

Two classes of bipartite networks: nested biological and social systems

Enrique Burgos,^{1,2} Horacio Ceva,¹ Laura Hernández,³ R.P.J. Perazzo,⁴ Mariano Devoto,⁵ and Diego Medan^{5,2}

¹*Departamento de Física, Comisión Nacional de Energía Atómica,
Avenida del Libertador 8250, 1429 Buenos Aires, Argentina*

²*Consejo Nacional de Investigaciones Científicas y Técnicas,
Avenida Rivadavia 1917, C1033AAJ, Buenos Aires, Argentina*

³*Laboratoire de Physique Théorique et Modélisation;
UMR CNRS, Université de Cergy-Pontoise,*

2 Avenue Adolphe Chauvin, 95302, Cergy-Pontoise Cedex France

⁴*Departamento de Investigación y Desarrollo, Instituto Tecnológico de Buenos Aires
Avenida E. Madero 399, Buenos Aires, Argentina*

⁵*Cátedra de Botánica, Facultad de Agronomía, Universidad de Buenos Aires
Avenida San Martín 4453, C1417DSE Buenos Aires, Argentina*

(Dated: October 25, 2018)

Bipartite graphs have received some attention in the study of social networks and of biological mutualistic systems. A generalization of a previous model is presented, that evolves the topology of the graph in order to optimally account for a given Contact Preference Rule between the two guilds of the network. As a result, social and biological graphs are classified as belonging to two clearly different classes. Projected graphs, linking the agents of only one guild, are obtained from the original bipartite graph. The corresponding evolution of its statistical properties is also studied. An example of a biological mutualistic network is analyzed in detail, and it is found that the model provides a very good fitting of all the main statistical features. The model also provides a proper qualitative description of the same features observed in social webs, suggesting the possible reasons underlying the difference in the organization of these two kinds of bipartite networks.

PACS numbers: 05.90.+m, 89.75.Fb, 87.23.Ge

I. INTRODUCTION

Bipartite networks have attracted considerable attention [1], [2] because they can describe social and ecological systems. These involve nodes of two kinds, and their edges only link nodes of different guilds.

The examples issuing from biology concern ecological systems. These are complex ensembles of living beings sharing a complicated pattern of mutual dependence and interacting in many intricate ways. A number of these systems provide valuable services to mankind and considerable attention is currently being paid to their stability taking into account human disturbance. A sustainable management of ecosystems can only be achieved if a proper understanding is reached concerning how these systems are assembled. As far as biological systems are concerned we will discuss the case of mutualistic systems. They involve two groups of species, usually animals and plants, that interact to fulfill essential biological functions such as feeding or reproduction. This is the case of systems involving plants and animals that feed from the fruits and disperse their seeds (*seed dispersal networks*). Another example is that of insects that feed from the nectar of flowers while pollinating them in the process (*pollination networks*).

Bipartite networks can also be found in social systems. Examples of this type involve the actors and movies they participate in [3] or the boards of directors of large companies and their members [1].

An important feature of bipartite networks is the de-

gree distributions of the nodes of both guilds. In social systems the statistical properties of the degree distributions of each guild are different. While the distribution associated to one guild approximately follows a power law, the degrees of the other distribute themselves as a bell shaped (Poisson-like) curve around some average value. In biological systems the degree distributions of *both* guilds decay slower than exponentially thus having fat tails. In spite of the fact that observed mutualistic systems are rather small, these distributions have been fitted by truncated power laws.

In addition it has been observed [4], [5] that in biological, mutualistic networks all the contacts (links) tend to be *nested* and limited by a curve [4], [6] defined as an *isocline of perfect order* [7].

In a nested network the nodes of both types can be ordered by decreasing degree in such a way that the set of species linked with each species in the list is contained in the set associated to the preceding one. This organization is such that the *generalists* of both type of guilds (i.e. those nodes interacting with a great number of nodes of the other guild) tend to interact among them while there are no contacts among *specialists* (i.e. nodes interacting with very few of the other guild). All these features indicate that these networks are far from being a random collection of interacting species, displaying instead a high degree of internal organization.

In preceding papers we have introduced the Self-organizing Network Model (SNM) [6], [8] to describe nested biological webs. Within that model, the topology of the network is the result of a self-organization process

in which its nodes progressively redefine their links obeying to a purely local rule that does not depend upon any global feature of the network. The network undergoes in this fashion an ordering process.

This self-organization process by no means represents any growth or assembling process of the ecological system. It represents instead the search of a pattern of contacts between both guilds that tends to optimally take into account some *contact preference rule* (CPR) that is assumed to prevail among the nodes of the network. The aim of this model is to trace a possible causal relationship between the details of a local rule governing the contacts between both guilds and the statistical features of the network. In fact, the results obtained in [6] under one specific assumption for such CPR accurately account for many observed statistical features of real mutualistic webs of widely different sizes.

In this article we present a generalization of the SNM to cast into a single framework the organization of both, mutualistic and social webs. We thus aim at establishing similarities and differences between social and biological networks by linking their statistical properties with the CPR that governs the interactions between both guilds.

The fact that nodes of one guild share contacts with nodes of the other kind, allows us to define a pattern of interactions among similar nodes [1]. Any bipartite network can also be regarded as describing two separate systems involving only nodes of one kind. The corresponding *projected graphs* are built by defining two nodes of the same guild as neighbors - therefore linked by an edge - when both share a contact with at least one node of the other guild. For instance, two plants are considered as neighbors if they are visited by the same animal species or two directors are neighbors if they belong to the same board.

Two nodes of one guild may share more than one contact with the nodes of the other guild. As a consequence, in the projected graphs not all edges have the same importance. Each edge carries a weight representing the number of common neighbors of the other kind thus providing a measure of the intensity of the corresponding interaction. This is the case for instance when more than one animal species visit the same pair of plants or two actors participate together in several films.

We also address the interesting question of how the gradual changes that are involved in the SNM are reflected both in the topology and the weights of the interactions in the projected graphs.

The aim of the previous analysis is to extract salient features of social and biological networks and not to provide precise fittings to empirical data. Nevertheless we compare in some detail theoretical predictions with the values observed in a real mutualist web [9] which is one of the largest mutualistic system reported in the literature, therefore allowing for statistical considerations.

The theoretical discussions presented in this work shed light on several questions. In the first place they allow to establish links between nestedness and the shape of

degree distributions of biological networks, in the second place they provide hints about possible reasons for the different shapes of the degree distributions of both guilds found in social networks. These two elements place biological and social webs into well differentiated classes of bipartite networks. Finally the theoretical predictions of the SNM are extended to the projected graphs and are found to provide a faithful description of the distributions observed in the mutualistic network of Ref. [9].

II. THEORETICAL BACKGROUND

A. The Self-organizing Network Model

We describe here a generalization of the SNM introduced in Ref. [6]. We refer the reader to that article for the details of the original model as well as for the comparison of its results with the empirical observations.

The interaction pattern of a bipartite network can be coded as an adjacency matrix in which rows and columns are labeled respectively by the plant and animal species involved in the network. Its elements $K_{p,a} \in \{0, 1\}$ represent respectively the absence or the presence of an interaction between the plant species p and the animal species a . In what follows we drop the term species specifying that when mentioning plants or animals we are not referring to the behavior of separate individuals but to all the members of a species.

The SNM is a computer model that starts from a random adjacency matrix in which the number of plants, animals and contacts between them are arbitrarily fixed provided that there are no species left without links with the other guild. Starting from this initial configuration plants and animals iteratively redefine their contacts by reallocating the 1's of the adjacency matrix. This reallocation obeys to some assumed CPR. In the following we consider a CPR that indicates that the agents of either guild prefer to set contacts with a species of the opposite guild having a greater (or lesser) number of contacts.

We implement such swapping with the following algorithm. In each iteration first a row and next a column are chosen at random. Once a row (column) has been chosen its contacts are reallocated with probability P_r (P_c). Reallocation consists in choosing at random a 1 and 0 belonging to the same row (column), and swapping them according to a previously selected CPR that we discuss below in some detail. The row (column) is left unchanged with probability $1 - P_r$ ($1 - P_c$). In case that, upon swapping, a row or a column would be left with no links, the reallocation is not produced. This rule prevents the elimination of a node of the system as a consequence of being left without interactions.

The two probability parameters P_r and P_c must not be considered as independent because the only relevant differences appear when their ratio $R = P_r/P_c$ is changed i.e. when columns and rows are updated with different frequencies. We will consider in particular two limiting

situations, one in which $R \simeq 1$ and another in which $R \ll 1$ or $R \gg 1$. These respectively correspond to a situation in which rows and columns are updated with the same frequency or to the case in which rows (columns) are updated much more frequently than columns (rows).

The swapping process is continued until the CPR that has been imposed is optimally satisfied and no further swappings can take place. The network reaches then a perfectly ordered phase [10].

One possible CPR [strategy (I)] is that the degree of the new partner must be higher than the one of the previous partner. Within this CPR species of either kind tend to be as generalists as possible. An alternative possibility [Strategy (II)] is just the opposite, namely that the new partner has fewer contacts than the previous one. In this case species tend to be as specialists as possible. Strategy (I) bears some similarity with the rule of preferential attachment of Ref. [11]. This is a stochastic attachment rule by which new nodes are added to a growing network attaching to the existing nodes with a probability that is proportional to their degree. There are however several important differences between preferential attachment and our strategy (I).

In the first place the approach in Ref.[11] deals with a population of entities, that are represented by the nodes of the graph, that grows constantly. Our model deals instead with a closed system in which new nodes are not added. It consequently involves a change of the topology of a network with a *constant number* of nodes and links. In the second place preferential attachment is clearly a non local process because the particular attachment of a new node is governed by the degree distribution of all the nodes of the network. Opposed to this, the present model follows a purely local rule. The reallocation of contacts with both CPR's involves only the information of the current and of the target nodes of its counterparts in the bipartite network and has no relation whatsoever to any global feature of the network. It could be thought of as one species of animals changing its current choice as a consequence of the better conditions offered by an alternative species of plants that is more highly or poorly visited.

As it is well known the fact that the decision rule is local is an important feature if the problem of the re-allocation of all the contacts of the network is cast into the form of the optimization problem of fulfilling a given CPR. Within this particular framework the SNM can be regarded as an heuristic solution for it.

B. The projected graphs

The information contained in a bipartite network can be used to construct two separate graphs, each composed of nodes belonging to a single guild. This is done extracting two projected graphs fulfilling the rule that two nodes of the same guild are neighbors - and therefore linked by an edge - if they share a contact with at least one node

of the other type in the bipartite network [1] .

Let K be the adjacency matrix with elements $K_{p,a} \in \{0, 1\}$ denoting the contacts between the plant p and the animal a . K^T is the transposed of K . The two matrices

$$\begin{aligned} W_{p,p'}^P &= K K^T = \sum_a K_{p,a} K_{a,p'}^T (1 - \delta_{p,p'}) \\ W_{a,a'}^A &= K^T K = \sum_p K_{a,p}^T K_{p,a'} (1 - \delta_{a,a'}) \end{aligned} \quad (1)$$

encode the weighted adjacency matrix of the projected graphs [12] for plants (W^P) and animals (W^A). The diagonal elements:

$$D^P(p) = \sum_a (K_{p,a})^2 \quad (2)$$

$$D^A(a) = \sum_p (K_{a,p}^T)^2 \quad (3)$$

that are canceled from the sums in Eq.(1) are the degrees of the plant and animal nodes in the bipartite graph. The non vanishing off diagonal elements of $W^{A,P}$ carry the information of the number of different paths linking two nodes of the same kind involving not more than one node of the other guild. These weights could be interpreted as the intensity of the interaction between such pair of species. A suitable generalization of the concept of degree for weighted graphs is just the total number of paths connecting some given node with all nearest neighboring nodes of the same kind, namely:

$$S^{A(P)}(i) = \sum_j (1 - \delta_{i,j}) W_{i,j}^{A(P)} \quad (4)$$

This is defined as the *strength* [2] of the node. It provides a measure of the relevance of the species i in the plant-or animal systems. The usual degree of the i -th animal or plant in the projected graph is denoted by $D_\pi^{P(A)}(i)$ and is given by the number of non zero elements in each row of the matrices $W^{A(P)}$.

Besides the above distributions, the projected graphs can also be characterized by the distribution of its clustering. The clustering C_i of the i -th node of any graph is defined (Ref.[3]) as

$$C_i = \frac{e_i}{k_i(k_i - 1)/2} \quad (5)$$

where e_i is the number of edges among the neighbors of the i -th node and k_i is its degree. The clustering coefficient is the fraction of first neighbors of a node that are themselves, neighbors among them.

C. Properties of the projected graphs

It is convenient to derive some analytical results for the properties of the projected graphs under the changes in the topology of the original bipartite graph. To this end

we assume a perfectly ordered bipartite graph described by an adjacency matrix with m rows and n columns and a given probability of contacts ϕ and discuss the degree distributions of the projected graphs.

We first consider an adjacency matrix with the same number of 1's in all its rows. This is the case for the perfect order produced by SNM using the CPR of strategy (II). As discussed below it also approximately represents the situation of a random adjacency matrix.

Let $k = n\phi$ be the number of 1's in each row. The probability that any two rows share no contacts with the same species of the other guild - and are therefore *not* neighbors in the projected graph - is:

$$q_{n,k} = \frac{\binom{n-k}{k}}{\binom{n}{k}} = \frac{(n-k)!^2}{n!(n-2k)!} \quad (6)$$

therefore the probability that a given row has ℓ neighbors and hence has degree ℓ in the projected graph is

$$P_{\ell|m} = \binom{m-1}{k} (1 - q_{n,k})^\ell q_{n,k}^{m-1-\ell} ; \quad \ell = 1, 2, \dots, m-1 \quad (7)$$

The number of rows with degree ℓ is $N_{\ell|m} = mP_{\ell|m}$. The average degree of the row-species in the projected graph therefore is

$$N_m = \sum_{\ell=0}^{m-1} \ell N_{\ell|m} = m(m-1)(1 - q_{n,k}) \quad (8)$$

Since $k = n\phi$ this degree distribution is fully specified by the dimensions of the matrix and the probability of contacts ϕ . A completely symmetric argument can be made for the column-species changing n by m .

The degree distribution for the opposite case, i.e. when the Strategy (I) is used and the system reaches an asymptotic order of perfect nestedness is simpler to obtain. If there are no species with no contacts and the pattern of interactions is nested, there exists at least one species of each guild that is a full generalist, i.e. has contacts with *all* species of the other kind. Under this condition all the species of each guild have contacts with the generalist of the other guild and it is therefore a neighbor of all the other species of the same type. Such perfectly nested system gives therefore rise to two projected graphs that are "tiny worlds": all species are neighbors of each other[13].

The above Eq. 6 can also be used to derive a close estimate of density of contacts $\phi_\pi^{P,A}$ of the two projected graphs for plants and animals, provided that the bipartite adjacency matrix is random. This is

$$\phi_\pi^P(n, \phi) = 1 - q_{n,k=n\phi} = 1 - \frac{(n - n\phi)!^2}{n!(n - 2n\phi)!} \quad (9)$$

The density for the projected graph for animals $\phi_\pi^A(m, \phi)$ is obtained from Eq.9 by changing n by m . This probability of contacts between nodes of the same guild is a rapidly growing function of ϕ , the probability of contacts in the rectangular adjacency matrix. Hence, in general, even very sparse adjacency rectangular matrices give rise to densely connected projected networks.

III. RESULTS

A. Results for the bipartite graphs

In the following, if not stated otherwise, we will discuss numerical examples concerning Strategy (I). The reason for this is two-fold: on one hand strategy (I) has a greater biological significance and it has been successfully used in Ref.[6] to account for the degree distributions of several observed mutualistic systems of a wide range of sizes. On the other hand the ordered patterns emerging from Strategy (II) can well be approximated by a random adjacency matrix. The reason for this is simple. The use of this strategy leads to a different situation in which all nodes of the same kind tend to have the same number of links [14]. If contacts are randomly assigned all species have *on average* the same degree. Thus, the iterative ordering of the SNM only tends to produce a sharper delta-like function in the degree distributions, centered at the corresponding average number of links.

Whenever strategy (I) is used the model always leads to a perfectly nested pattern, no matter the relative updating frequency of rows and columns, as shown in Fig.1. These perfectly ordered systems have been obtained starting from a random adjacency matrix of 50×150 with a probability of contacts between both guilds of 10% and running the SNM algorithm for a very large number of iterations until no further swappings take place. The different panels of Fig. 1 have different values of R and yet perfect nestedness is found in all cases.

The sole fact that interactions are arranged in a nested pattern does not define the shape of the degree distributions. They do indeed differ drastically with R . Several different shapes of this distribution can be found that are nevertheless compatible with a nested pattern of interaction. As we will soon see, the shape of the degree distribution actually provides some information about the way in which the CPR is actually enforced among the row- or column- species.

We discuss the numerical results obtained with the SNM by comparing them with the real mutualistic system described in Ref.[9]. Real systems such as this are not perfectly ordered. To obtain a theoretical prediction from the SNM an initial configuration has to be chosen that involves a random adjacency matrix with the same number of species and interactions as the real system. The iterative ordering process starts from this initial state and is stopped before a perfect order has been reached using some appropriate stopping criterion that takes into consideration the particular empirical situation under analysis. This is in fact the only adjustable parameter of the model. The results shown here correspond to 100000 iterations of the SNM. In this case the stopping criterium is based on a statistical estimate of the departure from the isocline of perfect order. The algorithm is stopped when the value of this estimate is close to the empirically observed one.

In Fig.2 we show theoretical and empirically observed

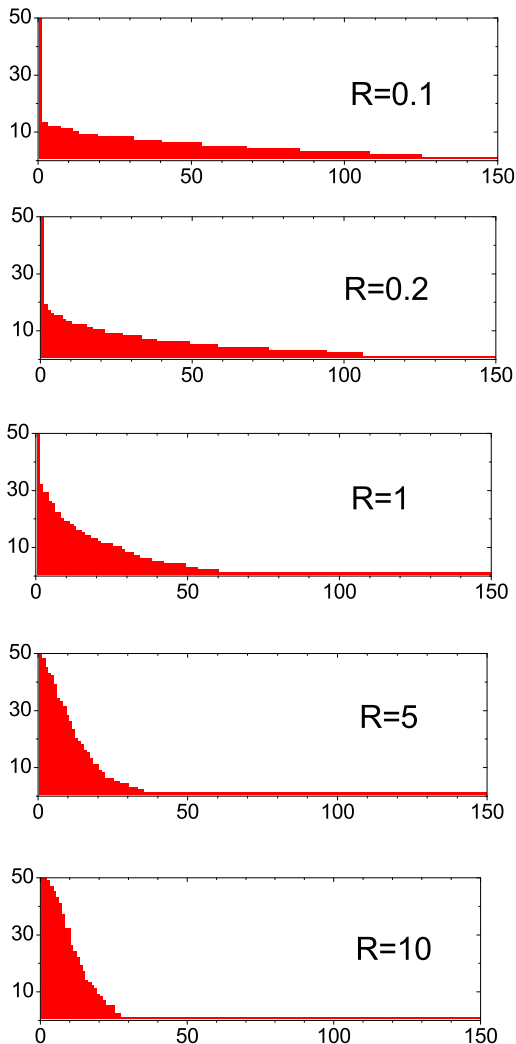


FIG. 1: Asymptotic adjacency matrices of a bipartite network of 50×150 . Each contact is shown as a black pixel. All panels display the adjacency matrix obtained with the SNM using Strategy (I) for both rows and columns and after 5×10^6 iterations.

[9] cumulative degree distributions [15] for three values $R = 1.0$, $R = 0.1$ and $R = 10.0$. The degree distributions for both guilds that are obtained with $R = 1$ and the above number of iterations, closely follow truncated power laws, truncation being here a finite size effect. In the limit of perfect order and $R = 1$ the distributions for plants and animals can be shown to map into each other [6] through the application of a simple scaling transformation.

The distributions for $R \ll 1$ or $R \gg 1$ for rows and columns shown in the right panels of Fig. 2 have quite different behaviors and strongly depart from the observed distributions of the mutualistic system. These curves show the seemingly paradoxical result that the degrees of the guild that is updated *less frequently* distribute according to truncated a power law, while the *more frequently* updated guild has a distribution that is bell-shaped thus indicating that the distribution of degrees have not been greatly changed by the self organization process and have a distribution that resembles the original random pattern. This can be understood because when, say, columns are frequently updated most swapings take place within each column. The contacts that are changed are therefore those of the row-agents while columns keep their degrees with little change. Thus, the degree distribution of the rows changes while that of the column-agents remains close to the original random matrix producing a bell shaped curve. However this is not a transient-like behavior by which a power law could be reached for both guilds with a larger number of iterations. The progressive ordering of contacts actually prevents this from happening thus giving rise to a perfectly nested system with a different order. A similar situation in which both guilds have different degree distributions has been described [1] for social webs such as films and actors and boards and directors of large companies.

B. Results for the projected graphs

The interactions among mutualist species are blended into the weights and strengths of the projected graphs. In what follows we discuss the results of the corresponding distributions in comparison with empirically observed data. These are shown in Figs.3, 4 and 5. All figures have the same organization of Fig.2, namely upper panels correspond to animals (columns) while lower panels correspond to plants (rows). Theoretical values are deduced from the rectangular adjacency matrix whose degree distributions are shown in Fig.2. We show results that correspond to $R = 1$, $R = 0.1$ and $R = 10.0$. Empirically observed values are always displayed as a reference in spite of the fact that values of R that are different from 1 are not expected to represent biological networks.

1. Degree and clustering distributions.

In Fig. 3 we show the degree distributions of the projected graphs for plants and animals. For a perfectly ordered system under Strategy (I) and for any value of R both distributions should approach a delta like function located at the corresponding number of species. Since the convergence to this limiting distribution is extremely slow, a partially ordered system is expected to show significant departures from such extreme distributions.

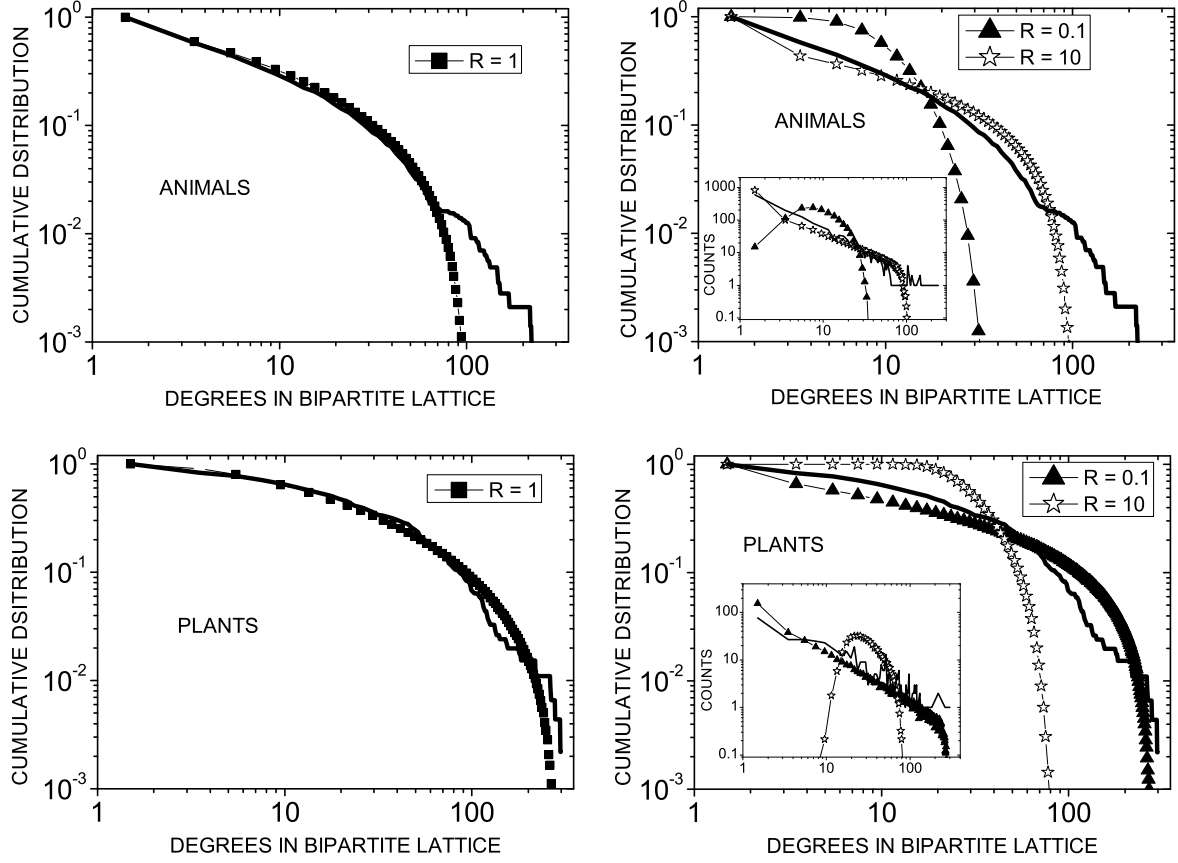


FIG. 2: Cumulative degree distributions of plants and animals of a bipartite network with the same dimensions (456×1428) as in Ref.[9], for different values of R . In the two panels on the right the corresponding non cumulative distributions are shown in the insets. The empirical distributions for plants and animals are always shown in heavy continuous line. Theoretical results are averaged over 100 realizations of the original random adjacency matrix. All distributions have $\text{bin}=2$; this is the main reason for the noisy appearance of the empirical data. Notice that in the plots of the right, stars or triangles fail to account *simultaneously* the empirical data. The non-cumulative degree distribution shown in the insets illustrate the different organizations of the networks with $R = 0.1$ and $R = 10$

For $R \ll 1$ or $R \gg 1$ either columns or rows are updated more frequently than rows or columns respectively. As explained above this causes one of the two guilds to develop a prominent peak at the corresponding number of species. This is the situation shown in the two right panels of Fig. 3 in which filled triangles and stars exchange roles showing a peak at the extreme right.

For this same reason, the distributions for both guilds and $R = 1$ are not similar and indicate that one of the two guilds has reached a more ordered configuration than the other. Indeed, while plants display a maximum at the number of plant-species, animals have not yet developed such pattern showing a maximum close to the origin. Since there are more columns than rows even for $R = 1$ each row is randomly selected for updating more frequently than each column. As a consequence plants are closer to a situation of perfect order. This effect is hard to observe directly in the bipartite graph. Theo-

retical values obtained for $R = 1$ are seen to closely reproduce the empirically observed distributions while the SNM run with $R \ll 1$ or $R \gg 1$ gives rise to projected graphs of a completely different nature.

We have also analyzed the distribution of clustering in the projected graphs. The results obtained for this confirm those already shown for the degree distributions. Upon a perfect nested order the distributions also tend to be delta functions located at a maximum value of 1. This agrees with the gradual approach to a tiny world pattern in which the projected graphs are complete graphs, no matter the value of R . Such approach however strongly depends upon the relative updating frequency of rows and columns. When R is widely different from 1, one of the two guilds shows a distribution of clustering that is a bell shaped while the other guild develops a strong peak at the maximum possible clustering equal to 1. For $R = 1$ the distributions that are obtained are in good

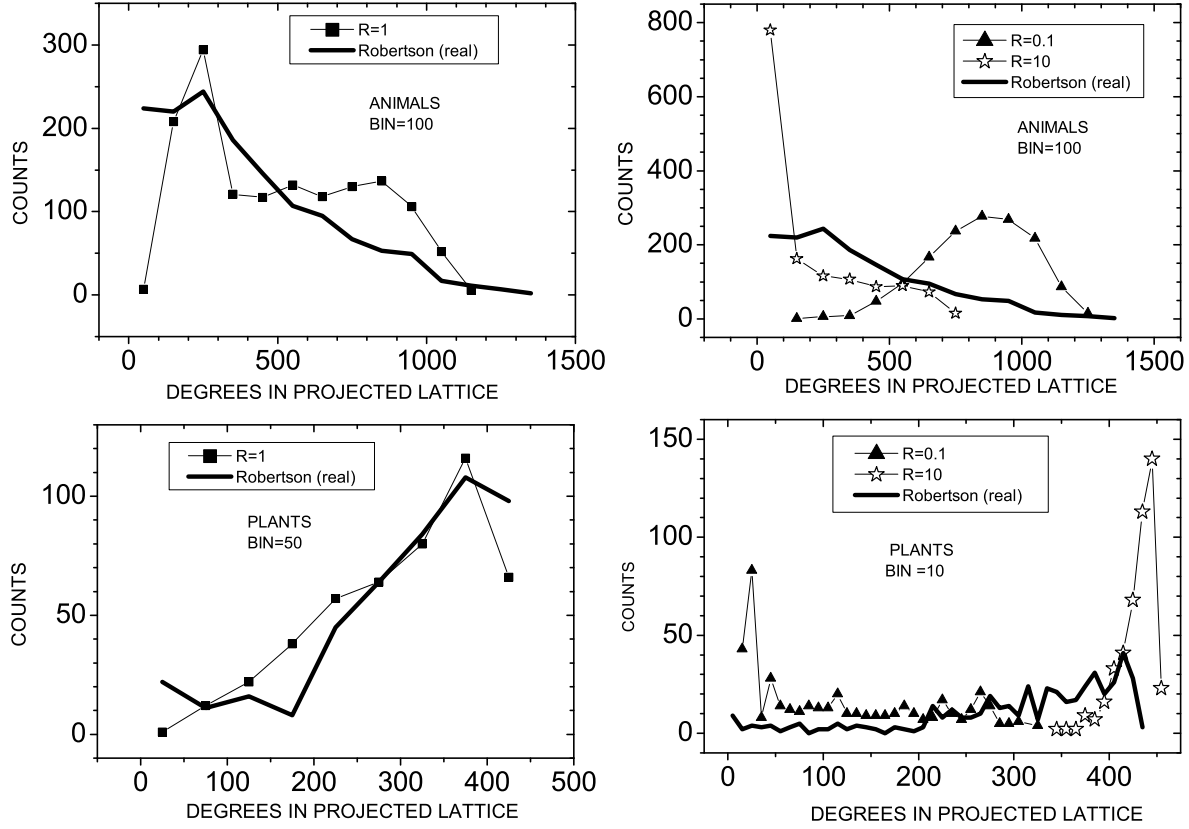


FIG. 3: Degree distributions in the projected graphs for animals (upper panels) and plants (lower panels), for different values of R . The shape of the full curves in the lower panels are different because of the binning.

qualitative agreement with the observed data in which both guilds appear not to be equally ordered: while animals have a heavily skewed distribution with a maximum at clustering equal to 1, plants have a more even distribution between clustering 0.8 and 1.0.

2. Distribution of strengths.

The relative importance of the different species in both projected systems is displayed by the distributions of strengths. These are shown in Fig.4. These distributions provide insight about the relative relevance of the different species in the two separate systems because they combine into a single distribution the number of neighbors with the weights of the interactions linking them. For a nested system with $R \simeq 1$, distributions approach a (truncated) power law with a vast majority of nodes having a low strength, close to their degree in the projected graph. On the other hand, few nodes with many neighbors have a very high strength. If $R \gg 1$ or $R \ll 1$ one of the two strength distributions is shaped as a bell

indicating little change with respect to the original random distribution, while the other follows the pattern explained above. General features of empirical values are also well described by the results obtained with the SNM (left panel of Fig. 4)

3. Distribution of weights.

As pointed up above, updating the interactions of one guild changes the world that is seen by the other. The weights of the projected graphs indicate how each guild mediates the relationship between individuals of the other. Within the SNM such mediation changes with R . In Fig.5 we show the theoretical and the observed distribution of weights for plants and animals with the same conventions of the preceding figures. In the limit of perfect order and $R = 1$, weights within the animal or plant systems approach the decay of a truncated power law. The real system is not perfectly ordered and therefore the distributions have a different decay rate. This is seen in the two left panels of Fig.5. Real data for animals

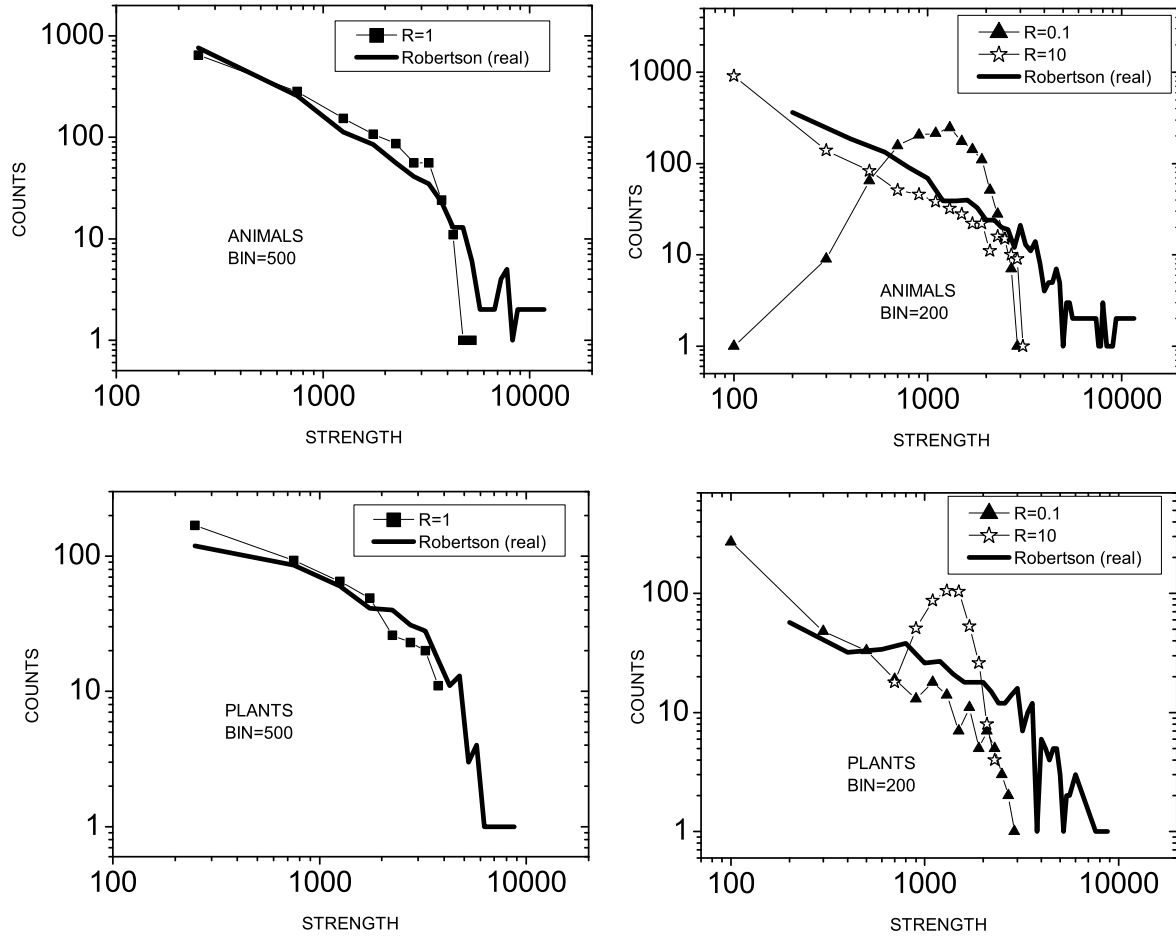


FIG. 4: Strength distributions in the projected graphs for animals (upper panels) and plants (lower panels), for different values of R .

is seen to have a distribution of weights that is closer to a power law than the corresponding one of plants. This result is consistent with what has been previously observed in connection with the degree distributions of the projected graphs. The cases shown in the right panels confirm that values of R that differ from 1 lead to a power-law distribution of strengths for only one of the two guilds.

Although we have not attempted a detailed fit of empirical data, this is seen to be qualitatively consistent with values $R \simeq 1$.

4. Distribution of paths of minimum length.

Besides the degrees, the strengths, the clustering coefficients, and the weights of the links, the projected graphs are also described by the distribution of the (minimal) path-lengths between any pair of nodes. This distribution is strongly dependent upon the probability of con-

tacts ϕ_π defined in Eq.(9), between two species of the same guild, that in turn depends upon the ordering process stemming from the SNM.

The distribution of minimal path lengths has a different pattern depending upon the value of R and upon the CPR that is used in the ordering process. In Table (I) we show as an example the results obtained with the SNM in several circumstances together with data of the observed system described in Ref [9]. For social type networks i.e. when rows and columns of the adjacency matrix are updated with very different frequencies, the distribution of path lengths has a different shape for each guild. The less frequently updated guild (in the example shown in Table (I) this corresponds to the columns) has a larger fraction of longer paths.

The occurrence of longer paths can only take place through minute alterations of a perfectly nested order of the bipartite network thus turning the distribution of minimal path lengths into a powerful tool to detect such alterations. This follows from the data of the network

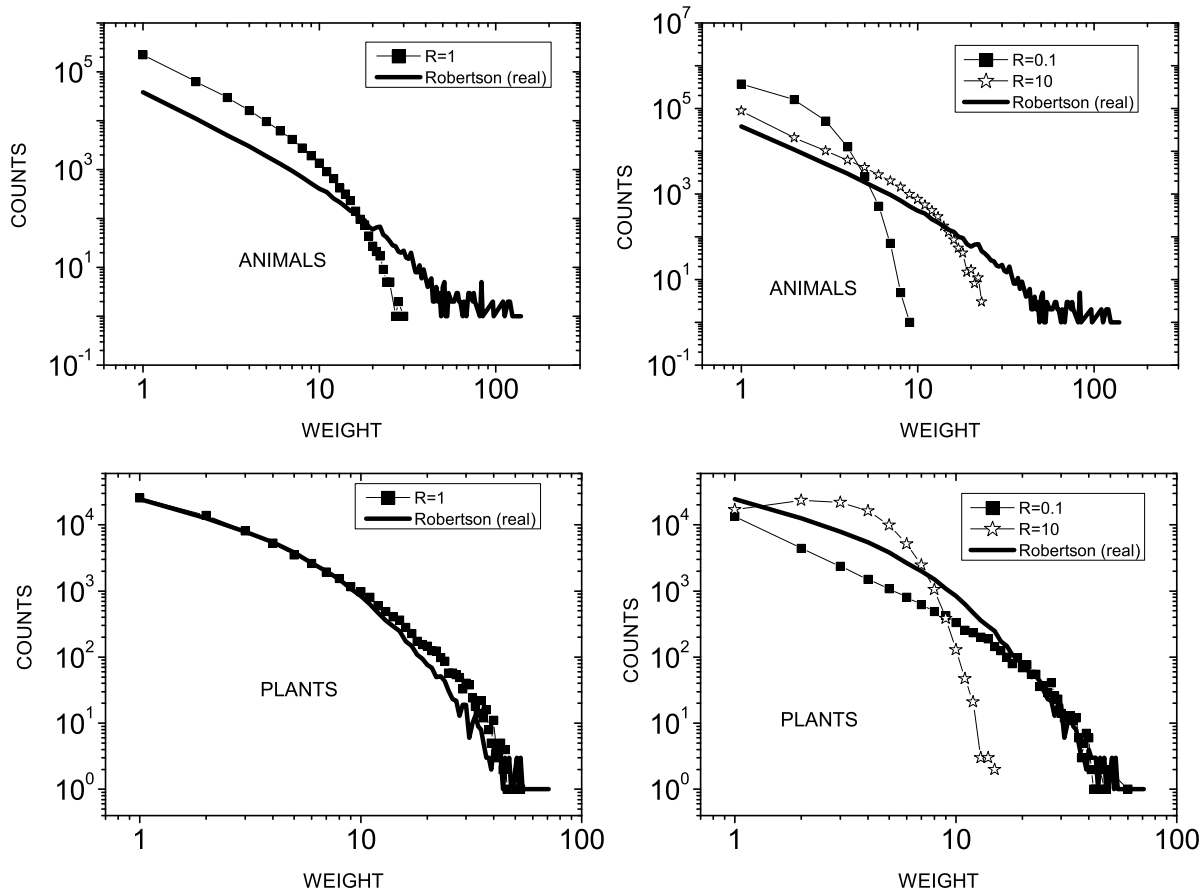


FIG. 5: Weight distributions of the links of the projected graphs for animals (upper panels) and plants (lower panels), and different values of R .

reported in Ref.[9]. In this case one certainly checks the gross feature of a great majority of shorter paths. Besides this, a small but significant fraction of paths of length 3 is also present. This can not be expected to result from fluctuations in the random initial conditions used in running the SNM and is never reproduced for biologically sound values of the parameters of the SNM. A way to understand this is the following. The 1.4 % of paths of length 3 are a total of almost 14,000 paths. This fraction of longer paths can be obtained from the presence of a very small set of perhaps a tenth of nodes that are linked by single vertices to a densely interconnected core built up by the other nearly 1400 nodes that have minimal paths only of lengths 1 and 2. Since the SNM is a statistical model that deals equally with all species of both guilds one should not expect to account for these sort of details.

IV. CONCLUSIONS

We have presented a generalization of the SNM (Self-organizing Network Model) that aims at finding the topology of a bipartite network that optimally takes into account some local contact preference rule (CPR) between the agents of the two guilds. To achieve this the rows and the columns of the adjacency matrix alternatively and iteratively update their contacts following such rule.

The CPR that favors contacts with a counterpart with as many links as possible provided the best description of real mutualistic networks (Ref.[6]). Thus an insect prefers to visit a flower that has many other species visiting it and a flower tends to attract a wider variety of insects. The opposite CPR that consists in developing some kind of specialization by which contacts are as few as possible is not observed in nature and gives rise to degree distributions that are sharply peaked at one value.

We have also considered an extension of the SNM that amounts to change the updating frequency of the con-

tacts of both guilds. When this extra degree of freedom is used, the model can also qualitatively account for the difference between the degree distributions of the two guilds that is present in social networks such as boards and directors. These results indicate that nested bipartite networks may belong to two well differentiated classes. While $R \simeq 1$ represent the situation of ecological systems, $R \ll 1$ or $R \gg 1$ correspond instead to social networks[1].

The distributions that have been observed in social networks indicates that the CPR's are not the same for

both guilds as in the case of mutualistic webs. While the degree distribution of one guild (say the distributions of the number of seats of a board) may follow some random process around a mean that represents some common practice, the degree distributions of its counterparts (directors) may instead be governed by a non random process obeying some specific CPR similar to that of either plants or animals in a mutualistic web. Thus, executives sitting in these boards may be the outcome of a selection process based upon the special merit of sitting already in several other boards (see Fig.8 of Ref.[1]).

Table 1

GUILD ⁽¹⁾	$\phi_\pi(\%)$	D_1 ⁽²⁾ (%)	$D_2(\%)$	$D_3(\%)$	$D_4(\%)$	COMMENTS
ANIMALS	26.6	26.7	71.9	1.4	.004	Observed Ref.[9]
PLANTS	68.0	68.5	31.2	.3	-	Observed Ref.[9]
ANIMALS	22.1	22	78	-	-	Random
PLANTS	54.0	57	43	-	-	Random
ANIMALS	32.9	32	68	-	-	70,000 iter. of SNM ⁽³⁾
PLANTS	65.0	65	35	-	-	70,000 iter. of SNM ⁽³⁾
ANIMALS	77.1	77	23	-	-	1,000,000 iter. of SNM ^{(3),(4)}
PLANTS	86.8	87	13	-	-	1,000,000 iter. of SNM ^{(3),(4)}
COLUMNS	15.1	15	84	.5	-	70,000 iter. of SNM ⁽⁵⁾
ROWS	89.5	90	10	-	-	70,000 iter. of SNM ⁽⁵⁾

Empirical distribution of minimal path lengths (first two rows) for the system described in Ref.[9] and several results of the SNM using Strategy I with an adjacency matrix of the same dimensions and the same number of contacts.

(1) Plants correspond to rows and animals to columns.

(2) D_j are the fraction of paths of length j expressed as percentages of the total number of paths. Theoretical results are rounded to the nearest integer.

(3) Plants and animals equally updated.

(4) Bipartite network symmetrically nested, closer to perfect order than any biological system.

(5) Columns updated 10 times less frequently than rows. This simulation would correspond to a social type bipartite network

The presence of fat tails in biological mutualistic networks has traditionally been attributed to the nested pattern of contacts between both guilds. Indeed, when $R = 1$ we have found that such is precisely the case. However the present model indicates that there is not a close relationship between the two concepts. With the present model *any* bipartite network that is adapted under the SNM *always* reaches a perfectly nested pattern of interactions independently of the updating frequency of rows and columns. However, the degree distributions strongly depend upon the different updating frequencies or, equivalently, by the prevailing order within each guild. Thus nestedness has to be considered under a new light.

The particular degree distributions observed in mutualistic webs should be attributed primarily to the particular way in which the pattern of interactions is achieved or, to put it into different words, to the way in which the CPR is actually enforced within the two guilds of the bipartite web.

Another extension that we have considered is the study of the two projected graphs and the changes that are induced on them by the SNM. We stress the contribution of this study to the understanding of the differences between social-type and ecological-type networks. In addition we have also checked that the results of the SNM for the projected graphs with $R = 1$ are also in good qualitative agreement with empirical observations of real biological systems. Moreover the projected graphs can reveal if plants and animals have achieved a different degree of order, something that is difficult to observe directly from the bipartite matrix.

We have studied the distribution of minimal path lengths within the projected graphs. This distribution is strongly dependent upon the probability of contacts. Since this is a rapidly growing function of the density of contacts in the bipartite matrix, the projected systems tend to always be tiny worlds of very densely interconnected species. Moreover, the theoretical estimates of the distribution of minimal path lengths for the system

of ref.[9] shed some light on possible reasons of minute departures from perfect order. The lack of a small fraction of paths of length 3 may perhaps be taken as a hint of the presence of species within the system having different CPR's that, in turn may produce within the ecosystem

what in ecology are called *compartments* (*communities* in complex network language), i.e. groups of species that while strongly connected among themselves, are weakly connected to the rest of the network.

-
- [1] M.E.J. Newman, S.H. Strogatz and D.J. Watts Phys.Rev. **E64**, 026118 (2001)
- [2] S. Boccaletti, V. Latora, Y. Moreno, M. Chavez, D.-U. Hwang, Phys. Rep. **424**, 175-308 (2006)
- [3] D.J.Watts and S.H. Strogatz, Nature **393**, 440 (1998)
- [4] W. Atmar and B.D. Patterson, Oecologia **96**, 373-382 (1993)
- [5] J. Bascompte, P. Jordano, C.J. Melián, and J.M. Olesen, Proc. Nat. Acad. Sci. USA **100**, 9383-9387(2003); P.Jordano, J. Bascompte, J.M. and Olesen, Ecol. Lett. **6**, 69-81, (2003); P. Jordano, J. Bascompte, and J.M. Olesen, in *Plant-pollinator interactions. From specialization to generalization* N. Waser and J. Ollerton, ed., University of Chicago Press. pp 173-199(2006)
- [6] D. Medan, R.P.J. Perazzo, M. Devoto, E. Burgos, M. Zimmermann, H. Ceva and A.M. Delbue, J. of Theor. Biol. **246**, 510 (2007)
- [7] In Refs.[4] - [6] the curve is also named *extinction curve* or *isocline of perfect nestedness*. We prefer here to call it isocline of perfect *order* for reasons that will become clear in what follows.
- [8] E. Burgos, H. Ceva, R.P.J. Perazzo, M. Devoto, D. Medan, M. Zimmermann, and A.M. Delbue, J. of Theor. Biol. **249**, 307 (2007)
- [9] C. Robertson, Science Press Printing Company, Lancaster, Pennsylvania, USA (1929).
- [10] The states that are reached in this way may however not have all contacts placed below the isocline of perfect order. One can construct a pattern of interactions that acts as a trap -i.e. a local minimum - stagnating the ordering process. Thus if during the iterative process the system falls into one of these configurations it will not undergo any further reorganization and yet will not correspond to an optimal allocation of contacts. Such traps could be avoided for instance by mapping the self-organization process into the solution of an optimization problem through simulated annealing. The occurrence of these traps is however not relevant to our present analysis because they are not important when dealing with real biological webs that are usually far from an asymptotically ordered pattern. If one aims at fitting empirical data the self-organizing process has therefore to be stopped at a moderate number of iterations. We will therefore ignore this problem for the moment.
- [11] A.-L. Barabási and R. Albert, Nature **393**, 440 (1998)
- [12] M.E.J. Newman, Phys.Rev. **E70**, 056131 (2004)
- [13] J.M. Olesen, J.Bascompte, Y.L.Dupont and P. Jordano, J. of Theor. Biol. **240**, 270-276 (2006)
- [14] In this particular case, the asymptotically ordered state may not be a static configuration. Some nodes may exchange links keeping the same average degree. This however does not change any statistical consideration.
- [15] In the rest of the work we only discuss degree distributions and not *cumulative* degree distributions such as it is a usual practice in the biological or ecological communities.