

Complex networks: two ways to be robust?

Carlos J. Melián* and Jordi Bascompte
 Integrative Ecology Group,
 Estación Biológica de Doñana,
 CSIC Apdo. 1056, E-41013
 Sevilla, Spain
 *Correspondence: E-mail:
 cmelian@ebd.csic.es

Abstract

Recent studies of biological networks have focused on the distribution of the number of links per node. However, the connectivity distribution does not uncover all the complexity of their topology. Here, we analyse the relation between the connectivity of a species and the average connectivity of its nearest neighbours in three of the most resolved community food webs. We compare the pattern arising with the one recently reported for protein networks and for a simple null model of a random network. Whereas two highly connected nodes are unlikely to be connected between each other in protein networks, the reverse happens in food webs. We discuss this difference in organization in relation to the robustness of biological networks to different types of perturbation.

Keywords

Complex networks, food webs, protein networks, randomly assembled networks, topology.

Ecology Letters (2002) 5: 705–708

INTRODUCTION

With the recent growth of empirical information, biological networks are becoming better resolved. This empirical work is providing insight into how these complex networks are assembled and how they remain stable to deleterious perturbations (Albert *et al.* 2000; Williams & Martinez 2000; Solé & Montoya 2001). Previous studies of biological networks have focused on the connectivity distribution, that is, the probability density distribution of the number of links per node. This connectivity distribution has been shown to have longer tails than would be expected for an exponential distribution, meaning that some species may be extremely connected and that the network is very heterogeneous (Ulanowicz & Wolff 1991; Amaral *et al.* 2000; Jeong *et al.* 2000; Montoya & Solé 2002; Jordano, Bascompte & Olesen, unpublished Ms; see however, Camacho *et al.* 2002 and Dunne *et al.* 2002a). However, the connectivity distribution does not necessarily capture all the topological complexity of biological networks (Dorogovtsev & Mendes 2002). A first step towards a more detailed characterization of biological networks concerns the study of connectivity correlation, that is, the relation between the number of interactions of a node and the average connectivity of its nearest neighbours (Krapivsky & Redner 2001).

Recently, Internet and protein networks have been analysed by plotting their connectivity correlation (Pastor-Satorras *et al.* 2001; Maslov & Sneppen 2002), a method

never used before in ecology. Two types of protein networks have been analysed: physical interaction, and transcription regulatory networks. Protein connectivity represents the fraction of pairs of proteins that interact, forming a network with functional and structural relationships (Maslov & Sneppen 2002). Here, we analyse the connectivity correlation in three of the most resolved community food webs to date and compare the arising pattern with that recently reported for protein networks. Protein networks show an inverse relationship between the connectivity of a node and the average connectivity of its nearest neighbours. That is, neighbours of highly connected proteins have low connectivity and, similarly, low connected proteins are connected with highly connected proteins. This means that links between highly connected proteins are systematically suppressed. That is, the network is compartmentalized in sub-networks organized around a highly connected node with few links among such sub-networks (Maslov & Sneppen 2002).

In this paper we first study the connectivity correlation in food webs, and compare the observed pattern with characteristic values for protein networks. We discuss differences between both types of networks in relation to their robustness to perturbations.

METHODS

Connectivity correlation (Fig. 1a) is best represented by the conditional probability $P_c(k'|k)$, which defines the

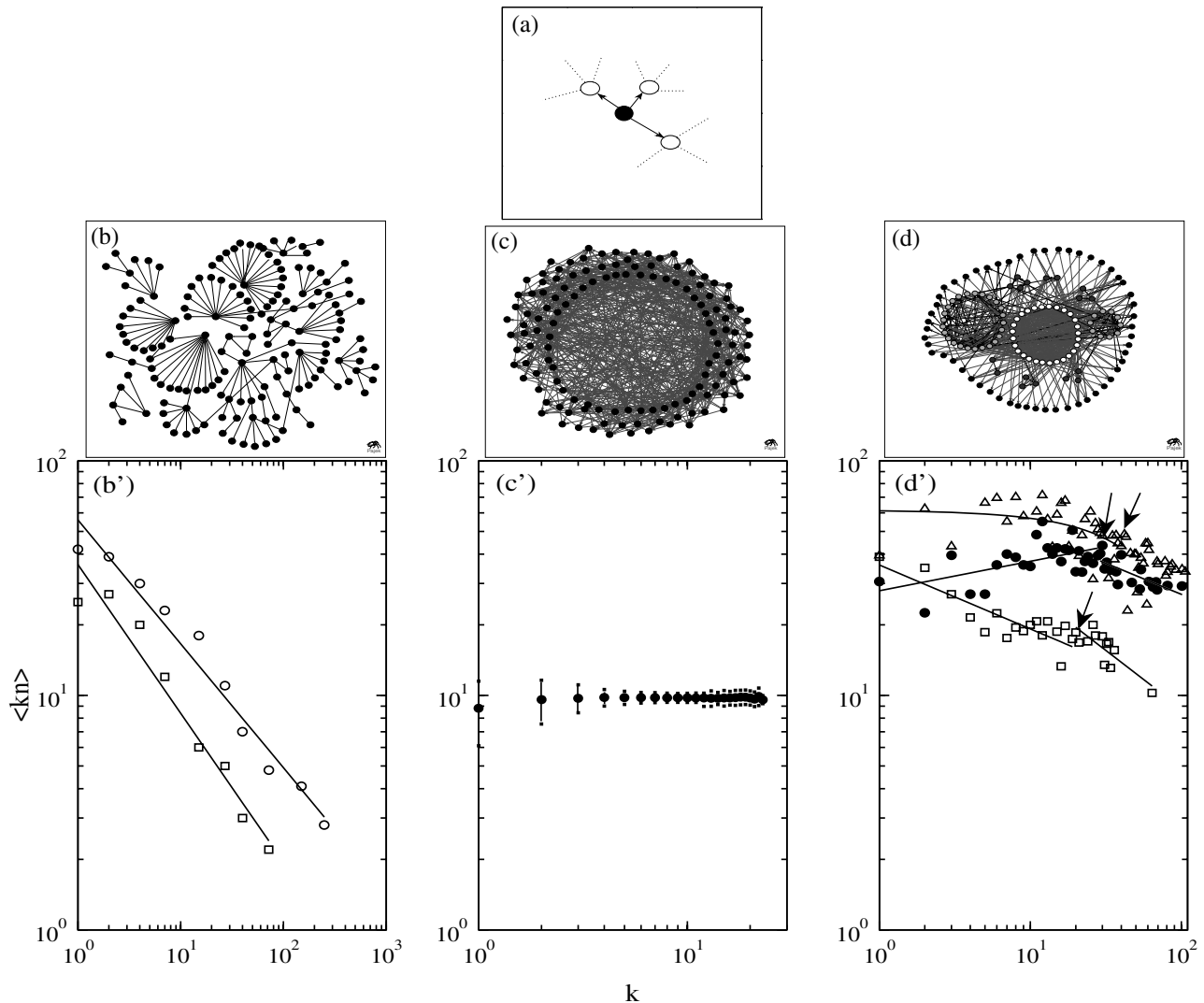


Figure 1 (a) A hypothetical food web graph. The average connectivity of the neighbours of the black node with $k = 3$ links is $\langle k_n \rangle = 4$. (b) A subset of the network of physical interactions between nuclear proteins (modified from Maslov & Sneppen 2002); (c) a single random replicate of the Ythan Estuary food web, and (d) the graph of the Ythan Estuary food web. (b') The average connectivity $\langle k_n \rangle$ of the neighbours of a link with connectivity k as a function of k in interaction (○) and regulatory (□) protein networks; (c') the average and standard deviation of 1000 randomly assembled networks; and (d') the average connectivity of food webs (Little Rock Lake (△) (Martinez 1991); El Verde (●) (Reagan & Waide 1996); and Ythan Estuary (□) (Huxham *et al.* 1996)). Arrows point to the threshold in connectivity (k_c) where a significant shift in the relationship appears. Note that links between highly connected proteins are systematically suppressed, generating a compartmentalized network (b and b'), whereas links between highly connected species are common in food webs, generating a cohesive network (d and d'). Randomly assembled networks show uncorrelated connectivity (c and c'). The network visualization was carried out using the PAJEK program for large network analysis: http://vlado.fmf.uni-lj.si/pub/networks/pajek/pajekman.htm.

probability that a link belonging to species with connectivity k points to a species with connectivity k' . If $P_c(k'|k)$ is independent of k , there is no correlation among species' connectivity. The average connectivity ($\langle k_n \rangle$) of the species directly connected (nearest neighbours) to a species with connectivity k can be expressed as:

$$\langle k_n \rangle = \sum_{k'} k' P_c(k'|k). \quad (1)$$

To detect shifts in the relationship between the connectivity of a node (k) and the average connectivity of its nearest neighbours ($\langle k_n \rangle$) we used split-line regression

(Schmid *et al.* 1994; Bersier & Sugihara 1997). Provided that a shift was detected in the slope of the regression, the threshold value (k_c) was calculated, and the data were divided into two groups: one including the data with values below the threshold, and the other including the rest of the data. Different subsets are thus determined in base to significant differences in the slope of the regression. As a benchmark to compare the connectivity correlation pattern we generated 1000 randomly assembled networks with the same number of species and connectivity in a similar way to Newman *et al.* (2001). For species with connectivity k we calculated the average connectivity and standard deviation of the nearest neighbours across all generated networks. The basic rules operating in the assemblage process were as follows.

- 1 At time $t = 0$, n_0 nodes with $n_0 - 1$ links each were created.
- 2 At each time step, a new node was added to the network, and ingoing and outgoing links with nodes already present were established with the same probability. That is, a link between two nodes was treated as a random event, independent of the presence of other links.

Although some patterns may depend on the choice of the nature of the links considered (ingoing links, outgoing links, or both; Camacho *et al.* 2002; Montoya & Solé 2002), in this paper we consider both ingoing and outgoing links following the analysis by Maslov & Sneppen (2002). We can thus directly compare our results with the ones observed for protein networks. Also, the results presented here are based on binary interactions. Future work will determine to what extent results based on binary interactions stand when quantitative information (i.e. interaction strength) is incorporated (Ulanowicz & Wolff 1991; Ulanowicz 2002).

RESULTS

The three types of network compared here differed in their internal topology (see Fig. 1). For both interaction and regulatory protein networks (Fig. 1b) correlation existed across all domains of connectivity (k), with connectivity correlation ($\langle k_n \rangle$) decaying as a power law $\langle k_n \rangle \propto k^{-0.6}$ (Maslov & Sneppen 2002; Fig. 1b'). On the other hand, randomly assembled networks (Fig. 1c) showed uncorrelated connectivity across all the domain of connectivity, that is, an absence of correlation between a species connectivity and the average connectivity of its nearest neighbours (Fig. 1c').

In contrast to protein and random networks, food webs (Fig. 1d) showed a connectivity threshold k_c in the response of $\langle k_n \rangle$ with increasing k ($k_c=19$ interactions for Ythan Estuary; $k_c=39$ for Little Rock Lake; and $k_c=28$ for El

Verde, Fig. 1d'). That is, food webs had two different domains with significantly different slopes across the range of values of species' connectivity. Specifically, both of Ythan Estuary's subsets best fit a power law ($P < 0.05$), with slopes of -0.27 and -0.49 above and below the threshold, respectively; Little Rock Lake's first subset best fits a linear regression ($P < 0.05$) with a slope of -0.48 ; the relationship is nonsignificant below the threshold; El Verde best fits a power law ($P < 0.05$) in both subsets with slopes of 0.12 and -0.26 above and below the threshold, respectively.

The above pattern suggests the existence of two assembly patterns at different scales of connectivity. In the first domain, connectivity of the nearest neighbours either decays very slowly or does not decay at all with k . In the second domain, $\langle k_n \rangle$ decays with k in a similar way to that found for protein networks. Globally, the average connectivity of the nearest neighbours does not decay as fast with the connectivity of a focal node as in protein networks.

SUMMARY AND DISCUSSION

The internal topology of the two types of biological network compared here depart from randomly assembled networks. Interaction and regulatory protein networks are structured so that two highly connected nodes are not connected to each other. The distribution of connections is highly heterogeneous, the network being organized as a series of highly connected nodes isolated from each other. In other words, the network is compartmentalized.

Recent papers on complex networks have studied the robustness of a network with regard to two different types of perturbation: robustness to the spread of a deleterious mutation (Maslov & Sneppen 2002), and robustness to the fragmentation of the network as an increasing number of nodes is deleted (Albert *et al.* 2000; Solé & Montoya 2001; Dunne *et al.* 2002b). How is the connectivity correlation pattern observed for food webs related to these two types of robustness?

As suggested by Maslov & Sneppen (2002) the compartmentalized pattern observed in protein networks increases the overall robustness of the network by isolating the cascading effects of deleterious mutations. In contrast, the food webs studied here have a pattern that is neither similar to the structure of randomly assembled webs, nor similar to protein networks. Food webs show two well-defined domains in the connectivity correlation distribution. In contrast to protein networks, two highly connected species within a food web are likely to interact among each other. This is likely to decrease the level of compartmentalization, a traditional concept in food web studies (Pimm & Lawton 1980). In this regard, food webs are likely to be more susceptible to the spread of a contaminant. However, the connectivity correlation pattern here described for food

webs, with their low level of compartmentalization (densely connected species connected to each other), may confer on them a higher resistance to fragmentation if a fraction of the species were removed. Thus, there are different ways of being robust related to different types of perturbations.

Previous authors have explored the effect of the connectivity distribution on the resistance of complex networks to fragmentation (Albert *et al.* 2000; Solé & Montoya 2001; Dunne *et al.* 2002b). However, a given connectivity distribution may be organized in different patterns of connectivity correlation. Our results build on previous work focusing on connectivity distribution patterns by pointing out that the pattern of connectivity correlation may also be important for understanding how food webs respond to perturbations. We suggest that the connectivity correlation provides an additional characterization of both the structure of food webs and their susceptibility to perturbations. Further work based on assembly models of biological networks incorporating both qualitative and quantitative information (Ulanowicz 2002) will give more insight into the relationship between connectivity distribution, connectivity correlation, and their importance to network responses to disturbances.

Through this and related papers we have looked at structural properties of food webs and their influence on the network response to perturbations. This work complements traditional theoretical approaches based on the stability of linearized dynamical systems (May 1972; Rozdilsky & Stone 2001). Further work is needed to integrate these two perspectives.

In summary, the pattern of connectivity correlation of complex networks reveals intrinsic features of their topology. The suppression of links between highly connected proteins, but their presence in food webs, reflects both differences in their structure and in their response to different perturbations.

ACKNOWLEDGEMENTS

We thank Pedro Jordano, Sandy Liebhold, and Miguel Angel Rodríguez for useful comments on a previous draft. Funding was provided by the Spanish Ministry of Science and Technology (Grant BOS2000-1366-C02-02 to J. B and Ph.D. Fellowship FP2000-6137 to C. J. M).

REFERENCES

- Albert, R., Jeong, H. & Barabasi, A.-L. (2000). Error and attack tolerance of complex networks. *Nature*, 406, 378–382.
- Amaral, L.A., Scala, A., Barthélemy, M. & Stanley, H.E. (2000). Classes of small-world networks. *Proc. Nat. Acad. Sci.*, 97, 11149–11152.
- Bersier, L.-F. & Sugihara, G. (1997). Scaling regions for food web properties. *Proc. Nat. Acad. Sci.*, 94, 1247–1251.
- Camacho, J., Guimera, R. & Amaral, L.A. (2002). Robust patterns in food web structure. *Phys. Rev. Lett.*, 88, 228102.
- Dorogovtsev, S.N. & Mendes, J.F.F. (2002). Evolution of networks. *Adv. Phys.*, 51, 1079.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002a). Small networks but not small worlds: unique aspects of food web structure. *Proc. Nat. Acad. Sci.*, in press.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002b). Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.*, 5, 558–567.
- Huxham, M., Beaney, S. & Raffaelli, D. (1996). Do parasites reduce the changes of triangulation in a real food web? *Oikos*, 76, 284–300.
- Jeong, H., Tombor, B., Albert, R., Oltvai, Z.N. & Barabasi, A.-L. (2000). The large-scale organization of metabolic networks. *Nature*, 407, 651–654.
- Krapivsky, P.L. & Redner, S. (2001). Organization of growing random networks. *Phys. Rev. E*, 63, 066123.
- Martinez, N.D. (1991). Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecol. Monogr.*, 61, 367–392.
- Maslov, S. & Sneppen, K. (2002). Specificity and stability in topology of protein networks. *Science*, 296, 910–913.
- May, R.M. (1972). Will a large complex system be stable? *Nature*, 238, 413–414.
- Montoya, J.M. & Solé, R.V. (2002). Small world pattern in food webs. *J. Theor. Biol.*, 214, 405–412.
- Newman, M.E.J., Strogatz, S.H. & Watts, D.J. (2001). Random graphs with arbitrary degree distributions and their applications. *Phys. Rev. E*, 64, U153–U168.
- Pastor-Satorras, R., Vazquez, A. & Vespignani, A. (2001). Dynamical and correlation properties of the Internet. *Phys. Rev. Lett.*, 87, 258701.
- Pimm, S.L. & Lawton, J.H. (1980). Are food webs divided into compartments? *J. Anim. Ecol.*, 49, 879–898.
- Reagan, D.P. & Waide, R.B. (1996). *The Food Web of a Tropical Rain Forest*. University of Chicago Press.
- Rozdilsky, I.D. & Stone, L. (2001). Complexity can enhance stability in competitive systems. *Ecol. Lett.*, 4, 397–400.
- Schmid, B., Polasek, W., Weiner, J., Krause, A. & Stoll, P. (1994). Modeling of discontinuous relationships in biology with censored regression. *Am. Nat.*, 143, 494–507.
- Solé, R.V. & Montoya, J.M. (2001). Complexity and fragility in ecological networks. *Proc. Roy. Soc. B*, 268, 2039–2045.
- Ulanowicz, R.E. (2002). The balance between adaptability and adaptation. *BioSystems*, 64, 13–22.
- Ulanowicz, R.E. & Wolff, W.F. (1991). Ecosystem flow networks: loaded dice? *Math. Biosci.*, 103, 45–68.
- Williams, R.J. & Martinez, N.D. (2000). Simple rules yield complex food webs. *Nature*, 404, 180–183.

Editor, P. J. Morin

Manuscript received 25 May 2002

First decision made 22 August 2002

Manuscript accepted 28 August 2002