EFFECTS OF TOPOLOGY ON ROBUSTNESS IN ECOLOGICAL BIPARTITE NETWORKS

Juan Manuel Pastor

Dept. Ciencia y Tecnología Aplicada a la I.T. Agrícola, and Grupo de Sistemas Complejos
Universidad Politécnica de Madrid, 28040-Madrid, Spain

Silvia Santamaría

Área de Biodiversidad y Conservación
Universidad Rey Juan Carlos, Móstoles, Spain

Marcos Méndez

Área de Biodiversidad y Conservación
Universidad Rey Juan Carlos, Móstoles, Spain

Javier Galeano

Dept. Ciencia y Tecnología Aplicada a la I.T. Agrícola, and Grupo de Sistemas Complejos
Universidad Politécnica de Madrid, 28040-Madrid, Spain

Abstract. High robustness of complex ecological systems in the face of species extinction has been hypothesized based on the redundancy in species. We explored how differences in network topology may affect robustness. Ecological bipartite networks used to be small, asymmetric and sparse matrices. We created synthetic networks to study the influence of the properties of network dimensions asymmetry, connectance and type of degree distribution on network robustness. We used two extinction strategies: node extinction and link extinction, and three extinction sequences differing in the order of species removal (least-to-most connected, random, most-to-least connected). We assessed robustness to extinction of simulated networks, which differed in one of the three topological features. Simulated networks indicated that robustness decreases when (a) extinction involved those nodes belonging to the most species-rich guild and (b) networks had lower 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.

1. **Introduction.** During the last decade, improvements in computing and the development of network analysis have allowed a qualitative advance in understanding the structure, function and robustness of complex networks. In a seminal work, Albert and Barabasi [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 (called 'errors') but extreme fragility when node removal was ordered from the most to the least connected node (called 'attacks'). They explained these contrasting results as a consequence of a highly heterogeneous degree

distribution of links among nodes, corresponding to a power law function. Albert and Barabasi's work [1] encouraged the assessment of the relationship between degree distribution and robustness of complex networks in several fields, from power distribution [22] to genetics [21] or ecology [24]. Patterns shown by Albert et al. [1] also apply to skewed degree distributions, not only to power law ones [6] and robustness increases with increases in connectance [6, 7], i.e., the proportion of observed interactions from the total possible in the network. Other works focus on cascade-based attacks [17, 13] study the vulnerability of real unipartite networks when the loads of nodes can be redistributed in case of intentional attacks. In ecology, robustness of ecological networks is focused on species extinctions [16, 12].

Our interest is focused on robustness in ecological networks, in particular, in mutualistic networks. Ecological mutualistic networks are formed by two type of species. In these relationships both species benefit from the interaction, and it is considered that there is not interaction between species of the same type. For example, in plant-pollinator interactions a pollinator feeds on a plant and the plant get its pollen dispersed by the pollinator. Thus, this type of ecological network is bipartite. This type of networks can show special features different from unipartite networks. For example, considering sexual contact network as bipartite (heterosexual contacts) leads to different epidemic threshold in the spreading of sexually transmitted diseases [10].

Despite a substantial increase in the understanding of the structure of empirical ecological networks (reviewed in [3]), few studies have addressed the robustness and its relation with the network structure [16, 12]. These empirical studies, based on a few networks, have concluded that mutualistic networks were relatively robust because of their asymmetry in network dimensions (for example, redundancy in number of floral visitors per plant) and their nested interactions pattern.

Memmott et al. [16] and Kaiser-Bunbury et al. [12] constitute a very valuable first step but fall short of allowing any general claim about pollinator network robustness. Among other gaps, understanding of how differences in network structure may affect robustness is lacking for bipartite networks. Here, we provide a broader assessment of robustness for pollination networks and explore how differences in network structure may affect robustness.

In large unipartite networks one can study the 'diameter', cluster distribution evolution in the extinction sequence, or relative size of the largest cluster and isolated clusters as a function of the fraction of removed nodes [1]. However, ecological bipartite networks are represented by small (typically less than 100 nodes), asymmetric and sparse matrices. For example, typical mutualistic networks have about 10% of possible links [19]. Moreover the degree distributions of rows or columns are heterogeneous, mainly power-law or truncated power-laws [11]. In this work we evaluate these ideas in simulated bipartite random networks controlling key structural features which allow us to directly assess their influence on bipartite network robustness. A companion paper, to be published elsewhere, will address robustness in empirical alpine plant-pollinator networks[23].

The overall aim of this study is to determine the effect of topology of bipartite network structure on robustness and, in particular, the robustness of mutualistic networks to species extinction and to interaction extinction.

2. **Methods.** In ecological mutualistic networks, robustness evaluation has been carried out by assessing the proportion of 'secondary extinctions' caused by the

accumulation of 'primary extinctions', following the tradition of simulation studies in (unipartite) food webs [7, 2] and its adaptation to bipartite pollination networks by Memmott et al. [16]. This approach assumes that a species becomes secondarily extinct as a result of having lost all their mutualistic interactions. In this paper, we quantified network robustness by modifying a common index for food webs, R50, which should facilitate future comparisons. Adapted to (bipartite) plant-pollinator networks, R50 is the percentage of primary species extinctions that have to occur in order to result in 50% of secondary extinctions [6]. For example, in plant-pollinator networks, R50 ranks from 100 (maximum robustness) to $100/A$ (minimum plant robustness) or $100/P$ (minimum pollinator robustness), where A is the number of animals species and P is the number of plant species. In addition, we introduce a new method of assessing robustness, based on link, not node, extinction (see below).

2.1. **Simulated networks.** We created simulated bipartite networks which differed in one of three network structural features: (i) Asymmetry in network dimensions, (ii) Connectance and (iii) Degree distribution. A short description of each feature and its relevance for networks follows. Asymmetry (A) is the ratio between matrix dimensions, i.e., $N_r : N_c$, where N_r is the number of rows and N_c is the number of columns. Connectance (C) is the percentage of non-zero values in the distribution of the number of links which connect the elements in a system [9] (equivalent to the occupation probability p in Random-Graph Theory). This parameter has long been used as an indicator of ecological network complexity and its influence on stability has been extensively discussed for food webs [6, 15, 14, 26]. Applied to bipartite networks, it is the fraction of actually observed mutualistic interactions (I) of all possible $N_r \times N_c$ interactions: $C(\%) = I/(N_r \times N_c) \times 100$. Although a high correlation between connectance and several other indices such as nestedness, degree distribution, dependence asymmetry, and extinction slope has been found for bipartite networks [5], the relationship between connectance and robustness has been tested only for unipartite networks [6].

Degree distribution refers to the distribution of connectivity or degree (number of links per node) in a network. Jordano et al. [11] found that most of the mutualistic ecological networks show a power-law or truncated power-law species degree distribution, differing from random assembled networks, which show Poisson degree distribution. Numerous studies based on simulations of extinction sequences suggest the existence of a relationship between degree distribution type and network robustness [1, 24, 6, 16, 4, 25]. However this relationship have not been tested for bipartite networks.

By way of null model, we created Poisson random bipartite networks with the same size (10000 potential interactions) and modified either asymmetry in network dimensions, or connectance, C. Firstly, we fixed C = 12% (the average of the 51 networks analyzed by Olesen et al. [20]) and explored seven values of asymmetries, 25:1, 4:1, 1.6:1, 1:1, 1:1.6, 1:4 and 1:25 respectively. Secondly, for symmetric matrix dimension we explored five levels of connectance: 10, 20, 30, 60 and 90%. In order to assess the effect of the degree distribution type on robustness we chose power-law and exponential degree distributions, which represent the two extreme cases found for empirical pollination networks [11]. In these skewed distributions, size could not be fixed to 10000 potential interactions due to the impossibility of simultaneously achieve a given degree distribution while keeping other network parameters unmodified. In total, we created 15 types of networks. Random networks have been averaged over 100 simulations. This set of simulated networks includes

the range of values for each feature which can take real mutualistic networks. They also extended it so that it is possible to detect the effect of the bipartite network structure on robustness beyond what it is possible using only realistic networks.

2.2. **Extinction scenarios.** Simulated networks were virtually subjected to two different extinction scenarios with three different sequences to explore the possible variability in mutualistic networks responses to robustness assessment.

Node extinction scenario. In node-extinction scenario we remove nodes, as 'primary extinctions' and evaluate the proportion of 'secondary extinctions' caused by the accumulation of 'primary extinctions'. In the ecological network, a node extinction corresponds to a species extinction.

Link extinction scenario. An equally possible, yet previously untested, procedure to model an ecological network extinction is removing interactions instead of nodes. In this scenario we removed links between species. The species 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. An interaction becomes extinct when species do not maintain biotic relationships. In our model the species interactions are presented by a matrix. In this way a species become extinct when all its interactions are extinct.

2.3. **Extinction sequences.** We simulated three different sequences of node (species) removal. In the first extinction sequence we remove species (from rows or columns) ranked from the most-linked to the least-linked species $(+ \rightarrow -)$ and represents the worst possible case [1, 24, 6, 16]. The second extinction sequence simulates the opposite situation, i.e., species extinctions ranked from the least-linked to the most-linked species $(- \rightarrow +)$ and it is considered the most likely case by Memmott et al. [16]. The third extinction sequence removes species randomly and it represents a null model against which the two above sequences can be compared [15, 16]. These sequences will be referred to as most- to-least $(+ \rightarrow -)$, least-to-most $(- \rightarrow +)$ and random sequences, respectively. The random sequence was averaged for 100 iterations.

In the link extinction scenario we used the adjacency matrix of the network. Then we removed links (change 1 to 0 in the matrix) according to species connectivity. In the 'most-to-least' sequence links are removed from the most connected species (in both rows and columns) to the least connected one. In the least-to-most sequence we started removing links from the least-connected species. As a null model links are removed randomly.

3. **Results.**

3.1. **Node extinction.** In order to study the robustness of small bipartite networks we proceeded to remove nodes following the three sequences: most-to-least, least-to-most and random in simulated matrices. In Fig.1, we illustrate the typical robustness behavior of an empirical plant-pollinator network and compare it with a random null model network with 80×125 dimensions. Fig.1a shows extinction patterns removing nodes in a empirical network and in Fig.1b we have plotted the same sequences for random networks of similar dimensions (averaged over 100 realizations). In both figures, we have used squares for most-to-least sequence, triangles for least-to-most and circles for random sequences. In both cases random is placed between the systematic extinction sequences.
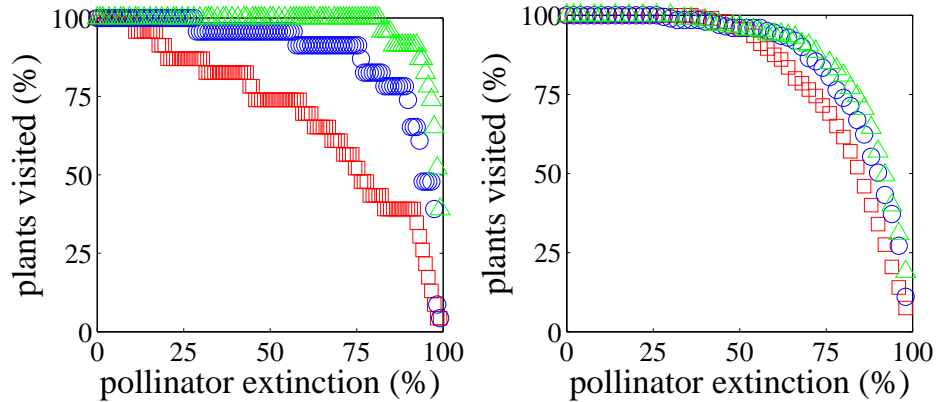
FIGURE 1.   Extinction patterns removing nodes with three dif-
ferent sequences: most-to-least, squares; random, circles; least-to-
most, triangles. **a**) Example of plant-pollinator network [8], data-
base in [18]. **b**) Random network with similar dimensions.

In order to study the effect of asymmetry in the matrix dimensions, we created
random matrices of different asymmetries, from 25:1 to 1:25. In all cases differences
between the three extinction sequences were similar to, although smaller than, those
for empirical mutualistic networks [23], and random sequence was always between
most-to-least and least-to-most. Consequently, in the following asymmetry analysis
we have focused the simulated networks on the random sequence. Fig.2a shows only
the random sequence for seven values of asymmetry, in networks with 10000 poten-
tial links and $C = 12\%$. These simulated networks exhibited the same behavior as
mutualistic networks: robustness increased with increases the asymmetry whenever
primary extinctions affected to shorter dimension of the matrix (secondary extinc-
tions began at higher primary extinctions). However, asymmetries greater than 4:1
only produced slight increases in robustness (Fig.2a).

Secondly, we have studied the influence of the connectance on the secondary
extinction. In Fig.2b the random extinction sequence is depicted for five different
connectances, from 10% to 90%. With connectances of 10%, the first secondary
extinction occurred after removing 40% of species respectively, while networks with
connectances of 60% and 90% remained intact until removal of more than 95%
of species.There was an increase in robustness with increases in the connectance.
Simulated networks confirmed that higher connectance leads to increased robustness
of bipartite networks (Fig.2b).

Finally, we have confirmed the importance of the degree distribution in the net-
work robustness. By contrast to Poisson networks, power-law (Fig.3a) and expo-
nential (Fig.3b) networks showed important differences in robustness depending on
the type of extinction sequence. Fig.3c and Fig.3d depicts a Poisson distribution
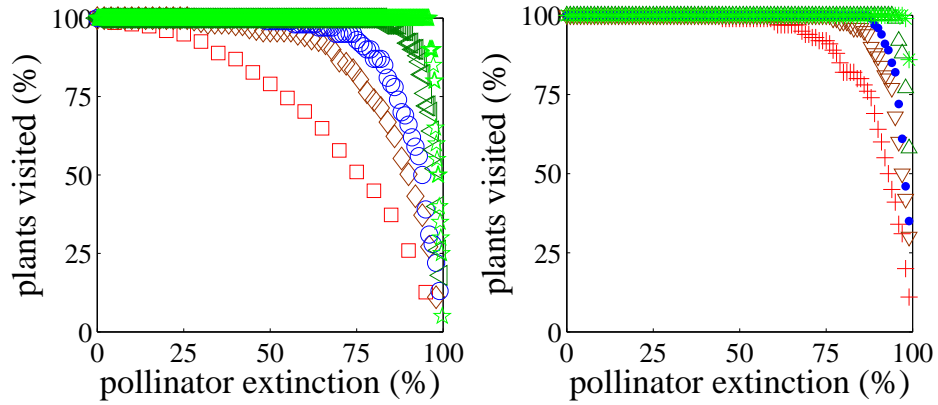with similar asymmetry and connectance than Fig.3a, and Fig.3b, respectively.

FIGURE 2. Extinction patterns removing nodes with **a**) different asymmetries: squares 200×50, diamonds 125×80, circles 100×100, left-triangles 80×125, stars 50×200; **b**) different connectance: pluses 10%, down-triangles 20%, dots 30%, up-triangles 60%, and asterisks 90 %.
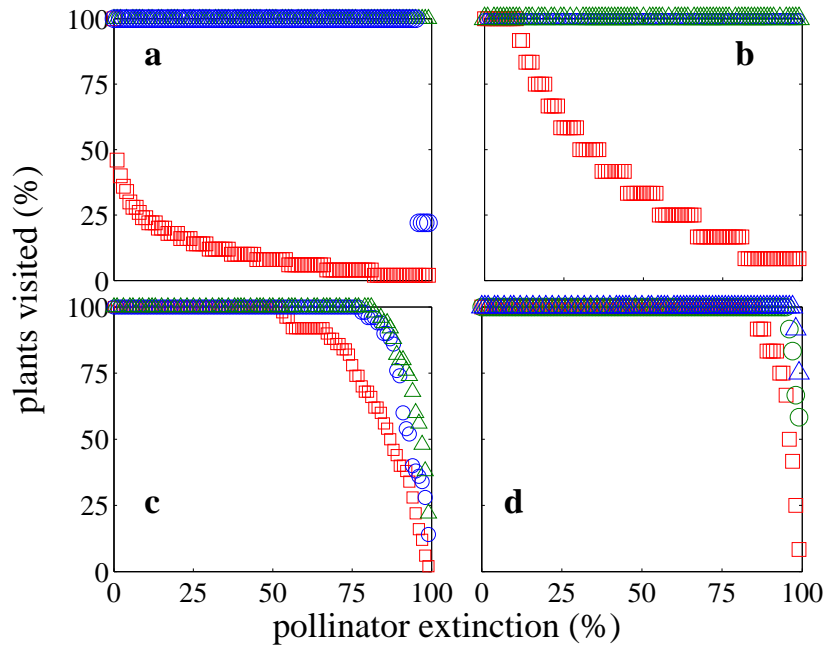

FIGURE 3. Extinction patterns removing nodes with different degree distribution: a) Power law distribution; b) exponential distribution; c) and d) Poisson distribution with similar asymmetry and connectance than a) and b), respectively. Symbols have the same meaning as in Fig.1.

The simulated power-law network was less robust than its corresponding Poisson network in the most-to-least extinction sequence (Fig.3a and Fig.3c). While in the power-law network R50 was10%, in the Poisson network it was 80%. In the least-to-most extinction sequence the opposite happened; the simulated power-law network was more robust than its corresponding Poisson network. In the random sequence, secondary extinctions were staggered, although R50 was 100%.

The simulated exponential network was less robust than its corresponding Poisson network (Fig.3b, Fig.3d), for the most-to-least and random extinction sequences: R50 was approximately 30% in the exponential network, whereas in the corresponding Poisson network it was approximately 90%. In the least-to-most extinction sequence exponential network showed the maximal R50. In summary, the simulated power law network was less robust than its corresponding Poisson network in the most-to-least extinction sequence ('attacks'). In the least-to-most extinction sequence the opposite happened (natural evolution). The simulated exponential network was less robust than its corresponding Poisson network, for the most-to-least and random extinction sequence.
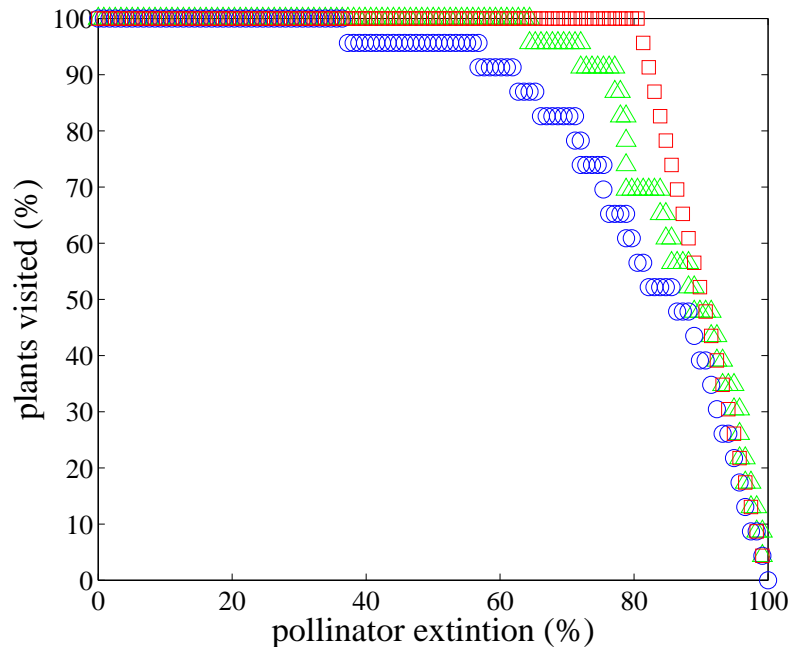

FIGURE 4. Extinction patterns removing links of the same empirical plant-pollinator network as Fig.1a. Symbols have the same meaning as in Fig.1.

3.2. **Links extinction.** 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. Although in the link-extinction scenario networks seem less robust than in the node-extinction scenario (Fig.4), this effect is due to the axes used in the representation.

This type of plot proposed by Memmott [16] depicts the fraction of survival species when an increasing number of nodes are deleted in the other guild. However, in the links extinction scenario removing a link may cause deletion of none or any of the two guilds.
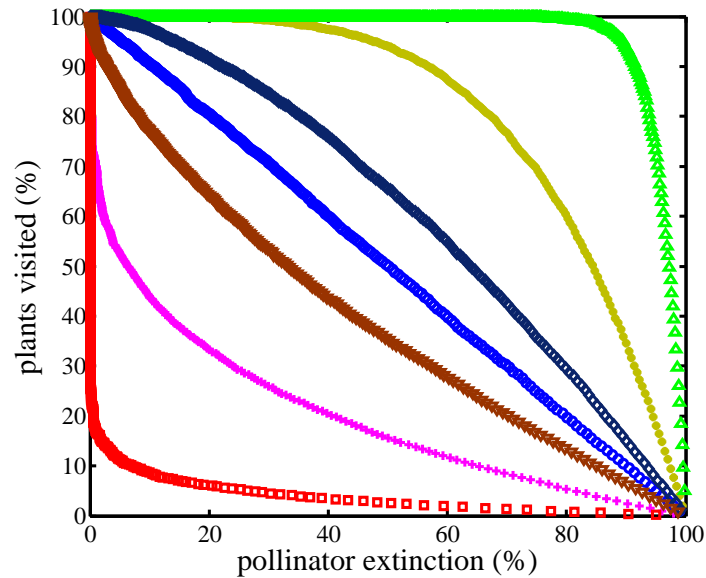

FIGURE 5. Extinction patterns removing links of simulated networks of different asymmetries: 500×20 squares, 200×50 pluses, 125×80 down-triangles, 100×100 circles, 80×125 diamonds, 50×200 stars, 20×500 up-triangles.

Furthermore the asymmetry effect was greater in this new scenario (Fig.5). In this case the extinctions affect simultaneously both plants and pollinators because a link removal may overcome a plant extinction, a pollinator extinction or both (Fig.5).

Instead of plotting species remaining connected versus primary extinction, in the following we have plotted secondary extinction versus primary extinction in log-log scales because it is useful for finding cascades. In symmetric random networks secondary extinctions follow primary extinction at the same rate. For example, in Fig.6 extinction sequences of 100×100 Poisson networks are in the diagonal (note the log-log scale).

In asymmetric random networks, (200×50) extinction sequences $(+ \rightarrow -,$ $- \rightarrow +,$ rnd) follows a power-law starting at 40 (Fig.7a). At low connectance the secondary extinctions occur regularly with the primary extinctions. However, at high connectance, the secondary extinctions, for $+ \rightarrow -$ and $- \rightarrow +$ (not random), occurs preferentially in events (not uniformly) (Fig 7b).

4. **Discussion.** Extinction patterns in simulated networks confirmed the influence on robustness of asymmetry in network dimensions, connectance and degree distribution. Thus, they may shed light on the robustness evaluation of empirical bipartite networks. Simulated networks clearly showed the protective effect of increasing
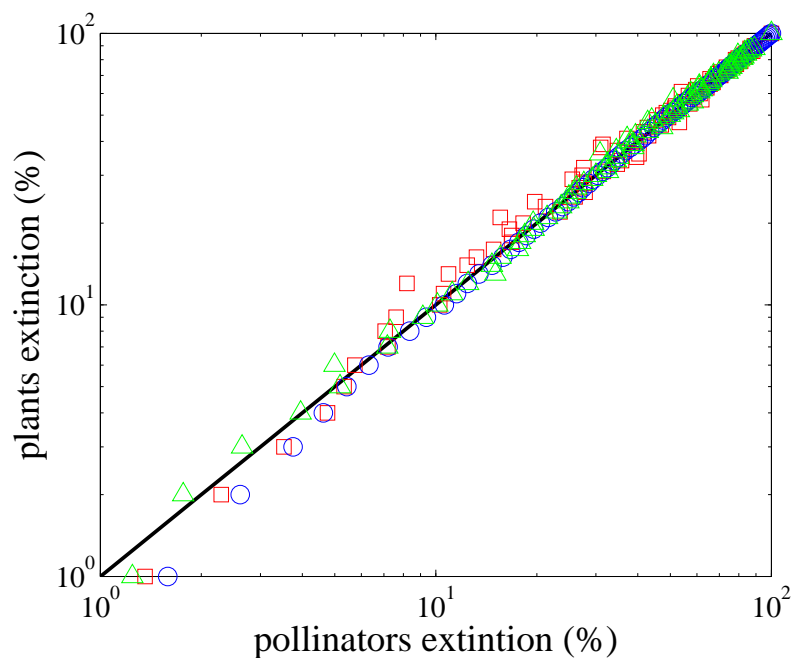
FIGURE 6. Extinction patterns removing links of 100×100 Poisson matrices and $C = 20\%$. Symbols have the same meaning as in Fig.1.
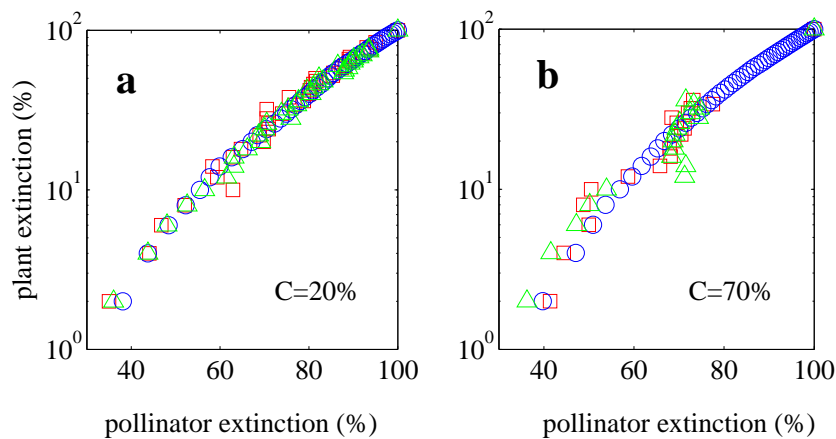

FIGURE 7. Extinction patterns removing links in 200x50 matrices with different connectances: a) $C = 20\%$, b) $C = 70\%$. Symbols have the same meaning as in Fig.1.

asymmetry. In general, robustness was dependent on the extinction scenario and decreased in the order least-to-most > random > most-to-least. Although the most-to-least sequence yields the fastest evolution, however, this extinction evolution does

not end up in a network collapse. The redundancy of ecological network leads to a slow extinction process during all the sequence. This evolution can be seen in Fig.8a, where the secondary extinction rate (normalized by primary extinctions) is plotted against primary extinctions. On the other hand, random sequences lead to a smaller extinction rates until the last high-connected nodes are removed (Fig.8b).
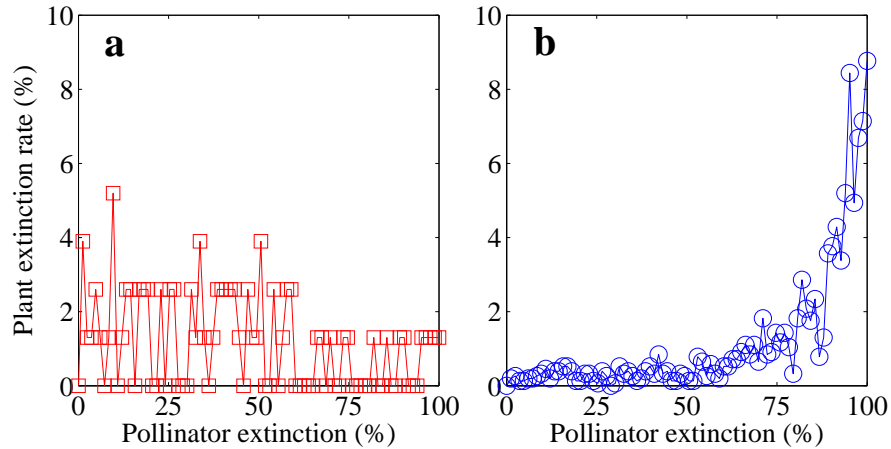

FIGURE 8. Extinction rates removing nodes in a plant-pollinator network [23]: a) most-to-least; b) random.

As with empirical networks, simulated networks were more robust to the extinction of nodes belonging to the most species-rich subset, i.e., the secondary extinctions are developed at higher values of primary extinctions. For all values of asymmetry and connectance tested, robustness was consistently highest in the least-to-most sequence, middle in the random sequence and lowest in the most-to-least sequence. These simulated networks exhibited the same behavior as mutualistic networks: robustness increased with increases in asymmetry and also with the connectance. In Fig.2b the random extinction scenario is depicted for five different connectances, from 10% to 90%. Therefore, in agreement with Dunne et al. [6], network response to these extinction sequences is not restricted to power law degree distribution, but greater differences between sequences coincide with the most skewed distributions. This heterogeneous degree distribution will determine a major interaction redundancy when node deletion begins from the least connected species. The extinction patterns for empirical mutualistic networks (Fig.1a) more closely resembled those of Poisson networks than those of power law ones (Fig 4a). This finding supports the protective effect of truncated power law distributions to most-to-least extinction sequence with respect to power law ones [11]. In the link extinction scenario the patterns change substantially. In this case primary extinction values are not in linear progression but they depend on how many nodes become extinct when a link is removed.

5. **Conclusions.** The robustness assessment of small empirical bipartite networks (like mutualistic ecological networks) cannot be done in terms of evolution of diameter or average path length of the largest cluster [1]. Instead of that, ecologists depict

secondary extinctions versus primary extinctions. The present study indicates that robustness of small bipartite networks dependent on the structure of each network. In particular, our simulations show a large importance of three structural features: degree distribution, connectance and asymmetry in network dimensions, which influence secondary extinctions by affecting interaction redundancy. The variability in robustness found in empirical mutualistic 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 sequences coincide with the most skewed distributions. This heterogeneous degree distribution will determine a major interaction redundancy when node deletion begins from the least connected species.

Removing links (in random sequence) reveals the important effect of asymmetry on the secondary extinction sequence. Plotting plant extinction versus pollinator extinction one can observe their relations in the extinction sequences. In symmetric networks the extinction patterns always follow the diagonal (Fig.6), i.e., species from both guilds become extinct at the same rate. In asymmetric networks species from the guild with a greater number of species become extinct at higher rate than species from the other guild. This scenario, more realistic than node removal, involves more dependence between the two subsets of species in the extinction sequence.

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E-mail address: juanmanuel.pastor@upm.es

E-mail address: silvia.santamaria@urjc.es

E-mail address: marcos.mendez@urjc.es

E-mail address: javier.galeano@upm.es