Population Dynamics on Complex Food Webs

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Abstract

In this work we analyze the topological and dynamical properties of a simple model of complex food webs, namely the niche model. We describe the system as an oriented weighted graph and we assign a Lotka-Volterra population dynamics on the structure created by the niche model. After this we introduce "predators" and "prey" weighted graphs from which we underline patterns of competition among species. We measure topological properties of such graphs comparing simulated food webs with real data. We find that, using a combination of projections weights as competition kernel in the Lotka-Volterra equations, the stability of food webs decreases with its complexity (measured as the average degree of the web).

Keywords: Complex Networks, Food Webs, Population Dynamics

1. Introduction

The study of food webs has recently attracted the interest of complex systems scientists as one of the clearest example of a network structure whose property can only be understood by looking at the system as a whole. A food web is the collection of the predation relations in an environment and assumes naturally the form of a network that is a mathematical object composed by vertices (the biological species) and their edges (the predation relations). Such a structure is very widespread and can be recovered with similar statistical properties in a variety of other situations from WWW[1] and the Internet[2] to protein interactions[3] and social systems[4]. Despite this similarity, food webs represent one of the most interesting cases of study for their particular topology. For example vertices can be divided in classes thanks to their biological meaning (i.e. prey/predators). Also, the structure is naturally layerized when considering the minimum distance of species from the external resources. All these properties make these structures extremely interesting for testing models and algorithms related to complex networks. Similarly, some of the ideas developed in the area of computer science turned out to be useful in the case of food webs, signalling some biological meaning hidden in this topology[5].

Traditionally, the most important quantities in a food web are the number of vertices N and the number of edges L. Since the maximum number of edges you may have in such a system grows as N^2 (precisely $N(N-1)$ for a directed graph) one also considers the density of edges L/N^2, a quantity known in ecology as the *directed connectance*. The edges are directed and each of them follows the convention (based on the flux of nutrients) of drawing the edge from prey to predator. In this work we will consider only *trophic webs*, where all species which have exactly the same predators and prey are merged. Another characterization can be obtained by considering all the species that have no predators. They are usually indicated as the *top* (T) species. Similarly, the species with no prey are called *basal* species (B). All the others form the *intermediate* (I) class. All the species are ultimately sustained by the transformation into biomass of external resources like water, mineral sunlight by means of the basal species. It is then customary to describe this situation with the introduction of an external node, called zero node, which points to all basal species i.e. to that nodes with only out-edges. Given this structure, it is easy to define layers of species given by the distance (i.e. the minimum path) towards the zero node of external

resources. The distance is measured as the number of edges the biomass has to travel. As in the Internet[6] some loops can be present in the system and they account for the stability and resilience of these structures[7]. Food webs have been modelled in many ways, and the different models have been validated with the experimental data available. Here we focus on one recent and successful model on which we create a suitable population dynamics by means of Lotka-Volterra equations whose parameters are self-determined by the topology created by the model itself.

2. Niche Model

There are many static models of food webs which reproduce the features of real ecosystems such as fractions of top, basal and intermediate species, number of food chains, average chain length, and connectance [8]. The simplest way is to create suitable graphs [9, 10, 11], where (given the linkage density and the number of nodes), directed edges are assigned to randomly chosen pairs of nodes. The agreement between real and simulated food webs is not very good. This is not surprising, since this simple model has many unrealistic features such as the assumption that every species can in principle be the predator of every other species.

Recently William and Martinez introduced another static model, called "niche model" [12]. The authors found a remarkable agreement between real webs and the synthetic ones generated by the model (much better than the one measured for cascade model [13]). This is particularly true when considering features such as cycles and species similarities. The external parameters of the model (i.e. the quantities fixed from the beginning) are the number of species S and the directed connectance $C = L/S^2$. To every node is assigned a uniformly distributed number n_i into the interval $[0, 1]$, the niche space. A species i is characterized by its niche parameter and its list of prey. Prey are chosen for all species according to the following rule: a species i preys on all species j with niche parameters n_j inside a segment of length r_i centered in a position chosen randomly inside the interval $[r_i/2, n_i]$, with $r_i = xn_i$ and x a random variable with probability density function

$$p_x(x) = \beta(x, 1, b) = b(1 - x)^{(b-1)} \tag{1}$$

Choosing $b = (1/2C) - 1$ is possible to generate graphs with the desired size

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and connectance[1].

Niche model estimates the central tendency of empirical data remarkably well [12]. Its topological and analytical properties have been widely studied [15, 16] and it has been shown that the predictions of the model are robust with respect to the specific form of the $p_x(x)$ chosen[17, 18].

3. Population Dynamics

Given the network structure, we want to define a population dynamics for the individuals of the species described in this food web. To each node i we associate a population i.e. a function of time $N_i(t)$ which represents the density of individuals of the same trophic species per unit of area.

To describe population dynamics we use the generalized Lotka-Volterra equations :

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - \sum_{j=1}^{S} \alpha_{ij} N_j}{K_i} \right) \tag{2}$$

where r_i is the intrinsic growth rate of species i, K_i his carrying capacity and α_{ij} represents the effect species j has on the population of species i. Pulling the carrying capacity into the interaction term the equations became

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \sum_{j=1}^{S} \overline{\alpha_{ij}} N_j \right) \tag{3}$$

This doesn't actually change the equations, but only how the interaction $\overline{\alpha_{ij}} = \alpha_{ij}/K_i$ is defined. For simplicity all self-interacting terms $\overline{\alpha_{ii}}$ are set to 1.

One can represent both the populations and the growth rates as rows of numbers (vectors) and the interaction term α as a matrix, called also *competition kernel*. Let us suppose that we have only one type of external resource R produced with a constant rate y (*renewability* of resources) and let us also suppose that each basal species consumes a fraction X at a rate c_i. The equation for the resources is:

$$\frac{dR(t)}{dt} = R(y - \sum_{i=1}^{S} c_i N_i) \tag{4}$$

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[1]In the niche model species with no prey and predators are eliminated and species with the same list of prey and predators, that is trophically identical species, are merged.

where the first term considers the renewability and the second one gives the total rate of consume[2].

If we consider the equilibrium conditions for equations that is 2 and 4, $dN_i/dt = 0$ and $dR/dt = 0$, we find a relationship between the ecological parameters given by

$$y = \sum_{ij}^{S} c_i \alpha_{ij}^{-1} K_j \tag{5}$$

This gives a fundamental constraint on all the parameters (except the r_i), especially on the competition kernel which must be invertible.

Some authors use as competition kernel a function of the distances between species in niche space [19, 20]. The problem with such a choice is that the topology of the food web is not included in the equations; a simple way to incorporate it is to use a combination of projections weights, an issue treated in the next section.

4. Projections Graphs

An adjacency matrix A of S rows and columns represents an aggregated food web with S trophic species. The elements a_{ij} is taken 1 if species j predates on species i and 0 otherwise. The ecosystem can also be represented as a bipartite graph [21] where two classes of nodes are present: predators (top and intermediate species) and prey (basal and intermediate species) and each directed edge is always disposed between nodes belonging to different classes. Such a graph can be projected into the predators-network, where two predators are connected with an edge weighted proportionally to the numbers of prey they have in common and, correspondingly, into the prey-network, where two prey are connected according to the number of predators they share.

The projection graphs are two undirected, weighted graphs whose sizes are the number of predators and the number of prey in the food web respectively. The corresponding adjacency matrices A^{pred} and A^{prey} are symmetric and we

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[2]here is assumed that $c_i \neq 0$ only for basal species.

define their elements in the following way:

$$a_{ij}^{pred} = \frac{\sum_{k=1}^{S} \delta_{a_{ki},1}\delta_{a_{kj},1}}{S(B+I)} \tag{6}$$

$$a_{ij}^{prey} = \frac{\sum_{k=1}^{S} \delta_{a_{ik},1}\delta_{a_{jk},1}}{S(T+I)} \tag{7}$$

We choose to normalize the predators weights over all possible prey, and the prey weights over all possible predators. Note that $a_{ij}^{pred} = a_{ji}^{pred}$ and $a_{ij}^{prey} = a_{ji}^{prey}$. Since the change in the size of the graphs (without loss of generality) we relabel the vertices in the two graphs and keep the information about the species they represent [14].

The weights of the projections' graphs are a measure of the interspecific competition for resources, giving information on how two species compete (or are object of competition) in the predation interaction. A more significant meaning of this quantity should be derived by the analysis of an original weighted food web where the strength of the predation is also considered. For this reason, considering equation 2 we propose the following competition kernel that joins in a self-organized way[22] the topology with the dynamics:

$$\alpha_{ij} = a_{ij}^{pred} - a_{ij}^{prey} \tag{8}$$

This means that the influence of population i on population j is negative if species i and j share some prey and positive if they share some predators. The competition between two species increases with respect to the number of prey species they share and vice versa. Using the elements defined in eq. 8, it is possible to simulate a population dynamics on both model and empirical food webs.

5. Results

The stability of empirical and model food webs has been tested numerically following this steps:

1. *Food web adjacency matrix.* We generate it using niche model, where the input parameters are connectance C and size S. In real cases this is done considering empirical food webs data.
2. *Competition kernel.* We derive the competition kernel $\alpha_{ij}(C)$ from equation 8.

3. *Ecological parameters.* We fix the parameters r_i, c_i and K_i:

- As a first approximation the intrinsic growths r_i are set all equals for all species. This means that in the ideal condition of no competition and infinite resources, all the populations should grow at the same rate. Varying these parameters one can simulate the different lifetimes of species and their reproduction strategies.

- Setting the carrying capacities K_i of the species means that, in the ideal condition of no interspecific competition ($\alpha_{ij} = 0$), the maximum number of individuals per unit of space which are sustainable from the external environment is fixed for every species.

- the consuming rates c_i has been set to 0.1 only for basal species. This is quite realistic because basal species are, by definition, the species which directly feed on the external environment.

- At this point using equation 5 we fix the renewability of resources y which depends basicly on the topology of the graph. To avoid indefinite growth, for simulated food webs, we fix the maximum renewability $y_M = 10$ and generate graphs with the same connectance and size until we obtain the desired renewability ($0 < y \leq y_M$).

4. *Integration of equations.* Once we have the competition kernel and the desired y we solve the equations 2 using the 4th order Runge-Kutta algorithm

5. *Stability.* The results have been collected in the steady state.

5.1. Projections Topological Properties

We measured topological properties of projections graphs for both empirical and model food webs. The data we used have been selected to be the largest and highest-quality empirical trophic food webs present in literature. They represent a wide range of ecosystems, from freshwater habitat (Skipwith Pond SWP, Little Rock Lake LRL, Bridge Brooke Lake BBL) to freshwater-marine interface (Chesapeake Bay CPB, Ythan Estuary YE) to terrestrial habitats (Coachella Valley CDE, Saint Martin Island SMI)

The measure of all topological features (except for averaged weights) is made by considering the binary matrices of projections where all weights different from 0 are put to 1.

Looking at the empirical graphs we find a very symmetric topology (Fig.2, 3). Some projections show the formation of isolated communities both in predators and in prey graphs (Fig. 4, 5) and sometimes we find only isolated nodes i.e. specialists in predation or in being a prey. This possibility of community formation is not considered in directed food webs. In fact, in both empirical and model graphs, there are no isolated nodes or clusters (in niche model isolated species are removed).

We can measure this feature by considering the matrices of path lengths whose elements are given by

$$d_{ij}^{pred/prey} = min\{ \sum_{k,l \in P_{ij}} a_{kl}^{pred/prey} \} \qquad (9)$$

where P_{ij} is a path connecting node i and j. Putting $d_{ij} = 0$ when the distance between i and j is infinite i.e. when the nodes are in different clusters. We compute average path length using two different normalizations:

$$l_G = \frac{1}{n(n-1)/2} \sum_{i>j} d_{ij} \qquad l_R = \frac{1}{[n(n-1)/2] - (l_0/2)} \sum_{i>j} d_{ij} \qquad (10)$$

where l_0 is the number of zeros in the matrix of path lengths. With this definitions l_G is the average path length over all possible paths and l_R is the average path length over all real paths. We have $0 \leq l_G/l_R \leq 1$ being 0 when all nodes are isolated and 1 when all nodes are in the same cluster. Together with this we measure other topological quantities such as clustering, diameter and average weight, for both projections (Table 1).

One of the first evidences is that the formation of communities is always common to both projections. Connectance varies from 0.24 of CDE to 0.92 of SWP, indicating that projections graphs are strongly connected in comparison to the original food webs. Average weights, the only quantities measured considering projections as weighted graphs, vary from 0.04 to 0.21 for predators and from 0.05 to 0.22 for prey. It seems that $\langle w \rangle$ is independent from original connectance and takes high values compared to model projections. Furthermore we can say that projections of food webs present all the characteristics of small world networks i.e. small diameter and large clustering [23].

We then compute the same quantities for projections of graphs derived from niche model and random graphs in function of the mean degree of original directed graphs (Fig. 6). We expect averaged topological properties

of random projections to be the same for predators' and prey's graphs because in and out degree distributions of random digraphs have the same form [11]. Comparing the curves with empirical data we find good agreement for clustering and average path lengths. The model represents the formation of competitive communities better than random projections while it overestimates diameters and underestimates average weights. We see how empirical D is better described through random projections, and how $\langle w \rangle$ of empirical projections is larger than model and random averaged weights. We can explain this trend considering the feeding rule of niche model which assigns prey from a single portion of niche space. This reduces the probability of sharing different resources to a single, well distributed interval, augmenting the diameter and reducing weights of projections graphs. On the other side, empirical food webs are not strictly interval and do exhibit a strong bias towards contiguity of prey [24]. This result suggest that empirical observed niches, once mapped onto a single dimension, should be composed of various intervals along niche space.

5.2. Dynamical properties

We tested the stability of these Lotka-Volterra systems using both empirical and model food webs. We remarked that, among all possible behaviors, using coefficients 8 as competition kernel, the system reaches quite always the steady state for small S and C. Otherwise the system is no longer stable and populations sizes go to infinity when complexity, measured as SC, grows. We tested steady states changing initial conditions, and ecological parameters.

The only stable empirical food web is Chesapeake Bay (CPB) which is the one with the lowest complexity. In Fig 7 we present population dynamics obtained setting initial population's densities to 1 for all species and changing the intrinsic growth of the species. We remarked that the r_i are a measure of the speed of convergence of populations sizes. Augmenting the intrinsic growths the steady state is reached faster. Populations' sizes at the steady state should be equal to the carrying capacities, but the presence of competition kernel changes the real K_i of every species. We remarked, however, that this parameters give the size's order of stable populations and when $K_i = K_P$ mean population is always K_p. We obtain the same result changing the initial conditions.

To conclude our analysis we simulated population dynamics on niche model. We fixed S and C and generated 100 realizations of population dy-

namics on model graphs for a relevant number of points. We counted how many times the system reaches the steady state and how many times it diverges. Again we find that, using expression 8 as competition kernel, these are the only two observed behaviors. The probability of reaching a steady state decreases with complexity (Fig. 8 and 9). Population dynamics on graphs from niche model is stable only for small S and C which is no longer true for empirical food webs. Simulating dynamics on graphs with more than 50 nodes is a hard computational task. However it is evident that the model is stable for $SC < 2$ and that stability decreases linearly between $SC = 2$ and $SC = 5$. This results are robust under the change of initial conditions and ecological parameters.

With this we show that it is possible to avoid chaotic behaviors of Lotka-Volterra systems using weights of projections' graphs as competition kernel. When a fixed food web topology gives raise to stable populations, its complexity must be small. This confirms recent findings of theoretical ecology that complex food webs are not necessarily stable.

[1] A.-L. Barabási, R. Albert, *Emergence of scaling in random networks*, Science, **286**, 509-512 (1999).

[2] G. Caldarelli, R. Marchetti and L. Pietronero, *The Fractal Properties of the Internet*, Europhysics Letters **52**, 386-391 (2000).

[3] H. Jeong, B. Tombor, R. Albert, Z.N. Oltvai, and A.-L. Barabási *The large-scale organization of metabolic networks*, Nature **407**, 651-654 (2000).

[4] M. Catanzaro, G. Caldarelli, L. Pietronero, *Assortative model for social networks* Physical Review E **70** 037101 (2004).

[5] S. Allesina, M. Pascual, *Googling Food Webs: Can an Eigenvector Measure Species' Importance for Coextinctions?*, PLoS Comput Biol **5**, e1000494 (2009).

[6] G. Bianconi, G. Caldarelli, A. Capocci *Loops structure of the Internet at the autonomous system level* Physical Review E **71** 066116 (2005).

[7] D. Garlaschelli, G. Caldarelli, L. Pietronero, *Universal Scaling Relations in Food Webs*, Nature **423**, 165 (2003).

[8] J. A. Dunne, R. J. Williams, N. Martinez, *Food web structure and network theory: The role of connectance and size*, PNAS, **99**, 12917-12922 (2002)

[9] B. Bollobás, *Random Graphs*, Academic Press, New York (1985)

[10] P. Erdős, A. Rényi, *On random graphs*, Publicationes Mathematicae, **6**, 290-297 (1959)

[11] M. E. J. Newman, *Random graphs as models of networks*, Preprint cond-mat/0202208v1 (2002)

[12] R. J. Williams, N. Martinez, *Simple rules yield complex food webs*, Nature, **404**, 180-183 (2000)

[13] J. E. Cohen, C. M. Newman, *A stochastic theory of community food webs. I Models and aggregated data*, Proc. R. Soc. Lond. B, **224**, 421-448 (1985)

[14] J. E. Cohen, *Food Webs and Niche Space*, Princeton University Press, (1978)

[15] R. J. Williams, E. L. Berlow, J. A. Dunne, A. L. Barabási, N. Martinez, *Two degrees of separation in complex food webs*, PNAS **99**, 12913-12916 (2002)

[16] J. Camacho, R. Guimerà, L. A. Nunes Amaral, *Analytical solution of a model for complex food webs*, Physical Rewiew E, **65**030901 (2002)

[17] D. B. Stouffer, J. Camacho, R. Guimerà, C. A. Ng, L. A. Nunes Amaral *Quantitative patterns in the structure of model and empirical food webs*, Ecology, **86**, 1301-1311 (2005)

[18] J. Camacho, R. Guimerà, L. A. Nunes Amaral, *Robust patterns in food web structure*, Physical Review Letters, **88** 228102 (2002)

[19] S. Pigolotti, C. López, E. Hernández-García, *Species clustering in competitive Lotka-Volterra models*, Preprint cond-mat q-bio/0702035v1 (2008)

[20] S. Pigolotti, C. López, E. Hernández-García, K. H. Andersen, *On the robustness of Gaussian competition in niche models*, Preprint cond-mat q-bio/08023274v1 (2008)

[21] G. Caldarelli, M. Catanzaro, *The corporate boards networks*, Physica A **338**, 98-106 (2004)

[22] D. Garlaschelli, A. Capocci, G. Caldarelli, *Self-organized network evolution coupled to extremal dynamics* Nature Physics **3** 813-817 (2007)

[23] D. J. Watts, S. H. Strogatz, *Collective dynamics of "small world" networks*, Nature, **393**, 440-442 (1998)

[24] D. B. Stouffer, J. Camacho, L. A. N. Amaral *A robust measure of food web intervality*, PNAS, **103**, 19015-19020 (2006)

6. Figures and Tables
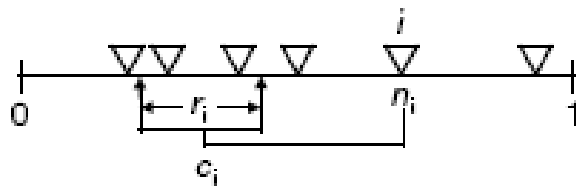
Figure 1: Diagram of the niche model. To each of the S species (for example $S = 6$, each shown as an inverted triangle) is assigned a "niche value" parameter (n_i) drawn uniformly from the interval $[0, 1]$. Species i consumes all species falling in a range (r_i) that is placed by uniformly drawing the center of the range (c_i) from $[r_i/2, n_i]$.
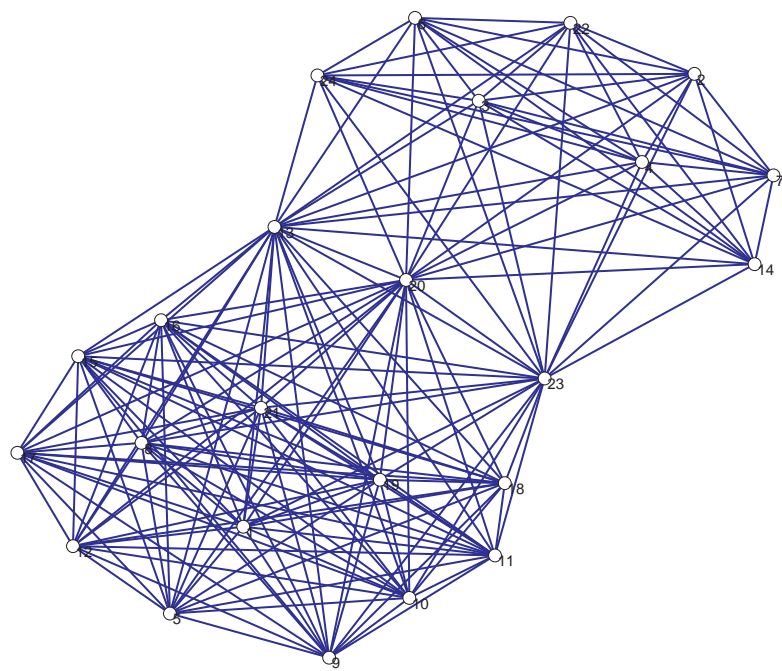
Figure 2: Graph of predators' projections for the food web of Skipwith Pond (SWP)
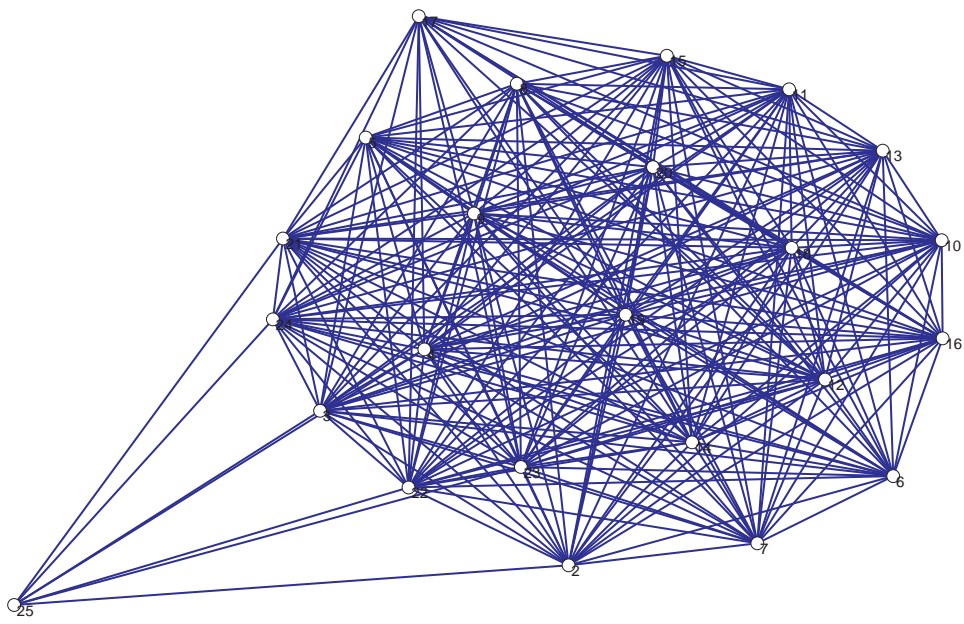
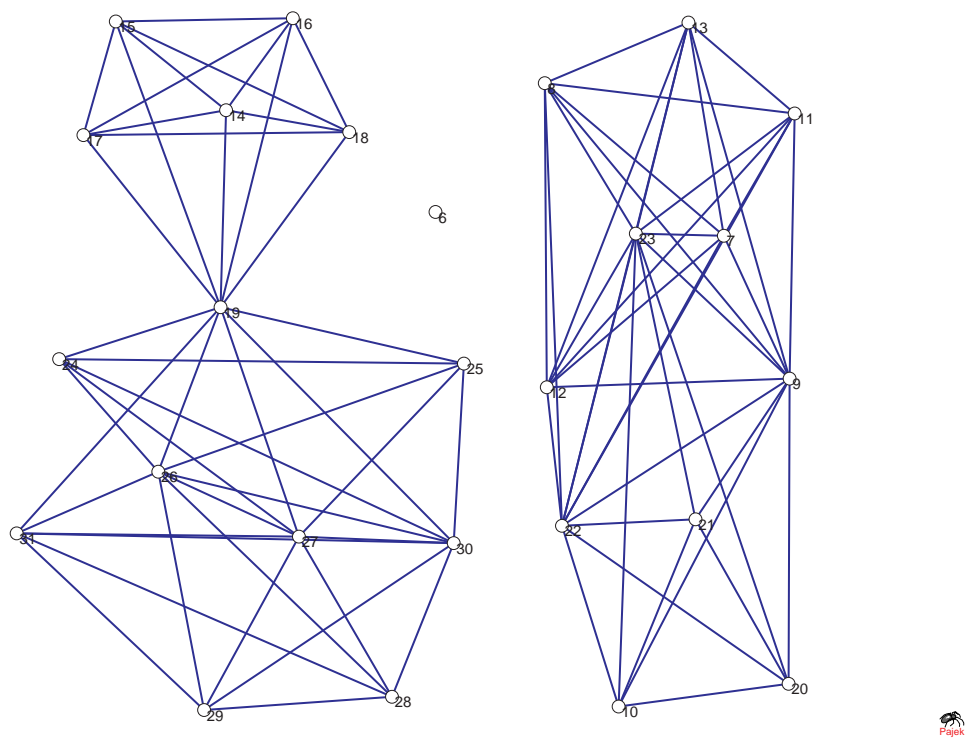Figure 3: Graph of prey's projections for the food web of Skipwith Pond (SWP).

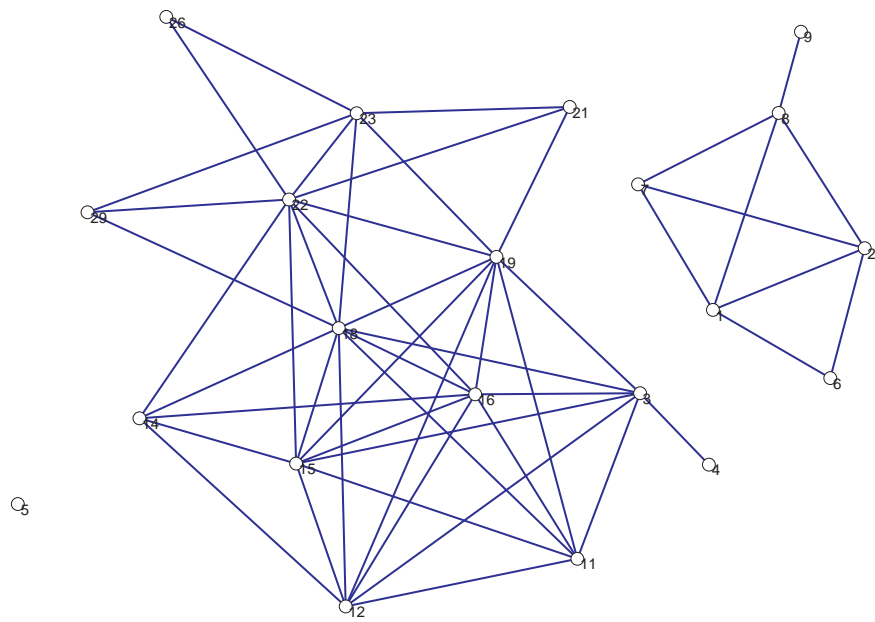Figure 4: Graph of predators' projection for the food web of chesapeake bay (CPB)

Figure 5: Graph of prey's projections for the food web of Chesapeake Bay (CPB), note the formation of communities and isolated species.
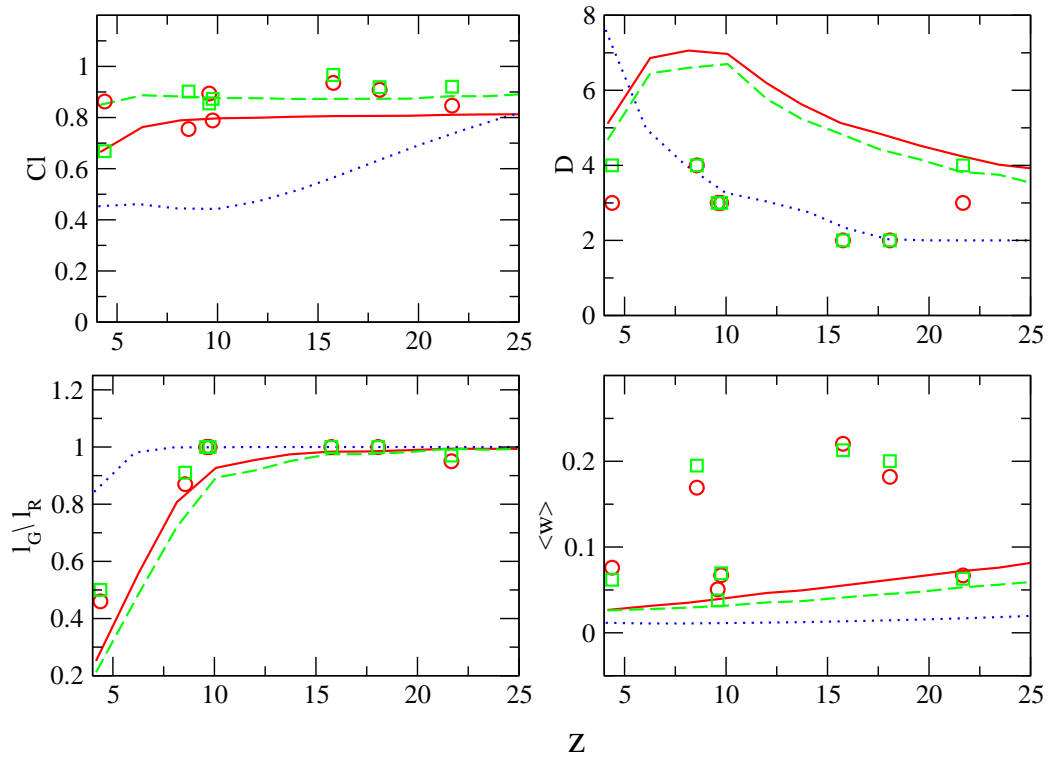
Figure 6: Measure of topological properties of prey's (dashed line) and predators' (continuos line) projections in function of mean degree of original food web, averaged over 100 realizations of niche graphs with $S = 100$, compared with empirical food webs (squares for prey's network and circles for predators' network), and random projections (dotted line)
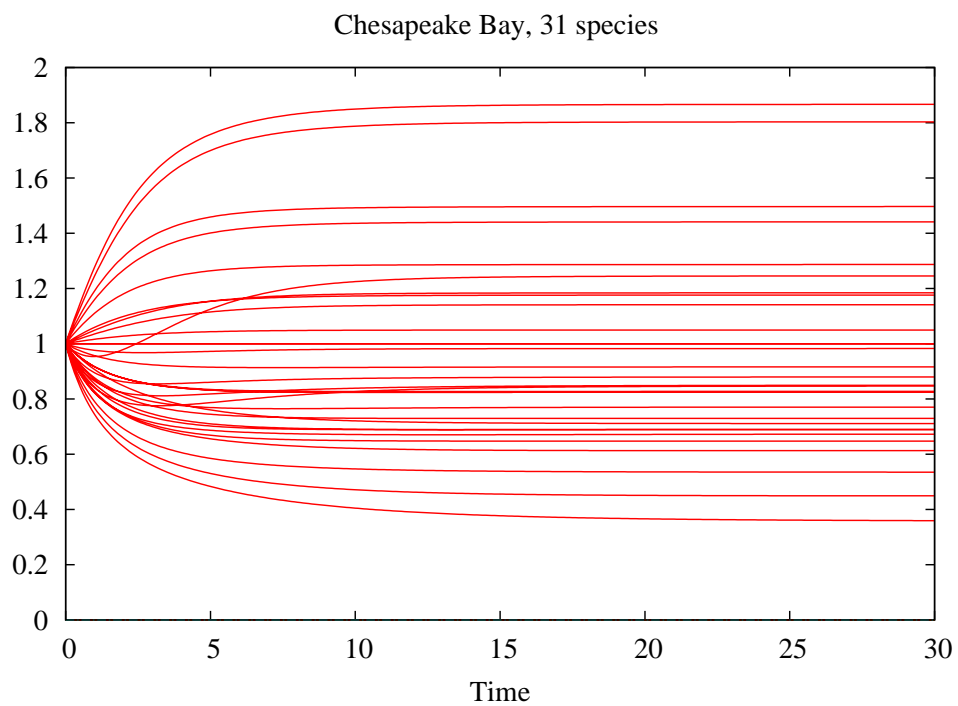
Figure 7: Population densities in function of time: each line represents the population of one species. The ecological parameters are fixed, r_i are uniformly distributed between 0 and 0.5, $K_i = 1$, $c_i = 0.1$ for basal species. All initial population densities are set to 1.
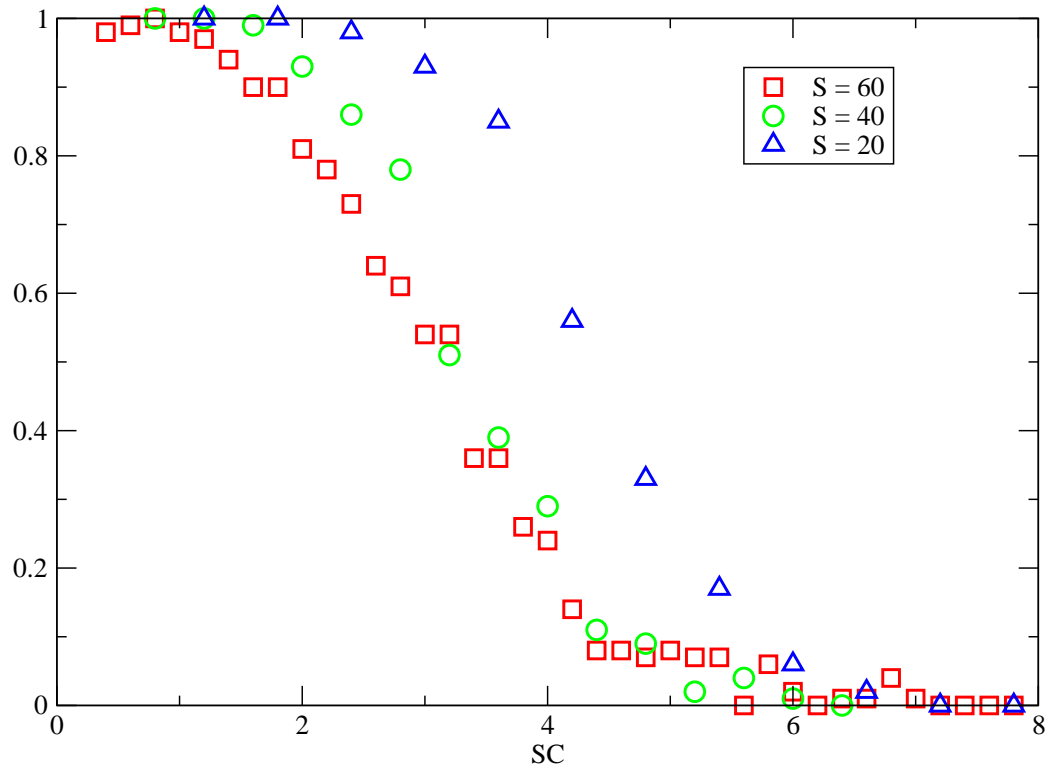
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Figure 8: Stability of niche model: plot of the averaged and normalized number of steady states for 100 realization of niche graphs in function of SC for $S = 20, 40, 60$. where S and C are fixed as input parameters of niche model.
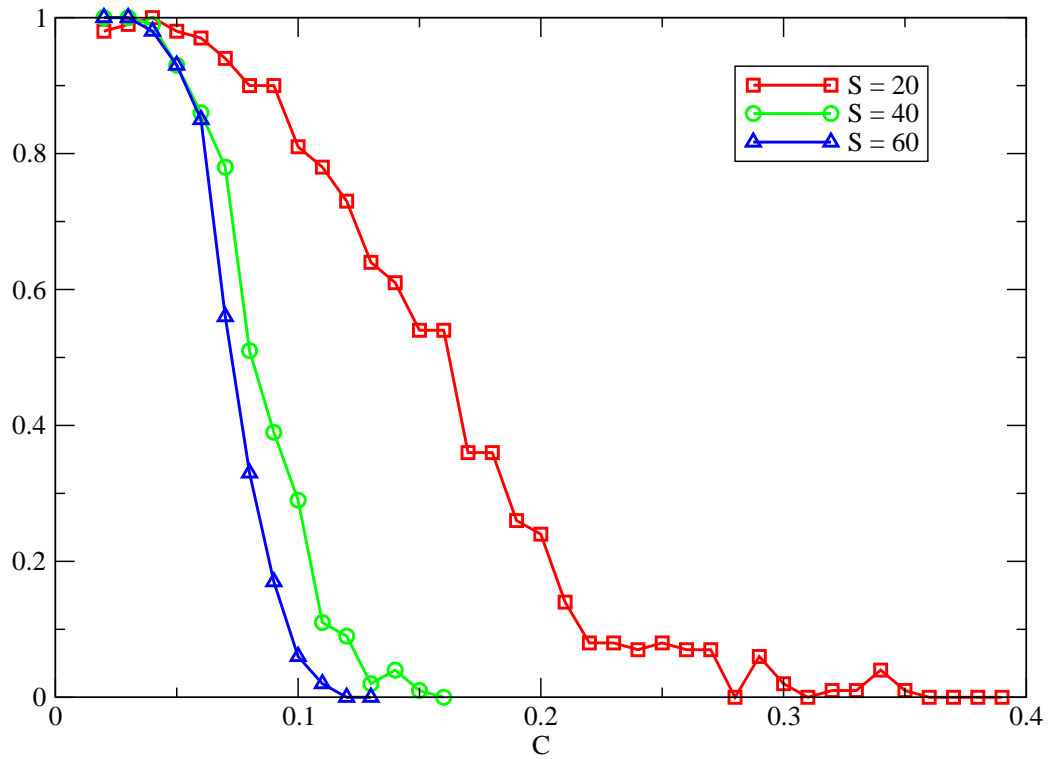
Figure 9: Stability of niche model: plot of the averaged and normalized number of steady states for 100 realization of niche graphs in function of C for $S = 20, 40, 60$. where S and C are fixed as input parameters of niche model.

Food Web	BBL	SWP	CDE	CPB	SMI	YE	LRL
S	25	25	29	31	42	78	92
L	107	197	262	68	205	374	997
C	0.171	0.32	0.31	0.072	0.12	0.061	0.12
PREDATORS							
S_{PRED}	17	24	26	26	36	71	80
L_{PRED}	61	169	278	83	296	989	1129
z_{PRED}	3.58	7.04	10.69	3.19	8.22	13.9	14.11
C_{PRED}	0.448	0.61	0.85	0.25	0.47	0.4	0.35
Cl_{PRED}	0.75	0.93	0.9	0.86	0.79	0.89	0.84
$<w>_{PRED}$	0.17	0.22	0.18	0.07	0.06	0.05	0.07
D_{PRED}	4	2	2	3	3	3	3
$((l_G)_{PRED}$	1.51	1.39	1.14	0.7	1.56	1.76	1.63
$(l_R)_{PRED}$	1.72	1.39	1.14	1.5	1.56	1.76	1.72
$(l_G/l_R)_{PRED}$	0.87	1	1	0.46	1	1	0.95
PREY							
S_{PREY}	25	25	29	21	35	49	91
L_{PREY}	132	255	318	51	363	694	3133
z_{PREY}	5.28	10.62	10.9	2.42	10.37	14.16	34.4
C_{PREY}	0.44	0.92	0.78	0.24	0.61	0.59	0.756
Cl_{PREY}	0.9	0.96	0.92	0.67	0.87	0.85	0.92
$<w>_{PREY}$	0.19	0.21	0.2	0.06	0.07	0.04	0.06
D_{PREY}	4	2	2	4	3	3	4
$(l_G)_{PREY}$	1.59	1.08	1.22	0.81	1.43	1.42	1.25
$(l_R)_{PREY}$	1.73	1.08	1.22	1.62	1.43	1.42	1.25
$(l_G/l_R)_{PRED}$	0.91	1	1	0.5	1	1	0.97

Table 1: topological properties of empirical food webs' projections. The measure of clustering, Cl, diameter D and average path lengths l_g and l_R, is made considering the binary matrices of projections where weights are all put to 1.