Robustness during network evolution

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Abstract—**Robust networks can maintain their characteristics under perturbation, which is rooted in the different topology structure. However, previous study of the relationship between network robustness and topology structure is based on a static context. We study the effects of network topology on the network robustness from an dynamic points of view. We explore robustness to two types of perturbation on two categories of networks during network evolution to perform some pre-established function. We demonstrated that scale-free networks perform inferior to homogenous random graph on mutational robustness, which facilitates the evolutionary search to perform the target function; while they are superior on robustness of attractors to random graph, which demonstrates the higher tolerance to state inversion. These results may highlight the ubiquitous existence of scale-free topologies in nature.**

Index Terms—**Network Robustness, Boolean Network, Mutational Robustness, Attractor, Network Evolution, Evolutionary Algorithm**

I. INTRODUCTION

Network robustness has been largely attributed to its topology structure. It was demonstrated that a power-law distribution of connectivity, scale-free topology, is more tolerable against random failures but extremely vulnerable against selective attack[1]. However, this study is based on a static context. We address the relationship between network robustness and its topology structure using an evolutionary approach. We apply a simple evolutionary algorithm to evolve two categories of networks, homogenous random graphs and scale-free networks, to perform specific function, and investigate the robustness behavior respectively during the evolution process.

Since the introduction of the Random Boolean Networks(RBN) model in the lately 1960s[2],many researchers modified it to model real networks[3][4][5]. It has been widely used to successfully model central biological dynamical processes such as the cell cycle in yeast[6] and the expression of the polarity genes in *Drosophila* segments[7], and also applied to evolution and social models. In addition, Boolean Network (BN) has been used to model the robustness in specific real-world genetic regulatory systems[8][9][10][11][12]. It is natural to use BN to model the evolution of both categories of networks, and investigate the network robustness. We utilize the evolutionary model in [13], and explore the robustness behavior os homogenous random graph and scale-free network.

We measure the robustness of BN by two means: mutational robustness and the robustness of attractors. On the one hand, a network's mutational robustness is simply the fraction of its immediate neighbors in topology spaces that have the

same attractor given the same initial state as the original network[15][16]. On the other hand, robustness of Boolean networks is linked to the long-term behavior of the networks, which is defined by the attractors[9][17][18]. As the attractors represent the steady states of Boolean networks, it is essential to study the robustness of the attractors when concerning the robustness of the networks[19].

In out study, we demonstrated that scale-free networks perform inferior to homogenous random graph on mutational robustness, which facilitates the evolutionary search to perform the target function; while they are superior on robustness of attractors to random graph, which demonstrates the high tolerance to noise. These results may highlight the ubiquitous existence of scale-free topologies in nature.

The paper is organized as follows. Section 2 gives formal definitions of Boolean Network models, and the different topology of BNs. In Section 3 we briefly outline the evolutionary algorithm to drive the network evolution, and the method to evaluate the fitness value of BNs. Section 4 presents the robustness measures of BNs and our simulation results are given in Section 5. Finally, in Section 6 we conclude the paper and discuss our further investigations into the robustness during network evolution.

II. BOOLEAN NETWORK MODELS

A Boolean Network consists of N nodes, $\sigma_1, \sigma_2, \ldots, \sigma_N$, each of which may take the values 0 or 1, representing the active and the inactive state, respectively. A node σ_i has $k_i(k_i \leq N)$ parent nodes $\sigma_{i1}, \ldots, \sigma_{ik_i}$, with $\{\sigma_{i1}, \ldots, \sigma_{ik_i}\} \subset \{\sigma_1, \ldots, \sigma_N\}$. The value of σ_i at time $t+1$ is determined by its parent nodes at time t through a Boolean function

$$\sigma_i = f_i(\sigma_{i1}, \ldots, \sigma_{ik_i}) \tag{1}$$

Once each node $\sigma_i(1 \leq i \leq N)$ has been provided with an initial state, the network dynamics are then given by the simultaneous updating of all the nodes of the network. The Boolean function used in out study is

$$\sigma_i(t+1) = \begin{cases} 0, & \text{if } \sum_{j=1}^{N} w_{ij}\sigma_j(t) < 0 \\ 1, & \text{if } \sum_{j=1}^{N} w_{ij}\sigma_j(t) > 0 \\ \sigma_i(t), & \text{if } \sum_{j=1}^{N} w_{ij}\sigma_j(t) = 0 \end{cases} \tag{2}$$

Starting from an initial state, the network will eventually reach an equilibrium state $\{S(1), S(2), \ldots, S(z)\}$, called an attractor cycle that it will cycle through each state endlessly, where $S(i)(1 \leq i \leq z)$ is a N-dimensional binary vector representing the i-th state of the network.

In homogeneous random networks, the number of connections per node, k, is Poisson distributed $P_{rand}(k) = e^{-\langle K \rangle} \langle K \rangle^k / k!$. The mean connectivity $\langle K \rangle$ is the relevant topological parameter to characterize the random network architecture. Conversely, the topology of scale-free networks is heterogeneous and the number of connections per node is power-law distributed $P_{SF}(k) = k^{-\gamma} / \sum_{k=1}^{\infty} k^{-\gamma}$, where the associated topological parameter is the degree exponent γ. Scale-free networks here have both in-degree and out-degree distributions that are power-law distributed.

III. EVOLUTION OF BNs

In the model of this study, a simple evolutionary algorithm is used to drive the evolution of networks towards a pre-established target function which is random chose and kept fixed throughout the evolutionary run.

During an evolutionary run, each network has a fixed output node which is randomly selected when the network is generated. After the network reaches its attractor given random initial states, the values of the output node form a time series which we define as the function of the network. And the fitness function is defined as the hamming distance of the function of the network and the target function. With certain mutations to weight, the distribution of incoming connections remains fixed such that homogenous random networks still remain random during the evolution and vice versa, but the network's function is changed. We select those networks with high fitness value, and then apply mutations on them to produce offsprings. No crossover is used during evolution.

A. Mutation

A variety of mutations are applied on the network topology. At each generation we mutate each node of each network in the population with fixed rate μ so that the expected number of mutations in each network is μN, where N is the size of the network. For each mutative process we randomly choose a node, and we either change one of its input connections or its weight in the associated updating rule. For such mutations the distribution of incoming connections remains unaltered, so that a population of networks that starts as scale-free (random) remains scale-free (random) throughout an evolutionary run. On the other hand, the distribution of outgoing connections can change. For random populations the final distribution of outgoing connections is identical to the initial one, whereas for scale-free populations the distribution evolves as it would if there were only random mutations without any selection.

B. Fitness evaluation

To calculate the fitness for each network, the nodes states are updated according to the dynamical rules until the networks falls within an attractor. The fitness of each network is defined using the hamming distance of the network's function to the pre-established target function:

$$F = max\{1 - \frac{1}{L \cdot L_c} \sum_{k=1}^{L \cdot L_c} |\sigma(t_k) - \sigma_{target}(t_k)|\}. \quad (3)$$

With this definition, the fitness value is between 0 and 1, and it will be 0.5 when the networks are randomly chosen and 1 for a network the function of which exactly matches the target function.

The maximum is calculated over all cyclic permutations of the target function. The sum on the right-hand side is the time average of the distance between the output node and a given target function during the cycle of the network. The sum is taken over $L \cdot L_c$, where L_c is the length of the target and L is the cycle length of the whole network.

C. Selection

Initially a population of N_{pop} networks that have either a homogeneous random (with a fixed patameter $\langle K \rangle$) or heterogeneous scale-free topology (with a fixed parameter γ) is randomly generated. Then we increase the size of the population to include both the non-mutated parent networks and the mutated offspring. Each network from the population will have an offspring of three mutated networks. The size of the population will then be $M = (3 \text{ mutants} + 1 \text{ parent})N_{pop}$. After that, a new generation of N_{pop} networks that have the highest fitness among the non-mutated parent networks and the mutated offspring is selected for the new generation.

IV. ROBUSTNESS MEASURE

We utilize two robustness measures in out study: mutational robustness and the robustness of attractors.

A. Mutational robustness of Boolean Network

A Boolean Network's mutational robustness R_μ is the fraction of its immediate neighbors in topology that have the same attractor with the original network given one initial state.

To calculate the mutational robustness of a Boolean Network, we perturb the weight w_{ij} between the node σ_i and σ_j to a random value for several times. Given the same initial state of the original network, we test if it reaches the same attractor. For all node pairs (σ_i, σ_j) $(1 \leq j < i \leq N)$, we do perturbations on the weight w_{ij}, and get the returning number N_μ. The mutational robustness can be calculated as follows:

$$R_\mu = \frac{N_\mu}{\binom{N}{2}} \quad (4)$$

B. Robustness of attractors

The robustness of attractors can be measure by external perturbation of an inversion of the binary state of one or more nodes.

Given an initial state of each node of a BN, the network states will falls into an attractor $\{S(1), S(2), \ldots, S(z)\}$ eventually. The length of the attractor is z, which means that there are z steps to return to the original state. For each state belonging to the attractor, we invert the binary state of one node $\sigma_i(1 \leq i \leq N)$ in the network as a single-node perturbation at a time $t_j(1 \leq j \leq z)$. Such a perturbation does not alter the topology structure of the BN and has no influence on its steady-state properties; however, it does affect the network dynamics by replacing the original time trajectory
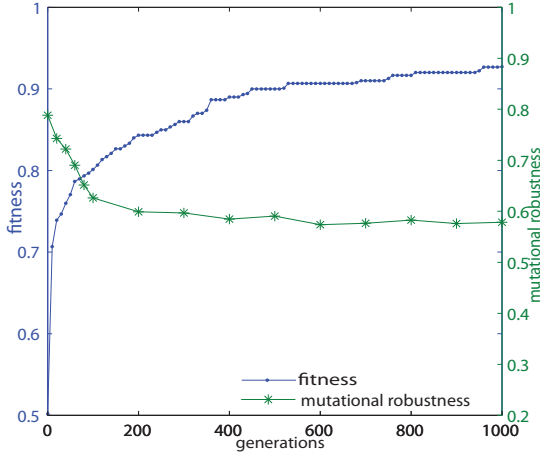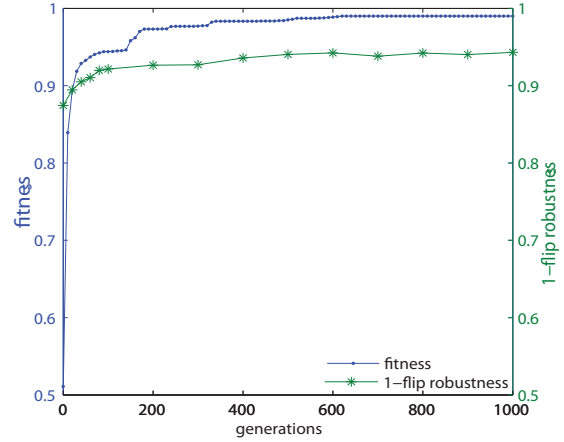
(a) Fitness and mutational robustness of Random Graph
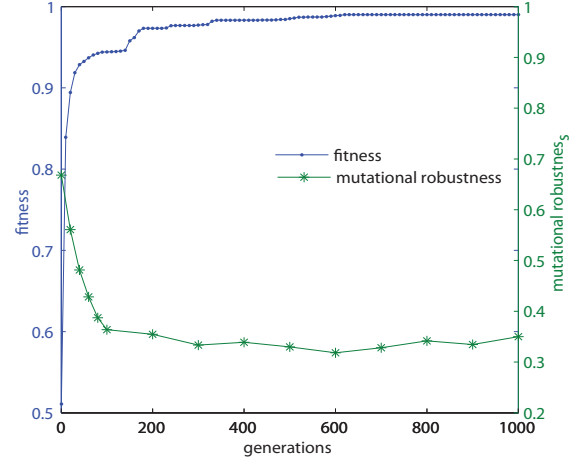
(b) Fitness and mutational robustness of Scale-free Network
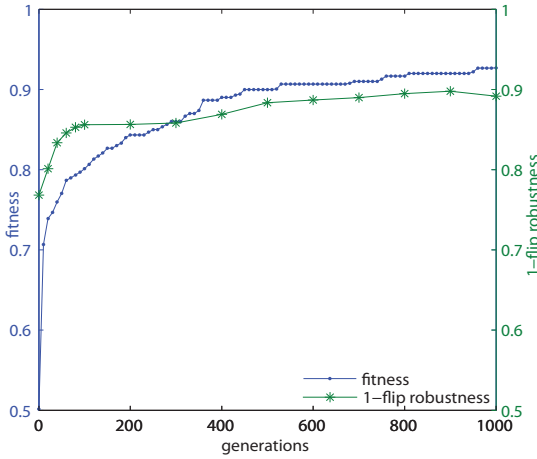
(c) Fitness and 1-flip robustness of Random Graph

(d) Fitness and 1-flip robustness of Scale-free Network

Fig. 1: The evolutionary path of Random Graph and Scale-free Network. The parameter is $\langle K \rangle = 1.9$ for Random Graph and $\gamma = 2.5$ for Scale-free Network. The network size is $N = 50$.

with a new trajectory. If the new trajectory converges to the original attractor after the perturbation, then it is desirable that the BN be stable or dynamically robust, meaning that it has a tendency to resist disturbance of the state and converge to its original attractor.

Repeat single-node inverting on all the nodes and all the states of the attractor, we get the returning number N_{attr1}, which is the number of perturbations that doesnot cause the shift of network's attractor. We define the returning rate of single-node inversion R_{n1} as the robustness of attractors to node inversion (1-flip robustness):

$$R_{n1} = \frac{N_{attr1}}{N \cdot z} \qquad (5)$$

where N is the network size, and z is the attractor length. Similarly, we can define the double-node inversion returning rate R_{n2} which stands for the robustness of attractors to

double-node inversion (2-flip robustness) of all the states in the attractor

$$R_{n2} = \frac{N_{attr2}}{\binom{N}{2} \cdot z} \qquad (6)$$

where N_{attr2} is the returning number with double-node inversion of all the states in the attractor.

V. RESULT

A. Evolutionary path of fitness and robustness

When evolving to perform specific target function, homogeneous random graph and scale-free network exhibit drastically different evolutionary path of fitness and robustness (Fig 1). From Fig 1.a and Fig 1.b, we can see that homogenous random graph evolve by sparse punctuated steps, and scale-free network evolve rapidly and continuously[13]. Furthermore, we
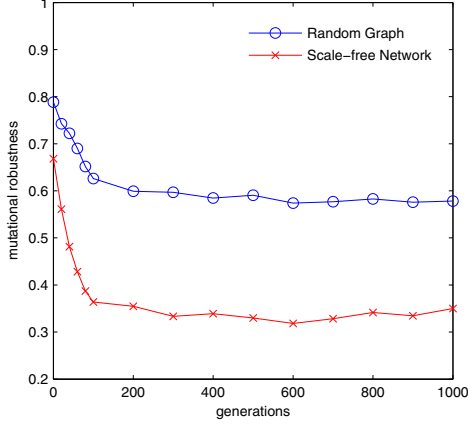
Fig. 2: Mutational robustness comparison between Random Graph with $\langle K \rangle = 1.9$ and Scale-free Network with $\gamma = 2.5$. The network size is $N = 50$.

found that the fitness value had a very strong negative relationship with the mutational robustness for both two categories of networks. For random graph, the fitness value increases very slowly, while the mutational robustness decrease slowly. However, for scale-free network, the mutational robustness decrease very quickly to some extent while its fitness increase quickly. At the same time, the robustness of attractors of both types of networks increase during the evolution.

B. Mutational robustness

Figure 2 shows a representative mutational robustness performance during an evolutionary run of homogenous random graph with $\langle K \rangle = 1.9$ and scale-free network with $\gamma = 2.5$, such that networks of both categories have the same number of average connections $\langle K \rangle$ and the same number of nodes N. The data is an averaged value of 50 independent evolutionary run. Before evolution, homogenous random graphs have an average value 0.8 of mutational robustness, while scale-free networks only have average value with 0.68. In the beginning several hundreds generations, both homogenous random graph and scale-free networks' performance decrease to certain value, and then fluctuate during that value, while scale-free network decrease more than random graph. The inferior performance of scale-free network suggests that one weight perturbation have more tendency to produce offsprings with new attractors than random graph, thus the mutation on scale-free networks produce offsprings with more different attractors, which facilitates the evolutionary search of networks to perform specific target functions. The conclusion is in accordance with those in [13], which states that scale-free networks evolves rapidly and continuously, and homogenous random graphs require a specific tuning of their connectivity to optimize their ability to evolve.
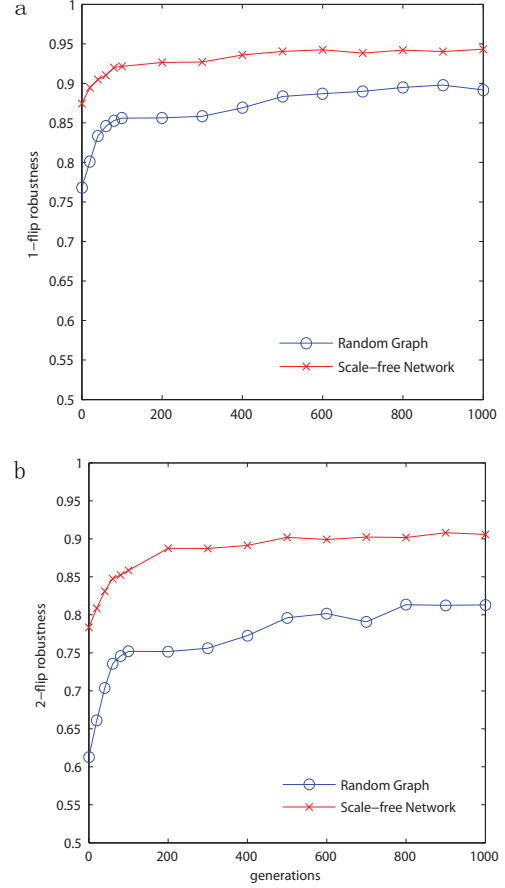

Fig. 3: Robustness of attractor comparison. (a) 1-flip robustness. (b) 2-flip robustness. Random Graph with $\langle K \rangle = 1.9$ and Scale-free Network with $\gamma = 2.5$. The network size is $N = 50$.

C. Robustness of attractors

Fig 3 shows the robustness of attractor performance during network evolution of homogenous random graph and scale-free network.

For 1-flip robustness (Fig 3.a), before the evolution, the scale-free network performance better than random graph. In the few hundreds generation during evolution, the 1-flip robustness of both the two type of networks increase rapidly to a summit. Then the robustness value fluctuate around the summit. However, the scale-free Network is still superior to Random Graph after evolution on 1-flip robustness. This illustrates that the scale-free network is more robust to state perturbation, one node state inversion is less likely to cause the network attractor moving to a new one, which suggests higher tolerance of state inversion of scale-free network to random graph.

We got similar results of 2-flip robustness (Fig 3.b). The only difference is that 2-flip robustness of both types of networks is less than the 1-flip robustness counterpart.

VI. Summary and discussion

In this article, we investigate the robustness performance of homogenous random graph and heterogenous scale-free network during evolution to perform a pre-established target function. Due to the evolutionary search for attractors whose fitness equals 1, both categories of networks' mutational robustness decreased. However, the scale-free networks perform inferior to homogenous random graphs so that scale-free networks evolves rapidly and continuously while random graph evolves slower. Furthermore, the performance of scale-free networks on robustness of attractors to state inversion is superior to homogenous random graph. More adaptable to new environments, and more robust to maintain its attractors, this may highlight the ubiquitous existence of scale-free topologies in nature.

Since biological networks are modular with a design that can be separated into units that perform almost independently, it has been demonstrated that modularly varying goals lead to the spontaneous evolution of modular network structure and network motifs[20]. We would like to investigate the different evolutionary path of homogeneous random graph and scale-free network to modularly varying goals. We are also interested in the different robustness performance and quantity of network motifs of the two categories of networks during their evolution to modular varying goals.

References

[1] R. Albert, H. JeongH and A.-L. Barabási. Attack and error tolerance of complex networks. *Nature* 406:378-382, 2000.

[2] S. Kauffman. Metabolic stability and epigenesis in randomly constructed genetic nets. *Journal of Theoritical Biology*, 22:437-467, 1969.

[3] S. Kauffman, C. Peterson, B. Samuelsson and C. Troein. Genetic networks with canalyzing Boolean rules are always stable. *Proceedings of the National Academy of Sciences of the USA*, 101(49):17102-17107, 2004.

[4] M. Aldana. Boolean dynamics of networks with scale-free topology. *Physica D*, 185(1):45-46, 2003.

[5] I. Shmulevich, H. Lahdesmaki, E. Dougherty, J. Astola, and W. Zhang. The role of certain Post classes in Boolean network models of genetic networks. *Proceedings of the National Academy of Sciences of the USA*, 100(19):10734-10739, 2003.

[6] F. Li, T. Long, Y. Lu, Q. Ouyang and C. Tang. The yeast cell-cycle network is robustly designed, *Proceedings of the National Academy of Sciences of the USA*, 101(14):4781-4786, 2004.

[7] R. Albert, and H. Othmer. The topology of the regulatory interactions predicts the expression pattern of the segment polarity genes in Drosophila melanogaster. *Journal of Theoritical Biology* 223:1-8, 2003.

[8] S. Kauffman, C. Peterson, B. Samuelsson and C. Troein, Random Boolean network models and the yeast transcriptional network. *Proceedings of the National Academy of Sciences of the USA*, 100(25):14796-14799, 2003.

[9] C. Espinosa-Soto, P. Padilla-Longoria and E. Alvarez-Buylla. A gene regulatory network model for cell-fate determination during Arabidopsis thaliana flower development that is robust and recovers experimental gene expression profiles. *Plant Cell*, 16(11):2923-2939, 2004.

[10] M. Chaves, R. Albert and E.D. Sontag . Robustness and fragility of Boolean models for genetic regulatory network. *Journal of Theoritical Biology*, 235(3):431-449, 2005.

[11] M. Aldana and P.Cluzel. A natural class of robust networks. *Proceedings of the National Academy of Sciences of the USA* 100(15):8710-8714, 2003.

[12] K. Klemm and S. Bornholdt. Topology of biological networks and reliability of information processing. *Proceedings of the National Academy of Sciences of the USA*, 102(51):18414-18419, 2005.

[13] P. Oikonomou and P. Cluzel. Effects of topology on network evolution. *Nature Physics*, 2(8):532-536, 2006.

[14] S. Maslov and K. Sneppen. Specificity and Stability in Topology of Protein Networks. *Science*, 296:910-913, 2002.

[15] S. Ciliberti, O.C. Martin and A. Wagner. Innovation and robustness in complex regulatory gene networks. *Proceedings of the National Academy of Sciences of the USA*, 104(34):13591-13596, 2007.

[16] S. Ciliberti, O.C. Martin and A. Wagner. Robustness can evolve gradually in complex regulatory gene networks with varying topology. *PLoS Computational Biology*, 2007.

[17] G. Von Dassow, E. Meir, E.M. Munro and G.M. Odell. The segment polarity network is a robust developmental module. *Nature* 406, 188-192, 2000.

[18] I. Shmulevich, I. Gluhovsky, R.F. Hashimoto, E.R. Dougherty and W. Zhang. Steady-state analysis of genetic regulatory networks modelled by probabilistic Boolean networks. *Comparative and Functional Genomics*, 4(6):601-608, 2003.

[19] S. Kinoshita, K. Iguchi and H.S. Yamada, Robustness of Attractor States in Complex Networks. *AIP Conference Proceedings*, 982:768-771, 2008.

[20] Kashtan N, Alon U. Spontaneous evolution of modularity and network motifs. *Proceedings of the National Academy of Sciences of the USA*, 102(29):13773-13778, 2005.

[21] H. Kitano. Biological robustness. *Nature Reviews Genetics*, 5:826-837, 2004.

[22] A. Hintze, C. Adami and L.A. Meyers. Evolution of Complex Modular Biological Networks, *PLoS Computational Biology*, 4(2):e23, 2008.

[23] A. Esmaeili and C. Jacob. Evolution of discrete gene regulatory models, *Proceedings of the 10th annual conference on Genetic and Evolutionary Computation Conference* 2008.

[24] M. Aldana, E. Balleza, S. Kauffman and O. Resendiz. Robustness and evolvability in genetic regulatory networks, *Journal of Theoretical Biology*, 245(3):433-448, 2007.

[25] Y. Xiao and E.R. Dougherty, The impact of function perturbations in Boolean networks, *Bioinformatics*, 23(10):1265-1273, 2007.