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Predicting criticality and dynamic range in complex networks: effects of topology

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The collective dynamics of a network of coupled excitable systems in response to an external stimulus depends on the topology of the connections in the network. Here we develop a general theoretical approach to study the effects of network topology on dynamic range, which quantifies the range of stimulus intensities resulting in distinguishable network responses. We find that the largest eigenvalue of the weighted network adjacency matrix governs the network dynamic range. Specifically, a largest eigenvalue equal to one corresponds to a critical regime with maximum dynamic range. We gain deeper insight on the effects of network topology using a nonlinear analysis in terms of additional spectral properties of the adjacency matrix. We find that homogeneous networks can reach a higher dynamic range than those with heterogeneous topology. Our analysis, confirmed by numerical simulations, generalizes previous studies in terms of the largest eigenvalue of the adjacency matrix.

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Numerous natural [1, 2] and social [3] systems are accurately described as networks of interacting excitable nodes. The collective dynamics of such excitable networks often defy naive expectations based on the dynamics of the single nodes which comprise the network. For example, the collective response of a neural network can encode sensory stimuli which span more than 10 orders of magnitude in intensity, while the response of a single neuron (node) typically encodes a much smaller range of stimulus intensities. More generally, the range of stimuli over which a network's response varies significantly is quantified by *dynamic range* and is a fundamental property, whether the network is comprised of people, cell phones, genes, or neurons. In neural networks, recent experiments [4] suggest that dynamic range is maximized in a critical regime in which neuronal avalanches [5] occur, confirming earlier theoretical predictions [2]. It has been argued [2, 4] that this critical regime occurs when the effective mean degree of the network is one, i.e. the expected number of excited nodes produced by one excited node is one. However, this criterion is invalid for networks with broad degree distributions [6, 7]. A general understanding of how dynamic range and criticality depend on network structure remains lacking. In this Letter, we present a unified theoretical treatment of stimulus-response relationships in excitable networks, which holds for diverse networks including those with random, scale free, degree-correlated, and assortative topologies.

As a tractable model of an excitable network, here we consider the Kinouchi-Copelli model [2], which consists of N coupled excitable nodes. Each node i can be in one of m states x_i . The state $x_i = 0$ is the resting state, $x_i = 1$ is the excited state, and there may be additional refractory states $x_i = 2, 3, \dots, m - 1$. At discrete times $t = 0, 1, \dots$ the states of the nodes x_i^t are updated as follows: (i) If node i is in the resting state, $x_i^t = 0$, it can be excited by another excited node j , $x_j^t = 1$, with probability A_{ij} , or independently by an external process with probability η . The network topology and strength of interactions between the nodes is described by the connectivity matrix $A = \{A_{ij}\}$. In this model, η is considered the stimulus strength. (ii) The nodes that are excited or in a re-

fractory state, $x_i^t \geq 1$, will deterministically make a transition to the next refractory state if one is available, or otherwise return to the resting state (i.e. $x_i^{t+1} = x_i^t + 1$ if $1 \leq x_i^t < m - 1$, and $x_i^{t+1} = 0$ if $x_i^t = m - 1$).

An important property of excitable networks is the dynamic range, which is defined as the range of stimuli that is distinguishable based on the system's response F . Following [2], we quantify the network response with the average activity $F = \langle f \rangle_t$ where $\langle \cdot \rangle_t$ denotes an average over time and f^t is the fraction of excited nodes at time t . To calculate a system's dynamic range, we first determine a lower stimulus threshold η_{low} below which the change in the response is negligible, and an upper stimulus threshold η_{high} above which the response saturates. Dynamic range (Δ), measured in decibels, is defined as $\Delta = 10 \log_{10} \eta_{high} / \eta_{low}$. To analyze the dynamics of this system, we denote the probability that a given node i is excited at time t by p_i^t . For simplicity, we will consider from now on only two states, resting and excited ($m=2$) [8]. Then, the update equation for p_i^t is

$$p_i^{t+1} = (1 - p_i^t) \left(\eta + (1 - \eta) \left[1 - \prod_j^N (1 - p_j^t A_{ij}) \right] \right) \quad (1)$$

which can be obtained by noting that $1 - p_i^t$ is the probability that node i is resting at time t , and the term in large parentheses is the probability that it makes a transition to the excited state. We note that, in writing this probability, we treat the events of neighbors of node i being excited at time t as statistically independent. As noted before [3, 9–11], this approximation yields good results even when the network has a non-negligible amount of short loops.

In Ref. [2], the response F was theoretically analyzed as a function of the external stimulation probability η using a mean-field approximation in which connection strengths were considered uniform, $A_{ij} = \sigma/N$ for all i, j . It was shown that at the critical value $\sigma = 1$, the network response F changes its qualitative behavior. In particular, $\lim_{\eta \rightarrow 0} F = 0$ if $\sigma < 1$ and $\lim_{\eta \rightarrow 0} F > 0$ if $\sigma > 1$. In addition, the dynamic range of the network was found to be maximized at $\sigma = 1$. The pa-

parameter σ is defined in Refs. [2, 4] as an average branching ratio, written here as $\sigma = \frac{1}{N} \sum_{i,j} A_{ij} = \langle d^{in} \rangle = \langle d^{out} \rangle$, where $d_i^{in} = \sum_j A_{ij}$ and $d_i^{out} = \sum_j A_{ji}$ are the in- and out-degrees of node i , respectively, and $\langle \cdot \rangle$ is an average over nodes. For the network topology studied by Ref. [2] $\sigma = 1$ marks the critical regime in which the expected number of excited nodes is equal in consecutive timesteps. Such critical branching processes result in avalanches of excitation with power-law distributed sizes. Cascades of neural activity with such power-law size distributions have been observed in brain tissue cultures [4], awake monkeys [12], and anesthetized rats [13]. While $\sigma = 1$ successfully predicts the critical regime for Erdős-Rényi random networks [2], this prediction fails in networks with a more heterogeneous degree distribution [6, 7]. Perhaps more importantly, previous theoretical analyses [2, 6, 7] do not account for features that are commonly found in real networks, such as community structure, correlation between in- and out-degree of a given node, or correlation between the degree of two nodes at the ends of a given edge [14]. Here, we will generalize the mean-field criterion $\sigma = 1$ to account for complex network topologies.

To begin, we note that $\lim_{\eta \rightarrow 0} F = 0$ corresponds to the fixed point $\vec{p} = 0$ of Eq. (1) with $\eta = 0$. To examine the linear stability of this fixed point, we set $\eta = 0$ and linearize around $p_i^t = 0$, assuming p_i^t to be small, obtaining $p_i^{t+1} = \sum_j^N p_j^t A_{ij}$. Assuming $p_i^t = u_i \lambda^t$ yields

$$\lambda u_i = \sum_j^N u_j A_{ij}. \quad (2)$$

Thus, the stability of the solution $\vec{p} = 0$ is governed by the largest eigenvalue of the network adjacency matrix, λ , with $\lambda < 1$ being stable and $\lambda > 1$ being unstable. Therefore, the critical state described in previous literature, occurring at various values of $\langle d \rangle$, should universally occur at $\lambda = 1$. Importantly, since $A_{ij} \geq 0$, the Perron-Frobenius theorem guarantees that λ is real and positive [15]. Other previous studies in *random* networks have also investigated spectral properties of A to gain insight on the stability of dynamics in neural networks [16] and have shown how λ could be changed by modifying the distribution of synapse strengths [17]. An important implication of Eq. (2) is that, when p and η are small enough, p should be almost proportional to the right eigenvector u corresponding to λ , so we write $p_i = C u_i + \epsilon_i$, where C is a proportionality constant and the ϵ_i error term captures the deviation of actual system behavior from the linear analysis. To first order, the constant C is related to the network response F since, neglecting ϵ , we have

$$F = \langle f \rangle_t = \frac{1}{N} \sum_i p_i \approx \frac{1}{N} \sum_i C u_i = C \langle u \rangle. \quad (3)$$

The linear analysis allowed us to identify $\lambda = 1$ as the point at which the network response becomes non-zero as $\eta \rightarrow 0$. In what follows, we use a weakly nonlinear analysis to obtain approximations to the response $F(\eta)$ when η is small. As we will show, these approximations depend only on a few spectral properties of A . Assuming $A_{ij} p_j \ll 1$ (which is valid

near the critical regime if each node has many incoming connections), we approximate the product term of Eq. (1) with an exponential, obtaining in steady state

$$p_i = (1 - p_i) \left(\eta + (1 - \eta) \left[1 - \exp \left(- \sum_j p_j A_{ij} \right) \right] \right) \quad (4)$$

which we expand to second order using Eq. (3) and $Au = \lambda u$,

$$C u_i + \epsilon_i = (A\epsilon)_i + \eta(1 - C u_i) + (1 - \eta) \lambda C u_i - \left(\lambda + \frac{1}{2} \lambda^2 \right) C^2 u_i^2. \quad (5)$$

To eliminate the error term ϵ_i from Eq. (5), we multiply by v_i , the i th entry of the left eigenvector corresponding to λ , and sum over i . We use the fact that $v^T A \epsilon = \lambda v^T \epsilon$, where v^T denotes the transpose of v , and neglect the resulting small term $(1 - \lambda) \sum_i v_i \epsilon_i$ close to the critical value $\lambda = 1$, obtaining

$$C \langle uv \rangle = \eta (\langle v \rangle - C \langle uv \rangle) + (1 - \eta) C \lambda \langle uv \rangle - \left(\lambda + \frac{1}{2} \lambda^2 \right) C^2 \langle v u^2 \rangle. \quad (6)$$

This equation is quadratic in C [and therefore in F , via Eq. (3)] and linear in η , and may be easily solved for either. For $\eta = 0$ the nonzero solution for F is

$$F_{\eta=0} = \frac{(\lambda - 1)}{(\lambda + \frac{1}{2} \lambda^2)} \frac{\langle uv \rangle \langle u \rangle}{\langle u^2 v \rangle}. \quad (7)$$

A more refined approximation than Eq. (6) can be obtained by repeating this process without expanding Eq. (4), which yields the linear equation for η

$$C \langle uv \rangle = \sum_i (1 - C u_i) (\eta + (1 - \eta) [1 - \exp(-\lambda C u_i)]). \quad (8)$$

Before numerically testing our theory, we will explain how it relates to previous results. For a network with correlations between degrees at the ends of a randomly chosen edge (assortative mixing by degree [14]), measured by the correlation coefficient $\rho = \langle d_i^{in} d_j^{out} \rangle_e / \langle d^{in} d^{out} \rangle$, with $\langle \cdot \rangle_e$ denoting an average over edges, the largest eigenvalue may be approximated by $\lambda \approx \rho \langle d^{in} d^{out} \rangle / \langle d \rangle$ [20]. In the absence of assortativity, when $\rho = 1$, $\lambda \approx \langle d^{in} d^{out} \rangle / \langle d \rangle$. If, in addition, there are no correlations between d_{in} and d_{out} (*node degree correlations*) or if the degree distribution is sufficiently homogenous, then $\langle d^{in} d^{out} \rangle \approx \langle d \rangle^2$ and the approximation reduces to $\lambda \approx \langle d \rangle$. In the case of Ref. [2], $\lambda \approx \langle d \rangle$ applies, and in the case of Refs. [6, 7], $\lambda \approx \langle d^{in} d^{out} \rangle / \langle d \rangle$ applies.

We test our theoretical results via direct simulation of the Kinouchi-Copelli model on six categories of directed networks with $N = 10,000$ nodes: (category 1) Random networks with no node degree correlation between d^{in} and d^{out} ; (category 2) Random networks with maximal degree correlation, $d^{in} = d^{out}$; (category 3) Random networks with moderate correlation between d^{in} and d^{out} ; (category 4) Networks with power law degree distribution with power law exponents $\gamma \in [2.0, 6.0]$, with and without node degree correlations; (category 5) Networks constructed with $\langle d \rangle = 1$, and assortativity coefficient ρ varying in $[0.7, 1.3]$; (category 6) Networks with weights which depend on the degree of the node from

which the edge originates, $A_{ij} = \alpha/d_i^{out}$.

We created networks in multiple steps: first, we created binary networks ($A_{ij} \in \{0, 1\}$) with target degree distributions as described below; next, we assigned a weight to each link, drawn from a uniform distribution between 0 and 1; finally, we calculated λ for the resulting network and multiplied A by a constant to rescale the largest eigenvalue to the targeted eigenvalue. This process was restarted from the first step for every network used in categories 1-4, creating a structurally different network for each simulation. The initial binary networks in categories 1-3 were Erdős-Rényi random networks, constructed by linking any pair of nodes with probability $p = 10/N$ [18]. Maximal degree correlation resulted from creating undirected binary networks and then forcing $A_{ij} = A_{ji}$ for $i < j$ while assigning weights. Moderate degree correlation resulted from making undirected binary networks but allowing $A_{ij} \neq A_{ji}$ when weights were assigned. The algorithms for constructing the initial binary networks of categories 4-6 placed links randomly between nodes with specified in- and out-degrees via the configuration model [19]. For this model, we generated in- and out-degree sequences from a power law distribution of desired exponent γ by calculating the expected integer number of nodes with each integer degree, from minimum degree 10 to maximum degree 200. In creating category 5 networks, we initially created one scale free network with power law exponent $\gamma = 2.5$ and $\lambda = 1$. Then, to change the degree of assortativity, we modified this original network by choosing two links at random and swapping them if the resulting swap would change the assortativity in the direction desired. This process was repeated until a desired value of ρ was achieved. Importantly, this swapping makes it possible to leave the degree distributions of the network unchanged, while still changing the assortative or disassortative properties of the network as in [14, 20]. Therefore, by this method we may maintain exactly the same degree distribution and mean degree, yet modify λ by virtue of $\lambda \propto \rho$.

In the six network types tested, results of simulations unanimously confirm the hypothesis that criticality occurs only for largest eigenvalue $\lambda = 1$. We present representative results in Fig. 1 (a), noting that each line and set of points corresponds to a single network realization, implying that the effect of the largest eigenvalue on criticality is robust for individual systems. Fig. 1 (a) shows the response F as a function of stimulus η for scale-free networks with exponent $\gamma = 2.5$, constructed with no correlation between in- and out-degree, highlighting the significant difference between the regimes of $\lambda < 1$ and $\lambda > 1$, with the critical data corresponding to $\lambda = 1$. The lines were obtained by using Eqs. (3) and (8). Fig. 1 (b) shows Δ as a function of λ , using $\eta_{high} = 1$ and $\eta_{low} = 0.01$, with the maximum occurring at $\lambda = 1$. Similar results showing criticality and maximum dynamic range at $\lambda = 1$ are obtained for networks of all categories 1-5. Fig. 2 shows $F_{\eta \rightarrow 0}$ for networks of categories 3-5, confirming the transition predicted by the leading order analysis in Eq. (2). The symbols show the result of direct numerical simulation of the Kinouchi-Copelli model, the solid lines were obtained

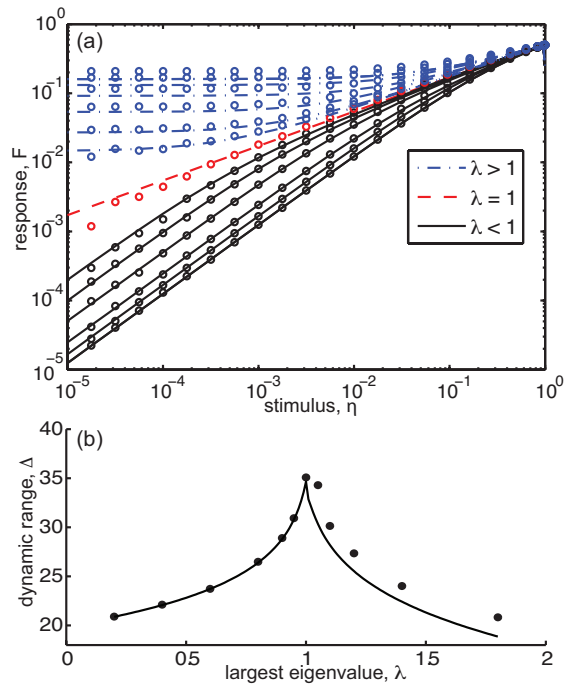


FIG. 1: (color online) (a) Response F vs. stimulus η for power law networks with exponent $\gamma = 2.5$ and no correlation between d_{in} and d_{out} . Eq. (8) (lines) captures much of the behavior of the simulation (circles), particularly for low levels of η and F , as expected from approximating Eq. (1). (b) Dynamic range Δ is maximized at $\lambda = 1$ in both simulation results (circles) and Eq. (6) (line).

by iterating Eq. (1), and the dashed lines were obtained from Eq. (7). Fig. 2(a) shows that criticality occurs at $\lambda = 1$ (indicated by a vertical arrow) rather than at $\langle d \rangle = 1$ for a category 3 random network. Fig. 2(b) shows that criticality occurs at $\lambda = 1$ for scale-free networks (category 4). Correlations between d_{in} and d_{out} affect the point at which $\lambda = 1$ occurs (vertical arrows). In Fig. 2(c), the mean degree was fixed at $\langle d \rangle = 1$, while λ was changed by modifying the assortative coefficient ρ . As predicted by the theory, there is a transition at $\lambda = 1$ even though the mean degree is fixed.

We now explore the question of what network topology will best enhance dynamic range. In many of the systems we simulate, a majority of the variation in dynamic range from one stimulus-response curve to another occurs due to variation at the low stimulus end of the curve, since most of the systems tend to saturate at around the same high stimulus levels (though this may not be the case for neuronal network experiments [4]). We therefore consider the following approximate measure of dynamic range, Λ , obtained by setting η_{high} to one in the definition of Δ , $\Lambda = 10 \log_{10} 1/\eta_*$, where η_* is the stimulus value corresponding to a lower threshold response F_* . Since dynamic range is maximized at criticality, we set $\lambda = 1$, solve Eq. (6) for η_* , substitute it into the definition of Λ using Eq. (3), retaining the leading order behavior to get

$$\Lambda_{MAX} = 10 \log_{10} \frac{2}{3F_*^2} - 10 \log_{10} \frac{\langle vu^2 \rangle}{\langle v \rangle \langle u \rangle^2}. \quad (9)$$

The first term of this equation shows that Λ_{MAX} depends on F_* . Since the entries of the right (left) dominant eigen-

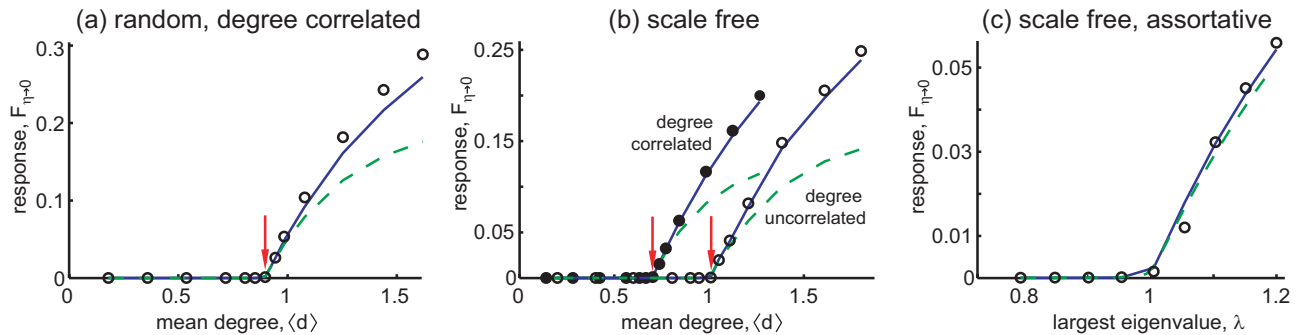


FIG. 2: (color online) $F_{\eta \rightarrow 0}$ obtained from direct numerical simulation of the Kinouchi–Copelli model (symbols) plotted against $\langle d \rangle$ (a, b) and λ (c). Blue solid lines result from iterating Eq. (1) and green dashed lines result from Eq. (7). Small arrows show where $\lambda = 1$ predicts a phase transition. (a) A set of random networks (category 3) showing that criticality occurs at $\lambda = 1$ (arrow), but not $\langle d \rangle = 1$. (b) Criticality in scale free networks (category 4) with node degree correlation also occurs at $\lambda = 1$ (arrow), but not $\langle d \rangle = 1$. (c) Category 5 networks are tuned through criticality by changing assortativity, without changing the degree distributions and fixed $\langle d \rangle = 1$.

vector are a first order approximation to the in-degree (out-degree) of the corresponding nodes [21], the second term suggests that maximum dynamic range should increase (decrease) as the degree distribution becomes more homogeneous (heterogeneous). For example, consider the case of an undirected, uncorrelated network, in which $v_i = u_i \approx d_i$. The second term is then approximately $-10 \log_{10} (\langle d^3 \rangle / \langle d \rangle^3)$, which is maximized when d_i is independent of i . This corroborates the numerical findings in Refs. [2, 7] that random graphs enhance dynamic range more than more heterogeneous scale free graphs, and that the heterogeneity of the degree distribution affects dynamic range [7]. To test our result, we simulate scale free networks with different power law exponents $\gamma \in [2.0, 6.0]$, yet with $\lambda = 1$ to maximize dynamic range in each case. Results of simulation (circles) plotted against the prediction of Eq. (9) (line) are shown in Fig. 3.

In summary, we analytically predict and numerically confirm that criticality and peak dynamic range occur in networks with largest eigenvalue $\lambda = 1$. This result holds for diverse network topologies including random, scale-free, assortative, and/or degree-correlated networks, and for networks in which edge weights are related to nodal degree, thus generalizing previous work. Moreover, we find that homogeneous (heterogeneous) network topologies result in higher (lower) dynamic range. Previous demonstrations of how λ governs network dynamics in many other models (see [21] and references

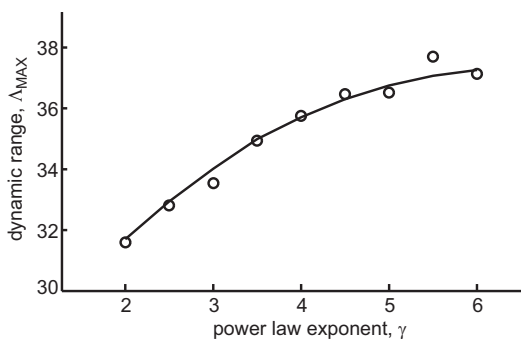


FIG. 3: For power-law degree distributions with $\lambda = 1$, peak dynamic range increases monotonically with network homogeneity, as measured by power law exponent γ . Simulations (circles) agree well with our predictions [Eq. (9); line].

therein) suggest that the generality of our findings may extend beyond the particular model studied here. Previous model studies have shown that mutual information between stimulus and response is also maximized at criticality [5]. Our findings suggest that peak mutual information will also be determined by $\lambda = 1$, but verifying this will require additional investigation. Taken together with related experimental findings [4], our results are consistent with the hypotheses that 1) real brain networks operate with $\lambda \approx 1$, and 2) if an organism benefits from large dynamic range, then evolutionary pressures may act to homogenize the network topology of the brain.

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- [1] L. L. Gollo *et al.*, PLoS Comput. Biol **5**(6): e10000402 (2009).
- [2] O. Kinouchi *et al.*, Nature Physics **2**, 348 (2006).
- [3] S. Gomez *et al.*, EPL **89** 38009 (2010).
- [4] W. L. Shew *et al.* J. Neurosci **29**(49):15595 (2009).
- [5] J. M. Beggs *et al.*, J. Neurosci **23**: 11167-11177 (2003).
- [6] M. Copelli *et al.*, Eur Phys. J. B **56** 273 (2007).
- [7] A. Wu *et al.*, Phys. Rev. E **75** 032901 (2007).
- [8] Our approach is easily generalized to include more refractory states. We also note that, in analogy to Ref. [10], our method can be generalized to include transmission delays and asynchronous updating. This will be discussed in a forthcoming publication.
- [9] J. G. Restrepo *et al.*, Phys. Rev. Lett **100**, 058701 (2008).
- [10] E. Ott *et al.*, Phys. Rev. E **79**, 056111 (2009).
- [11] A. Pomerance *et al.*, PNAS **106**, 20 (2009).
- [12] T. Petermann *et al.*, Proc. Natl. Acad. Sci. USA **106**:1592115926 (2009).
- [13] E. D. Gireesh *et al.*, Proc. Natl. Acad. Sci. USA **105**:7576 7581 (2008).
- [14] M. E. J. Newman, Phys. Rev. E. **67**, 026126 (2003).
- [15] C. R. MacCluer, SIAM Rev **42**:487 (2000).
- [16] R.T. Gray *et al.*, Neurocomputing **70**: 1000 (2007).
- [17] K. Rajan *et al.*, Phys. Rev. Lett **97**, 188104 (2006).
- [18] P. Erdős *et al.*, Publicationes Mathematicae **6** (1959).
- [19] M. E. J. Newman, SIAM Rev **45** 167 (2003).
- [20] J. G. Restrepo *et al.*, Phys. Rev. E **76**, 056119 (2007).
- [21] J. G. Restrepo *et al.*, Phys. Rev. Lett. **97**, 094102 (2006).