Effects of community structure on the dynamics of random threshold networks

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Phys. Rev. E **87**, 012810 — Published 22 January 2013
DOI: 10.1103/PhysRevE.87.012810

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Random threshold networks (RTNs) have been widely used as models of neural or genetic regulatory networks. Network topology plays a central role in the dynamics of these networks. Recently it has been shown that many social and biological networks are scale-free and also exhibit community structure, in which autonomous modules are wired together to perform relatively independent functions. In this study, we use both synchronous and asynchronous models of RTNs to systematically investigate how community structure affects the dynamics of RTNs with scale-free topology. Extensive simulation experiments show that RTNs with high modularity have more attractors than those RTNs with low modularity and RTNs with smaller communities tend to have more attractors. Damage resulting from perturbation of initial conditions spreads less effectively in RTNs with higher modularity and RTNs with smaller communities. In addition, RTNs with high modularity can coordinate their internal dynamics better than RTNs with low modularity under the synchronous update scheme, and it is the other way around under the asynchronous update. This study shows that community structure has a strong effect on the dynamics of RTNs.

PACS numbers: Valid PACS appear here

I. INTRODUCTION

Boolean networks have been widely used to model the dynamic properties of complex networks such as biological networks, neural networks, ecological networks, and social networks [1–4]. In Boolean networks, the nodes are characterized by two qualitative states, usually referred to as 1(ON) and 0(OFF), and each node updates its state based on its regulation by other nodes of the network. Random Boolean networks (RBNs) and random threshold networks (RTNs) are two representative types of Boolean networks wherein the regulatory relationships contain a large degree of randomness. In classical models of RBNs and RTNs, all nodes are synchronously updated at each time step, and thus the network dynamics are deterministic. Since the number of states of a Boolean network is finite, after a transient period the system will reach a steady state (also called fixed point) or a set of regularly recurring states called limit cycle, which are collectively referred to as attractors.

RBNs were initially introduced by Kauffman [1] and have been extensively studied since then [5–7]. The dynamics of a RBN falls into ordered, chaotic (disordered) and critical regimes. In the ordered regime, all the attractors of the network are fixed points (steady states) and the system is very robust against transient perturbation of individual nodes. In the chaotic regime the system is very sensitive to perturbations and even small perturbations can change the entire behavior of the system. The regime in between order and chaos is called critical; in this regime the system maintains a balance between robust behavior against the majority of random perturbations and flexible switching in response to select perturbations. It has been shown that many topological and state parameters, such as node indegree (the number of inputs), degree distribution, and expression bias in lookup tables, determine the dynamic regimes of random Boolean networks [5, 7–9].

RTNs were initially proposed as artificial neural network models [2] and have also been studied in the context of spin glasses [10]. RTNs also exhibit a rich range of dynamics with a transition between frozen and chaotic phases. The criticality of random threshold dynamics has been extensively studied as well [11–16]. The parameters that affect the dynamical regimes of RTNs include node indegree, activation thresholds, and connection weights [15, 18]. Threshold networks have been used to model yeast cell-cycle regulation and ecological community assembly and yielded important biological insights [4, 19]. Zañudo et al. studied the dynamical properties of RTNs with different node indegrees, activator-repressor proportions, activator-repressor strengths and different thresholds, and identified the set of parameters that lead to networks that show dynamical properties observed in biological systems [20].

Many empirical networks exhibit a scale-free topology [21], i.e., the degrees of nodes are heterogeneous and follow a power-law distribution. In addition to this scale-free nature, recently it has been shown that most social and biological networks also have a modular or community structure, in which relatively autonomous modules are wired together [22, 23]. Communities are typically densely connected internally but sparsely connected to the rest of the network. There are several quantitative definitions for communities which compare the numbers of internal and external edges [24, 25]. As the heterogeneity of node degree, the sizes of communities are also heterogeneous and vary in a rich range. It is hypothesized that community structure has significant effects on the dynamics and stability of Boolean networks; however this question has not been studied systematically.

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Poblanno-Balp and Gershenson studied coupled RBNs with multiple modules and increased the number of links between modules to see how modularity affects the dynamics of the RBNs [26]. Their model simulates different modularity by changing the links between modules and inside modules, but the degree of each node may not be conserved and iterations of the network may not satisfy the definition of having a community structure when considered separately. In addition, their networks do not possess scale-free nature, and thus may not represent the real topological properties of social and biological networks.

To date there have not been any studies on coupled threshold networks and on modular RTNs. The effects of community structure on the dynamics of RTNs have not been investigated yet. In addition, most studies on RTNs are based on the classical synchronous update scheme wherein the states of all nodes are updated simultaneously according to the last state of the system. This type of update implicitly assumes that the time scales of all events in the system are similar and the state transitions of nodes are synchronized, an assumption which may not be realistic for social networks and biological networks [27]. In contrast, asynchronous models can account for the presence of multiple time scales. It is not known whether the update schemes modulate the effects of community structure.

In this study, we use both synchronous and asynchronous models to systematically investigate how community structure affects the dynamics of RTNs with scale-free topology. First, we investigate the effect that community structure has on the number and length of attractors of RTNs by increasing the strength of network modularity and the size of communities. Then we describe damage spreading from multiple types of perturbations of initial conditions in RTNs with and without community structure. We also consider the effect of communities with varying strength and size on the ability of RTNs to coordinate their internal dynamics, measured by the mutual information of node pairs' state sequences. All of our results indicate the importance of community structure in the dynamics of RTNs.

II. METHODS

A. Models

A random threshold network (RTN) consists of N randomly interconnected nodes. Each node is characterized by a binary state variable $\sigma_i \in \{0, 1\}$. The transfer function of each node in RTNs is an additive sign function as follows:

$$\sigma_i^* = \psi\left\{\sum_{j=1}^{N} \omega_{i,j}\sigma_j + T_i\right\} \tag{1}$$

where * denotes the next state of node i. $\psi(x) = 1$ if $x > 0$, and $\psi(x) = 0$ if $x \le 0$. $\omega_{i,j}$ is the interaction weight between node i and node j. $\omega_{i,j} > 0$ represents that node j activates node i, $\omega_{i,j} < 0$ means that node j inhibits node i, and $\omega_{i,j} = 0$ indicates that node j does not directly regulate node i. T_i is the threshold parameter for node i, controlling how many signals are needed for the activation of this node. Although most studies on RTNs assume that $\omega_{i,j}$ take discrete integer values $\{-1, 1\}$ with equal probability and T_i are fixed and identical for all nodes, some studies investigate how interaction weights and inhomogeneous thresholds affect the phase transition of RTNs [15, 18]. In this study, we assume $\omega_{i,j} = 1$ with a probability p and set the threshold parameter T_i to be zero for all nodes.

In classic RTNs, the states of nodes are updated deterministically and synchronously, i.e., the state of each node i at time step $t + 1$ is determined by the states of its regulators at time step t:

$$\sigma_i(t+1) = \begin{cases} 1 & \text{if } \sum_{j=1}^{N} \omega_{i,j}\sigma_j(t) + T_i > 0, \\ 0 & \text{if } \sum_{j=1}^{N} \omega_{i,j}\sigma_j(t) + T_i \le 0. \end{cases} \tag{2}$$

In synchronous RTN models, the state trajectory from each initial condition is unique and deterministic. Synchronous models assume that the time scales of all events are identical and the state transitions of all nodes are synchronized, which may not be realistic for real-world networks [27–29]. Therefore, we also consider asynchronous RTN models which allow the presence of different time scales. There exist deterministic asynchronous schemes updating each node according to its fixed time scale [30], but stochastic schemes are better options if one is interested in general trends of dynamics. There are different stochastic asynchronous schemes wherein all nodes are updated according to a random order, or at each time step one randomly selected node is updated [29, 31]. In this study, we adopt a random order-based asynchronous model, i.e., at each time step, a node order is chosen uniformly at random from all possible permutations of the nodes, and the state of each node in the network is updated according to this order:

$$\sigma_i(t+1) = \begin{cases} 1 & \text{if } \sum_{j=1}^{N} \omega_{i,j}\sigma_j(t_j) + T_i > 0, \\ 0 & \text{if } \sum_{j=1}^{N} \omega_{i,j}\sigma_j(t_j) + T_i \le 0. \end{cases} \tag{3}$$

where $t_j \in \{t, t + 1\}$ denotes the most recent time step at which node j was updated, depending on its position in the order. This update method guarantees that each node is updated exactly once during each unit time interval. Because of the stochasticity of this asynchronous model, the network dynamics are not deterministic and the same initial condition can lead to different state trajectories.

B. Identification of attractors

A RTN with N nodes has a total of 2^N states, making up its state space. Since the number of the system states is finite, during its evolution from an initial condition the system's state sooner or later will reach an attractor, namely a fixed point or a set of recurring states called complex attractor. The number of states in an attractor is called the length of the attractor. For synchronous RTNs the set of recurring states is referred to as a limit cycle; the system traverses these states in a fixed order. Since fixed points are time-independent, they are the same in both synchronous and asynchronous models of a RTN. In contrast, complex attractors can be different in deterministic and stochastic asynchronous Boolean models. Limit cycles present in the synchronous model of a RTN may disappear if asynchronous updating schemes are used. For asynchronous RTNs, the set of recurring states is alternatively referred to as a loose attractor since the system may oscillate irregularly within this set of states [29]. All the possible transitions among system states can be represented by a directed graph called state transition graph, wherein nodes are states of the system and edges denote the possible transitions among the states. State transition graphs of a RTN can be different under the synchronous and asynchronous models since update schemes affect the state trajectories of the system.

The state space of a RTN increases exponentially with the number of nodes in the network. Thus enumerating all attractors for a large RTN is a challenging problem under both synchronous and asynchronous schemes. As in other studies [4, 14, 26, 32], we adopt a procedure of randomly sampling initial conditions from which the system's state evolves until an attractor is reached. We find attractors by taking advantage of the properties of the state trajectories of synchronous and asynchronous models. In a synchronous model any system state can have only one successor in the state transition graph, which may be a different state or the same state again. Therefore, if the model reaches a state that has already appeared in the last time step, then this state must be a fixed point. If the model reaches a state that has already appeared in the current trajectory but not in the last time step, the set of states between these two repetitions of the state forms a limit cycle, as shown in FIG. 1(a). For our chosen asynchronous RTN model, the fixed points can be identified in the same way as for the synchronous scheme. Since one system state can have multiple successors in the state transition graph of an asynchronous RTN model, when the model reaches a state that already appeared in the current trajectory, it does not necessarily mean that a loose attractor is reached. However, if we run the model for sufficient time and the system stays in a set of recurring states, which form a strongly connected component without outgoing edges in the state trajectory, we can conclude that the model reached a loose attractor, as shown in FIG. 1(b). The number of time steps that the model needs to reach a fixed point or a complex attractor can be calculated straightforwardly.

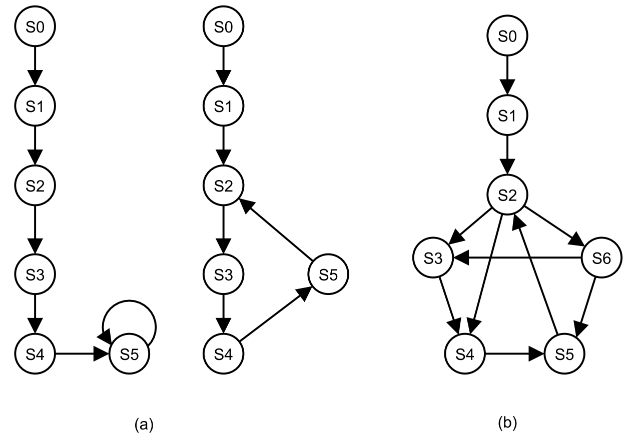

FIG. 1: Examples of state transitions in synchronous and asynchronous RTNs. (a) State transitions in synchronous RTNs. In the left subfigure S5 is a fixed point, and in the right subfigure {S2, S3, S4, S5} is a limit cycle. (b) State transitions in asynchronous RTNs. {S2, S3, S4, S5, S6} is a loose attractor.

C. Damage spreading and coordination of internal dynamics

One way to characterize the dynamic regime of a RTN is to measure its sensitivity to initial conditions, i.e., whether small differences in initial states lead to similar or different system states. This sensitivity analysis is similar to damage spreading and stability analyses of RTNs [9, 14]. We use both transient and permanent perturbations to study the effects of community structure on the damage spreading in RTNs. In transient perturbations, for each initial condition S_0 in a set of randomly sampled initial system states, an initial condition S_0', differing from S_0 in the state of one randomly chosen node, is generated and used for the subsequent simulation. In permanent perturbations, for each initial condition S_0, we randomly choose a node and maintain its state observed in S_0 permanently, and then generate another initial condition S_0', the same as S_0 but the node is kept in the opposite state permanently. The damage is measured by the Hamming distance between the two system states after a certain number of time steps. $\langle d \rangle$ is the average damage over the sampled set of initial system states and the ensemble of RTNs. When we examine the damage spreading under the asynchronous update scheme, we use the same sequence of node orders for unperturbed and perturbed initial conditions to rule out the effects of the stochasticity existing in asynchronous update.

The widely studied problem of synchronization of oscillators in complex networks [33, 34] led to the introduction of measures that quantify the coordination of a system's internal dynamics. For Boolean networks, the mutual information contained in the time series (state sequences) of two nodes measures how well their activities are coordinated [32, 35]. Let p_0 and p_1 be the probabilities of state 0 and state 1 respectively occurring in the time series $\Sigma_i = \{\sigma_i(0), \sigma_i(1), \sigma_i(2), ...\}$ of node i. Then the entropy of Σ_i, characterizing the state uncertainty in the time series, is defined as $H[\Sigma_i] = -p_0 \log_2 p_0 - p_1 \log_2 p_1$. The joint entropy of time series Σ_i and Σ_j, measuring the state uncertainty associated with the two time series, is defined as $H[\Sigma_i, \Sigma_j] = -p_{00} \log_2 p_{00} - p_{01} \log_2 p_{01} - p_{10} \log_2 p_{10} - p_{11} \log_2 p_{11}$, where p_{xy} is the probability of state pairs xy occurring in Σ_i and Σ_j, $x, y \in \{0, 1\}$, and $0 \log_2 0 = 0$ for the special case where any of the probabilities is zero.

In the above formulae, the probabilities can be estimated from the state sequences of nodes by running the dynamic model from all possible initial states for a very large number of time steps. However, this will be prohibitively time-consuming. Therefore, we again start from a set of randomly sampled initial conditions and run the model to a certain number of time steps. The probability p_x is estimated by the fraction of time steps for which the state of a node is x, and the probability p_{xy} is estimated by the fraction of time steps for which the state of node i is x and one time step later the state of node j is y. The mutual information of Σ_i and Σ_j, quantifying the dependency between the two time series, is defined as

$$I[\Sigma_i, \Sigma_j] = H[\Sigma_i] + H[\Sigma_j] - H[\Sigma_i, \Sigma_j].$$

For example, if the system reaches a fixed point right after an initial condition and the state sequences of node i and node j in the fixed point are $\Sigma_i = \{0, 0, 0, ...\}$ and $\Sigma_j = \{1, 1, 1, ...\}$, then $I[\Sigma_i, \Sigma_j] = 0$. If the system reaches a limit cycle and the state sequences of node i and node j in the limit cycle are $\Sigma_i = \{0, 1, 0, 1, ...\}$ and $\Sigma_j = \{1, 0, 1, 0, ...\}$, then $I[\Sigma_i, \Sigma_j] = 1$. $I[\Sigma_i, \Sigma_j]$ measures the extent to which information about node i at time t influences node j at time $t + 1$. It also reflects how well the activities of node i and node j are coordinated. The average of the mutual information over all pairs $\langle I \rangle$ measures the ability that the system can coordinate its internal dynamics. We study the effects of community structure on the coordination of internal dynamics of RTNs.

III. RESULTS

We used the software tool from [36] to generate directed scale-free networks with different community structure (modularity) (designated as mRTN hereafter). The software has a couple of parameters which allow users to generate different types of networks, including network size N, average indegree $\langle k_{in} \rangle$, mixing parameter μ (controlling the modularity of the networks), the exponent t_1 of the indegree distribution ($P(k_{in}) \sim k_{in}^{-t_1}$) and the exponent t_2 for the community size distribution ($P(C) \sim C^{-t_2}$), the minimum community size $C_{\min}$ and the maximum community size $C_{\max}$. We randomly choose the values of interaction weights such that the directed edges are activating with probability p and inhibitory with probability $1 - p$. Since we have observed that the conclusions (the relative relations between the results on shuffled RTNs and on modular RTNs) using $p = 0.3$ and $p = 0.7$ are similar to those using $p = 0.5$, we set $p = 0.5$ which means that $\omega_{i,j}$ was set to 1 or -1 with equal probability. To generate RTNs without modularity (designated as sRTN hereafter), we randomly shuffle the modular RTNs while keeping their degree distribution unchanged.

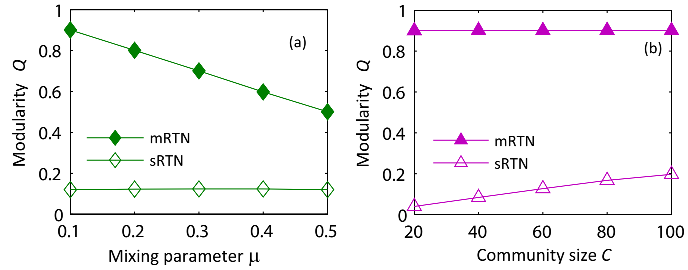

FIG. 2: Modularity of the generated directed networks. (a) The modularity of the model networks, and of their shuffled counterparts, for different mixing parameters. (b) The modularity of the model networks, and of their shuffled counterparts, with different sizes of communities.

In this study, we chose $N = 500$ which is large enough to consider the modularity of complex networks. We vary the mixing parameter μ from 0.1 to 0.5 to generate networks with decreasing modularity, keeping $t_1 = 2$, $t_2 = 1$, $C_{\min} = 20$ and $C_{\max} = 100$. In addition to modularity, we also examine the effects of community size on network dynamics. To do this, we keep a fixed mixing parameter ($\mu = 0.1$) and vary community size C from 20 to 100 (i.e., $C_{\min} = C_{\max} = 20, C_{\min} = C_{\max} = 40$, and so on). To investigate the effects of the heterogeneity of community size, we set $C_{\max} = 50$ for some simulations and compare the results with those using $C_{\max} = 100$. When we investigated the effects of community structure on the number of attractors of RTNs, we set $k_{in} = 2.0$ which allows the networks to be critical and have a fair amount of fixed points and complex attractors [12, 16–18, 32]. To study the effects of community structure on the damage spreading in RTNs and on the coordination of internal dynamics, we set $k_{in} = 5.0$ which is expected to take the networks into the chaotic regime [12, 16–18, 32]. For each set of parameters, we generate 100 networks and report the averaged results over the ensemble of 100 realizations.

FIG. 2 shows the modularity of the networks with $k_{in} = 2.0$, where the modularity was calculated using the modularity measure Q for directed networks [37] based on the community assignment of nodes. The figure confirms that increasing the mixing parameter induces a linear decrease in the network's modularity, whereas changing community sizes has no effect on the network's modularity. On the other hand, shuffled networks do not have significant modularity. The modularity of the networks with $k_{in} = 5.0$ is similar to that of the networks with $k_{in} = 2.0$.

The state space of RTNs increases exponentially with the number of nodes, thus it is impossible to check all initial conditions. We sample 1000 initial conditions and observe the behaviors of RTNs based on these sampled initial conditions. For the initial conditions, we randomly assign 0 or 1 with equal probability to each node. We run both synchronous and asynchronous models for 200 time steps unless noted otherwise.

A. Effects of community structure on attractors

We first run the RTN models described in the Methods section for 200 time steps which is large enough to reach attractors, and then examine the effects of introducing community structure into the network topology on the number of attractors. The number of fixed points and limit cycles of RTNs under the synchronous update scheme is shown in FIG. 3. The inset in the first panel of the figure is the result from sampling 10,000 initial conditions, confirming that 1000 initial conditions are sufficient to indicate the trends. We can see that RTNs with higher modularity (lower mixing parameter) tend to have more attractors. In contrast, the shuffled RTNs, which do not exhibit high modularity, have fewer attractors and significantly fewer limit cycles than RTNs with a distinct community structure. This is mainly because a RTN with distinct community structure behaves as a collection of weakly coupled community RTNs. The attractors of these relatively independent community RTNs combine in different ways to form the attractors of the whole RTN. For RTNs with high modularity, less initial conditions lead to fixed points and more lead to limit cycles, while for RTNs with low modularity, more initial conditions lead to fixed points than those leading to limit cycles. This may be because, although the average indegree of a RTN without modularity is not large enough to lead the system to the chaotic phase, the relatively independent modules in a RTN exhibiting highly modular structure can be chaotic because of the high indegree of nodes inside modules, and thus the whole RTN has many limit cycles caused by the combination of limit cycles of the modules. The number of time steps that the models need to reach a fixed point or a limit cycle does not show a clear trend with respect to the modularity of the networks (data not shown). In addition, RTNs with distinct community structure tend to have longer limit cycles than RTNs without community structure, supporting the conclusion that these limit cycles are combinations of the individual communities' limit cycles. The above results indicate that community structure in network topology does affect the criticality of random threshold dynamics.

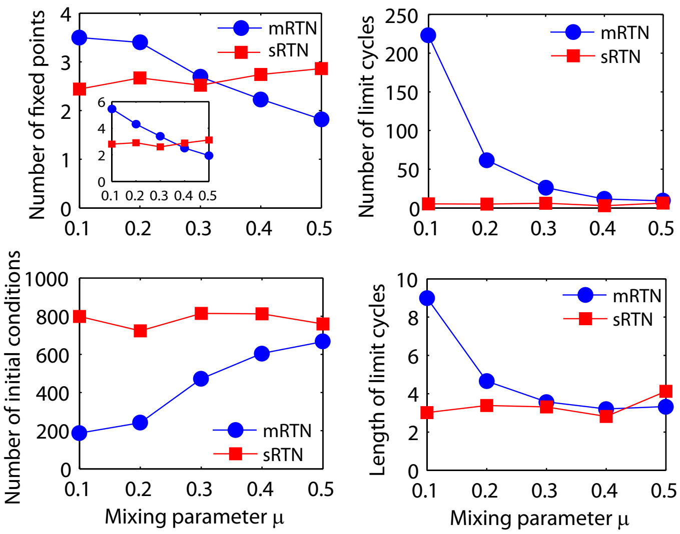

FIG. 3: Attractors of RTNs with different modularity under the synchronous update scheme. The inset in the first panel is the number of fixed points based on 10,000 initial conditions. The third panel gives the number of initial conditions leading to fixed points; the number of initial conditions leading to limit cycles is 1000 minus the values shown.

The number of fixed points and loose attractors of RTNs under the asynchronous scheme is shown in FIG. 4. Like synchronous RTNs, asynchronous RTNs with higher modularity tend to have more fixed points and complex attractors. The shuffled asynchronous RTNs, which do not exhibit significant modularity, have fewer attractors than asynchronous RTNs with distinct community structure. Comparing the asynchronous models with the corresponding synchronous models, we can see that asynchronous RTNs reach a fixed point much more easily than synchronous RTNs, and synchronous RTNs have more limit cycles than asynchronous RTNs have loose attractors, consistent with the previous observations on asynchronous update in other systems [38–40]. The lack of loose attractors mainly origins from the stochasticity of the asynchronous update scheme which makes the systems difficult to stay in a set of recurring states. Similarly, for the same reason the vast majority of initial conditions lead to fixed points and only a few lead to loose attractors in asynchronous RTNs. Like synchronous RTNs, asynchronous RTNs with distinct community structure tend to have longer attractors than asynchronous RTNs without modularity. The results based on the asynchronous update scheme are consistent with those based on the synchronous scheme, confirming the effects of community structure on the attractors of RTNs.

Similarly to the way that the heterogeneity of degree and the connectivity of nodes affect the network dynamics, community size may affect the dynamics of RTNs as

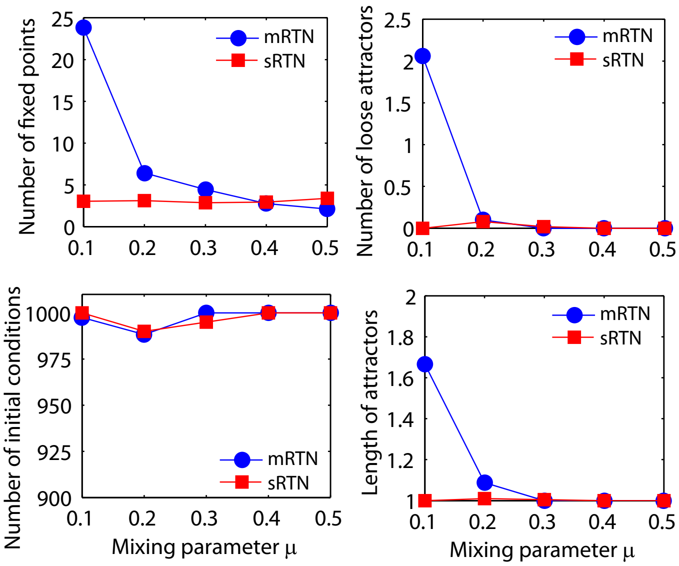

FIG. 4: Attractors of RTNs with different modularity under the asynchronous update scheme. The third panel gives the number of initial conditions leading to fixed points; the number of initial conditions leading to loose attractors is 1000 minus the values shown.

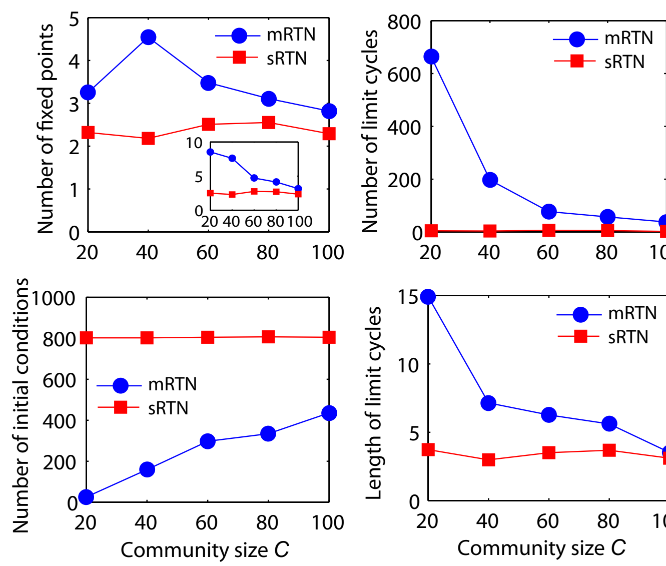

FIG. 5: Attractors of RTNs with communities of different sizes under the synchronous update scheme. The inset in the first panel is the number of fixed points found from 10,000 initial conditions. The third panel gives the number of initial conditions leading to fixed points; the number of initial conditions leading to limit cycles is 1000 minus the values shown.

well. To examine this point, we kept the mixing parameter as 0.1 which makes the network modularity remain high (see FIG. 2) and added constraints to the community size. We generated networks with communities of 20, 40, 60, 80 and 100 nodes. The networks contain one community with a larger than designed size if the network size is not exactly dividable by the community size. The results under the synchronous update scheme are shown in FIG. 5. The inset in the first panel of the figure is the result from sampling 10,000 initial conditions, suggesting that the lower value at community size 20 for 1000 initial conditions is a finite-size effect. We can see that RTNs with small communities tend to have more attractors (fixed points and limit cycles) than RTNs with large communities, probably because RTNs with small communities have more relatively independent small modules whose attractor combinations lead to more attractors of the whole networks than RTNs with large communities. In RTNs with small communities, very few initial conditions lead to fixed points and the reachability of fixed points is higher in RTNs with large communities. In addition, limit cycles in RTNs with small communities tend to be longer than RTNs with large communities. Collectively, we can conclude that in addition to modularity, community size also affects the criticality of random network dynamics.

The effects of community size on network dynamics under the asynchronous scheme are demonstrated in FIG. 6. As in synchronous RTNs, asynchronous RTNs with smaller communities tend to have more attractors, and the number of initial conditions leading to fixed points increases with the community size. Asynchronous RTNs with smaller communities tend to have longer attractors. Again, the results based on the asynchronous update scheme are consistent with those based on the synchronous scheme and confirm the effects of community size on the attractors of RTNs.

B. Effects of community structure on damage spreading

In the last subsection we studied the effects of community structure on the dynamics of ordered or critical RTNs. We continue in this subsection by examining how community structure affects the dynamics of chaotic RTNs. The results on damage spreading caused by transient perturbation of initial conditions in RTNs with different community structure are shown in FIG. 7. We can see that under both synchronous and asynchronous schemes, RTNs with distinct community structure are more robust to transient perturbation of initial conditions than RTNs without community structure and shuffled RTNs without modularity. In other words, damage resulting from transient perturbations spreads less effectively in highly modular RTNs than in RTNs without modular topology. Community size also has dramatic effects on the damage spreading resulting from transient perturbations in RTNs. Damage spreading is more difficult in RTNs with small communities than in RTNs with large communities. We hypothesize that this may be

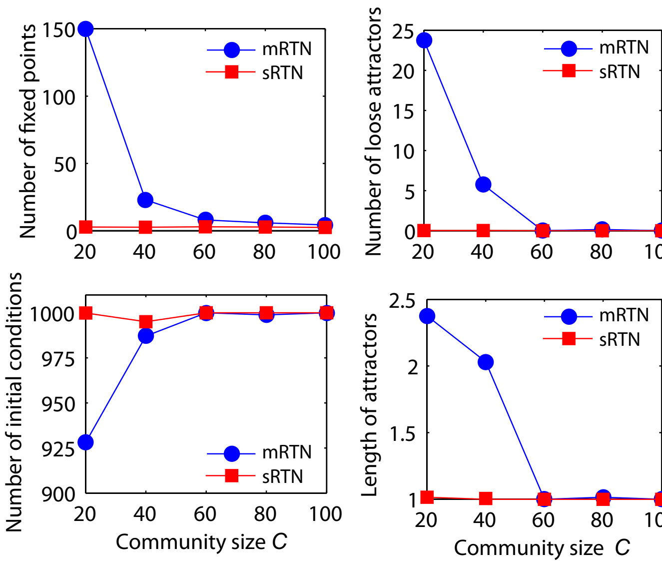

FIG. 6: Attractors of RTNs with communities of different sizes under the asynchronous update scheme. The third panel gives the number of initial conditions leading to fixed points; the number of initial conditions leading to loose attractors is 1000 minus the values shown.

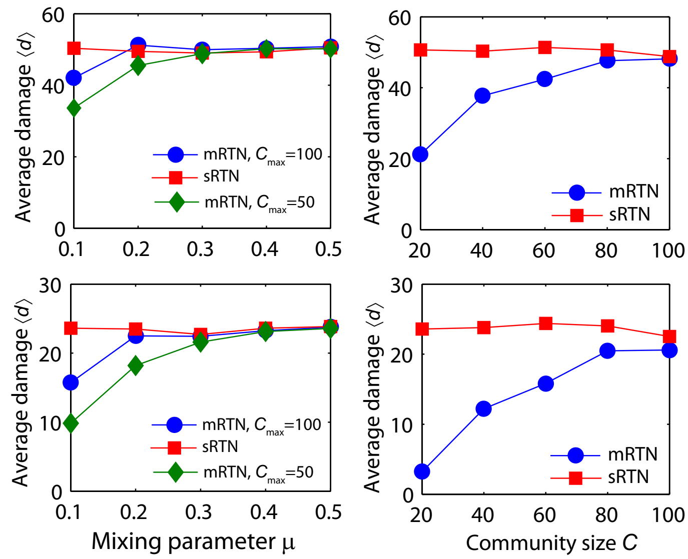

FIG. 7: Damage spreading from transient perturbations of initial conditions in synchronous and asynchronous RTNs. The upper two panels are for the synchronous update scheme and the bottom two panels are for the asynchronous update scheme.

because nodes that connect communities act as bottlenecks of damage propagation and make damage difficult to spread across communities. In agreement with this hypothesis, setting a lower maximum community size, $C_{\max}$=50 instead of 100, lowers the average damage even more for the two highest modularity values, indicating that the heterogeneity of community size has nontrivial effects on the stability of network dynamics. In addition, asynchronous RTNs tend to exhibit smaller damage in response to transient perturbation of initial conditions than synchronous RTNs, indicating that the stochastic asynchronous update scheme can slow down or weaken the damage.

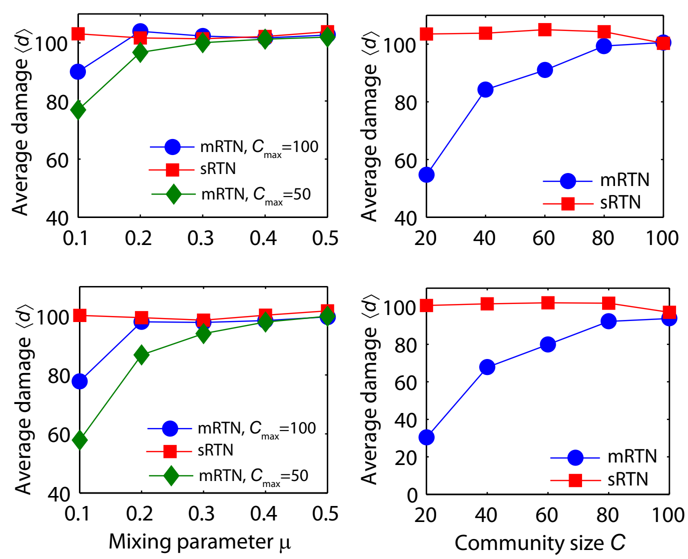

FIG. 8: Damage spreading from permanent perturbations of initial conditions in synchronous and asynchronous RTNs. The upper two panels are for the synchronous update scheme and the bottom two panels are for the asynchronous update scheme.

Damage spreading resulting from permanent perturbation of initial conditions in synchronous and asynchronous RTNs is shown in FIG. 8. We can see that the effects of community structure on damage spreading caused by permanent perturbations are similar to those on damage spreading caused by transient perturbations. As expected, damages resulting from permanent perturbations are larger than those resulting from transient perturbation of initial conditions in both synchronous and asynchronous RTNs. We conclude that modularity, community size and the heterogeneity of the community sizes all have considerable impact on the stability of random threshold dynamics.

C. Effects of community structure on internal dynamics

The average of the mutual information over all pairs $\langle I \rangle$ measures how well the system can coordinate its internal dynamics. Usually $N\langle I \rangle$ is used because it approaches a nonzero constant when the network size N is infinitely large [33, 34]. For RTNs with average indegree 2, we did not see a clear difference between the coordination ability of RTNs with and without modular topology, because all the networks reach fixed points very soon, and thus have very low average mutual information. For RTNs with average indegree 5.0, i.e., when the networks are in their chaotic regime, we do see that RTNs with strong community structure have different dynamic coordination abilities compared to RTNs without modularity. According to the definition of $\langle I \rangle$, the more time steps we run the model, the more accurate estimation of the mutual information we have. Therefore we run the models for 500 time steps and discard the first 50 time steps to remove any bias from the transient dynamics. The mutual information of RTNs with and without community structure is given in FIG. 9. We can see that under the synchronous scheme RTNs with high modularity can coordinate their internal dynamics better than RTNs with low modularity and shuffled RTNs. This is consistent with the previous observation that oscillators in the same community are synchronized more easily than those across communities [33, 34]. Community size also affects the coordination ability of synchronous RTNs. RTNs with small communities coordinate their internal dynamics better than RTNs with large communities and RTNs without community structures.

Coordination of internal dynamics is different in asynchronous RTNs than in synchronous RTNs. Overall synchronous RNTs coordinate their internal dynamics better than asynchronous RTNs. In addition, asynchronous RTNs with distinct community structure coordinate their internal dynamics less effectively than RTNs without community structure, and asynchronous RTNs with small communities coordinate their internal dynamics less effectively than RTNs with large communities. Note that synchronous and asynchronous RTNs have similar coordination of their internal dynamics when their networks do not exhibit modular topology. This inverted behavior of synchronous versus asynchronous RTNs is supported by the observed non-monotonic coordination properties of synchronous Boolean networks [32, 35]. Boolean networks in the ordered regime are dynamically frozen and all the attractors of the network are fixed points, which make the average mutual information $\langle I \rangle$ close to zero. Boolean networks in the chaotic phase are sensitive to small differences in initial conditions, thus it is difficult to coordinate their internal dynamics. Critical Boolean networks have maximal coordination of internal dynamics. On one hand, we observed more limit cycles in synchronous RTNs with high modularity than in synchronous RTNs with low modularity; no fixed points were found in these RTNs. Oscillating node pairs in the same limit cycle can have high mutual information since their states occur predictably. That may be why synchronous RTNs with modular topology have higher mutual information than synchronous RTNs without modular topology. On the other hand, asynchronous RTNs

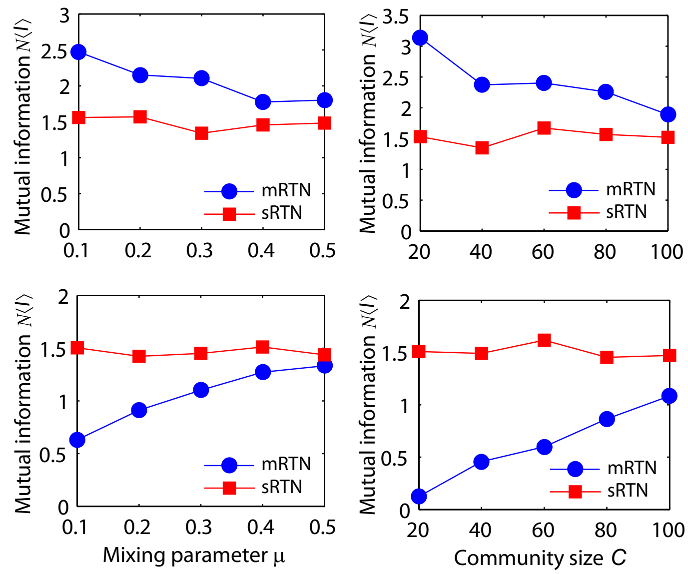

FIG. 9: Mutual information of time series in synchronous and asynchronous RTNs with different community structure. The upper two panels are for the synchronous scheme and the bottom two panels are for the asynchronous scheme.

with high modularity have more fixed points and more loose attractors than asynchronous RTNs with low modularity, and it is difficult for node pairs in the same fixed points and loose attractors to highly coordinate their activities since their states are not predictive of each other. Therefore asynchronous RTNs with high modularity do not coordinate their internal dynamics better than asynchronous RTNs with low modularity.

IV. CONCLUSIONS

We systematically investigated the effects of community structure on the dynamics of RTNs with scale-free topology by using both synchronous and asynchronous models. We have shown that RTNs with highly modular topology tend to have more attractors than RTNs without modular topology. We have also shown that damage resulting from transient or permanent perturbations of initial conditions is more difficult to spread in RTNs with high modularity than RTNs with low modularity.

Our study significantly expands the investigation of the differences between deterministic and stochastic dynamics in Boolean networks. We found that it is much easier for asynchronous RTNs to reach a fixed point than synchronous RTNs, and synchronous RTNs have more limit cycles than asynchronous RTNs have loose attractors, consistent with the previous observations on asynchronous update in other systems [38–40]. Asynchronous RTNs tend to more easily correct small perturbations than synchronous RTNs. This is probably due to the overall smaller number of loose attractors and the higher reachability of fixed points in asynchronous RTN models.

Finally we have shown that RTNs with high modularity can coordinate their internal dynamics better than RTNs with low modularity under the synchronous scheme, whereas asynchronous RTNs with high modularity do not have better coordination of their internal dynamics than asynchronous RTNs without modularity. We also observed that synchronous RTNs coordinate their internal dynamics better than asynchronous RTNs. Overall this study shows that average indegree is not the only factor that affects the criticality of random threshold dynamics, and that local structure has strong effects on the dynamics of RTNs.

Acknowledgments: This work is supported by NSF grants MCB 1121612 and PHY 1205840. We thank Dr. Colin Campbell for helpful discussions.

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