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Random walk networks

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Abstract

Random Boolean networks are among the best-known systems used to model genetic networks. They show an on-off dynamics and it is easy to obtain analytical results with them. Unfortunately very few genes are strictly on-off switched. On the other hand, continuous methods are in principle more suitable to capture the real behavior of the genome, but have difficulties when trying to obtain analytical results. In this work, we introduce a new model of random discrete network: random walk networks, where the state of each gene is changed by small discrete variations, being thus a natural bridge between discrete and continuous models. (© 2004 Elsevier B.V. All rights reserved.

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1. Introduction

Random Boolean networks (RBN) are a classical discrete approach in complex systems to gene networks [1,2]. In RBN, each gene have only two states (on/off) with a dynamic based in Boolean functions. Nevertheless, very few genes are strictly on–off switched, rather they have continuous behavior [3]. In order to handle this

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continuous behavior, models of many-genes activity based on differential equations have been developed, although they have evident computational and analytical problems. In Ref. [4], it is proposed a continuous-discrete hybrid set of piece-wise linear differential equations in order to get round this problem. Unfortunately, it is difficult to obtain analytical results in such continuous or semi-continuous models.

In this paper, we introduce random walk networks (RWN). These networks work with small variations in the gene states, being in this way a discrete approach to differential equations. RWN are formed by N automata, each one connected with another K automata in a random manner. Each automaton can be in a number s of possible states ranging from 1 to s and the changes among states occur in discrete steps of $\{+1, -1\}$. The dynamics of each automaton is constrained by two reflecting states: 1 and s. These extreme states represent null activity and saturation activity respectively, and they act as barriers for the automaton. A function rule table of K variables, generated in a random manner, is associated with each automaton. This function has as input the state values of the K input automata.

In contrast with RBN, the output of this function does not define the new value of the automaton, but a variation +1 or -1 in its value, and hence its link with differential equations. These variations modify the state of a given automaton producing (in the chaotic case) a random walk-like behavior of its value, which gives the name to these networks. For example, let us suppose K = 2 and s = 4 and the automaton i with state in time t, $x_i^t = 2$. Let us also suppose that its two automata input have states $x_{i_1}^t = 1$ and $x_{i_2}^t = 3$ in time t. We search the input combination (1,3) in the rule table for the automaton i and find +1 as output. Then the value $x_i^t = 2$ is updated as $x_i^{t+1} = 2 + 1 = 3$ in time t + 1. In the case $x_i^t = 4$ (saturation state) the update would be $x_i^{t+1} = 4$. Similarly, if the automaton has a value of $x_i^t = 1$ (null activity) and the output is -1 the update will be $x_i^{t+1} = 1$. That is, the extreme values act as barriers. As in RBN, the evolution of the system is updated synchronously and we can define a new parameter p, the bias [5], but here it is the probability of having +1 as the output value in the rule tables (and having -1 with probability (1-p)) when we generate in a random manner all the rule tables at the beginning of the definition of the network. Note that connections and rule tables are generated in a random manner at the beginning of the definition of each network but afterwards are maintained (quenched) in time.

RWN present complex dynamical behavior and similar order–disorder transition as RBN [5], random threshold networks [6] or asymmetric neural networks [7], for example. For a fixed number *s* of states, two well-defined phases appear in RWN, separated by a critical line in the space p - K:

- (1) an ordered phase when the value of the bias p is far away from 0.5 and/or the connectivity K is low, in which the networks freeze in a pattern after a short transient. In this phase, almost all of the automata remain in a completely frozen state, and
- (2) a disordered phase, in the contrary case for p and K, where all patterns are lost and the automata appear to be in a completely disordered state, switching from one state to another seemingly at random.



Fig. 1. Up: dynamics of a RWN with N = 100 automata, K = 2, p = 0.79 and s = 10. The horizontal axis represents time steps and the vertical axis shows the 100 automata. Different gray intensities indicate different states for each automaton, ranging from 1 (white) to 10 (black). Down: evolution of the automata states (automata values) in time for the same RWN. For simplicity we only show automata number 33 (broken line), 53 (dotted line) and 88 (solid line). The positions of these automata are marked in the vertical axis of the upper figure.

We can observe that RWN reduces to RBN when s = 2. In this sense, RWN are a generalization of RBN. Fig. 1 shows the time evolution of an example RWN with N = 100, K = 2, p = 0.79 and s = 10.

2. Annealed and quenched model

Following Ref. [8], we can obtain the boundaries separating order and disorder for the RWN annealed model. For the annealed model, in contrast with quenched RWN, we define the automata inputs and the functions of each automaton each time step in order to avoid correlations or system memory. This is strictly true for other systems, as RBN, but for annealed RWN the memory dependence is not totally avoided. Here, the state values x_i^t have influence in the values x_i^{t+1} . Nevertheless, the RWN annealed system shows an ordered–disordered transition and we can compute it as a mean field of the quenched RWN.

The behavior of each automaton is constrained by the reflecting states 1 and s. For a given network automata, we define P_n as the probability of being in state $n \in \{1, 2, ..., s\}$, that is, having value *n*. If we assume absence of correlations, we can write the evolution of the probabilities as

$$\begin{cases}
P_{1}(t+1) = (1-p)(P_{1}(t) + P_{2}(t)) \\
\vdots \\
P_{i}(t+1) = (1-p)P_{i+1}(t) + pP_{i-1}(t) \\
\vdots \\
P_{s}(t+1) = p(P_{s-1}(t) + P_{s}(t))
\end{cases}$$
(1)

with i = 2, 3, ..., s - 1.

Following the annealed model [8], we need to compute the overlap between two annealed replicas, with initial state conditions randomly chosen. The overlap in time t: $a(t) \in [0, 1]$ is defined as the normalized number Na(t) of elements with common states in two annealed replicas. The time evolution of the overlap in the annealed model is given by

$$a(t+1) = a(t)[a^{K}(t) + (1 - a^{K}(t))(p^{2} + (1 - p)^{2})] + \frac{2(1 - a(t))}{1 - \sum_{n=1}^{s} P_{n}^{2}} \left[a^{K}(t)(pP_{s-1}P_{s} + (1 - p)P_{1}P_{2}) + (1 - a^{K}(t))(p^{2}P_{s-1}P_{s} + (1 - p)^{2}P_{1}P_{2} + p(1 - p)\sum_{n=2}^{s-1} P_{n-1}P_{n+1} \right].$$

$$(2)$$

This equation has as fixed point, the value $a^* = 1$ and a stability analysis leads to the following critical surface separating the ordered and disordered phases for annealed RWN:

$$K \frac{\left(1 - \sum_{n=1}^{s} P_n^2\right)}{1/pP_s^2 + 1/(1-p)P_1^2} = 1 , \qquad (3)$$

where now P_n are the stationary values of $P_n(t)$ calculated from Eq. (1) in the limit when $t \to \infty$:

$$P_n = \frac{1}{z} \left(\frac{p}{1-p}\right)^{n-1} \tag{4}$$

being $z = \frac{1 - (\frac{p}{1-p})^s}{1 - p/(1-p)}$ the normalization constant.



Fig. 2. Evolution of the overlap a(t) as a function of the number of states *s*. Left: Evolution of the overlap a(t) for annealed RWN for K = 2, p = 0.65 and different values of *s*. In all of them we have taken as initial conditions a(0) = 1/s. Each point represents the average of 100 different networks, with N = 10000 automata each one. Solid lines represent the theoretical evolution using Eqs. (1) and (2). Right: Evolution of the overlap a(t) for quenched RWN for the same parameter values and initial conditions than left. Again, each point represents the average of 100 different networks, with N = 10000 automata each one.

As expected, using s = 2 in the critical surface equation (Eq. (3)) this value leads to the well-known critical curve for RBN [5]:

$$K2p(1-p) = 1. (5)$$

3. Numerical simulations

Fig. 2 shows the results in the evolution of the overlap a(t) between two given configurations of the same system. Solid lines in Fig. 2 left are the theoretical predictions of the evolution for the annealed RWN from Eqs. (1) and (2), meanwhile points (circles, squares, diamonds and triangles) are the simulation results for the annealed RWN. *K* and *p* have a fixed value and it shows the effect of the variations in *s*. As can be seen, the agreement between theory (continuous line) from Eqs. (1) and (2) and simulation is complete. Compare it with Fig. 2 right, corresponding to the quenched RWN. It is clear how the values of the overlap a(t) in the annealed RWN (left) are always smaller than the values in the quenched RWN (right). Thus, due to the strong correlations of the quenched system, the annealed model underestimates the quenched one and the critical surface obtained for the annealed model is not applicable to the quenched model (unlike RBN).

Fig. 3 shows the dependence with p and s of the stationary value of the overlap, a^* , i.e.: a(t) when t tends to infinity. As can be seen in these figures, $1 - a^*$ acts as order parameter, having order when $1 - a^* = 0$ and disorder otherwise. Fig. 3 left corresponds to the theoretical annealed RWN from Eqs. (1) and (2) when $t \to \infty$, and Fig. 3 right to the quenched model. As can be seen, both cases show a clear transition from order to disorder, although the annealed model predicts a critical p bigger than the quenched one.



Fig. 3. Behavior of the stationary value of the overlap, a^* , as a function of the bias p. We plot $1 - a^*$, which acts as an order parameter, versus p. Left: Theoretical representation of $1 - a^*$ as a function of p for the annealed RWN. Each curve corresponds from the bottom to the top to s = 3, 4, 5, 6, 7, 8, 9. Right: Numerical simulations of $1 - a^*$ as a function of p for the quenched system. Each point in the curves has been obtained by averaging 100 simulations. Each curve corresponds from the bottom to the top to s = 3, 4, 5, 6, 7, 8, 9, for quenched RWN with N = 10000 and K = 2.

4. Summary

The RBN was one of the first ways proposed to statistically study genome global properties. Unfortunately, this is a model of all-nothing behavior where the state of a given gene is completely determined by the input genes and where smooth variations of state are not allowed, in contrast with the real genome. On the other hand, systems of differential equations, which in principle should give a better understanding of such continuous behavior, are difficult to solve and it is hard to obtain analytical results. In this paper, we have proposed RWN, a new simple random network model which has great resemblances with real genetic networks. RWN are a natural link between discrete all-nothing models (like RBN) and continuous systems of differential equations, as RWN allow small, almost continuous variations in the behavior of the genome. RWN have a clear order–disorder transition and allow analytical treatment. In this paper, we have deduced the critical frontier for the annealed model, although due to the memory of the system, the annealed solution does not coincide with the quenched critical frontier.

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