Evidence of universality for the May-Wigner stability theorem for random networks with local dynamics

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We consider a random network of nonlinear maps exhibiting a wide range of local dynamics, with the links having normally distributed interaction strengths. The stability of such a system is examined in terms of the asymptotic fraction of nodes that persist in a nonzero state. Scaling results show that the probability of survival in the steady state agrees remarkably well with the May-Wigner stability criterion derived from linear stability arguments. This suggests universality of the complexity-stability relation for random networks with respect to arbitrary global dynamics of the system.

The relation between the structure of a network and its dynamical properties has been a problem of long-standing importance in many fields, especially in theoretical ecology [1]. A major advance in this area was the suggestion by May that the stability of a network can be inferred from an analysis of the interactions between the network elements [2]. Confining attention only to the local stability of an arbitrary equilibrium of the dynamics, one can ignore explicit dynamics and look at only the leading eigenvalues of the linear stability matrix. Assuming that the network interactions are random, rigorous results on the eigenvalue spectra of random matrices can be applied [3]. If the stability matrix is comprised of elements from a normal distribution with zero mean and variance σ^2, then the network is almost certainly stable if $NC\sigma^2 < 1$, and unstable otherwise. N is the number of nodes in the network and C is the network connectivity, i.e., the probability that any two given elements of the network are coupled to each other, as reflected in the sparsity of the matrix [2,4]. This result is often referred to as the May-Wigner stability theorem [5].

May's suggestion that increasing network complexity leads to decrease in stability was supported by earlier numerical simulations [6], but it ran counter to the empirically established conventional wisdom that biodiversity promotes ecosystem stability. The original result has been criticized on the ground that it is obtained by linearizing about an assumed equilibrium, and so is inapplicable when either the perturbations from the equilibrium are large, or, the dynamics does not settle down to a fixed point attractor (e.g., they might undergo periodic oscillations as in a Lotka-Volterra-type system). The ensuing stability versus diversity debate in ecology has resulted in a large body of literature attempting to resolve this issue one way or another [7]. Although much of the controversy may have been due to the methods that different groups used to measure complexity and stability [8], and the two apparently opposing conclusions have been resolved in the specific context of a community assembly model [9], the general question of whether network complex-

ity is conducive to the long-term persistence of the nodes remains unresolved. In addition to ecological networks, phenomena where the survival of nodes in a network may be of relevance are power grid breakdown, financial market crashes, etc.; in short, any system that is susceptible to sudden collapse. Further, since the present problem is related to the persistence of a trajectory in a high-dimensional space with absorbing boundaries, it is also of considerable relevance to the general question of persistence in nonequilibrium systems that has seen a huge spurt of interest recently [10].

In this paper, we report results on the role that network complexity plays on global stability (in contrast to local stability) of a network, by looking at the persistence of individual nodes in a network of randomly coupled nonlinear maps undergoing a wide range of local dynamics. We observe that the results of the May-Wigner theorem seem to be valid universally, namely, increasing the number of interactions per node or increasing interaction strength will give rise to increased likelihood of extinction. This evidence of universality (in the sense of being independent of the local dynamics at the nodes) has bearing on network problems in general [11,12], as it addresses an issue which arises in many different contexts, namely: *What is the significance of local dynamics on network stability, especially in situations where the dynamics can be widely varying?*

Previous work on including explicit dynamics in network models mostly involved generalized Lotka-Volterra-type ordinary differential equations (ODEs) [13]. However, in the absence of interaction between the nodes, the local dynamics in such a system is trivial. In contrast, considering randomly coupled maps as a model for the dynamical network allows us to consider *very general local dynamics, including chaos*. In the specific context of ecological networks, this is a reasonable assumption for the population dynamics of individual species. In addition, the use of coupled maps allow us to work with much larger networks, compared to models incorporating realistic consumer-resource configurations used to analyze simple communities with very few species, whose results are difficult to scale to larger ecosystems [14].

Our model has N dynamical elements in a network with random nonlocal connectivity, for instance, representing an

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ecological network of N interacting species. Each node i $(=1\ldots N)$ is associated with a continuous state variable $x_n(i)$ which represents the relative population density of the ith species at time n. The interaction between two species is represented by Lotka-Volterra-type relation, with the sign of the coupling coefficient J_{ij} determining either a predator-prey relation $(J_{ij}>0, J_{ji}<0)$, competition $(J_{ij}, J_{ji}<0)$, or mutualism $(J_{ij}, J_{ji}>0)$. The time evolution of the system is given by

$$x_{n+1}(i) = f[x_n(i)\{1 + \Sigma_j J_{ij} x_n(j)\}], \tag{1}$$

where f represents the local on-site dynamics. For the results shown in this paper we have chosen f to be the exponential map,

$$f(x) = xe^{r(1-x)}, \quad \text{if } x > 0; = 0, \quad \text{otherwise}, \tag{2}$$

with r being the nonlinearity parameter leading from periodic behavior to chaos [15]. This is a much more realistic model of population dynamics than the logistic map, and in contrast to the latter, is defined over the semi-infinite interval $[0, \infty]$ rather than a finite, bounded interval. Our results also hold for other models of population dynamics such as the Bellows map, $f(x) = rx/(1+x^b)$ [16]. These maps have the property that they do not go extinct in the absence of coupling, as we are interested not in intrinsic instability of the species, but rather in the instability induced by network interactions.

The connectivity matrix $\mathbf{J} = \{J_{ij}\}$ is a sparse matrix with probability $1-C$ that an element is zero. The diagonal entries $J_{ii}=0$ indicate that in the absence of interaction with other species, the exponential map (2) completely determines the population dynamics of each species. The nonzero entries in the matrix are chosen from a normal distribution with mean 0 and variance σ^2. Note that we have also used uniform distribution over the interval $[-\sigma, \sigma]$ without any qualitative changes in the results. The results reported below are for parallel updating; similar results hold for random sequential updating. Also, our results hold for interaction couplings other than the one used above. For example, the following type of coupling:

$$x_{n+1}(i) = f[x_n(i)] + \Sigma_j J_{ij} f[x_n(i)] f[x_n(j)],$$

gives results similar to that reported in this paper.

The linear stability criteria for random networks provides a relation between the parameters N, C, and σ. However, since we are considering explicit local dynamics, we have an additional parameter, r. In our work, instead of looking at linear stability, we shall consider persistence, i.e., the probability that a site has a nonzero value of x, as the measure of stability of the system. Although some early work on survival and extinction of species in a coupled network were done in restricted contexts of exclusively competitive [17] or cooperative interactions [18], no systematic study has been previously made on whether the May criterion is valid in the presence of local dynamics, incorporating all kinds of interactions between species.

Initially, all the N species have population values randomly distributed about $x=1$. Immediately after starting the simulation the number of persistent species (i.e., with $x>0$)
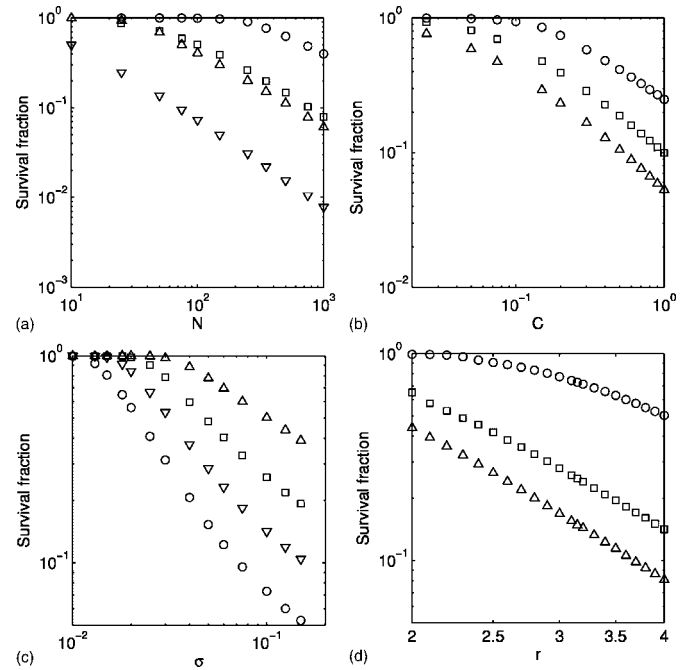

FIG. 1. The fraction of persistent nodes plotted against the model parameters: (a) the initial number of nodes, N ($\sigma=0.1$; $\bigcirc$: $C=0.1, r=2$, $\square$: $C=0.1, r=4$, $\triangle$: $C=1, r=2$, $\triangledown$: $C=1, r=4$); (b) connectivity, C ($N=100$, $\sigma=0.15$; $\bigcirc$: $r=2$, $\square$: $r=3$, $\triangle$: $r=4$); (c) standard deviation, σ ($N=100$, $r=4$; $\triangle$: $C=0.1$, $\square$: $C=0.25$, $\triangledown$: $C=0.5$, $\bigcirc$: $C=1$); (d) the nonlinearity parameter, r ($N=100$, $\sigma=0.1$; $\bigcirc$: $C=0.1$, $\square$: $C=0.5$, $\triangle$: $C=0.9$). The data is obtained after 10^4 iterations and averaged over 5000 realizations.

decreases rapidly, but eventually attains a steady-state value which is a function of the system parameters. Note that, if $x \leq 0$ for any species, it is removed from the system and subsequently plays no further role. After a series of such extinctions, the effective number of interacting species decreases and, consequently, the intensity of such extinction-inducing fluctuations is also reduced. We have continued the simulations for up to 10^4 iterations, when the probability of further extinctions was found to become extremely small. We then look at the fraction of species which survives as a function of the model parameters (Fig. 1). The results qualitatively agree with the May criterion for stability, in that, increasing complexity (in terms of size, connectivity, and interaction strength of the network) decreases stability, with a larger proportion of species liable to get extinct. Note that the May criterion was derived on the basis of local stability, whereas here we are considering the species' persistence, a measure of global stability.

Figure 1(a) shows the ratio of persistent species N_{pers} with respect to the initial number of species N. This ratio N_{pers}/N appears to vary as $1/N$ for large N. This indicates that the number of surviving species is independent of N. Agreement with Wigner-May stability results is also seen for the $1/C$ variation of the surviving fraction with connectivity [Fig. 1(b)]. Figure 1(c) shows that the fraction of survivors depend on the interaction strength parameter σ as $1/\sigma^z$ where the exponent z is an increasing function of the connectivity C. This dependence is expected because, if C is decreased while
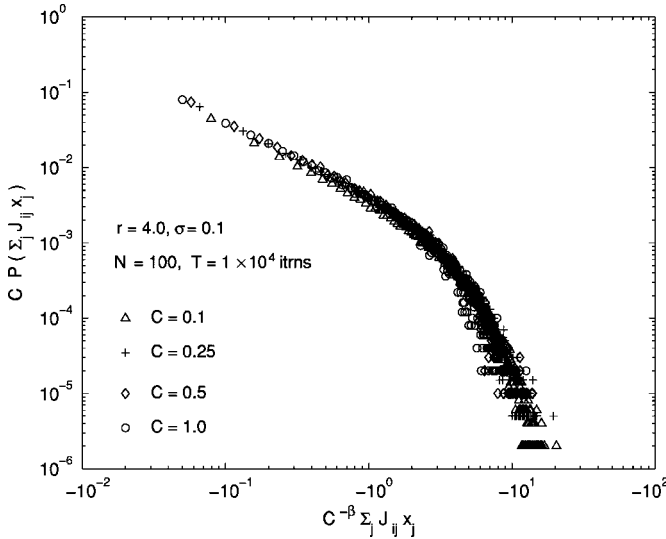
FIG. 2. The scaling of $\Sigma_j J_{ij}x_j$ with connectivity C for $N=100$, $\sigma=0.1$, and $r=4$. The data is obtained after 10^4 iterations and averaged over 5000 realizations.

FIG. 3. The scaling of $\Sigma_j J_{ij}x_j$ with σ, the standard deviation of normal distribution from which the connection weights are chosen ($N=100$, $C=1$, and $r=4$). The data is obtained after 10^4 iterations and averaged over 5000 realizations.

keeping N fixed, the effective number of other species that a species interacts with, is decreased. In the limit $C\rightarrow 0$, every species is independent of all other species, and will persist with probability 1. Finally, we display the survival fraction against the nonlinearity parameter r of the local map. It is clearly evident that one obtains a smooth monotonic variation of the survival fraction with respect to r [Fig. 1(d)]. This *a priori* may seem surprising, since the local map has a significant range of diverse dynamics including windows of periodic and chaotic behavior and this is not reflected at all in the figure.

To understand these results, we analyze the probability of survival of any species in the steady state. A species i will become extinct if its population x_i becomes negative at a particular time. By looking at the equations describing the system, one notes that this is only possible if $\Sigma_j J_{ij}x_j < -1$. Therefore, the probability of survival of a species is essentially equivalent to $P(\Sigma_j J_{ij}x_j > -1)$. The distribution of $P(\Sigma_j J_{ij}x_j)$ has a power-law distribution about its peak at zero, and Gaussian tails. We now scale this distribution with respect to the different network parameters, as scaling in nonequilibrium phenomena is the most sensitive and stringent test of universality.

Figure 2 shows the scaling of $P(\Sigma_j J_{ij}x_j)$ with the connectivity C which goes as $\sim C^{-1}g_c(C^{-\beta}\Sigma_j J_{ij}x_j)$, where g_c is the scaling function independent of C, implying $CP(\Sigma_j J_{ij}x_j > -1)\sim$ constant. Therefore, the probability of survival varies as $\sim 1/C$, in exact agreement with the results obtained from linear stability analysis. The exponent $\beta=0.2\pm 0.02$ for a wide range of values of σ and r. Similar agreement is seen for the variation of the probability of survival with σ (Fig. 3). The scaling data show that $P(\Sigma_j J_{ij}x_j)\sim \sigma^{-2}g_\sigma(\sigma^{-\alpha}\Sigma_j J_{ij}x_j)$, where g_σ is the scaling function, so that the survival probability varies as $\sim 1/\sigma^2$. The exponent α varies in the range 0.1–0.2, decreasing with r and with C.

The variation with the map nonlinearity parameter, however, has no analog in the previous work on random net-
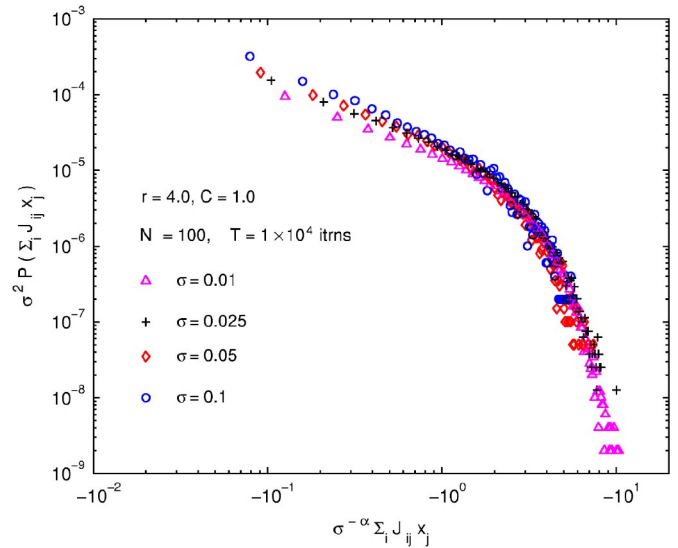
works. We observe that the relevant parameter is the image of the critical point of the map, rather than r itself. This point $x_r^{max}=e^{(r-1)}/r$ gives a measure of the width of the chaotic attractor [19]. Since this increases the interval over which the probability of $(\Sigma_j J_{ij}x_j)$ is observed, we have normalized the argument of the scaling function by dividing it by x_r^{max}. Figure 4 shows the scaling of $P(\Sigma_j J_{ij}x_j)$ $\sim (x_r^{max})^{-\gamma}g_r[(x_r^{max})^{-1}\Sigma_j J_{ij}x_j]$, where g_r is the scaling function. Therefore, the probability of survival varies as $(x_r^{max})^{-\gamma}$, with the exponent $\gamma=3.1\pm 0.1$ for a wide range of values of C and σ. Interestingly, when the local dynamics is given by the Bellows map, we again obtain $\gamma\sim 3$.
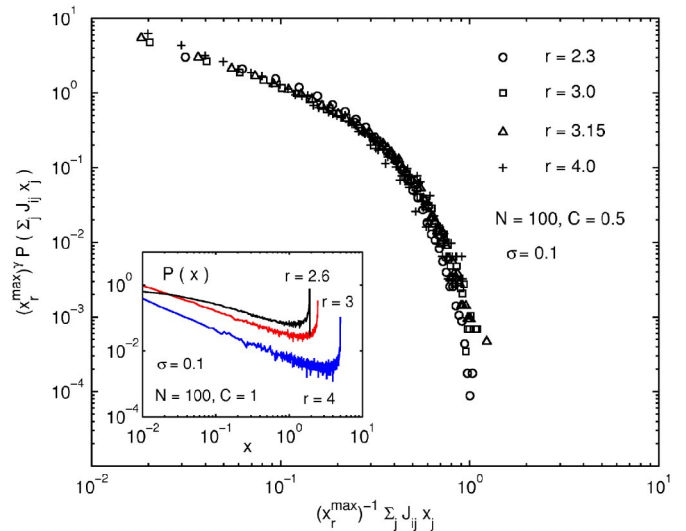

FIG. 4. The scaling of $\Sigma_j J_{ij}x_j$ with the width of the attractor x_r^{max} for $N=100$, $C=0.5$, and $\sigma=0.1$. The inset shows the power-law scaling behavior of the probability distribution of populations x ($N=100$, $C=1$, and $\sigma=0.1$). The data is obtained after 10^4 iterations and averaged over 5000 realizations.

The above scaling results show that the complexity-stability relations obtained by May hold true not only qualitatively, but also quantitatively, when we introduce explicit local dynamics of the network elements. The exact nonlinearity of the map, as would be reflected in, e.g., the Lyapunov exponent, does not enter any of the results, which suggests that these relations are universal and independent of details of the local dynamics. In addition, the results remain valid even if the local nonlinearity parameter r for all the N maps is not a constant, but varies according to a uniform random distribution between $r=2$ and $r=4$.

The power spectra of quantities such as the total system population, $\Sigma_{i=1}^{N} x_i$ (which can be identified with "biomass" in the ecological context), has a low-frequency scaling given by: $S(f) \sim f^{-\alpha}$ with $1 < \alpha < 2$. In addition, the distribution of populations $P(x)$ is a clear power law: $P(x) \sim x^{-\phi}$, with $\phi \sim 1$ for sufficiently high r (Fig. 4 inset) [20].

In summary, our work addresses one of the strong criticisms against the wider applicability of the May-Wigner results, namely their assumption of an equilibrium. Here we have a range of dynamics at the local level and certainly no dynamical equilibrium at the global level, as populations are always fluctuating. Rather, we have a nonequilibrium steady state where the survival fraction attains stationarity. The stability of our dynamically more complex network, however, still obeys the May criterion, and increasing complexity (in terms of size, connectivity, and interaction strength of the network) leads to greater instability, resulting in a larger proportion of species becoming extinct [21]. Scaling results of the probability distribution of the interaction term in the stationary state indicate that the stability of the network varies as $\sim 1/NC\sigma^2$, very much in agreement with the May-Wigner results. We also find that the stability of the network scales with the nonlinearity parameter of the local maps in a smooth monotonic fashion, with the relevant scaling variable being the maximum value that x can take (which depends monotonically on the nonlinearity). These observations hold for networks with widely varying local dynamics as well as for different updating and coupling schemes, underscoring a remarkable universality and increasing the scope of relevance of the May-Wigner stability theorem.

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