IJCSS International Journal of Complex Systems in Science

Int. J. Complex Systems in Science
vol. **1(2)** (2011), pp. 179–182

How robust are pollination networks?: an assessment using alpine pollination and simulated networks

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Abstract. High robustness of complex ecological systems in the face of species extinction has been hypothesized on the redundancy in species. We explored how differences in network topology may affect robustness. We created synthetic networks to study the influence of the properties of asymmetry of network dimensions, connectance and type of degree distribution on network robustness. In synthetic and pollination networks, we used two extinction strategies: node extinction and link extinction, and we simulated three extinction scenarios differing in the order of species removal (least-to-most connected, random, most-to-least connected), to evaluate the robustness of 10 alpine pollination networks. In addition, we assessed robustness to extinction of simulated networks, which differed in one of the three topological features. Our study indicated that robustness of alpine pollination networks is dependent on the topology of each network. Simulated networks indicated that robustness increases when (a) extinction involved those nodes belonging to the most species-rich trophic level and (b) networks had higher connectance. We also compared simulated networks with different degree-distribution networks, and they showed important differences in robustness depending on the extinction scenario. In the link extinction strategy, the robustness of synthetic networks was clearly determined by the asymmetry in the network dimensions, while the variation in connectance produced negligible differences.

Keywords: Network, Ecology, Robustness, Asymmetry, Connectance, Degree-Distribution
MSC 2000: 05C80, 90C35, 05C90

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Received: October 17, 2011
Published: October 24, 2011

1. Introduction

The recent network approach to biotic interactions has provided new tools for the old problem of assessing robustness of complex ecological systems in the face of species extinction. In a seminal work, Albert et al. [1] evaluated the tolerance of two networks (Internet and WWW) to the extinction of their nodes. They found high robustness when nodes were removed at random but extreme fragility when node removal was ordered from the most to the least connected node.

In this work we evaluate these ideas in plant-pollinator networks. From a complex network point of view, a pollinator network is a bipartite network because it consists of two subsets of nodes: pollinators and plants. In plant-pollinator interaction networks few studies have addressed the robustness theoretically or empirically [2]. Memmot et al. concluded that pollination networks were relatively robust because of their asymmetry in network dimensions and their nested interactions pattern. Here, we provide a broader assessment of robustness for alpine pollination networks and explore how differences in network structure may affect robustness.

2. Methods

We analyzed a set of 10 binary alpine pollination networks (APN). In order to quantify the effect of asymmetry in network dimensions, connectance (C) and degree distribution we created simulated networks which differed in one of three network topological features. Asymmetry in network dimensions is the ratio of animal (A) to plant (P) species involved in a pollination network. Connectance is the percentage of non-zero values, i.e., it is the fraction of actually observed interactions of all possible interactions. Degree distribution refers to the distribution of connectivity or degree (number of links per node) in a network. We created Poisson random bipartite networks with the same size (10000 potential links) and modified either asymmetry in network dimensions, or connectance, C. First, we fixed $C = 12\%$ (the average of the 51 real networks) and explored a wide range of pollinator:plant ratios. Second, for a symmetric matrix we explored four levels of connectance: 5, 10, 30 and 60%. In order to assess the effect of the degree distribution type on robustness we chose power law and exponential degree distributions and we compared each of them with Poisson networks with identical asymmetry and connectance. The results have been averaged over 100 simulations.

Robustness evaluation was carried out by assessing the proportion of "secondary extinctions" caused by the accumulation of "primary extinctions" [2].

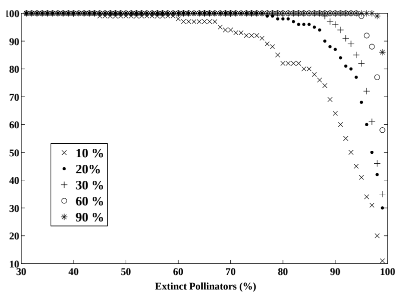
Both real and random networks were virtually subjected to two different extinction scenarios to explore the possible variability in pollination networks responses to robustness assessment.

Node extinction scenario. It includes three sequences of nodes removal which consist in the primary species extinction in one of the two trophic levels (plants or pollinators) to observe the number of secondary extinctions that occur in the other.

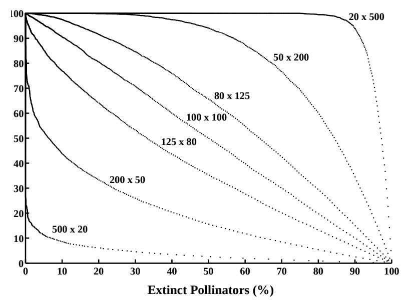
Link extinction scenario. In this scenario we removed links between species. The species (plant or pollinator) will become extinct when it loses all its links. The logic behind this scenario is that in the gradual decline in both plant and pollinator species abundance links disappear before the total extinction of the involved species.

3. Results

In general, APN robustness was dependent on the extinction scenario and decreased in the order least-to-most > random > most-to-least. As expected, higher connectances led to higher robustness.



(a) Extinction patterns removing nodes with different connectance



(b) Extinction patterns removing links with different asymmetries

In synthetic networks, for all values of asymmetry and connectance tested, robustness was consistently highest in the least-to-most sequence, middle in the random and lowest in the most-to-least sequence. These simulated networks exhibited the same behavior as APN networks: Robustness increased with increases asymmetry and also with the connectance. In Fig. (a) the random extinction scenario is depicted for five different connectances, from 10% to 90%. The simulated Power law network was less robust than its corresponding Poisson network in the most-to-least extinction sequence. In the least-to-most extinction sequence the opposite happened. The simulated Exponential network was less robust than its corresponding Poisson network, for the most-to-least and random extinction sequence.

Links extinction scenario produced extinction patterns qualitatively different from the node extinction scenario. The main difference between node and link extinction is the uniformity in the three extinction sequences. In general, APN were less robust in the link-extinction scenario than in the node-extinction scenario. Furthermore the asymmetry effect was greater in this new scenario. In this case the extinctions affect simultaneously both plants and pollinators, so extinction curves depicts this effect, as it can be seen in Figure (b). For a symmetric network both type of species become extinct consecutively, independently of the connectance.

4. Conclusions

The variability in robustness found in empirical APN suggests that robustness depends on network structure. Simulated networks clearly showed the protective effect of increasing asymmetry. Simulated networks confirmed that higher connectance leads to increased robustness of bipartite networks, but greater differences between scenarios coincide with the most skewed distributions. This heterogeneous degree distribution will determine a major interactor redundancy when node deletion begins from the least connected species. In the case of links removal APN are less robust than in node removing. Indeed, in symmetric networks the extinction patterns always follow the matrix diagonal. In summary, links removal shows clearly the dependence of robustness on asymmetry. This scenario, more realistic than node removal, involves more dependence between the two subsets of species in the extinction sequence.

Acknowledgements

We thank authors of database for making their data available and people of R.J.C University for their field work and specilists for insect identification of the network SANT. This work was supported by the project URJC-CM-2007-CET-1620, by the project 014/2009 from the Organismo Autónomo de Parques Nacionales (Spain), and by MODELICO-CM/S2009ESP-1691.

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