# The architecture of predator-prey and the relationship between complexity and stability

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Theoretical studies predict that the stability of an ecosystem is negatively correlated with its complexity, measured by the number of interacting species. On the other hand, empirical evidence indicates that food webs are highly interconnected. In this manuscript we present results on the stability two-level predator-prey food webs. We analyzed exhaustively all possible topologies of connections among species. Our findings show that those food webs fall into two classes with clearly distinct stability properties. In one of them stability is negatively correlated with complexity, and in the other group stability is positively correlated. For a positive relationship our results reveals highly structured food webs. The positive or negative relationship is related only to the topological structure of the food web. It is independent of the number of connections, strengths of predator-prey interactions or number of species. We review empirical evidence that corroborates our results.

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## Introduction

The complexity of association among species was found to influence the stability and balance of the community system (1,2). Early empirical and theoretical studies (3,4) suggested that increased complexity, measured by the number of connections among species, strengthen ecosystem stability. In the last few years, empirical evidence of aquatic and terrestrial food webs has been analyzed through complex networks theory (5,6), and showed that ecological networks have much higher complexity than other networks studied. According to that empirical evidence, the species within ecosystems present high levels of connectance.

On the other hand, theoretical studies of general complex systems (7) indicate that complex systems which are connected at random may be expected to be stable up to some critical level of connectance, and beyond this point to go suddenly unstable. Based on these studies, May (8, 9) performed an analytical investigation to clarify the relation between stability and complexity in ecological systems. He found, studying random community matrices, that stability tends to decrease with complexity. Recently, Gross et al. (10) studied several millions replicates of food webs, and also concluded that food web complexity is negatively correlated with stability.

The set of all possible theoretical ecosystems, where species are interacting through competition, mutualism or a general predator-prey relationship, is huge. For instance, for a ten species ecosystem there are $2^{10x10}$ possible food webs, topologically different and with same strength of interactions between species. The sheer size of this sample space (approximately $10^{30}$) requires the adoption of special strategies in the search for stable structures through new connections among species. In an attempt to find these special strategies, De Angelis (11) showed that if the food web incorporates a biologically reasonable constraint, of simple predator-prey relations, then an increased complexity can often lead to increased stability. Another biologically constraint was presented by Lawrence R. Lawtor (12), Lawrence examined competitive systems in natural communities and compared them with randomly constructed communities, and discovered that competitive processes are important in shaping stable communities. Recently Allesina et al. (13) made a statistical analysis, from ten thousand community matrices, and showed that when the interaction between species is constrained to consumer-resource relationships, large and highly interconnected communities exhibit a high probability of stability compared to the random case.

In this work we report a complete statistical analysis of the set of all possible community matrices. Here we assemble food webs, topologically different, connected by competition among prey, and constrained to a certain predator-prey structures. We repeat the process for all possible predator-prey structures. Our statistical analyses reveal the existence of two groups of samples, within all possible predator-prey structures. One of them, with 33.2 percent of the total, displays the same kind of negative correlation between complexity and stability found by Robert May (8,9) and Gross et al. (10). The other group, with 66.8 percent, contains highly structured food webs where complexity is positively correlated with stability, in agreement with empirical results (1, 2, 5).

We found that the condition for a negative or positive correlation between complexity and stability is related only to the topological structure of the food web. The sign of the correlation does not depend on the distribution of predator-prey interaction strengths, the number of predator-prey connections or the number of interacting species. For food webs with high levels of connectance, our results reveal that the positive correlation is found in highly nested structures and that is in agreement with recently empirical results from the Serengeti (14, 15). Our results and the results of Bastolla et al. (16) are pointing that nested structure in food webs permits an increase of complexity and biodiversity to strengthen ecosystem stability.

**Methods**

Our goal is to analyze the stability of all possible topologies of predator-prey food webs. The community matrix (May 1972, 1974) is a very useful concept for our analysis. It appears in the stability analysis of population dynamics, and is related to the functional form of the couplings (interactions) between species in a given ecosystem. If one writes the rate of change of the abundance $X_i$ of species $i$ as:

$$\frac{dX_i}{dt} = f_i(X_1 \dots X_N), \qquad (1)$$

where $N$ is the total number of species, each $f_i(X_1 \dots X_N)$ is composed by linear and non-linear functions. The non-linear functions represent strong interactions between species, i.e. intraspecific competition (self-regulation), interspecific competition, mutualism, and predation. The dynamical properties of the ecological system, Eq. (1), in the neighborhood of an equilibrium point, can be obtained by an analysis of the derivatives of $f_i(X_1 \dots X_N)$ with respect to the abundances $X_j$. Theses derivatives may be arranged to form the so-called community matrix $M$, whose entries are defined as:

$$m_{ij} = \left.\frac{\partial f_i}{\partial X_j}\right|_{X^*},$$

where $\left.\right|_{X^*}$ specifies that the partial derivative is evaluated in an equilibrium point, where all species coexist permanently, that is $X^*_i > 0$ for all $i$. If $X^*$ is a stable equilibrium point all eigenvalues of $M$ have negative real parts.

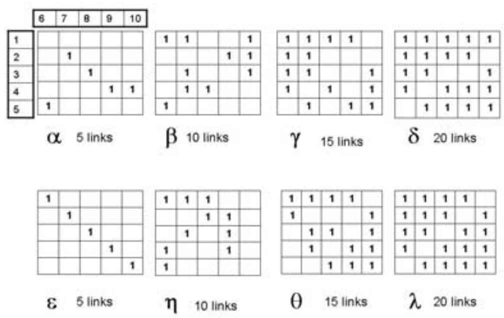


**Fig. 1. Illustration of the relationship between predator (1, 2, 3, 4 and 5) and prey (6, 7, 8, 9 and 10) species. The Greek letters represent eight different scenarios of predator-prey structures, taken from $2^{25}$ scenarios possible. The symbol 1 means that the predator given by the line number feeds on the prey given by the column number.**

In this work we modeled 10 species ( $N = 10$ ) predator-prey food webs by setting the community matrix elements to some specific values. We chose the diagonal elements of $M$ to be all equal to -1, which means that all species have a form of self-regulatory auto-interaction; this choice is identical to the choice made by May (*8*). We chose the off-diagonal coefficients according to biologically reasonable constraints. First, we fixed our studies in two trophic levels, and the $N = 10$ species were divided in two groups, five predators and five prey. Now we can look at two different sectors of the community matrix. One concerns the predator-prey interactions, and the other one represent prey-prey interactions,

If we assume that each matrix entry can be filled with either zero or non-zero number (which we chose to be +1 for predator-prey and -1 for prey-predator interaction), then there are $2^{25}$ distinct combinations for the predator-prey sector and $2^{10}$ combinations of the prey-prey sectors, resulting in a total $2^{35}$ (~$10^{10}$) possible community matrices.

In order to explore this rather large sample space, we adopted the following strategy: initially we chose a fixed predator-prey scenario, as illustrated in figure 1. The scenario α represent a food web with four predators (named 2, 3, 4 and 5) feeding on five preys (named 6, 7, 8, 9 and 10). The relationship between them is: predators 2, 3 and 5 are specialist and they are connected with the prey 7, 8, and 10, respectively, the predator 4 is a generalist and its resources are the prey 9 and 10. The interpretation is the same for the other scenarios. For each scenario we introduced Λ links between prey species (which we chose to be -1 for prey-prey interaction). For five prey species, Λ takes values from Λ=0 to a maximum of Λ=C(5,2)=10 links, where C(5,2) is the binomial coefficient. With Λ links between prey species we have C(10,Λ) combinations to assembled different food webs, in each scenario. We then calculate the eigenvalues (17) of the community matrix of each scenario and each combination of prey-prey interactions with Λ connections among prey.

## Results

We now proceed to show the results of our exhaustive exploration of the sample space of all possible community matrices with constraints presented in the previous section. We analyze separately the two groups of scenarios, α to δ and ε to λ presented in figure 1.

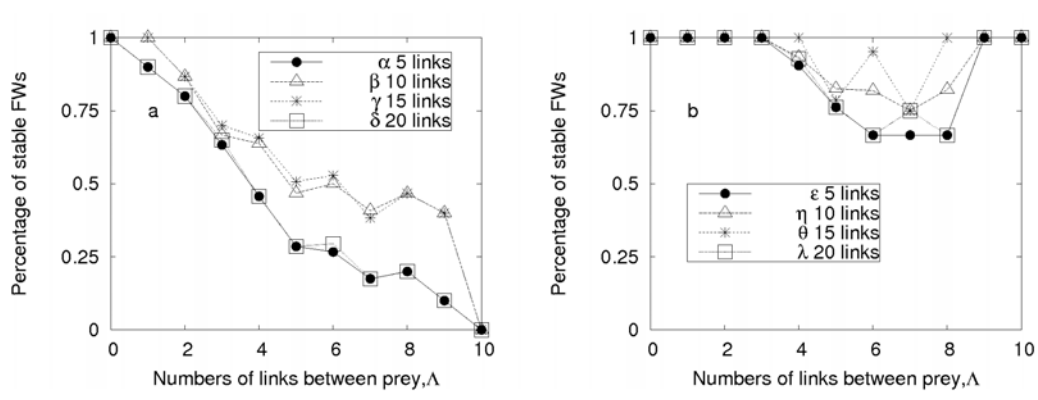


**Fig.2. In the y-axis the percentage of stable FWs, that is, the number of stable FWs normalized by C(10,Λ). (a) The scenarios, α, β , γ and δ, present a negative correlation between complexity and stability. (b) The scenarios ε, η, θ and λ, present a positive correlation for Λ>7.**

The analyses of communities matrices that represent from scenarios α to δ show that the fraction of stable food webs (FWs) clearly decreases with the increasing number Λ of prey-prey links, independently of the number of links between predator and prey, as can be seen in figure 2a. This behavior is qualitatively different from scenarios ε to λ, shown in figure 2b, whose stability behavior has little effect for $4<\Lambda<7$, and after $\Lambda>7$ the fraction of stable food webs increases with increasing number of prey-prey links. This indicates that prey-prey competition has a little effect on the stability of these structures. The behavior of figure 2b is showing that the structure of the food web is relevant for ecosystem stability and persistence of biodiversity.

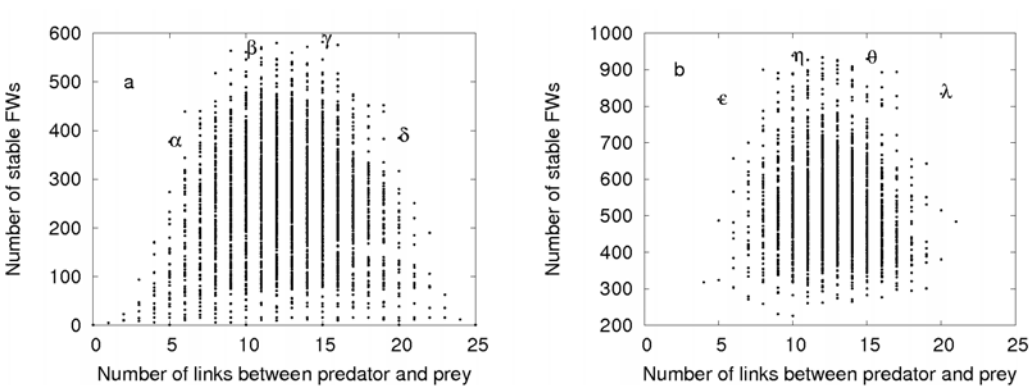


**Fig.3. The y-axis represents the total number of stable FWs for each scenario, and the x-axis denotes the number of links of predator-prey for each scenario. (a) The points denote all the scenarios with negative correlation, scenarios close to α, β, γ and δ of figure 2a. About 33.2 percent of the $2^{25}$ scenarios are present in this figure. (b) The points represent all the scenarios with positive correlation between complexity and stability, scenarios close to ε, η, θ and λ of figure 2b. There are about 66.8 percent of all scenarios in this figure.**

We showed eight scenarios of predator-prey structures however we analysis $2^{25}$ possible scenarios. In all of them was detected these two types of behavior, that we showed in figures 2a and 2b. In order to show the results for the other scenarios, we separate the structures that present a negative correlation from the structures that present a positive correlation. The figures 3a and 3b is showing in y-axis the total number of stable FWs for each scenario, and in x-axis the number of predator-prey links of each scenario. For scenarios that present a negative correlation the number of stable FWs is less than for scenarios with positive correlation, compare the scale of y-axis in figures 3a and 3b. For structures of figure 3a, negative correlation, and high levels of connectance among predator-prey we can see that the total number of stable FWs clearly decreases with increasing number of predator-prey links. However, for structures of figure 3b, positive correlation, it is not possible to say that the total number of stable FWs decreases with complexity because of the λ scenario. That means that structure presented by scenario λ leads to increasing ecosystem stability. If we do a zoom of figure 3b, on food webs highly connected, and print their topological structure then we found only nested structure, as can see in figure 4. This result is robust on the distribution of predator-prey interaction strengths or number of interacting species (Supplementary Information). That means: it is not possible to change the relationship between complexity and stability without changing the structure.

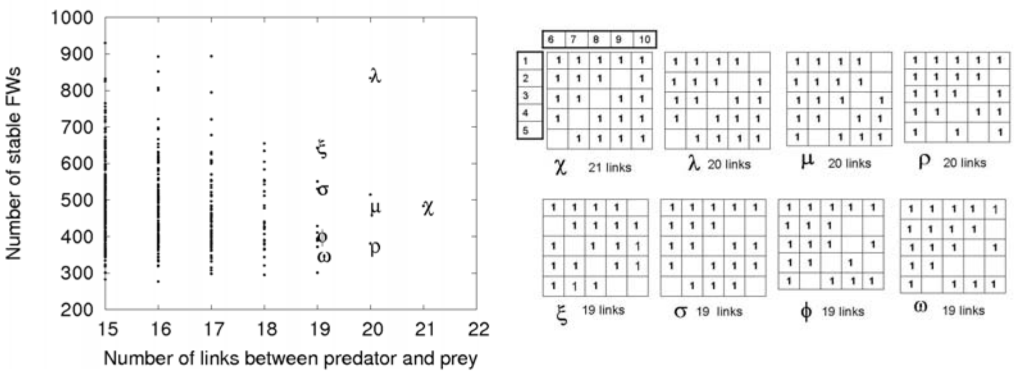


**Fig.4. A zoom of figure 3b and an illustration of the predator-prey structures for highly complex food webs.**

## Discussion

We analyzed all possible topologies for two-level food webs and discovered that there exist two groups of samples, within all possible predator-prey structures. The first group contains structures of food webs negatively correlated with complexity, figures 2a and 3a, found by May (8,9) and Gross et al. (10). The other group, with the majority of samples, contains highly structured food webs that permit a positive correlation between complexity and stability. Our results indicate that only the structure of predator-prey networks can control the relationship between complexity and stability (Supplementary Information).

For high levels of connectance among predator and prey species we found that this architecture is build by highly nested structures. The nested structures that we found are in agreement with empirical reports from species of the Serengeti (14, 15). These reports with 40 years of data reveal that the species interactions between herbivores and plants, and carnivores and herbivores are hierarchically nested. Our theoretical results contrast with studies of competitive systems and the increasing of stability in food webs (18-20). Moreover our results reveal asymmetric patterns, intrinsically presents in nested structures, of the interactions between predators and prey, to enhance ecosystem stability in agreement with empirical reports (21, 22).

From other food webs, empirical report of 52 mutualistic networks (*23*) showed that the assemblies of plants and animals are highly nested. A theoretical study (*16*) found that the architecture of mutualistic networks increases biodiversity, i. e. the number of coexisting species. That means the nested structure of food webs, mutualistic or predator-prey, are positively correlated with stability, complexity and biodiversity.

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