$ .

Let  $J_i$  be the event that there are at least  $(\rho - 2\delta)n^B$  vertices in  $S_i$  such that  $\hat{\xi}_{aR}^{\{x\}} \neq \emptyset$ . Using our binomial large deviation estimate (2.6)

$$P(J_i^c) \le \exp\left(-\gamma\left(\frac{\rho - 2\delta}{\rho - \delta}\right)(\rho - \delta)n^B\right) = \exp\left(-c_3(\delta)n^B\right).$$
(3.4)

So on the intersection  $E_i \cap H_i \cap J_i$  there is a set  $W_i \subset \hat{\xi}_{2aR-2}^{\{w_i\}}$  with  $|W_i| \ge (\rho - 2\delta)n^B$ , and each vertex of  $W_i$  is separated by a distance 2aR from other vertices of  $W_i$ . Hence using monotonicity of the threshold contact process  $\sigma_i \le \tau_i + 2aR$  on this intersection. So

$$P(\sigma_i > \tau_i + 2aR) \le P(E_i^c) + P(H_i^c | E_i) + P(J_i^c) \le 3\exp(-2C(\delta)n^B).$$

where  $C(\delta) = \min\{c_1(\delta), c_2(\delta), c_3(\delta)\}/2$ . Let  $K = \inf\{i \ge 1 : \sigma_i > \tau_i + 2aR\}$ . Then

$$P(K > \exp(C(\delta)n^B)) \ge \left[1 - 3\exp(-2C(\delta)n^B)\right]^{\exp(C(\delta)n^B)} \ge 1 - 3\exp(-C(\delta)n^B).$$

Since  $\sigma_i > \tau_i > \sigma_{i-1}$ ,  $\sigma_{K-1} \ge 2(K-1)$ . As  $|\hat{\xi}^A_{\sigma_{K-1}}| \ge (\rho - 2\delta)n^B$ , we get our result if we take  $T = \sigma_{K-1}$ .

As in the proof of Theorem 1, survival of the dual process gives persistence of the threshold contact process.

Proof of Theorem 3. Let  $0 < \delta < \delta_0$ ,  $\rho$ ,  $a = (1/4 - \delta)$  and  $B = (1/4 - 2\delta) \log(qr - \delta)/\log r$ be the constants from the previous proof. Define the random variables  $Y_x$ ,  $1 \le x \le n$ , as  $Y_x = 1$  if the dual process  $\hat{\xi}_t^{\{x\}}$  starting at x satisfies  $m(\hat{\xi}_{2aR-2}^{\{x\}}, 2aR) \ge (\rho - 2\delta)n^B$  and  $Y_x = 0$  otherwise.

Consider the event  $G_x$  as defined in Lemma 3.1. For large n,  $P(G_x) \ge P(B_x) - \delta = \rho - \delta$ . If  $G_x$  occurs, then  $|\hat{\xi}_{aR-2}^{\{x\}}| \ge n^B$  and clusters starting from any two vertices of  $\hat{\xi}_{aR}^{\{x\}}$  do not intersect until their size become  $n^a$ . Using arguments that led to (3.4)

$$P(m(\hat{\xi}_{2aR-2}^{\{x\}}, 2aR) < (\rho - 2\delta)n^B | G_x) \le \exp(-cn^B),$$

which implies that if n is large  $P(Y_x = 1) \ge \rho - 2\delta$ .

If we grow the cluster starting from x using a breadth-first search, then all the vertices at distance  $\leq 2aR$  from x are within the cluster of size  $n^{2a}$ . So if  $A_{x,z}$  be the event that the clusters of size  $n^{2a}$  starting from x and z do not intersect, then

$$P(Y_x = 1, Y_z = 1) - P(Y_x = 1)P(Y_z = 1) \le P(A_{x,z}^c) \le n^{-(1-4a)} = n^{-4\delta}$$

by Lemma 2.1. Using the bound on the covariances,

$$\operatorname{var}\left(\sum_{x=1}^{n} Y_x\right) \le n + n(n-1)n^{-4\delta},$$

and Chebyshev's inequality gives that as  $n \to \infty$ 

$$P\left(\left|\sum_{x=1}^{n} (Y_x - EY_x)\right| \ge n\delta\right) \le \frac{n + n(n-1)n^{-4\delta}}{n^2\delta^2} \to 0.$$

Since  $EY_x \ge \rho - 2\delta$ , this implies

$$\lim_{n \to \infty} P\left(\sum_{x=1}^{n} Y_x \ge n(\rho - 3\delta)\right) = 1.$$
(3.5)

If  $Y_x = 1$ ,  $m(\hat{\xi}_{T_1}^{\{x\}}, 2aR) \ge (\rho - 2\delta)n^B$ , for  $T_1 = 2aR - 2$ . Using Lemma 3.1, after an additional  $T_2 \ge 2 \exp(C(\delta)n^B)$  units of time, the dual process contains at least  $(\rho - 2\delta)n^B$  many particles with probability  $\ge 1 - 3 \exp(-C(\delta)n^B)$ . Using duality of the threshold contact process, for any subset S of vertices

$$P(\xi_{T_1+T_2}^1 \supset S) = P\left(\hat{\xi}_{T_1+T_2}^{\{x\}} \neq \emptyset \; \forall x \in S\right)$$
  

$$\geq P\left(|\hat{\xi}_{T_1+T_2}^{\{x\}}| \geq (\rho - 2\delta)n^B \; \forall x \in S\right)$$
  

$$\geq P(Y_x = 1 \; \forall x \in S) \cdot (1 - 3|S| \exp(-C(\delta)n^B))$$
  

$$\geq P(Y_x = 1 \; \forall x \in S) \cdot (1 - \exp(-n^{B/2})),$$

since  $|S| \leq n$ . Hence for  $T = T_1 + T_2$  using the attractiveness property of the threshold contact process, and combining the last calculation with (3.5) we conclude that as  $n \to \infty$ 

$$\inf_{t \le T} P\left(\frac{|\xi_t^1|}{n} > \rho - 3\delta\right) = P\left(\frac{|\xi_T^1|}{n} > \rho - 3\delta\right)$$
$$\ge P\left(\xi_T^1 \supseteq \{x : Y_x = 1\}, \sum_{x=1}^n Y_x \ge n(\rho - 3\delta)\right) \to 1,$$

which completes the proof of Theorem 3.

### References

Albert, R. and Othmer, H. G. (2003) The topology of the regulatory interactions predicts the expression pattern of the segment polarity genes in *Drosophila melanogaster*. Journal of Theoretical Biology, 223, 1–18

Athreya, K.B. (1994) Large deviations for branching processes, I. Single type case. Ann. Appl. Prob. 4, 779–790

Chaves, M., Albert, R., and Sontag, E.D. (2005) Robustness and fragility of Boolean models for genetic regulatory networks. *J. Theor. Biol.* 235, 431–449

Derrida, B. and Pomeau, Y. (1986) Random networks of automata: a simplified annealed approximation. *Europhysics Letters*, 1, 45–49

Durrett, R. (2006) Random Graph Dynamics. Cambridge University Press.

Flyvbjerg, H. and Kjaer, N. J. (1988) Exact solution of Kaufmann's model with connectivity one. *Journal of Physics A*, 21, 1695–1718

Kadanoff, L.P., Coppersmith, S., and Aldana, M. (2002) Boolean dynamics with random couplings. arXiv:nlin.AO/0204062

Kauffman, S. A. (1969) Metabolic stability and epigenesis in randomly constructed genetic nets. *Journal of Theoretical Biology*, 22, 437–467

Kauffman, S. A. (1993) Origins of Order: Self-Organization and Selection in Evolution. Oxford University Press.

Kauffman, S.A., Peterson, C., Samuelsson, B., and Troein, C. (2003) Random Boolean models and the yeast transcriptional network. *Proceedings of the National Academy of Sciences* 110, 14796–14799

Li, F., Long, T., Lu Y., Ouyang Q., Tang C. (2004) The yeast cell-cycle is robustly designed. *Proceedings of the National Academy of Sciences*, 101, 4781–4786.

Liggett, T. M.(1999) Stochastic Interacting Systems: Contact, Voter, and Exclusion Processes. Springer.

Nyter, M., Price, N.D., Aldana, M., Ramsey. S.A., Kauffman, S.A., Hood, L.E., Yli-Harja, O., and Shmuelivich, I. (2008) *Proceedings of the National Academy of Sciences*. 105, 1897–1900

Shmulevih, I., Kauffmann, S.A., and Aldana, M. (2005) Eukaryotic cells are dynamically ordered or critical but not chaotic. *Proceedings of the National Academy of Sciences*. 102, 13439–13444