Dragging as a mechanism of destruction of mutualistic network?

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Abstract.   Mutualism is the interaction between two kind of species that results advantageous for both. Mutualistic communities have an internal structure of bipartite network. Literature makes a distiction between *generalists* species, linked to several instances of the other class, and *specialists*, with few links. This property is called *nestedness* and provides stability and resilience. We describe *dragging* as a possible mechanism of destruction and how it is related to the K-core structure.

Keywords: Mutualism, nestedness, cascade extinction, dragging, K-core.

1.   Introduction

Mutualism is a benefitial interaction between two classes of species (for instance, pollinators and plants, or seed dispersers and plants). From an structural point of view these communities are bipartite networks [9],[7]. Besides, when we consider weighted links, these mutualistic networks can be seen as directed networks because there will be an interaction matrix of the benefit of plants on animals and another for the benefits of animals on plants. This fact is less stressed in the literature but quite important for their dynamics because it is a source of asymmetry.

Depending on the degree, there is a distiction between *generalists* species, linked to several instances of the other class, and *specialists*, tied only to a small number of them. In real networks, there is a core of generalists highly interconnected and a high number of specialists that usually link to the core. This property is called *nestedness* and provides stability [12] but the dynamics of destruction of this kind of communities is an open research field. We discuss *dragging* as a mechanism that might trigger cascade extinctions and how it is related to the K-core decomposition of the network [1].

2. Dynamics of mutualism

Classic models of mutualism derive from Verlhust's logistic equation [13], adding a third term as the mutualistic benefit. The first one was proposed by May [9]. May's equations for two species can be written as

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

where $N_1(N_2)$ is the population of the species $1(2)$; $r_1 (r_2)$ is the intrinsic growth rate of population $1 (2)$ and $K_1 (K_2)$ the carrying capacity. Another well known model is the so called *type II* [14], because mutualism is included as a type II functional response.

Depending on the intrinsic growth rate there are two possible behaviors: *facultative* and *obligatory*. In the facultative case, the species intrinsic growth rate is positive. Mutualist links only increase that figure but are not essential for survival. More interesting is *obligatory* mutualism, because each species depends on the others to live. For instance, some kind of plant whose polen is the only food for a pollinator that, in turn, is the unique vector for the plant sexual reproduction.

Both species must have a number of individuals above a survival minimum to guarantee that their effective groths rates (intrinsic rate + mutualistic benefit) are positive, otherwise system collapses.

We propose a modified model that includes the benefit as part of the *effective growth rate* and not as an independent term, to overcome some of the known drawbacks of *May* or *type II*. For 2-species, where we will call the plant species *1* and the pollinator species *2*, the new model [6] reads:

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

The main problem to check experimentally the accuracy of these mathematical tools is that field observation is rather difficult and time consuming, so discussion remains on a theoretical plane. As discussed in [3] *"essentially, all models are wrong, but some are useful"*, we are going to explain an observed quality of mutualistic communities trying to avoid modelling details.

Nestedness is a quite remarkable property of mutualism, and an active research topic [2, 5, 10, 11, 12]. It is commonly accepted that nestnedness

provides stability and resilience, but as interactions between species are non-linear and the network structure may become rather intricate hypotheses put focus in partial aspects of the global dynamics.

Here, we propose an explanation for a particular observed property of nested dynamics, that the survival chances of a newcomer species depends on the strength of its ties to the generalist core.

Let's start with the most simple example, that of two species, one of each kind, assuming that mutualism if obligatory. Benefit depends on the number of individuals of the other species, so we can write population dynamics equations as:

$$\frac{dN_1}{dt} = N_1 r_{\text{ef},1}$$
$$\frac{dN_2}{dt} = N_2 r_{\text{ef},2} \tag{3}$$

where the effective growth rates are functions of both populations:

$$r_{\text{ef},1} = f\left(r_1, N_1, N_2, b_{12}\right)$$
$$r_{\text{ef},2} = f\left(r_2, N_2, N_1, b_{21}\right) \tag{4}$$

Where coefficients b_{ij} represent the stregnth of unidirectional ties. Function f is, in general, nonlinear and may depend on other constant value parameters that are particular of each model, but we do not need to dive so deep for our discussion. No matter what model we are using, the system has at least three fixed points [4].

First one is stable, extinction. If both r_{eff1} and r_{eff2} are simulatenously negative, populations will decline towards zero and there they will remain. Second one is also stable, populations at *maxima* when both effective rates are positive. Maximum value depends on the model we are using. Usually is called *carrying capacity* but we prefer to avoid this expression since it is tighlty associated with the logistic formulation of Raymond Pearl that has major shortcomings [8]. The third fixed point is unstable, a saddle that appears when $r_{eff1} = r_{eff2} = 0$. Solving equation (4) with this condition we find N_1^*, N_2^* that is the vital minimum of the system. If $N_1 > N_1^*$ and $N_2 > N_2^*$ populations evolve towards maxima, on the other hand if $N_1 < N_1^*$ and $N_2 < N_2^*$ system collapses.

What happens when one population is above the vital minimum and the other below?. There is a watershed that divides life and death of the system. Intuition tells that if population 1 is high enough, population 2 may grow until it reaches the life area and before population 1 drops below N_1^*. The shape
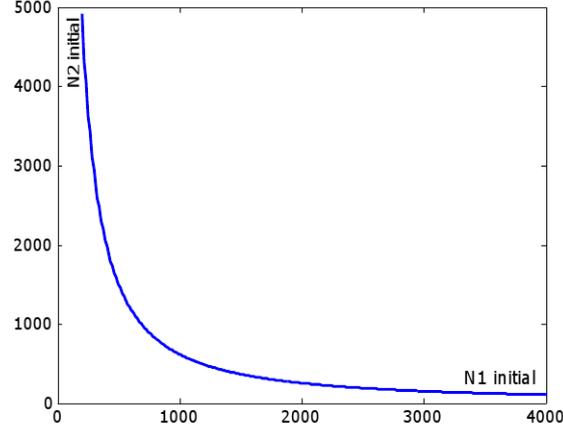
Figure 1: Exponential life watershed for a simple two species mutualistic community.

of this line depends on the model we are using. In fig. 1 we show an example with the formulation we are currently working in, where the watersehd is a power law. Anyway, for the purposes of this communication it would be valid any other silghtly different shape, provided that there are two distinct regions.

When the number of species increases, finding the vital minimum may produce strange results. We have to solve the set of n x m equations, for n species of class a and m of class p. This task will require usually a numeric solver.

$$r_{\mathrm{ef},i}^{a} = f\left(r_i^a, N_i^a, N_1^p, .., N_m^p, b_{1i}^{ap}, .., b_{mi}^{ap}\right) = 0 \ , \forall i = 1, n$$
$$r_{\mathrm{ef},j}^{p} = f\left(r_j^p, N_j^p, N_1^a, .., N_n^a, b_{1j}^{pa}, .., b_{nj}^{pa}\right) = 0 \ , \forall j = 1, m$$

$$(5)$$

The paradox is that some of the values $N*_j$ may be negative, even when there are only two species of one class and one of the opposite. The interpretation is simple. Imagine that there is an stable and strong network and a newcomer species arrives. The effect of the preexisting network on the newcomer is positive enough to balance its intrinsic negative rate for any combination of populations that is above the vital minimun. This is equivalent to facultative mutualism for the preexisting network and equivalent rate positive for the newcomer for any number of individuals. This fact is important for the resilience of the system.
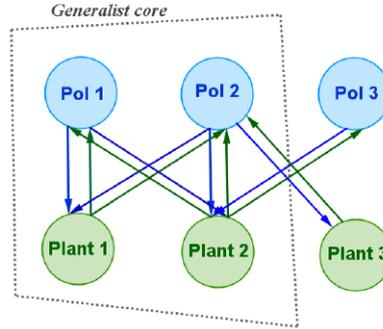
Figure 2: Example of simplified mutualistic community. Left, generalist core with two linked specialists. Right, two new specialist newcomers.

3.   Cascade extinction and dragging

When dealing with extinctions, it is important to know the event that triggers the catastrophe and the damage extension. A large extinction event (a locust invasion, a fire, a severe drought, etc.) destroys several species and might drive the system towards collapse. But for system survival is more important its resilience against individual species decline, and here is where nestedness plays an important role.

For our explanation we will use a simple network example (Fig. 2). Let's start with a generalist core of 2x2 species (pollinators and plants) and two specialists. Imagine that some generalist species suffers a catastrophic event, for instance, Plant-2, and all its individuals die. Its extinction will trigger that of Pollinator-3, an specialist that depends on Plant-2 to survive, but is quite probable that Pollinator-1 and Pollinator-2 may keep its population over vital minimum by the benefit of Plant-1. In this scenario it is also quite possible Plant-3 survival.

As the generalist core has more species and many links it is easier to understand its resilience when one of the species suffers a catastrophic event. It is also straightforward that a specialist linked to just one generalist may disappear even if the population of the generalist drops below the vital minimum.

But, why the distribution of newcomers does not follow a random pattern but a nested one? The explanation must be found in network structure and its ability to propagate extinctions.

We use K-core decomposition to describe distance from the strongly nested core. If we call $G = (V, L)$ our graph, composed of V vertices and L links between them, a $K - core$ is a maximum subgraph for which the degree of its nodes is at least K [1]. As we are working with a bipartite, bidirectional

graph, we will make a simplification. For our descriptive purposes we will assume that it behaves as unidirectional having in mind that this is not valid for numerical simulations.

We build a community with 8 species of plants and 7 species of pollinators (figure 4) and perform K-core decomposition. This example has only 3 levels. We define distance as the shortest path from any node to the maximum value k_{max}. Distances of nodes that belong to 3-core are 0. Plants 4, 5 and 7 and pollinators 4 and 6 are at distance 1. Pollinator 5 and plant 8 are at distance 2, plant 6 is at distance 3 and pollinator 7 at distance 4.
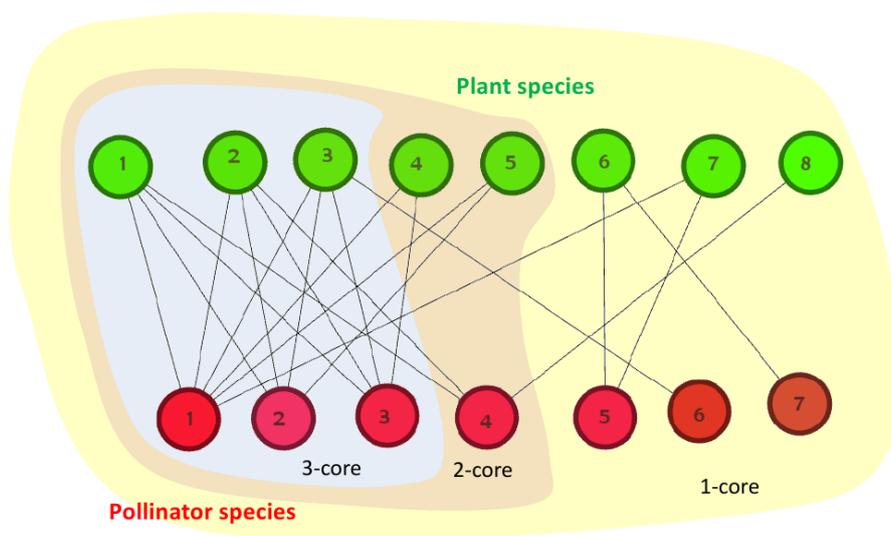

Figure 3: Simulated neetwork

Species of the 1-core are the specialists of this example. Pollinator 6 and plant 8 are linked to one generalist each. If we remove those nodes (plant 3 and pollinator 4) the specialists are destroyed but they do not propagate extinction, they are the edge of the chain.

Notice plant 6 and pollinators 5 and 7. They are not directly tied to the core but through are a long tail that starts at plant 7. All these species are in danger of destruction if any of the nodes of the chain suffers an external event.

In the numerical simulation, pollinator species 5 suffers a step growth of its yearly death rate by a 25%, this event leads it to extinction. As population of pollinator 5 drops, plant 6 losses one of their two sources of mutualistic benefit and also drops. Pollinator 7 suffers the same fate as it is only tied to plant 6. Eventually theses populations fall below their vital minimum and are
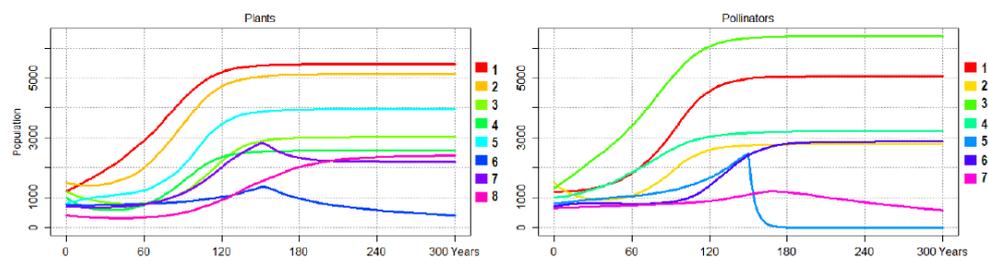
Figure 4: Pollinator 5 suffers an external events and drags other species

dragged to extinction by the event on pollinator 5.

Pollinator 7, at a distance 4, is the most endangered species because any extinction in the chain that links it to the core will spread towards it. On the other hand, the same simulation shows that plan 7 that is directly linked to pollinator 5 survives because of its link with the core. This is not a general rule, benefit provided by pollinator 1 could be not strong enough but is the most likely situation. When a newcomer links to any chain, the preexisting species are a viable tail of the community, so they can survive without the incoming one.

4.   Conclusions

We have described how topology is critical for extinction spread in mutualistic networks. The chances of survival of any species depends on its distance to the generalist core, and so nestedness appears as a result of mutualism. This is a work in progress, an accurate characterization of the concepts *generalist core* and *distance* will allow a probabilistic description of extinction spread.

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