Robustness of Attractor States in Complex Networks

Shu-ichi Kinoshita*, Kazumoto Iguchi† and Hiroaki S. Yamada**

*Graduate School of Science and Technology, Niigata University, Niigata 950-2181, Japan
†KazumotoIguchi Research Laboratory, 70-3 Shinhari, Hari, Anan, Tokushima 774-0003, Japan
**Yamada Physics Research Laboratory, Nishi-ku Aoyama 5-7-14, Niigata 950-2002, Japan

Abstract. We study the intrinsic properties of attractors in the Boolean dynamics in complex network with scale-free topology, comparing with those of the so-called random Kauffman networks. We have numerically investigated the frozen and relevant nodes for each attractor, and the robustness of the attractors to the perturbation that flips the state of a single node of attractors in the relatively small network ($N = 30 \sim 200$). It is shown that the rate of frozen nodes in the complex networks with scale-free topology is larger than that in the random Kauffman model. Furthermore, we have found that in the complex scale-free networks with fluctuations of in-degree number the attractors are more sensitive to the state flip of a highly connected node than to the state flip of a less connected node.

Keywords: Boolean dynamics; Attractor; Scale-free network; Intrinsic property; Robustness; Frozen nodes
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INTRODUCTION

Dynamics of Boolean networks is often used as a model for genetic networks inside cells, in which the genetic states are represented in terms of the language of attractors [1, 2]. A Boolean network consists of N nodes, each of which receives k_i inputs such that the degree is k_i. In the so-called *Kauffman model* – a random Boolean network (RBN) model, each node receives a certain fixed number of inputs such that the degree is $k_i \equiv K$.

In real systems each node has a different number of inputs, however. As a more realistic modeling of biological systems we expect that the fluctuation of the number of input-degree is treated as a random variable with a probability distribution function such as the inverse power-law distribution or the exponential distribution or the Poisson distribution. In fact, the in-degree distribution appears to be exponential in *E.coil* and to be power-law in yeast [3, 4, 5, 6, 7, 8, 9, 10, 11, 12].

Recently, the relationship between the Boolean dynamics and the network topology has been investigated by many authors from the view point of stability and evolvability of the network systems [10, 11, 12, 13, 14, 15, 16, 17]. They considered stability of the network dynamics when one node is noisily perturbed, and showed that the stability depends on the connectivity of nodes in a relatively small network $N = 19$ with scale-free topology.

In the present report, the number of in-degree k_i at the $i-$th node is determined by the preferential attachment rule that makes the system a complex network with scale-free topology (SFRBN)[9]. We do not deal with large networks(i.e. $N = 30 \sim 200$), focusing on the intrinsic properties of the Boolean dynamics on the complex networks. The details of the method for generating networks have been given in our previous paper [16]. As is numerically seen in the relatively small networks, the degree distribution functions $P(k)$ are not different from each other among networks with different topology. However, we would like to mention that the network size in our study is larger than the one used in the related previous studies by other researchers [10, 11, 12, 13, 14, 15, 16, 17], and that our study provides more details of the robustness of attractors and the frozen nodes in the attractors.

MODEL

The initial values for the nodes are chosen randomly and are synchronously updated in the time steps, according to the connectivity $\{k_i\}$ and the Boolean functions $\{f_i\}$ assigned for each node in the network as,

$$\sigma_i(t+1) = f_i(\sigma_{i_1}(t), \sigma_{i_2}(t), \cdots, \sigma_{i_{k_i}}(t)), \quad (1)$$

where $i = 1, ..., N$ and $\sigma_i \in \{0, 1\}$ is the binary state. All trajectories starting at any initial state run into a certain number of attractors(i.e. points or cycles). We study the directed RBNs, the directed SFRBNs, and the directed SFRBNs throughout this paper.

Figure 1 shows the time-dependence of the state which constitutes an typical attractor in the SFRBN with $\langle k \rangle = 2$.

Fig. 2(a) shows the histogram of the length ℓ_c of the attractors in the RBN with $K = 2$ and that in the SFRBN where the average degree of nodes $\langle k \rangle = 2$. Fig. 2(b) shows the median value $\bar{m}$ of the distribution of state cycle lengths with respect to N, the total number of nodes.

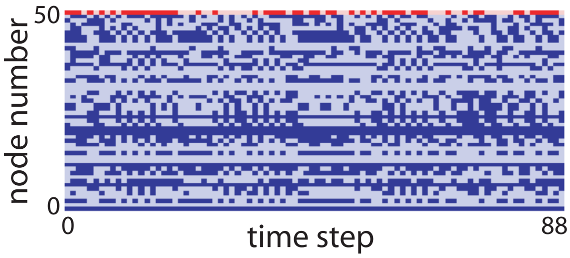

FIGURE 1. (Color online) Space-time diagram for an typical attractor with $\ell_c = 88$. in the SFRBN with $\langle k \rangle = 2$. The vertical axis denotes the node number that is in the high connectivity order. The dense or gray color corresponds to the binary values of the state. The static nodes of the attractor are frozen nodes. The network size is $N = 50$.

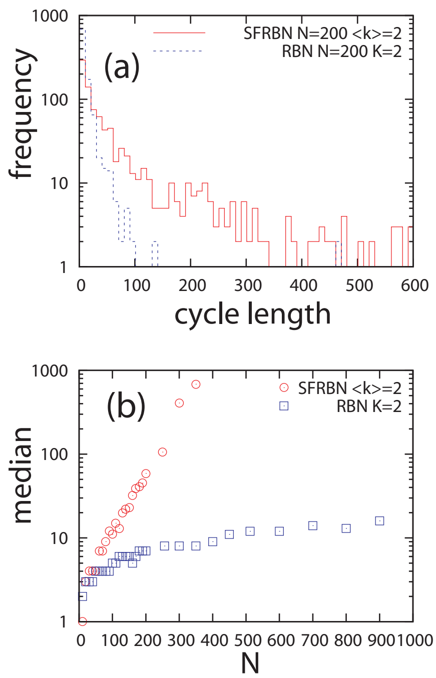

FIGURE 2. (Color online) (a) Histogram of the length ℓ_c of state cycles is shown for the RBNs and the SFRBNs, respectively, where the network size is $N = 200$. Each histogram is generated by 10^3 different sets of the Boolean functions and five different network structures. The maximum iteration number of the Boolean dynamics is 10^5 until the convergence to the cycle is realized. (b) Semi-log plots of the median value $\bar{m}$ of 1000 samples of the lengths of the state cycles with respect to the total number N of nodes for the directed RBNs and SFRBNs.

Apparently, the distribution of the attractor lengths in the SFRBN is much wider than that in the RBN, and the attractor length has longer period than that in the RBN. This is directly related to the diversity of attractors in the SFRBNs, which is of great importance for the stability of living cells. We investigated the function form $\bar{m}(N)$ in more detail in the previous paper [16], and found that the function form $\bar{m}(N)$ asymptotically changes from the algebraic type $\bar{m}(N) \propto N^{\alpha}$ to the exponential one as the average degree $\langle k \rangle$ goes to $\langle k \rangle = 2$.

Here we have a question: *How does the characteristics of the attractors depend on the network topology?* In the present paper we study the difference between attractors in the RBN and the SFRBN without a bias, focusing on the frozen nodes and the robustness of attractors against the external perturbations.

FROZEN NODES OF ATTRACTORS

In this section, we investigate the so-called frozen nodes of attractors whose values remain constant through a given trajectory of the attractors [2]. Frozen nodes arise through canalizing the Boolean functions and the homogeneity bias.

We count the number of frozen nodes N_f for each attractor and plot the histograms for some cases in Fig.3. The remarkably different peak structure exists between the cases in the SFRBN of $\langle k \rangle = 2$ and the RBN of $K = 2$. The distributions in the SFRBN have a peak around $N_f \sim N/2$, while the distributions in the RBN are broad with a peak at $N_f = N$. Note that $N_f = N$ corresponds to the point attractors that all nodes are frozen.

The fact that N_f is relatively smaller in the SFRBN would make the attractor period larger than that in the RBN, as seen in Fig.2. However, the role of the frozen nodes is not so clear in the network because all frozen nodes also are connected to the network and might influence the attractors. In the next section, we investigate the significance of each node in the respective attractor.

ROBUSTNESS OF ATTRACTORS TO STATE FLIP

One of the important properties in the scale-free topology is the existence of the highly connected hub node as seen in the yeast synthetic network and so on. In this section, we investigate the robustness of attractors to an external perturbation caused by an inversion of the binary state of a single node. We consider an attractor of period ℓ_c and flip the state of the single node at time $t \in [1, \ell_c]$ as a perturbation. The perturbation to the trajectory of the attractor may leap from the trajectory of the original attractor to another one, i.e. the attractor shift. The high homeostatic stability implies low reachability among different attractors.

We investigate the probability R_s that the attractor remains in the original attractor under the inversion of the single node state [1, 18], which is the rate returning

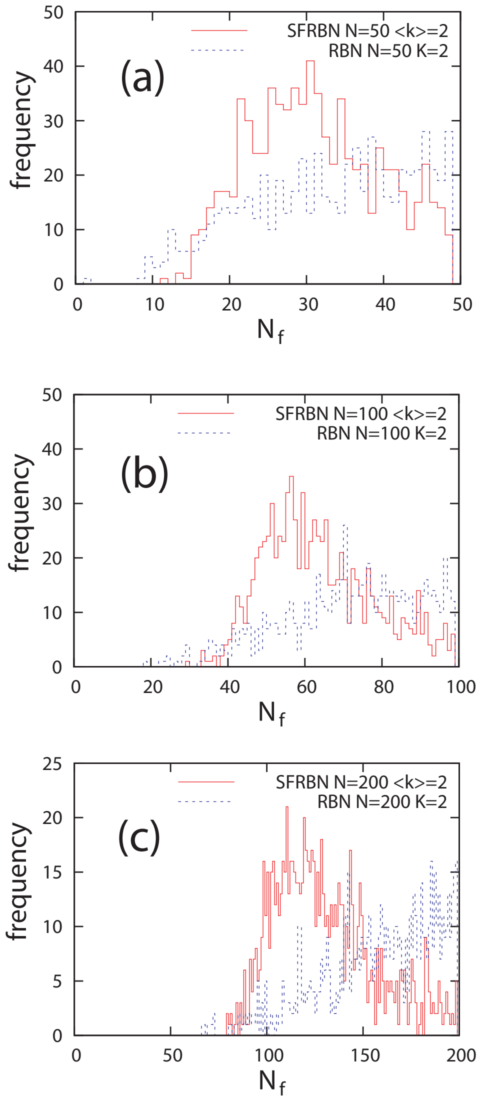

FIGURE 3. (a) Histograms of the number of frozen nodes N_f for 1000 attractors in the RBNs with $K = 2$ and the SFRBNs with $\langle k \rangle = 2$. The network size is (a) $N = 50$, (b) $N = 100$ and (c) $N = 200$. The scale out data at $N_f = N$ are not shown in the figures.

to the original attractor under the inversion. Here we call the rate the *robustness* of the attractor.

Figure 4 shows the robustness R_s of attractors with $\ell_c = 55$ in the SFRBN and $\ell_c = 48$ in the RBN, respectively. It follows that in the SFRBN the number of "active nodes" ($R_s < 1$) is much more larger than that in the RBN. On the other hand, in the RBN the perturbation to the active nodes influences effectively the shift of attractor ($R_s < 0.6$) although the number of active nodes is not so many [18]. As a result, in the SFRBN the perturbation to the highly connected hubs may give rise to the attractor shift, comparing with the one to the less connected

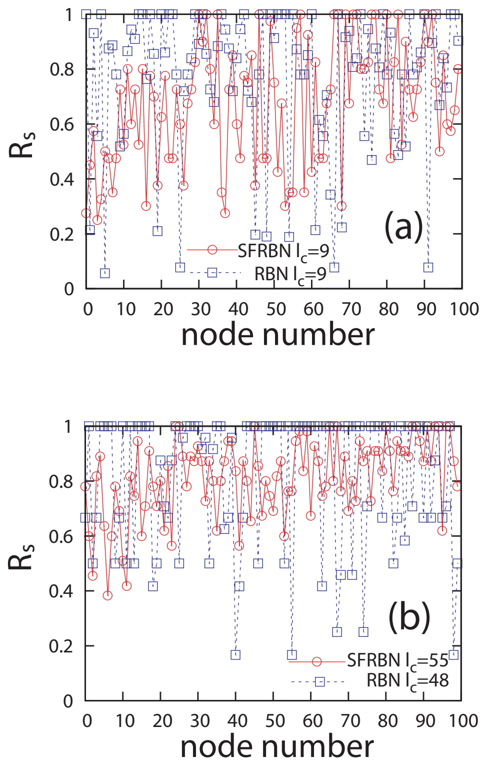

FIGURE 4. The rate R_s of returning to the original attractor as a function of numbered nodes in the order of the number of in-degree k_i. We used $N = 100$ in both the SFRBN with $\langle k \rangle = 2$ and the RBN with $K = 2$. The periods of the attractors are (a) $\ell_c = 9$ in the SFRBN and $\ell_c = 9$ in the RBN, (b) $\ell_c = 55$ in the SFRBN and $\ell_c = 48$ in the RBN, respectively. The horizontal axis denoted as "Node number" shows the node number in the order of the number of input-degree.

nodes.

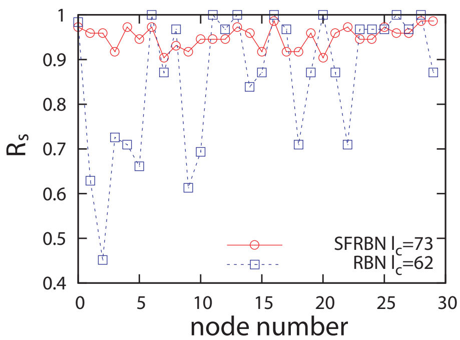

FIGURE 5. Robustness R_s for some attractors of the SFRBN with $\langle k \rangle = 4$ and the RBN with $K = 4$ in the network size of $N = 30$. The periods of attractors are $\ell_c = 73$ in the SFRBN and $\ell_c = 62$ in the RBN.

The robustness of some attractors in the SFRBN with $\langle k \rangle = 4$ and in the RBN with $K = 4$ is given in Fig.5. Although the whole structure is almost similar to that for the cases in Fig. 4, it is found that the effect of inversion of the single site state on the attractor shift is relatively small compared to the cases of $\langle k \rangle = 2$ and $K = 2$. There is a tendency that the attractors become more robust to the perturbation as the average number of input-degree $\langle k \rangle$ increases.

SUMMARY AND DISCUSSION

In summary, we have studied the Boolean dynamics of the Kauffman model with the directed SFRBN, comparing with the ones with the directed RBN for the relatively small network size. In this study we investigated some intrinsic properties of attractors between the RBNs and the SFRBNs, focusing on the frozen nodes and the robustness to a perturbation. The obtained results are as follows. (i) The number of frozen nodes in the SFRBN is smaller than that in the RBN and the property reflects on the much more widely distributed attractor lengths. (ii) The perturbation to the highly connected hubs may give rise to the attractor shift in comparison to the less connected nodes. (iii) The attractors becomes more robust to the perturbation as the average number of input degree $\langle k \rangle$ increases.

Although in this report we did not show the details of the attractor shifts by the perturbation, we will present the details of the numerical results for the diagram of transition among the attractors and the robustness to perturbation in our forthcoming paper [18].

Robustness against genetic mutations and environmental perturbations is one of the universal features of biological systems. And the robustness is important for understanding evolutionary processes and homeostasis of gene regulatory networks [18, 19, 20, 21, 22]. However, in this report we investigated only robustness to the single site inversion. For the purpose of the study, the other robustness of the SFRBN might become significant; for instance, robustness of attractors to the change of Boolean functions and to the breakdown of the network structures. We expect that such a study on the robustness of attractors provide some insights into important biological phenomena such as cellular homeostasis and apotosis.

Actually Aldana *et al* investigated the small SFRBN ($N \sim 15 - 20$) and found that the robustness of the ordered phase to the network damage in the SFRBN is lower than that in the RBN [19]. The result implies that there exists a possibility of evolution though mutation even in the ordered phase, despite of the Kauffman's conjecture that life evolves in "edge of chaos".

Moreover, recently, an interesting network model, the so called *feedback network* has been proposed by White *et al* [23]. The feedback networks can be a good model for describing the autocatalytic chemical reactions and the kinship, and so on, because the node selection, the search distance and the search path of networks are controlled by the attachment, the distance decay and the cycle formation parameters. It is interesting to investigate the features of the Boolean dynamics in the feedback networks from the point of view of frozen nodes and robustness [18].

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