DRAGGING IN MUTUALISTIC NETWORKS

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Abstract. Mutualistic networks are considered an example of resilience against perturbations. Mutualistic interactions are beneficial for the two sets of species involved. Network robustness has been usually measured in terms of extinction sequences, i.e., nodes are removed from the empirical bipartite network one subset (primary extinctions) and the number of extinctions on the other subset (secondary extinction) is computed. This is a first approach to study ecosystems extinction. However, each interacting species, depicted as a node of the mutualistic network, is really composed by certain number of individuals (population) and its shortage can diminish dramatically the population of its interacting partners, i.e. the population dynamics plays an important role in the robustness of the ecological networks. Although different models of population dynamics for mutualistic interacting species have been addressed, like Type II models, only recently a new mutualistic model has been proposed exhibiting bounded solutions and good properties for simulation. In this paper we show that population dynamics is as important as network topology when we are interested in the resilience of the community.

1. **Introduction.** The application of network theory to ecology has provided new insights in the study of natural systems. An important effort has been focused on their topologic properties. Links in ecological networks are defined according to the biological interactions between species [10, 4, 5, 11, 24]. A very common and important type of interaction is mutualism, that is beneficial for both involved species. In terms of network theory a biological community can be depicted as a bipartite network, in such a way that species in one subset only interact with species in the other subset. This set of interactions may be represented by an

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adjacency matrix, A, where rows represent species of one subset, columns the species of the other. Matrix elements a_{ij} are 1 when species i interacts with species j and 0 otherwise. Although most of ecological networks are binary, i.e., dataset only records if the interaction exists or not, many papers have reported the importance of getting the number of 'visits' as a measure of the interaction. With this kind of dataset one can work with a weighted network [2, 14].

A special feature of the adjacency matrix of mutualistic network is the nestedness. An interaction matrix is nested when the partners of a species is a subset of the partners of other species with higher degree. This property can be visualized if one rearranges rows and columns in terms of their degree. In this case one observes that interactions come together at one corner (core of *generalists*) and species with few links (*specialists*) have high-connected partners (in a triangle-like pattern). This property is said to be the key of the resilience of mutualistic networks [17, 4, 5, 15].

Only few models of population dynamics have been successfully applied to mutualistic networks because of the difficulties involved in the estimation of their parameters [15]. The first proposal of population dynamics for mutualistic communities was proposed by May (1981). It relied on the same idea that the prey-predator Lotka-Volverra model, that is a Verhulst equation plus an interacting term. In May's equation the additional term is always positive because in the mutualistic relationships the interaction is always beneficial.

The Verhulst's equation (also known as *logistic equation*) can be written as the Malthusian growth term minus a coefficient that limits the growth when population reaches a maximum value, $K > 0$, the so-called *carrying capacity*, i.e., the maximum population size given by environmental conditions of water, nutrients, space, etc.:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right). \tag{1}$$

The solution of this equation is, provided the *intrinsic growth rate*, r, is positive, a sigmoid that asimptotically tends to K.

The simplest way of including the mutualistic interaction is adding a term proportional to both interacting populations, with a positive coefficient. So, May's equations for two interacting mutualistic species can be written as:

$$\begin{aligned}
\frac{dN_1}{dt} &= r_1\,N_1\left(1 - \frac{N_1}{K_1}\right) + r_1\,N_1\,\beta_{12}\,\frac{N_2}{K_1}, \\
\frac{dN_2}{dt} &= r_2\,N_2\left(1 - \frac{N_2}{K_2}\right) + r_2\,N_2\,\beta_{21}\,\frac{N_1}{K_2},
\end{aligned} \tag{2}$$

where $N_1(N_2)$ is the species population 1(2); $r_1\,(r_2)$ is the intrinsic growth rate of population 1 (2) and $K_1\,(K_2)$ the carrying capacity; the mutualistic strength is driven by the coefficient $\beta_{12}\,(\beta_{21})$, as a *per capita* benefit for species 1 (2).

According to the sign of the intrinsic growth rate of involving species mutualism can be classified as: *mandatory*, when $r < 0$ and then the mutualistic term is necessary for avoiding species extinction; or *facultative*, when $r > 0$ and the species would survive without mutualism. We are interested in *mandatory* mutualism because in this case perturbations can induce species extinctions.

Altough this simple model is considered the starting point of any mutualistic model, it has an important drawback, as it leads to unbounded growth when $r < 0$ and the population is above the carrying capacity.

In order to solve this issue, different modification have been proposed. The most popular version is the so called *type II* [27], because mutualism is included as a type II functional response:

$$\frac{dN_1}{dt} = r_1\,N_1\,-\alpha_1\,N_1^2 + \frac{a\,b\,N_1\,N_2}{1 + a\,N_2\,T_H},$$
$$\frac{dN_2}{dt} = r_2\,N_2\,-\alpha_2 N_2^2 + \frac{a\,b\,N_1\,N_2}{1 + a\,N_1\,T_H}, \tag{3}$$

where a $(a > 0)$ is the effective search rate and b $(b > 0)$ is a coefficient that relates encounters between individuals of species 1 and 2, and T_H is a handling time.

The main disadvantage of this model is the dificulty for doing any analytical treatment and the very limited range of valid parameters for the simulations.

2. **A simple model of population dynamics with mutualism.** In this work we use a very recent population dynamics model of mutualism [12]. This model solves the unbounded growth problem of May's model with a cubic term that allows analytical and numerical treatment.

The main idea of this model is to include the mutualism in both the growing and limiting terms. Then the Verhulst-type equation for one species can be written as:

$$\frac{dN}{dt} = N\,r_{\text{eff}} = N\,(r_{\text{eff}}^m - a^m\,N), \tag{4}$$

where the superscript m stands for *mutualistic*; so the growth rate and the *per capita* limiting term include the populations of the interacting species.

For two species, let one subset species (for example, the plant) correspond to the index 1 and the other subset species (for example, the animal) to the index 2. The growth rate and the limiting terms can be written as:

$$r_{\text{eff},1}^m = r_1 + b_{12}\,N_2,$$
$$a^m = \alpha_1 + c_1 b_{12}\,N_2. \tag{5}$$

And then, the complete equations system for two mutualistic species is:

$$\frac{dN_1}{dt} = (r_1 + b_{12}\,N_2)\ N_1 - (\alpha_1 + c_1\,b_{12}\,N_2)\,N_1{}^2,$$
$$\frac{dN_2}{dt} = (r_2 + b_{21}\,N_1)\ N_2 - (\alpha_2 + c_2\,b_{21}\,N_1)\,N_2{}^2. \tag{6}$$

In these equations the variable r is the intrinsic growth rate, α is an intraspecific competition coefficient, b_{12} (b_{21}) is the *per capita* benefit for species 1 (2) from species 2(1) and c is a coefficient representing the weight of mutualism in the limiting term.

This polynomial model allows using standard methods for nonlinear equations system, in order to obtain the stationary solutions and their stability. The linear stability analysis of this model (see [12]) shows stable nodes at population maxima (carrying capacities that depend on the system state) and total extinction. Saddle points are found at partial extinctions and at the condition $r_{\text{eff},1,2} = 0$. Figure 1 depicts an example of the flow diagram for two mutualistic species (simulation parameters in the figure caption). All flow lines end at one of the two stable points (total extinction or populationmaxima). The two attraction points are located at carrying capacities, around $(130, 130)$, and at total extinction $(0, 0)$. Flow lines close to the saddle point change direction towards one of the two stable nodes.
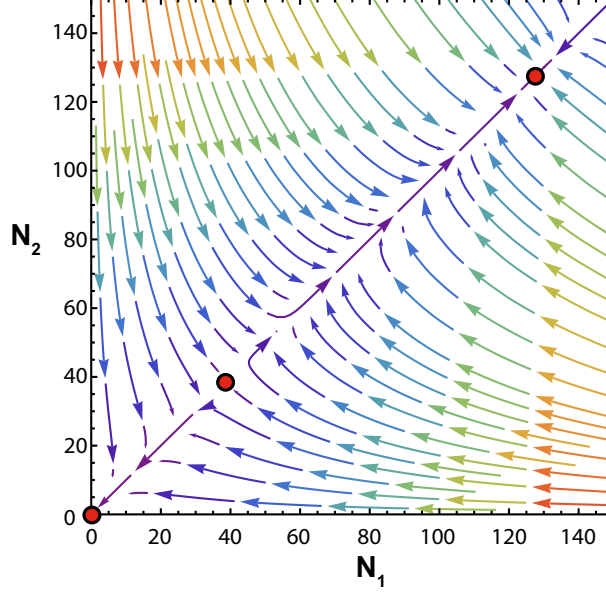
FIGURE 1. Flow diagram for two species with parameters: $r_1 = r_2 = -0.15$, $b_{12} = b_{21} = 0.015$, $\alpha_1 = \alpha_2 = 0.01$, $c_1 = 0.002$, and $c_2 = 0.003$.

In this paper we focus on the perturbation of a mutualistic system around the stable node at the carrying capacity. For a mutualistic system of n_a species of one guild and n_p species of the other guild, the equations system is:

$$\frac{1}{N_i^a}\frac{dN_i^a}{dt} = r_i + \sum_{k=1}^{n_p} b_{ik}\, N_k^p - \left(\alpha_i + c_i \sum_{k=1}^{n_p} b_{ik}\, N_k^p\right) N_i^a,$$

$$\frac{1}{N_j^p}\frac{dN_j^p}{dt} = r_j + \sum_{\ell=1}^{n_a} b_{j\ell}\, N_\ell^a - \left(\alpha_j + c_j \sum_{\ell=1}^{n_a} b_{j\ell}\, N_\ell^a\right) N_j^p \qquad (7)$$

where N_i^a is the population of the i-species of subset a, b_{ik} is the *per capita* mutualism benefit for the i-species from the k-species, α_i is the intra-specific competition coeficient for the i-species, c_i is the weight of the mutualism in the limiting term, and the same concepts apply for the j-species.

With the linear stability analysis one can find that this equations system (for many species) has also partial extinctions as stable fixed points (see [12]), as well as the total extinction and the carrying capacity.

2.1. **Numerical simulations.** In population dynamics models, the variable N refers to discrete number of individuals and the outcome in each time step must be an integer number. A good choice of simulation method is the Binomial Simulation, a stochastic extension of Continuous System Simulation, because the final result for an individual is being alive or dead [3], so it can be described by a Bernoulli process (over finite time intervals).

Let assume that the probability of breeding over an interval ΔT is exponentially distributed, and its average value is $1/r$, where r is the intrinsic growth rate. So,

the probability of reproduction is:

$$P = \int_0^{\Delta T} r e^{-r\,t}\,dt = 1 - e^{-r\,\Delta T}. \tag{8}$$

In particular, a population of N individuals at time t, with probability of reproduction P, at the next time step $t + \Delta T$ will be:

$$N(t + \Delta T) = N(t) + sgn\,(r)\,Binomial\,(N(t), P), \tag{9}$$

where $sign(x)$ is the sign function that extracts the sign of x and $Binominal$ is the result of a Binomial trial.

And now we can think of all the terms of equation (7) as an *effective* growth rate, so the set of equations (7) becomes in stochastic form:

$$
\begin{aligned}
N_j^a(t + \Delta T) &= N_j^a(t) + sgn\left(\hat{r}_{ef_j}^a\right) Binomial\left(N_j^a(t), P_j^a\right), \\
N_l^p(t + \Delta T) &= N_l^p(t) + sgn\left(\hat{r}_{ef_l}^p\right) Binomial\left(N_l^p(t), P_l^p\right),
\end{aligned}
\tag{10}
$$

where $\hat{r}_{ef_j}^a$ is jth-species effective growth rate in the simulation period and P_j^a, the probabilities of growth according to equation (8), and the superscript a stands for the animal and p for plant. In particular, working with one-day steps, as we do:

$$\hat{r}_{ef} = (1 + r_{ef})^{1/365} - 1. \tag{11}$$

Detailed numerical treatment of the equations is discussed in [12].

3. **Resilience of mutualistic networks.** As a general conception, mutualistic networks seem to be robust to perturbations due to their worldwide expansion over very different ecosystems. For example, plant-pollinator mutualism is responsible of about the 90% reproductive mechanism in tropical forest ecosystems [4].

Studies on the resilience of mutualistic networks are usually based on topology rather than on population evolution. Several works have studied the robustness of mutualistic networks in terms of secondary extinctions caused by the accumulation of primary extinctions [10, 17, 18, 13, 9, 19, 14, 21, 22]. Secondary extinctions happen when one species loses all its mutualistic partners. The main idea of this procedure is to observe how secondary extinctions occur on one subset (for example, plants) when one removes species from the other subset (primary extinctions) following predetermined specific sequence of removing nodes. The typical sequences are: starting from the most-connected node to the less-connected node in decreasing order, starting from the less-connected node to the most-connected node in increasing order, and randomly. These extinction sequences try to simulate two extreme scenarios where the extinction of primary species occurs according to species's degree: a gradual disturbance (*e.g.*, meteorological anomaly) will first affect specialists; on the other hand epidemic propagation spreads faster among highly connected species. The random sequence corresponds to a null model with non preferences in the election of the species to be extincted.

On this procedure one plots the surviving plants (percentage of species) *versus* percentage of pollinator extinction (sometimes called *attack tolerance curve* [5]). Some assessment indices have been proposed to quantify the robustness of this type of bipartite networks. The $R50$-index represents the percentage of primary extinction that produces a loss of $\geq 50\%$ of species [10], obtained from the interpolated extinction curve. The R-value is defined as the area under the extinction curve plotted with axes between 0 and 1 [5].

Other works based on dynamic model of plant-pollinator communities have been published [6]. They used a dynamic Boolean network-based model where species interactation can be mutually beneficial or beneficial for one species and detrimental for the other. The dynamic Boolean framework allows for a complete dynamical analysis after removing a species that describes the resulting behavior of the whole system [6].

However, resilience is just studied from the point of view of topology, removing nodes, one by one, as unitary elements. From the population point of view this represents that one removes all individuals from one species without changing the populations of its mutualistic partners.

A new approach may be attempted if we take populations into account. Starting from the stationary state at the populations maxima, we have implemented perturbations to one or several species for a period of time in order to study the recovery of the system. This way models the perturbation and disturbances occurring in natural ecosystems, due to plagues, human effects or climate change. In this case the population of one (o several) species decreases due to internal or external factors and this change in the number of individuals implies changes in population of its mutualistic parterns, and recursively, these changes will affect other connected species, and so on. This chain of perturbations can produce a progressive declining of populations that leads to a cascade of extinctions.

In conventional studies of mutualistic network resilience all information is contained in the topology, *i.e.*, no matter how many individuals the species have, no matter the type of dynamic behaviour. This is the reason why mutualistic networks are seen as robust: secondary extinctions only occur when *all* the mutualistic partners are extinct. However, recent papers alarm about extinctions threats of many species [16]. For example, *one common criterion used to classify extinction risk is a decline in abundance* [26] (the International Union for Conservation of Nature -IUCN- Red List classifies as critically endangered species when the decline in abundance is greater than 80% over 10 years or 3 generations and the mean extinction probability is about 15% by 2100).

In our model (Eq. 7) we have implemented external perturbations in a simple way: perturbations cause an increase in the death rate (decreasing the intrinsic growth rate, r_i). With this change in the parameter values we resume the simulation and observe if the system evolves towards populations maxima or if perturbations drive it into an unstable basin of partial or total extinctions.

The main goal of this work is to observe the influence of population dynamics when a nested mutualistic network is perturbed. For this purpose we have simulated three mutualistic networks in 7×7 matrices, with different topologies, in order to find out if the network substrate is the key in the resilience of mutualistic networks.

We have characterized the topology in terms of the nestedness. The assessment of nestedness has been made using the NODF measure [1, 25]. This measure is based on decreasing fill of rows and columns, when the matrix is packed in terms of their degree, and paired overlap, i.e., percentage of links of a row (column) at the same position that rows (columns) with higher position in the rearranged matrix.

For each adjacency matrix we have performed perturbations on two main species: *generalists* and *specialists*. The core of generalists is identified performing a *K-shell decomposition*. This procedure allows to classify nodes by the number of *effective* links that one has to prune to produce its extinction.

3.1. **K-shell decomposition.** The k-shell decomposition is a centrality measure for network analysis that identifies progressively internal 'shells' and decomposes the network, layer by layer, by an effective degree in cohesion ([8, 7]). The k-shell may be performed using the "prunning" algorithm: One starts prunning the nodes of degree one; after all nodes of degree one have been removed one looks again for nodes of degree one, in a recursively way, until no 1-degree node remains in the network. The subset of all removed nodes is the 1-shell. For the 2-shell one repeats the procedure prunning 2-degree nodes, and so on. The last subset, with the highest degree, is the *k-core*. An example of a k-shell decomposition is depicted in Fig. 2. In this case, animal species A5, A6, and A7 and plant species P6, P7, and P8 belong to K1-shell; animal species A4 and plant species P4 and P5 belong to K2-shell, and, finally, A1, A2, A3 and P1 P2 P3 are the generalist group or k-core. Note that A5 and P6 and P7 have two links (P7 has one link with the core), however, in the prunning process they behave as if they had one effective link with the network.

From this decomposition we can define the term *generalist* in a more precise way: the species belonging to the *kmax-core*.

With this decomposition we can study perturbation spreading along the network taking the species k-shell into account.
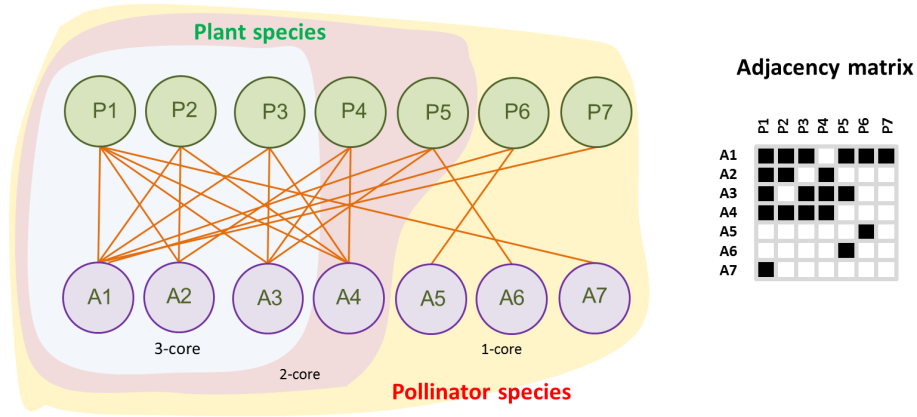

FIGURE 2. Network M1.

4. **Results.** Our main goal is to study the role of population dynamics in resilience of mutualistic networks. To this purpose we have performed simulations of the proposed equations (10), with an ad-hoc application written in Python 3 and run on a personal computer, and then, we have perturbed the steady state (for different mutualistic networks). Accesible empirical datasets [20] reveal that mutualistic networks are sparse (filled around 20%) and nested, i.e., when rows and columns are rearranged in terms of their degrees their adjacency matrix shows a triangle-type structure.

In order to reveal the role of connectivity we have disturbed species in three different mutualistic networks: a) $M1$, nestedness assessment NODF=16, with two plant species and three animal species in the 1-shell, one plant species in the 2-shell, and a core of generalists formed by four plant species and four animal species (see Figure 2); b) $M2$, NODF=30, with one plant species and one animal species in the

1-shell, three plant species and three animal species in the 2-shell, and a core of generalists with three plant species and three animal species (see Figure 3); c) $M3$, a perfectly nested matrix with triangular symmetry (NODF=67). This implies one plant species and one animal species in the 1-shell, in the 2-shell and in the 3-shell, and four plant species and four animal species in the 4-shell or k-core (Fig. 4).

In all cases, we have firstly performed simulations of the equation system 7 with the selected parameters (listed in Table 1, Table 3, and Table 4) in order to verify the stability of the system: populations of all species tend to their carrying capacities, the stationary solution, and remain in this state unless the system is externally perturbed. We have looked for the time the system reaches its steady state, and then we have perturbed one species. In some cases the perturbed species is the most generalist and in other cases we have perturbed a specialist to test the resilience of the network against 'attacks' to a hub or to a peripherical node.

Perturbations are implemented in a simple way, just increasing the yearly death rate during a chosen period, and the period is tunned to obtain species extinction.
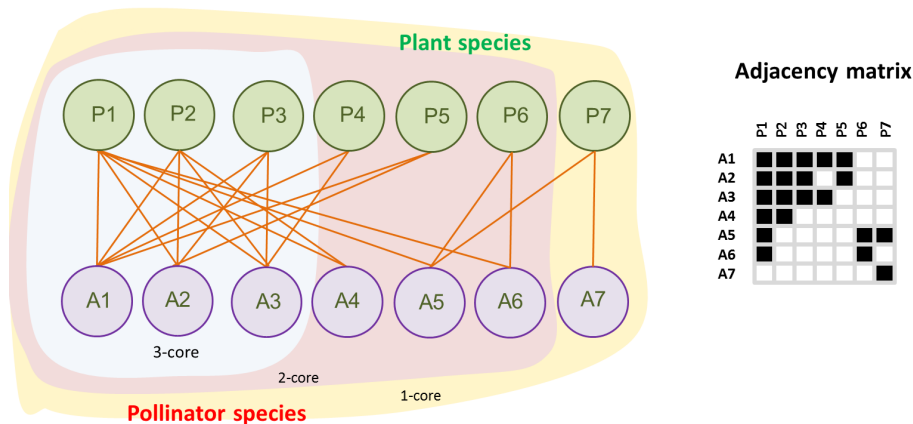

FIGURE 3. Network M2.

In all cases we have performed simulations lasting to the stationary state (each species reaches its *carrying capacity*). To test the stability of the model we have performed some simulations with initial populations greater than their carrying capacity to verify that population diminishes to reach the stable solution.

From this point on, we perturbed one species and let the system evolve to the new stationary solution.

Figure 5 depicts the time evolution of a mutualistic system with the topology of matrix $M1$. Note that in some cases initial population may be greater than its *carrying capacity* and they decrease until they reach the stationary solution. At year 200 (when the system has reached the stationary state) the generalist animal $A1$ suffers a *plague* (large perturbation) that leads the population close to extinction. Due to this large perturbation all populations decline, however all species recover except the specialist plant P7 that becomes extinct (Figure 5).

However, if we increase the mutualistic benefit of plant $P7$ and diminish it on animal $A7$ only this specialist species may become extinct (see Table 1). Figure 6 shows the perturbation of animal $A1$ for 8 years with a rate of 0.7: only animal $A7$ goes to extinct and all the plants can recover although their populations have
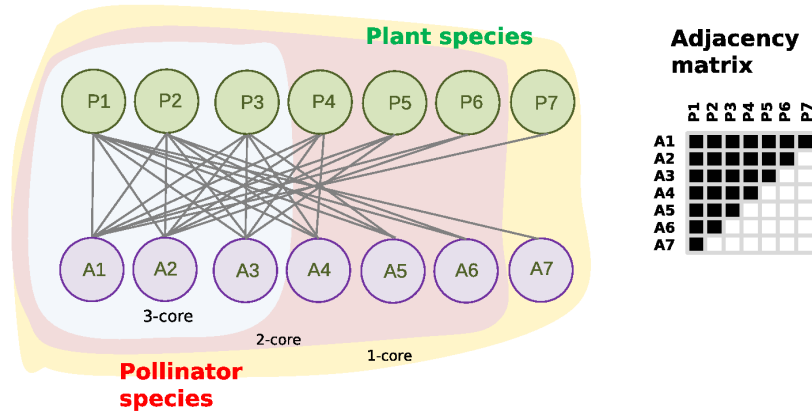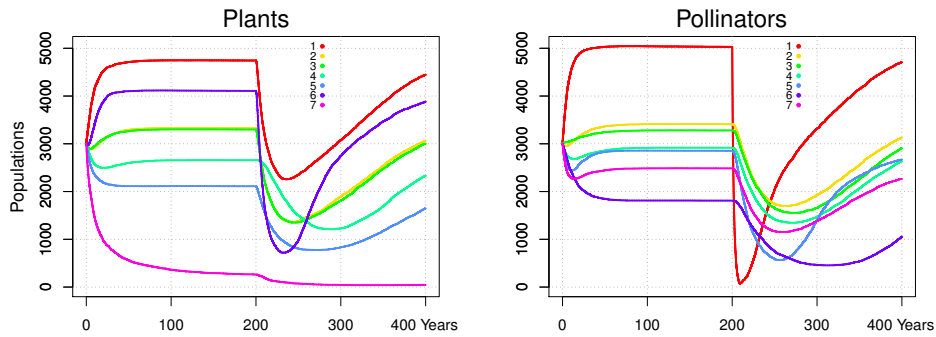
FIGURE 4. Network M3.

FIGURE 5. Population time evolution of community M1. At year 200 disturbances on animal A1 cause extinction of the specialist plant P7. All animal species and the rest of plant species can recover a new stationary population.

gone down close to extinction. Note that in this case the perturbation on one animal subset species induces an extinction of another animal species (they are not directly linked because they belong to the same subset), but no plant species becomes extinct. Simulation parameters are listed in Table 1.

The same mutualistic network $M1$, with the same beneficial matrix (see Table 1) may lead to the extinction cascade if the perturbation is greater. Figure 7 depicts the same system as Fig. 6 but the perturbation is of rate 0.8 lasting 10 years: the generalist animal $A1$ cannot recover its population and drags all other species to total extinction. Simulation parameters of Fig 5, Fig. 6 and Fig. 7 are detailed in Table 1.

A cascade extinction may be triggered not only by a generalist but also by a specialist. In Figure 8 is plotted the time evolution of the same mutualistic network (with some changes in the beneficial matrix as shown in Table 2) under a perturbation on the specialist animal $A7$ at time 200 lasting 20 years. Although this is a specialist species its generalist plant partner obtains an important benefit from this
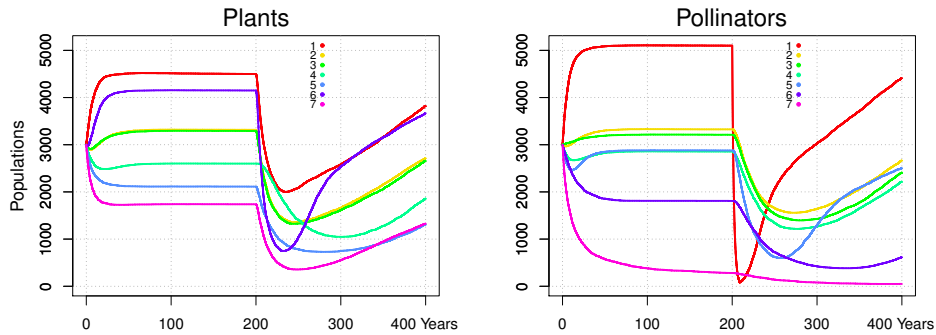
FIGURE 6. Population time evolution of community M1. At time 200 disturbations on animal A1 cause extinction of animal A7. All plants and the rest of animals can recover a new stationary population.
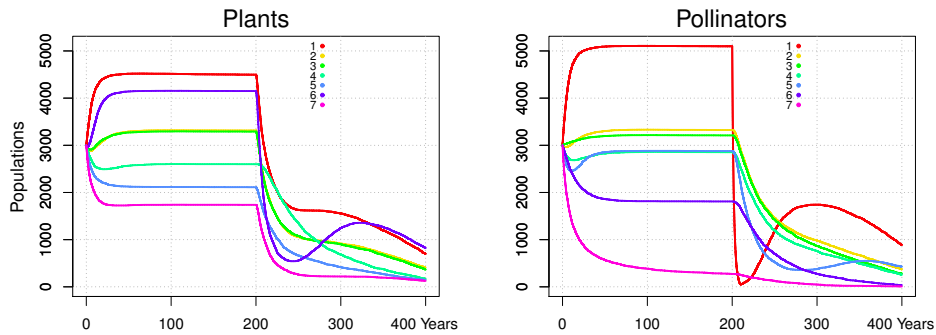

FIGURE 7. Population time evolution of community M1. At year 200 a perturbations on animal A1 produces a vanishing population that drags all plants and animal species, triggering a cascade extinction.

interaction. This large decay produces a serious disminishing of the generalist plant population that drags all species into cascade extinction. Simulation parameters are detailed in Table 2.

In mutualistic network $M2$, where species in the 1-shell are connected to a species in the 2-shell (see Fig. 3), the perturbation on the specialist animal $A5$ drags the specialist plants $P6$ and $P7$, and the animals $A5$, $A6$, and $A7$. The core of the network is stable and reaches a new stationary state with a bit lower *carrying capacities* (see Figure 9).

However, when the perturbed species is the generalist animal species A1, belonging to the k-core, this species goes to extinction dragging all species except the specialists that have strong links between them and the generalist plant species that shares links with the three specialist animals (Figure 10). Simulation parameters are listed in Table 3.

With minor changes in the interaction matrix, the same perturbation on the generalist $A1$ only leads to its own extinction (not shown).

FIGURE 8. Population time evolution of community M1. At year 200 a perturbation on the specialist animal A7 produces a vanishing population that drags all plants and animal species, triggering a cascade extinction.

FIGURE 9. Population time evolution of community M2. At year 500 perturbations on the specialist animal A5 produce a vanishing population that drags all plants and animal species in the 1-shell.
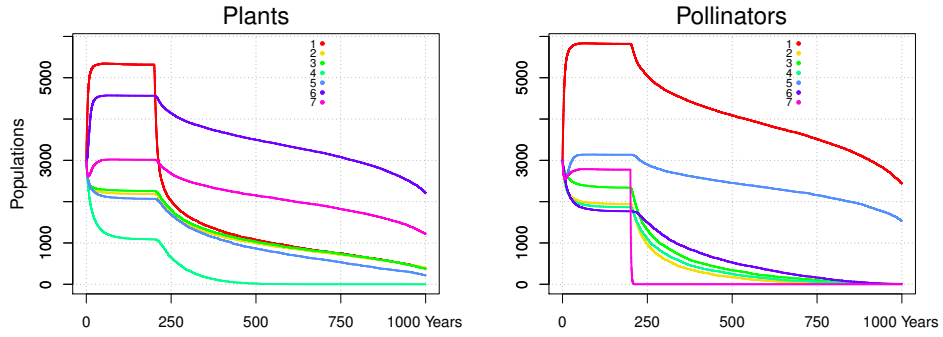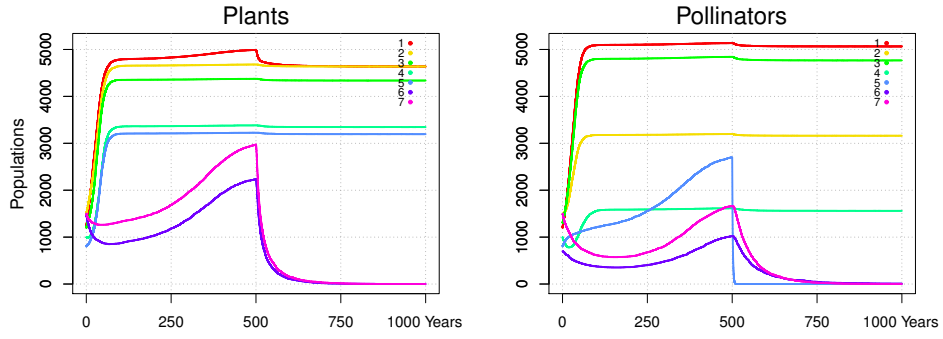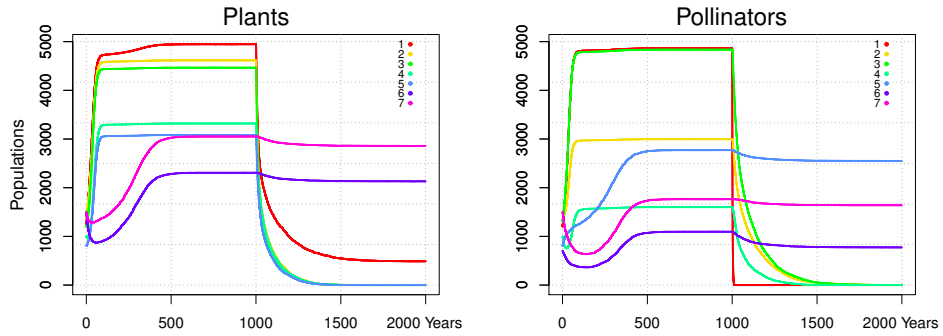

FIGURE 10. Population time evolution of community M2. At time 1000 disturbations on the generalist animal A1 produce a vanishing population that drags all generalist animal species and generalist plants except P1; species in the 1-shell are minimally affected.

Figure 11 shows population evolution of the community $M3$. At time 200 the specialist animal $A7$ is affected by an external *plague* for ten years that declines quickly its population to become extinct. Due to the minimal dependence of plants on this animal, the remainder of the network goes towards a stationary solution with lower *carrying capacities* (simulation parameters in Table 4).
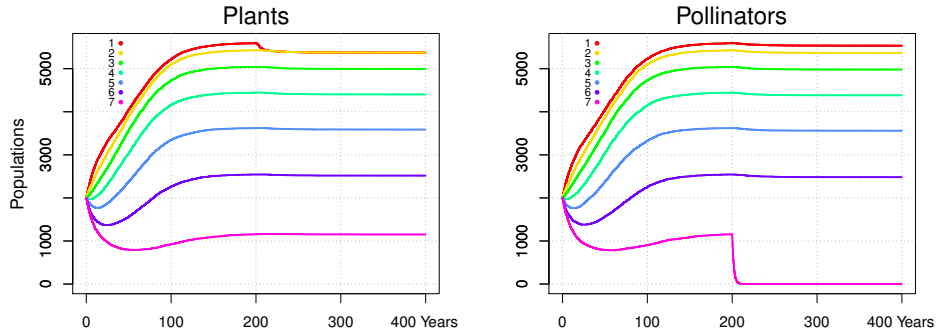
FIGURE 11. Population time evolution of community M3. At time 200 disturbations on animal PA cause its extinction.

In the next example of disturbation (Figure 12) we simulate a perturbation on the generalist animal A1 in the same community $M3$. With the same mutualistic parameters and with the same perturbation, now the *plague* affects to a generalist (A1) with an important role in the network. The drastic decay of population of A1 draggs all its mutualistic partners, ending at an extinction cascade.
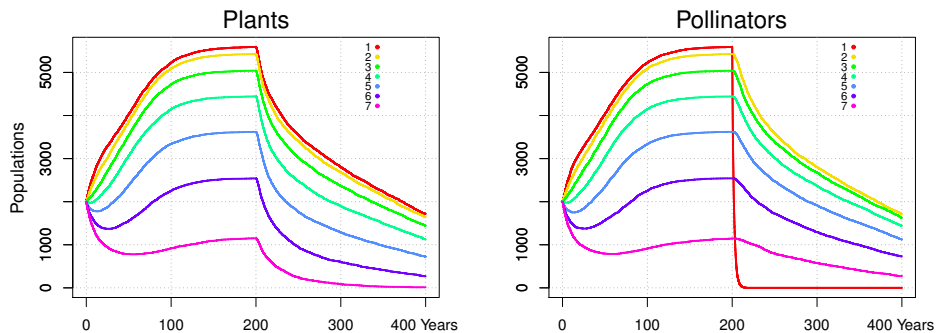
FIGURE 12. Population time evolution of community M1. At time 200 disturbations on animal A1 cause total extinction.

In Figure 13 we have plotted population evolution of the same community $M3$ with different mutualistic dependences than in previous cases (see Table 4), a different perturbation at time 200. At this time the generalist animal A1 is subject to a death rate of 80% for ten years. Now this highly connected species goes to extinction dragging the specialist P7, while the rest of the community reaches a new stationary state (with different carrying capacities). Table 4 contains the dynamics parameters used in these three examples.
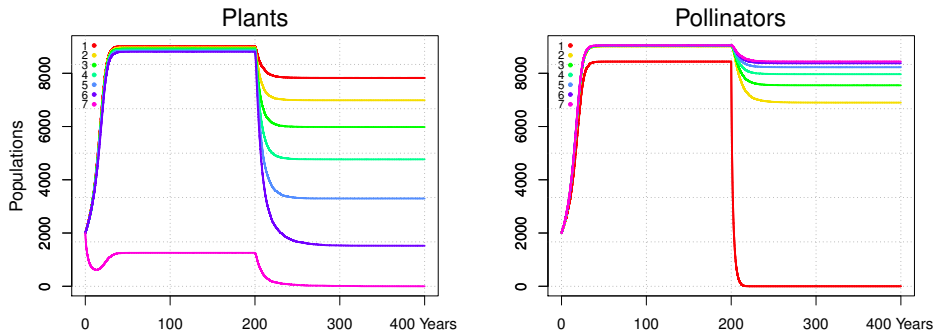
FIGURE 13. Population time evolution of community M3. At time 200 disturbances on the generalist animal A1 cause extinction of the specialist plant P7 and its own extinction.

5. **Discussion.** To our best knowledge, resilience and robustness studies on mutualistic networks have been done from the topology point of view. Conclusions about robustness of this kind of networks are extracted observing secondary extinctions when species are removed (primary extinctions) from the network following a predetermined sequence. A secondary extinction will occur only when *all* partners become extinct. However, dynamically a species can go to extinction when its population disminishes below a "vital" threshold as it states the International Union for Conservation of Nature (IUCN). Its Red List classifies as critically endangered species when the decline in abundance is greater than 80% over 10 years [26]. This opens a new approach in the resilience studies of mutualistic networks because of functional extinctions [23]. This phenomenon can occur even if the population of the target species recovers after the disturbance has disappeared (as it can be seen in Figures 6 and 5).

This new perspective may change the previous results on resilience with mutualistic networks. Some considerations must be taken into account: i) induced extinctions can occur when populations of partners are low enough (primary extinction is not required to get secondary extinctions); ii) dragging can affect any species linked, *i.e.* a species will become extinct when all its partners cannot supply mutualistic benefit enough to compensate the negative growth rates (the loss of a link can imply an extinction depending on the dynamical mutualistic parameters); iii) cascade extinction is a dynamical process that will occur when population decline of one species produces a continuous negative effective growth rate in all its partners, and these new population declines entail the same negative effects in all their partners, and so on.

Essentially, the resilience of this kind of network can be seen as the distance, in the flow diagram, from the *survival watershed* (as it is explained in [12]). When the system is close to one *survival watershed* a perturbation can move the system state to a extinction basin, or even to the total extinction basin.

Topology is not enough to measure the resilience of a mutualistic network. In three networks with very different topology we have found similar dragging effects when one species is damaged. We have found similar casuistry in all three topologies, with very different parameters: nestedness and k-shell distribution should be the relevant parameters to determine the resilience of a mutualistic network. For

each network we have found a variety of resilience behavior, from stability to extinction cascade depending on the mutualistic parameters of the equations system. As conclusion, one cannot predict the resilience behavior of a mutualistic networks attending only to topological properties.

This approach may be usefully applied in other systems where extinctions are involved and the role of dynamics on the vulnerability of the system can be assessed. This may be the case of spatially explicit metapopulations and metacommunities (e.g. networks of temporary ponds, islands in an archipelago, etc) where in addition to the features of the topological network that characterize them, the vulnerability of the system is also significantly determined by the dynamics of the populations.

Although we have studied only one model of population dynamics in mutualistic systems, other mutualistic models will have some parameters for the species interactions that could be tuned in order to produce dragging or stability as we have done in this model.

	P1	P2	P3	P4	P5	P6	P7	A1	A2	A3	A4	A5	A6	A7
$b_{j1}\left(10^{-5}\right)$	3	2	2	0	1.2	5	0.7	3	2	1.5	1.2	0	0	3
$b_{j2}\left(10^{-5}\right)$	1.5	1.5	0	2	0	0	0	2	2	0	1.2	0	0	0
$b_{j3}\left(10^{-5}\right)$	1.5	0	1.5	1.5	1.2	0	0	2	0	1.5	1.2	0	0	0
$b_{j4}\left(10^{-5}\right)$	1.2	1.5	1.5	1.2	0	0	0	0	1.5	1.5	1.2	0	0	0
$b_{j5}\left(10^{-5}\right)$	0	0	0	0	0	0.1	0	1	0	1.5	0	0	5	0
$b_{j6}\left(10^{-5}\right)$	0	0	0	0	1.2	0	0	1	0	0	0	4	0	0
$b_{j7}\left(10^{-5}\right)$	1	0	0	0	0	0	0	1	0	0	0	0	0	0
$N_{init\,j}$	3000	3000	3000	3000	3000	3000	3000	3000	3000	3000	3000	3000	3000	3000
$c_{j}\left(10^{-5}\right)$	8	8	8	8	8	8	8	8	8	8	8	8	8	8
$\alpha_{j}\left(10^{-5}\right)$	3.5	3.5	3.5	3.5	3.5	3.5	3.5	3.5	3.5	3.5	3.5	3.5	3.5	3.5
$r_{birth\,j}$	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003
$r_{death\,j}$	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02

TABLE 1. Mutualistic coefficients and conditions for the simulation of M1 in Fig. 5; in Fig. 6 and Fig. 7 $b_{P7A1} = 2$, $b_{A7P1} = 0.8$.

	P1	P2	P3	P4	P5	P6	P7	A1	A2	A3	A4	A5	A6	A7
$b_{j1}\left(10^{-5}\right)$	1.5	1.5	1.5	0	1.2	5	3	1.5	1.5	1.5	1	0	0	3
$b_{j2}\left(10^{-5}\right)$	1	1	0	1.5	0	0	0	1	1	0	1	0	0	0
$b_{j3}\left(10^{-5}\right)$	1	0	1	1	1.2	0	0	1	0	1	1	0	0	0
$b_{j4}\left(10^{-5}\right)$	1	1	1	1	0	0	0	0	1	1	1	0	0	0
$b_{j5}\left(10^{-5}\right)$	0	0	0	0	0	0.1	0	1	0	1	0	0	5	0
$b_{j6}\left(10^{-5}\right)$	0	0	0	0	1.2	0	0	1	0	0	0	4	0	0
$b_{j7}\left(10^{-5}\right)$	0.8	0	0	0	0	0	0	0.8	0	0	0	0	0	0

TABLE 2. Mutualistic coefficients for the simulation of M1 in 8. The rest of parameters are the same as in Table 1.

	P1	P2	P3	P4	P5	P6	P7	A1	A2	A3	A4	A5	A6	A7
$b_{1j}\left(10^{-5}\right)$	2	2	2	1.6	1.9	0	0	2	2	2	1	0.1	0.2	0
$b_{2j}\left(10^{-5}\right)$	2	2	2	0	2.2	0	0	2	2	2	1	0	0	0
$b_{3j}\left(10^{-5}\right)$	2	2	2	2	0	0	0	2	2	2	0	0	0	0
$b_{4j}\left(10^{-5}\right)$	2	2	0	0	0	0	0	2	0	1	0	0	0	0
$b_{5j}\left(10^{-5}\right)$	1	0	0	0	0	4	5	0.1	1	0	0	0	0	0
$b_{6j}\left(10^{-5}\right)$	1	0	0	0	0	0.11	0	0	0	0	0	0.5	2	0
$b_{7j}\left(10^{-5}\right)$	0	0	0	0	0	0	1	0	0	0	0	4	0	2
$N_{init\,j}$	1200	1500	1200	1000	800	1500	1500	1200	1500	1300	1000	800	700	1500
$c_j\left(10^{-5}\right)$	8	8	8	8	8	8	8	8	8	8	8	8	8	8
$\alpha_j\left(10^{-5}\right)$	3	3	3	3	3	3	3	3	3	3	3	3	3	3
$r_{birth\,j}$	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003
$r_{death\,j}$	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02

TABLE 3. Mutualistic coefficients and conditions for the simulation depicted in Fig. 9. In Fig. 10 all parameters are identical except $b_{P1A1} = b_{P2A1} = b_{P3A1} = 4$, $b_{P1A2} = b_{P1A3} = b_{P1A4} = 1$, $b_{P2A2} = b_{P2A3} = b_{P2A4} = 1$, $b_{P3A2} = b_{P3A3} = 1$, $b_{A1P4} = b_{A2P3} = 1$

	P1	P2	P3	P4	P5	P6	P7	A1	A2	A3	A4	A5	A6	A7
$b_{1j}\left(10^{-5}\right)$	1	1	1	1	1	1	1	1	1	1	1	1	1	1
$b_{2j}\left(10^{-5}\right)$	1	1	1	1	1	1	0	1	1	1	1	1	1	0
$b_{3j}\left(10^{-5}\right)$	1	1	1	1	1	0	0	1	1	1	1	1	0	0
$b_{4j}\left(10^{-5}\right)$	1	1	1	1	0	0	0	1	1	1	1	0	0	0
$b_{5j}\left(10^{-5}\right)$	1	1	1	0	0	0	0	1	1	1	0	0	0	0
$b_{6j}\left(10^{-5}\right)$	1	1	0	0	0	0	0	1	1	0	0	0	0	0
$b_{7j}\left(10^{-5}\right)$	1	0	0	0	0	0	0	1	0	0	0	0	0	0
$N_{init\,j}$	2000	2000	2000	2000	2000	2000	2000	2000	2000	2000	2000	2000	2000	2000
$c_j\left(10^{-5}\right)$	6	6	6	6	6	6	6	6	6	6	6	6	6	6
$\alpha_j\left(10^{-5}\right)$	3	3	3	3	3	3	3	3	3	3	3	3	3	3
$r_{birth\,j}$	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003	0.003
$r_{death\,j}$	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02

TABLE 4. Mutualistic coefficients and conditions for the simulation depicted in Fig. 11 and Fig. 12. In Fig. 13 dynamic parameters and mutualistic coefficients are the same except $b_{P2A1} = b_{A2P1} = 2$, $b_{P3A1} = b_{A3P1} = 3$, $b_{P4A1} = b_{A4P1} = 4$, $b_{P5A1} = b_{A5P1} = 5$, $b_{P6A1} = b_{A6P1} = 6$, $b_{P7A1} = 4$, $b_{A7P1} = 7$, $c_{P7} = 20$, $\alpha_{P7} = 18$, $r_{death\,P7} = 0.03$.

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