The trophic coherence of networks: Diversity and stability reconciled?

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Will a large, complex system be stable? Robert May asked this question in 1972, and showed that the answer was, in general, no – at least if the interactions between elements were randomly placed.[1] In the case of ecosystems, as well as financial and other complex systems, both received wisdom and empirical research suggested that size and link density increased stability, so the result became known as May's Paradox. In ecology the "diversity-stability debate" rages on, and it has often be conjectured that large, complex (i.e., dense) ecosystems are stable thanks to some unidentified structural property.[2]

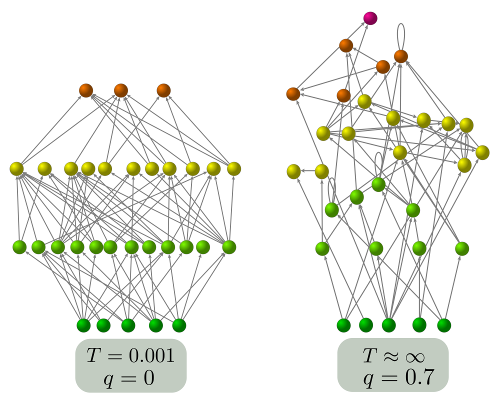

FIG. 1. Networks generated with the Preferential Preying Model (PPM), using the number of species and links of the Chesapeake Bay food web, for $T = 0.001$ (left) and $T = 10$ (right). The height of nodes represents their *trophic level*, defined for each node as the mean trophic level of its incoming nodes (e.g., prey), plus one. The network on the left has maximum trophic coherence, while the one on the right is highly incoherent; the parameter q captures this.

We show that *trophic coherence* – a hitherto ignored feature of food webs which current structural models fail to reproduce – is significantly correlated with ecosystem stability, whereas size and link density are not.[3] Together with cannibalism, trophic coherence accounts for over 80% of the variance in stability observed in a 16-food-web dataset. We propose the Preferential Preying Model (PPM), whose single free parameter, T, sets the degree of trophic coherence. For $T \simeq 0$ we obtain maximally coherent networks (left panel of Fig. 1), whereas very incoherent structures (similar to those produced by current food-web models) ensue from a high T (right panel of Fig. 1). By adjusting T to the empirical coherence of food webs, the PPM predicts their stability much more accurately than do other models, and is at least as successful as regards all other structural features analysed.

Most remarkably, the PPM shows that stability can increase with size and link density if networks are sufficiently coherent. As shown in Fig. 2, while for high T stability decreases with size and density according to the May-Wigner law, as in other food-web models, below a certain value of T the size-stability relationship is inverted. This suggests that it is trophic coherence which accounts for the high stability of large, dense ecosystems – such as rainforests or coral reefs – and may be significant for other complex dynamical systems. This result raises the concern that loss of a few elements (e.g., species or banks) could push a system into a regime of inherent instability. On the other hand, it may provide a way of diagnosing the risk of such a "tipping point".

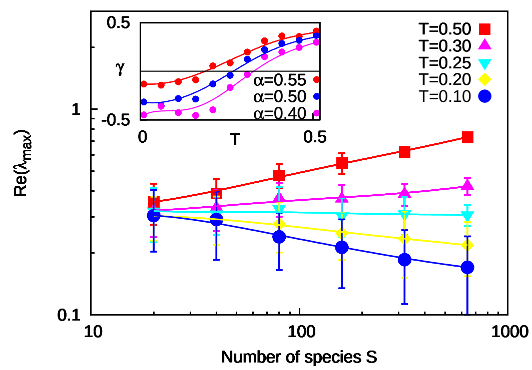

FIG. 2. Real part of the leading eigenvalue of the interaction matrix, $Re(\lambda_{max})$, against number of nodes, S, for networks generated with the PPM for different values of the parameter T. $Re(\lambda_{max})$ is the degree of self-regulation (e.g., intra-species competition in an ecosystem) required for the system to be (locally) stable; thus, the lower $Re(\lambda_{max})$, the more stable we consider the network. The density of links (complexity), K, is $K = S^{\alpha}$, with $\alpha = 0.5$ as recent estimates find for food webs. Inset: Slope of the stability-size curve, γ, against T for different exponents α.

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[1] R.M. May, "Will a large complex system be stable?" *Nature* **238**, 413–4 (1972)
[2] K.S. McCann, "The diversity-stability debate," *Nature* **405** 228–33 (2000).
[3] S. Johnson, V. Domínguez-García, and M.A. Muñoz, "The trophic coherence of food webs: Diversity and stability reconciled?," submitted to *Nature* (under review).