Are Scale-Free Networks Functionally Robust?

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This paper reexamines the claim that biological networks are robust due to their scale-free (SF) architecture, by presenting a basic and simple way to assess the role that this architecture plays in determining network robustness. Studying the error tolerance of the yeast protein-protein interaction network [7] to random node removal using the pertaining knockout data we show that it is only very marginally more robust than an equivalent Erdös-Rényi (ER) network, in contradistinction to the prevalent notion in the literature [2].

Albert et al. [2, 1] investigated the robustness of the two basic network models, the ER model [5] that produces a connectivity distribution with an exponential tail, and the SF model [3] with a power law tail. They quantified a network's tolerance to errors by characterizing the changes in its diameter and largest connected component while some of its nodes are being randomly removed. They found that SF networks display a markedly higher degree of robustness than ER ones, and reasoned that this is because power law distribution implies that the majority of nodes have only a few links, and thus nodes with small connectivity will be selected for removal with much

higher probability [2].

Our study of network robustness begins with the simple but basic observation that since comparable ER and SF networks consist of the same number of nodes and links, they have an identical mean rank (number of links of a node). Thus, if the damage to the network is *linearly* dependent upon a removed node's rank, the two networks will essentially exhibit the same level of error tolerance. A difference in the error tolerance of SF and ER networks will hence only take place if the damage as a function of a removed node's rank (the 'damage function', see Fig. 1) deviates from a linear function. As the power law connectivity distribution induces a larger variance of node ranks than an exponential one, then if the damage function is *concave*, SF networks will be more robust and vice versa if it is *convex*. Indeed, in the case of the structural measures studied by Albert et al., the decrease in the diameter and giant component size happens to be a concave function of the node's rank, resulting in the superior robustness of SF over ER networks.

While the behavior of structural indices may provide an important clue to network robustness, the main question is whether SF networks are indeed more *functionally* robust than ER ones. We study this fundamental question using the *Saccharomyces cerevisiae* protein-protein interaction (PPI) network [7], a SF network where the phenotypic effect of protein removal correlates strongly with its rank [8]. We regressed the proteins' essentiality [6] as a function of the rank (Fig. 1), and examined the concavity of the
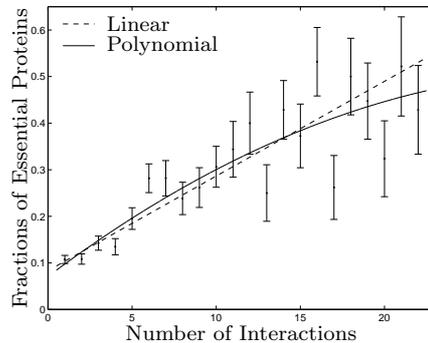
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Figure 1: The fraction of essential proteins (and standard error) versus their rank. Two regressions were applied to fit the data, using a line (dashed) and a second order polynomial (solid). Both regressors are based on a two-stage least squares regression for binary variables [4].

resulting regression function. While a linear regression is very significant (p-value $< 10^{-300}$), the addition of a second order term to the regression leads to a slightly concave polynomial regression but is, alas, borderline insignificant (p-value $= 0.073$).

To further study the functional robustness of the PPI SF network, we generated a SF network based on a preferential attachment model [3] and an ER network [5], both with the same number of nodes $(4, 718)$ and links $(15, 128)$ as in the PPI network. The level of damage to a network upon a node removal is the fraction of lethal outcomes upon the removal of nodes with that rank in the PPI data.[1] The mean damage when randomly removing a node in the ER network is 0.23 (standard error of 0.001) and 0.21 (0.0014) in the SF network. This statistically significant difference (p-value $< 10^{-300}$)

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[1] If there are no nodes with that rank in the PPI network, the closest rank is taken. This is the case for only 8 nodes in the ER network and for only 9 nodes in the SF one.

is very small.

In summary, this study makes two basic contributions: First, methodologically, we present a general way to examine the role of the SF architecture in determining a network's robustness by carefully studying the shape of its damage function. Second, we show that the available lethality data concerning the PPI network (addressed originally in [8]) do not support the prevalent view that SF networks are *functionally* more robust than ER ones; their relative robustness is either fairly minor (according to one test) or insignificant (according to the other). One should hence not hasten to make the conceptual leap between structural and functional robustness. It may well be that SF networks are prevalent in biological systems because of reasons other than robustness.

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