

# Build-up mechanisms determining the topology of mutualistic networks

Paulo R. Guimarães Jr.<sup>a,b,\*</sup>, Glaucio Machado<sup>c</sup>, Marcus A.M. de Aguiar<sup>d</sup>, Pedro Jordano<sup>b</sup>,  
Jordi Bascompte<sup>b</sup>, Alúcio Pinheiro<sup>e</sup>, Sérgio Furtado dos Reis<sup>f</sup>

<sup>a</sup>Programa de Pós-graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas, 6109, 13083-970 Campinas, SP, Brazil

<sup>b</sup>Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain

<sup>c</sup>Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 11294, 05422-970 São Paulo, SP, Brazil

<sup>d</sup>Instituto de Física Gleb Wataghin, Universidade Estadual de Campinas, 6165, 13083-970 Campinas, SP, Brazil

<sup>e</sup>Departamento de Estatística, Instituto de Matemática, Estatística e Computação Científica, Universidade Estadual de Campinas, 6065, 13083-859 Campinas, SP, Brazil

<sup>f</sup>Departamento de Parasitologia, Instituto de Biologia, Universidade Estadual de Campinas, 6109, 13083-970 Campinas, SP, Brazil

Received 29 July 2006; received in revised form 17 June 2007; accepted 7 August 2007

Available online 19 August 2007

## Abstract

The frequency distribution of the number of interactions per species (i.e., degree distribution) within plant–animal mutualistic assemblages often decays as a power-law with an exponential truncation. Such a truncation suggests that there are ecological factors limiting the frequency of supergeneralist species. However, it is not clear whether these patterns can emerge from intrinsic features of the interacting assemblages, such as differences between plant and animal species richness (richness ratio). Here, we show that high richness ratios often characterize plant–animal mutualisms. Then, we demonstrate that exponential truncations are expected in bipartite networks generated by a simple model that incorporates build-up mechanisms that lead to a high richness ratio. Our results provide a simple interpretation for the truncations commonly observed in the degree distributions of mutualistic networks that complements previous ones based on biological effects.

© 2007 Elsevier Ltd. All rights reserved.

**Keywords:** Complex networks; Forbidden links; Mutualisms; Plant–animal interactions; Pollination; Seed dispersal; Small networks; Species richness

## 1. Introduction

The notion of complex networks has recently emerged as a key concept to understand the interactions among elements of a system, whether they are physical, chemical, social, or biological (Strogatz, 2001). In ecology, the network approach has been applied to investigate the structure of food webs (Pascual and Dunne, 2006) and of other interspecific interactions (Guimarães et al., 2006; Jordano, 1987; Memmott, 1999; Vazquez et al., 2005). In the network formalism, species are represented by nodes, and interactions between species are described by links (reviewed by Pimm, 2002). The network approach is

helping to describe community-level patterns of interspecific interactions and understanding how interactions coevolve in species-rich assemblages (Bascompte et al., 2003, 2006; Guimarães et al., 2006; Jordano et al., 2003; Lewinsohn et al., 2006; Montoya et al., 2006; Prado and Lewinsohn, 2004). Our major challenge, however, is to infer what are the ecological and evolutionary factors that generate the observed community-level structure of ecological networks (Fig. 1A). In this context, community-level patterns of interactions are likely to uncover the importance of different ecological factors and coevolutionary processes (Lewinsohn et al., 2006; Olesen and Jordano, 2002; Thompson, 2005, 2006).

It was recently shown that the frequency distribution of interactions per species (i.e., degree distribution) within plant–animal mutualistic assemblages often decays as a power-law with an exponential truncation (Jordano et al., 2003; Fig. 1B). Although the degree distribution does not

\*Corresponding author. Present address: Instituto de Física Gleb Wataghin, Universidade Estadual de Campinas, 6165, 13083-970 Campinas, SP, Brazil. Tel.: +55 19 35215477; fax: +55 19 32893124.

E-mail address: [prguima@ifi.unicamp.br](mailto:prguima@ifi.unicamp.br) (P.R. Guimarães Jr.).

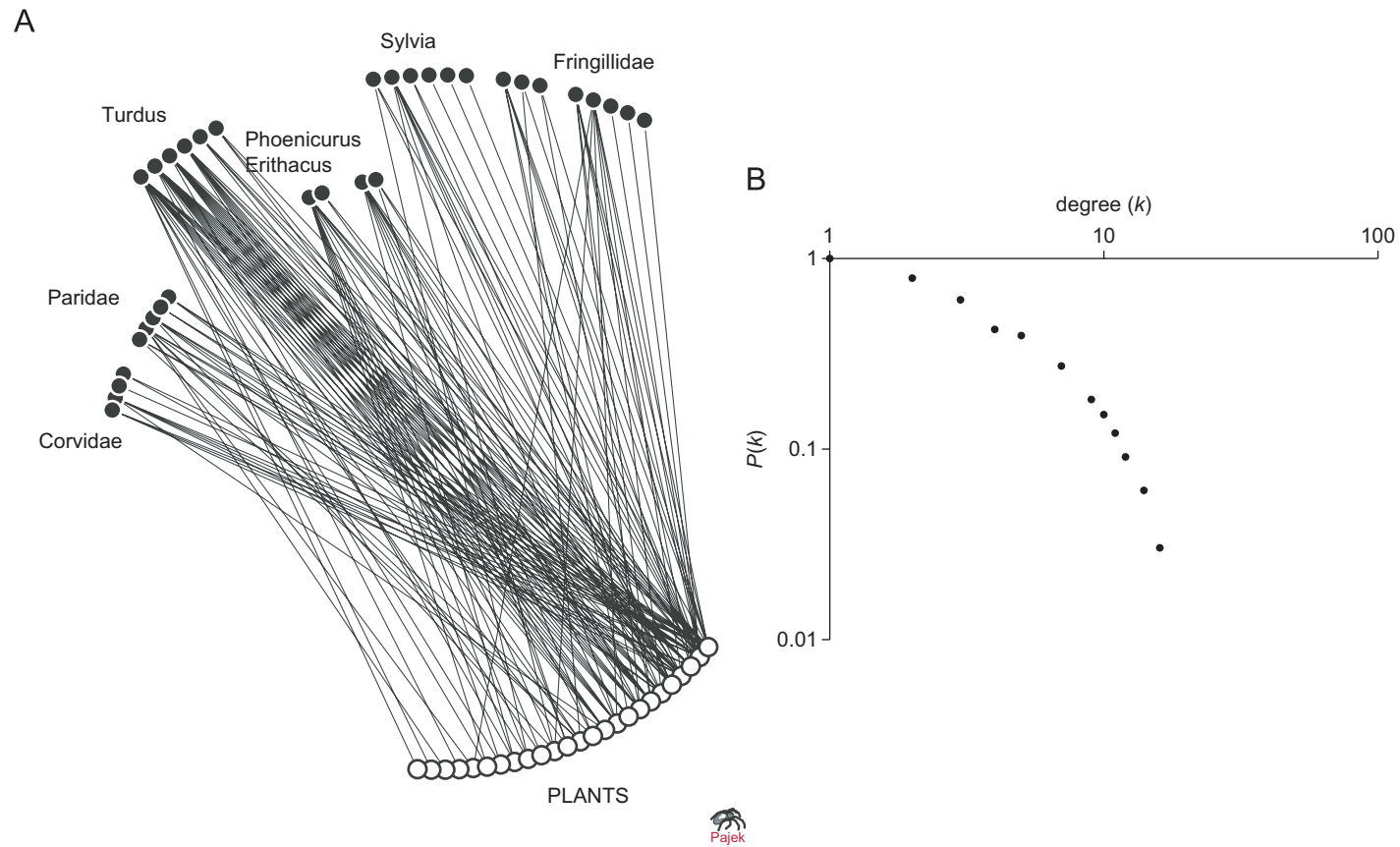


Fig. 1. (A) The network describing community-level patterns of interactions among frugivorous birds (black nodes, names indicating some bird taxa) and plants producing fleshy-fruits (white nodes) in Nava de las Correhuelas, SE Spain (Jordano, unpublished data). This network describes the mutualistic interaction involving seed dispersal services by the animals when consuming the fruits for food. (B) Log–log plot of the cumulative degree distribution describing the probability of finding a bird species that interacts with at least  $k$  plants in the same network.

describe all aspects of network structure (see Bascompte et al., 2003), it provides relevant information about the patterns of specialization within the communities and the processes that generate the observed distributions (Jordano et al., 2003). For example, power-law distributions can arise when recently arrived species are likely to interact with the most generalist species (Jordano et al., 2003). In contrast, exponential truncations have been associated with constraints limiting the existence of species with many interactions (Amaral et al., 2000; Jordano et al., 2003; Mossa et al., 2002) or with the random initial condition at the origin of network (Guimarães et al., 2005). However, few theoretical studies explore alternative explanations for exponential truncations that characterize typical features of plant–animal mutualisms (but see Vazquez, 2005).

Plant–animal mutualisms are best described as bipartite networks, in which there are two disjoint sets of species (animals and plants) and there are no interactions between species within the same set (Harary, 1969; Jordano et al., 2003). The bipartite structure *per se* does not affect the degree distribution (Ergun, 2002; Liljeros et al., 2001). However, we note that plant–animal mutualisms show marked differences in species richness between the animal and plant sets (high richness ratio, in which the ratio is here defined as the number of species of the richer set divided by the number of species of the poorer set; see Table 1). In fact, Fleming (2005) demonstrated that the species richness of mutualistic vertebrates (fruiting and nectar-eating bats and birds) clearly differs from the richness of their food plants. Along the same lines, Guimarães et al. (2007b) have shown that the species richness of fish clients is seven-fold higher than their mutualistic partners, i.e., cleaner fishes and shrimps. These high richness ratios are not likely to be generated by sampling bias, because in such cases network description is based on long-term, detailed field studies that largely represent enumerations of the actual interactions occurring in the field (Jordano et al., 2003). Therefore, these differences in species richness are likely to be a consequence of ecological processes acting during the build-up of the network. Thus, the question is whether processes that generate a high richness ratio also affect the degree distribution, eventually leading to truncated power-law distributions.

Here, we introduce build-up mechanisms that lead to high richness ratios in a simple network model that generates power-law degree distributions (Barabási and Albert, 1999). We use analytical predictions, numerical simulations and analyses of real data to explore the relationship between exponential truncations and ecological processes that lead to a high richness ratio. Our aim is to contribute to the study of community-level patterns of interactions in plant–animal mutualisms exploring the importance of species-level, build-up mechanisms to the observed network structure.

## 2. The model

In our model, species are represented by nodes and interspecific interactions by links. Thus, we present a species-level model such as those traditionally used in ecological networks (see Pimm, 2002). Consequently, the model ignores features such as the number of individuals of each species that may markedly affect sampling and ecological patterns and processes (Hubbell, 2001). However, because of its simplicity, the model allows exploring the effects of processes that lead to different species richness in mutualistic networks in the absence of complicating factors. Future studies should try to link individual and species-level descriptions of ecological networks. For example, differences in number interactions among species may be a result of differences in abundance among species.

In this paper, we incorporate bipartivity and mechanisms that lead to high richness ratios into one of the simplest models generating power-law degree distributions, the Barabási–Albert (BA) model (Barabási and Albert, 1999). The BA model is a minimal model that recognizes two aspects of the evolution of complex systems. First, many complex systems grow in time by adding new elements. Second, new elements often interact preferentially with the highly connected nodes in the network, which constitutes the so-called preferential attachment or ‘the rich gets richer’ phenomenon (Barabási and Albert, 1999). The BA model is defined by the following algorithm: (1) at time  $t = 0$ , one creates  $m_0$  disconnected nodes (Albert and Barabási, 2000); (2) at each time step, a new node with  $m$  edges is added to the network and connected to a node with probability  $\Pi$ ; (3) the probability  $\Pi$  that a new node

Table 1  
Examples of how widespread are differences in set sizes ( $S_A/S_B > 1$ ) in ecological bipartite networks

Mutualistic interactions	$n$	Median network size	Median $S_A/S_B$ ratio	Percentage of networks with significant deviation of 1:1 ratio
Plant–ant	3	26 (10–41)	1.6 (1.5–2.25)	33.3
Plant–pollinator	40	65 (39–115)	3.0 (2.1–4.0)	86.0
Plant–frugivore	28	27 (18–58)	1.8 (1.3–2.9)	46.4

Data analyzed of the main types of mutualisms, including the interactions between plants and defensive partners (plant–ant interactions), pollinators and seed dispersers—data from our dataset (Bascompte et al., 2003) and the Interaction Web Database (<http://www.nceas.ucsb.edu/interactionweb>). We defined  $S_A$  as the larger set and  $S_B$  as the smaller set. Numbers in parentheses are the first and third quartiles. For each network, we test the significance of  $S_A/S_B > 1$  against the binomial distribution.

will be connected to node  $i$  depends on the degree  $k$  of that node, so that

$$\Pi(k_i) = \frac{k_i + 1}{\sum_j (k_j + 1)}. \quad (1)$$

Here we propose a model that incorporates the intrinsic bipartivity of plant–animal mutualisms into the BA model: (i) at time  $t=0$ , one creates  $m_0$  disconnected nodes; (ii) a proportion of  $m_0$  is assigned to the set  $A$ ,  $m_{0A}$ , and the remaining nodes are assigned to the set  $B$ ,  $m_{0B}$ ; (iii) at each time step and independently of current state, a new node with  $m$  edges is added to the network; (iv) the new node belongs to set  $A$ , with probability  $(1-p)$ , or to the second set ( $B$ ) with probability  $p$ ; (v) to incorporate preferential attachment, we assume that the probability that a new node in set  $B$  will be connected to node  $i$  in set  $A$  follows Eq. (1) with the sum over  $j$  restricted to the set  $A$ . Similarly, the probability that a new node in set  $A$  will be connected to node  $i$  in set  $B$  follows Eq. (1) with the sum over  $j$  restricted to set  $B$ .

The above model allows modeling three general mechanisms that may account for the high richness ratios in plant–animal mutualisms here reported, and investigating their effect on the scale-free behavior of  $P(k)$ . In the first mechanism, called “differential starting size”, both sets grow with the same rate,  $p=0.5$ , but the initial core of disconnected nodes,  $m_0$ , is not equally divided between both sets, so that  $m_{0A} > m_{0B}$ . Thus, differences of set sizes are generated at the birth of the network. In the second mechanism, called “differential growth rate”, the two sets start with the same size,  $m_{0A} = m_{0B}$ , but have different growth rates, that is,  $p \neq 0.5$ . Consequently, the difference of set sizes results from the growing dynamics of each set. In the third mechanism, called “differential limiting size”, the two sets of the network have the same initial core,  $m_{0A} = m_{0B}$ , the same growth rate,  $p = 0.5$ , but one of the sets has a lower size limit, so that  $S_A < S_B$ . In this case, the difference between set sizes results from differential constraints of maximum size of each set. We note that this differential constraint can be modeled for set  $A$  by changing the value of  $p$  to  $p = 0$  after  $S_A$  has been reached. Therefore, for simplicity, we may assume that differential limiting size is a special case of differential growth rate. It is important to notice that these mechanisms can be implemented by simply tuning the parameters of the model ( $m_{0A}$ ,  $m_{0B}$ ,  $p$ ,  $S_A$ ,  $S_B$ ) without directly affecting preferential attachment. Thus, the proposed mechanisms cannot be interpreted as constraints acting on preferential attachment. This is an important difference in relation to previous mechanisms such as forbidden links or filtering information constraining the preferential attachment process (Amaral et al., 2000; Jordano et al., 2003; Mossa et al., 2002).

### 3. Analytic predictions and numerical results

We explore the differences between analytic predictions considering unipartite and bipartite networks. A reasonable

analytic prediction for the structure of bipartite networks may be derived by generalizing previous studies with unipartite networks. Barabási and Albert (1999) applied continuum theory to obtain the analytical predictions for the degree distribution in unipartite BA networks. The BA model predicts that, for large networks, the degree ( $k$ ) of a node  $i$  changes with time according to the dynamical equation:

$$\frac{dk_i}{dt} = m \frac{k_i}{\sum_{j=1}^{N-1} k_j} = m \frac{k_i}{2mt} = \frac{k_i}{2t}. \quad (2)$$

The solution to the above equation is

$$k_i = m \left( \frac{t}{t_i} \right)^\beta, \quad (3)$$

in which  $\beta = 1/2$  and  $t_i$  is an initial time when  $i$  has  $m$  connections, i.e., the time when the node is added to the network. The degree distribution can be interpreted as the probability that a randomly chosen node has  $k$  links and the prediction derived from Eq. (3) is

$$P(k) \sim 2m^{1/\beta} k^{-(1/\beta+1)}. \quad (4)$$

Data from real, plant–animal networks usually show power-laws with exponential truncations (Jordano et al., 2003). Additionally, numerical simulations suggest that finite-size fluctuations lead to truncations in unipartite networks and animal aggregation models (Guimarães et al., 2005; Keitt and Stanley, 1998). However, no previous study investigates if build-up mechanisms may also generate truncated power-laws. We introduce an additional analytic approach to explore the conditions that lead to exponential truncation. The introduced approach demonstrates that truncated power-laws observed in plant–animal mutualisms are expected if high richness ratio is occurring due to build-up mechanisms.

In the original BA model, each event leads to an increase in the network size and in the number of connections. In the bipartite model considered here, we have two different set sizes. Without loss of generality, we focus our analytical results in set  $A$ . By step (v) of our model, the number of connections of a node in set  $A$  can increase only at time events in which a new node enters in set  $B$ . Also, according to step (iv), a new node will be randomly assigned to either set  $A$  or  $B$ . Therefore, the growth rate of the number of connections of a node  $i$  in set  $A$  is proportional to  $m$ , to the probability  $p$  that nodes are assigned to  $B$ , and to the number of connections of node  $i$  relative to the total number of connections in set  $A$  (preferential attachment):

$$\frac{dk_i}{dt} = pm \frac{k_i}{\sum_{j \in A} k_j} = \frac{pk_i}{t}. \quad (5)$$

Integrating we obtain

$$k_i(t) = m \left( \frac{t}{t_i} \right)^p, \quad (6)$$



where  $t_i$  is the time where node  $i$  is inserted into set  $A$ . If  $p$  is not too close to 1, such that  $(1-p)t > m_{0A}$ , then the number of nodes added to set  $A$  in the growth process is much larger than the number of nodes in the initial set  $m_{0A}$  and we may assume that, typically, the node  $i$  is an added node. In this case, neglecting the initial set, we may proceed as in Barabási and Albert (1999) to write

$$prob(k_i < k) = prob\left(t_i > t\left(\frac{m}{k}\right)^{1/p}\right) = 1 - \left(\frac{m}{k}\right)^{1/p}, \quad (7)$$

where we have assumed that the probability density of nodes entering in set  $A$  is uniform. The cumulative probability is, therefore,

$$P(k_i \geq k) = \left(\frac{m}{k}\right)^{1/p}. \quad (8)$$

This is a power-law distribution which drops fast for small  $p$ .

If, on the other hand,  $p$  is close to 1, so that  $(1-p)t < m_{0A}$ , most of the nodes in set  $A$  are nodes of the initial set, for which  $t_i = 1$ . In this case  $k_i(t) = mt/m_{0A}$  and the number of connections of all nodes grows uniformly on the average. In this situation, preferential attachment does not lead to the high heterogeneity in the number of connections observed for unipartite networks. In fact, because the degree of all nodes in  $A$  grows uniformly in time, the attachment of nodes added to  $B$  to the nodes of  $A$  is essentially a random process, leading to an exponential distribution instead of a power-law. Therefore, the combined action of slow growth of the set and preferential attachment, lead to an exponential distribution in the number of connections of these nodes, with average degree equal to  $mt/m_{0A}$ . Writing this distribution as  $f(k) = C \exp(-\gamma k)$  and imposing  $\int_0^\infty f(k) dk = 1$  and  $\int_0^\infty kf(k) dk = mt/m_{0A}$ , we find  $1/C = \gamma = m_{0A}/mt$ . The cumulative distribution in this case is a pure exponential

$$P(k_i \geq k) = \int_k^\infty f(k') dk' = \exp\left[-\left(\frac{m_{0A}}{mt}\right)k\right]. \quad (9)$$

We use numerical simulations to investigate if the above analytic approach reproduces the behavior of degree distributions for small networks. Except when explicitly stated, the simulations are performed using  $m_{0A} = m_{0B} = 10$ ,  $p = 0.5$ , and  $m = 3$ . The simulations end when one of the set sizes reaches  $S_i = 5.0 \times 10^2$ . We plot  $P(k)$  for both sets separately,  $P(k_A)$  and  $P(k_B)$ , and both distributions are plotted as cumulative distributions (Jordano et al., 2003). Cumulative distributions are often used to improve the characterization of degree distributions (Strogatz, 2001).

In the simulation of “differential starting size”, we vary the initial core of set  $A$ ,  $m_{0A}$ , keeping the initial core of set  $B$  as  $m_{0B} = 10$ . In Fig. 2, we illustrate degree distributions of set  $A$  for different  $m_{0A}$ . All degree distributions follow power-laws, although the slopes of the degree distribution are affected by the increase of  $m_{0A}$ . Therefore, we conclude that “differential start size” does not affect qualitatively

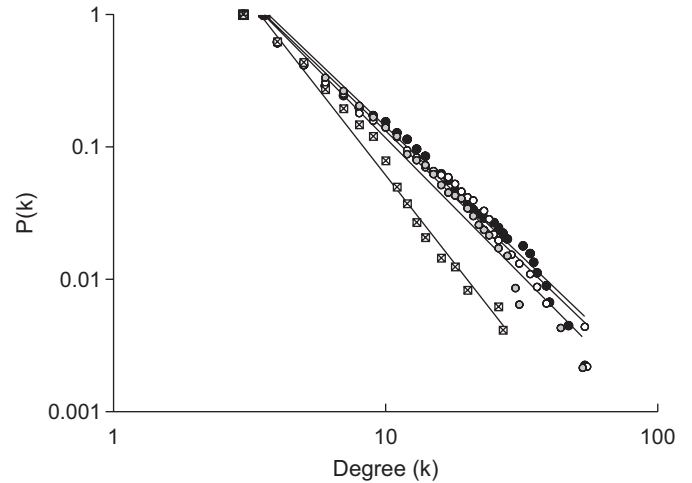


Fig. 2. Effects of differential starting size ( $m_{0A} > m_{0B}$ ) on degree distribution. Log-log plot of the cumulative degree distribution  $P(k_A)$  for distinct differential starting sizes (in all cases,  $m_{0B} = 10$ ):  $m_{0A} = 10$  (closed circles),  $m_{0A} = 15$  (open circles),  $m_{0A} = 30$  (gray circles), and  $m_{0A} = 60$  (crosses). Continuous lines illustrate the power-law behavior in all cases.

the functional form of  $P(k)$  predicted by the BA model even in small networks.

To test the effect of “differential growth rate” on  $P(k)$ , we vary  $p$ , the probability of a new node being assigned to set  $B$ , maintaining the initial size of the sets equal. We use  $m_{0A} = m_{0B} = 50$  nodes in all simulations, because  $m_{0A} = m_{0B} = 10$  does not allow an accurate determination of  $P(k_A)$  for  $p = 1$ . The results of the simulations demonstrate that  $p$  markedly affects the functional form of  $P(k_A)$ . First, the slope of degree distribution decays with  $p$ , as expected from the analytical prediction (Fig. 3A). Second, as predicted from the analytical analysis, the power-law behavior of  $P(k_A)$  is preserved for  $p$  closer to 0 ( $p \leq 0.5$ ), that is, when the size of set  $A$  increases faster or at the same rate than set  $B$  (Fig. 3A). However, if  $p$  is closer to 1 ( $p > 0.5$ ), that is, the set  $A$  increases slower than set  $B$ , exponential deviations appear for larger  $k$ , generating a  $P(k_A)$  that decays as a power-law with an exponential truncation (Fig. 3A). For the limiting case in which  $p = 1$ , there is no evidence of power-law behavior at all, and  $P(k_A)$  follows a slow-decaying exponential function  $P(k) \sim e^{-k\gamma}$ , with the slope following the analytical prediction ( $m_{0A}/mt$ ) (Fig. 3A). Therefore, in bipartite networks in which  $p \approx 1$ , preferential attachment generates slow-decaying exponential curves and not power-law degree distribution, as usually expected (Barabási and Albert, 1999). Exponential distributions of  $P(k)$  are generally associated to networks in which nodes are connected with a constant probability, a rule called random attachment (Albert and Barabási, 2002). However, it is noteworthy that the exponential distribution generated by  $p = 1$  decays slower than the distribution predicted by random attachment (Fig. 3B).

In the last simulation, aiming to test the effect of “differential limiting size” on  $P(k)$ , we vary the final size of

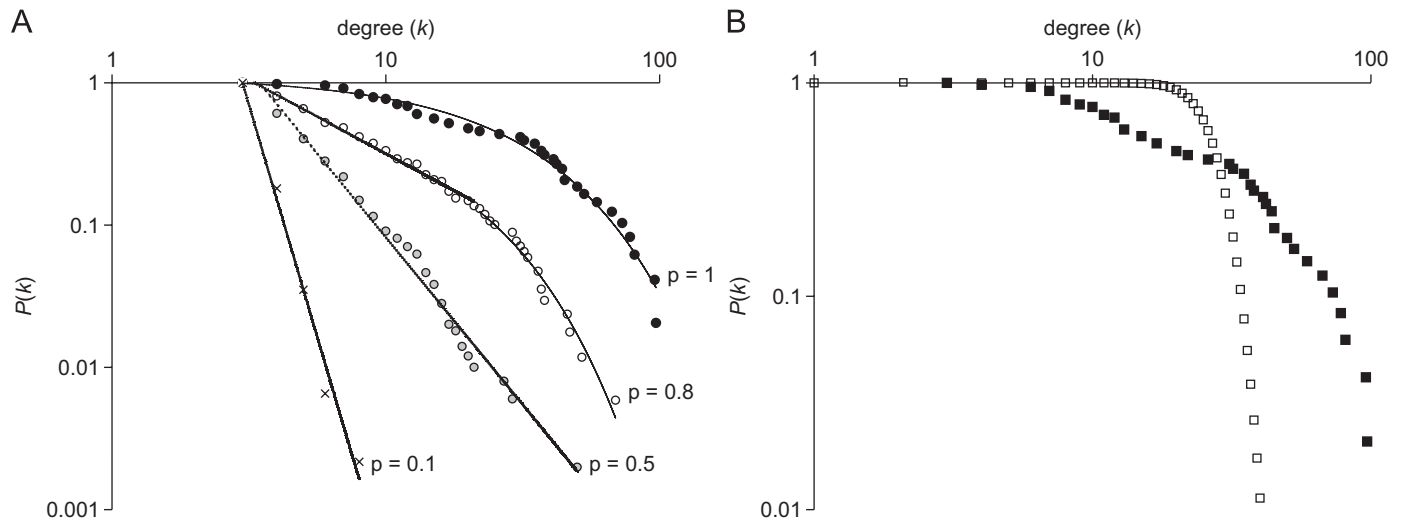


Fig. 3. Effects of the rate of increase of a set size (number of nodes),  $p$ , on its cumulative degree distribution  $P(k)$ . (A) Log–log plot of the cumulative  $P(k)$  for different values of  $p$ . Straight lines indicate the fit to a power-law distribution whereas curves indicate exponential deviations. Note that for  $p = 1$ ,  $P(k)$  is described solely by the exponential function with slope  $m_{0,A}/m$ . (B) The slow-decaying, exponential  $P(k)$  for  $p = 1$  (black squares) and the binomial  $P(k)$  expected for a random network (empty squares).

set  $A$ ,  $S_A$ , keeping the final size of set  $B$ ,  $S_B$ , constant ( $S_B = 1.0 \times 10^3$ ). In this simulation, the sets  $A$  and  $B$  have different size limits. If we let the simulation stop when one of the sets reaches the previously established limiting size, we preserve the scale-free behavior for both  $P(k_A)$  and  $P(k_B)$  (Fig. 4). However, if  $S_A \ll S_B$  and the simulation stops only when both sets reach the previously established limiting size we find that  $P(k_A)$  behaves as a slow-decaying exponential function (Fig. 4). This numerical result supports the notion that differential limiting size can be modeled as a special case of differential growth rate. In contrast,  $P(k_B)$  is characterized by an overrepresentation of nodes with the minimum of connections,  $m$ , but preserves the power-law behavior for  $k > m$  (Fig. 4). As the difference between  $S_A$  and  $S_B$  decreases, both degree distributions converge to power-laws (Fig. 4).

#### 4. Analyses of real plant–animal networks

We also explore if the differences observed in the degree distributions of plants and animals in real pollination and seed dispersal networks (Jordano et al., 2003) are in agreement with the predictions of “differential growth rate” and “differential limiting size”. The use of real networks to investigate the validity of the above mechanisms is difficult for at least three reasons. First, the available networks are static descriptions of these mutualistic interactions and there are no available data on how network structure changes in time. Second, we have no information about the initial conditions of these networks, and a recent theoretical study suggests that this initial condition may markedly affect the degree distribution of small networks (Guimarães et al., 2005). Finally, sampling effort may vary among networks and this may affect the described patterns of interactions (see Olesen and Jordano,

2002). We circumvent these problems by testing for simple, general patterns of relationships expected among degree distributions of different sets if “differential growth rate” or “differential limiting size” are operating.

The degree distribution can be described by two metrics,  $\langle k \rangle$  and  $k_x$ , in which  $\langle k \rangle$  is the average degree and  $k_x$  is the cut-off value, that is, the  $k$ -value beyond which the degree distribution departs from a power-law (Jordano et al., 2003; Guimarães et al., 2005). We used the standardized cut-off value,  $k_x/\langle k \rangle$ , to track changes in the degree distribution from power-law distributions (large  $k_x/\langle k \rangle$ ) to fast-decaying distributions (small  $k_x/\langle k \rangle$ ) (Fig. 5A). The cut-off value,  $k_x$ , was recorded from the literature ( $N = 41$  networks; Jordano et al., 2003) and  $\langle k \rangle$  was estimated for each set separately.

If “differential growth rate” or “differential limiting size” are operating we should expect that smaller sets usually show smaller values of  $k_x/\langle k \rangle$ . In fact, in 73.2% of the mutualistic networks, the smaller set shows smaller values of  $k_x/\langle k \rangle$  ( $p = 0.002$ , binomial test). Additionally, we should expect the differences between the ratio  $k_x/\langle k \rangle$  of both sets will increase with the difference between the richness of two sets. Again the prediction is supported: the differences between the values of  $k_x/\langle k \rangle$  of both sets increase with the differences in species richness, although with a lot of variation (see Fig. 5B).

#### 5. Implications for plant–animal networks

Ecological networks, as some large, sparse food webs (Dunne et al., 2002; Memmott et al., 2000), show power-law degree distributions. Preferential attachment may explain power-laws, although different mechanisms may lead to this pattern in complex networks (Albert and Barabási, 2002). Preferential attachment may explain

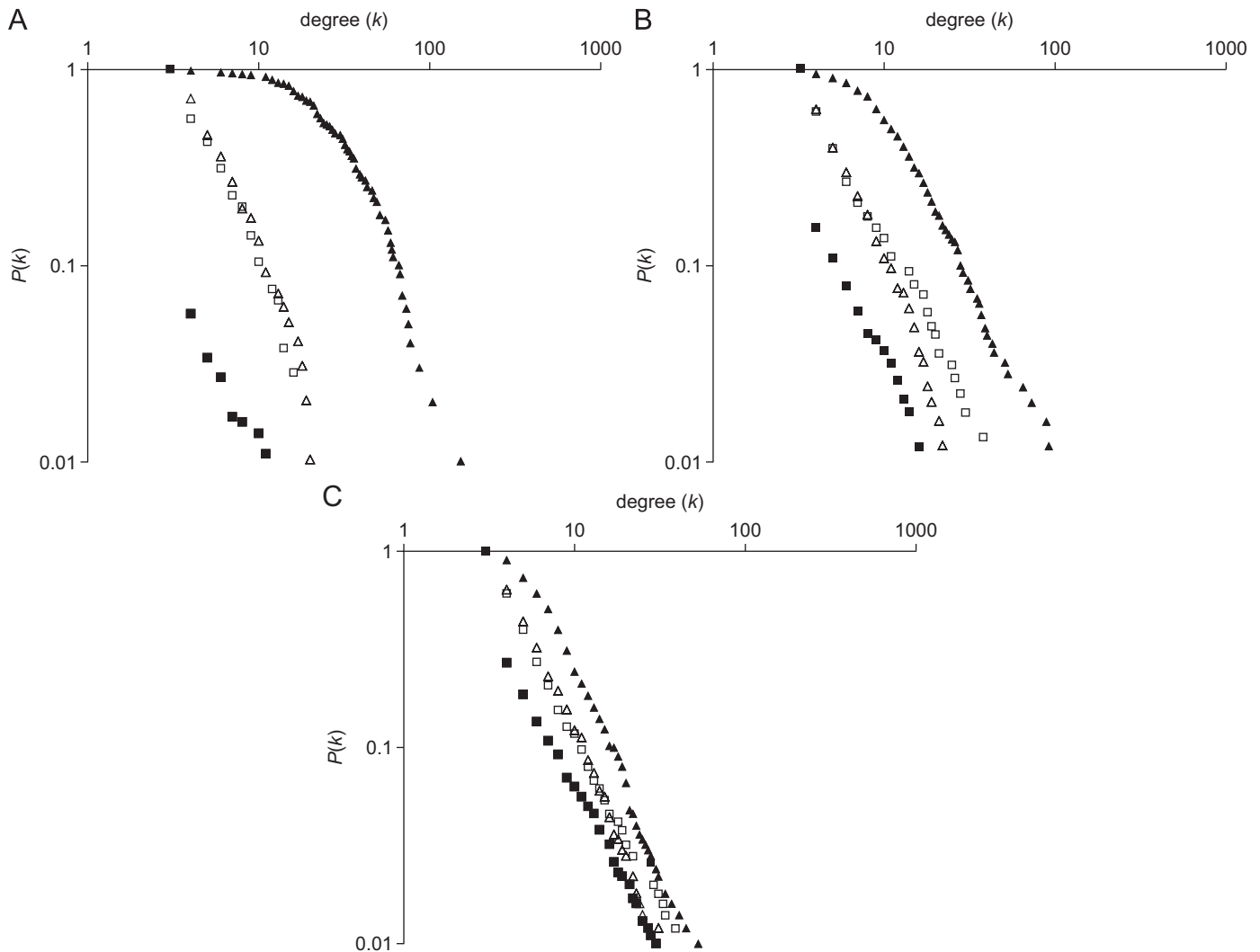


Fig. 4. Effects of differences of set size limits,  $S_A$  and  $S_B$  on  $P(k_A)$  and  $P(k_B)$ . Each figure has four degree distributions:  $P(k_A)$  and  $P(k_B)$  for a simulation in which network growth stops when the smaller size limit was reached (empty symbols) and  $P(k_A)$  and  $P(k_B)$  for a simulation in which network growth stops when both size limits were reached (filled symbols). Triangles represent records for smaller set size limits and squares represents records for larger set size limits. In all simulations  $S_B = 1.0 \times 10^3$  and (A)  $S_A = 1.0 \times 10^2$ ; (B)  $S_A = 2.5 \times 10^2$ ; (C)  $S_B = S_A = 1.0 \times 10^3$ .

power-laws, although different mechanisms may lead to this pattern in complex networks (Albert and Barabási, 2002). The exponential truncation observed in some degree distributions is usually interpreted as evidence of constraints limiting preferential attachment. Constraints such as filtering information acting on Internet evolution (Mossa et al., 2002), aging operating on movie-actor networks (Amaral et al., 2000), and costs of adding edges influencing the network of world airports have been proposed to explain exponential truncation of power-laws in non-biological systems (Amaral et al., 2000). In ecology, the truncation of power-laws was observed in many coevolutionary bipartite networks of plant–animal mutualisms. Jordano et al. (2003) proposed that in such systems truncation emerges as a consequence of “forbidden links”, which are interactions that *a priori* cannot occur due to biological constraints, i.e., structural zeroes in the interaction matrix.

Forbidden links do occur in natural communities and limit the number of interactions in biological systems (Bascompte and Jordano, 2006) as for example, when a given bird species is unable to interact with a fraction of plant species simply because they are not able to eat large fruits, or when a pollinator and a flowering plant species occur at different times of the year (with different phenologies). However, here we clearly demonstrate that exponential truncations can also emerge from processes associated with differences in species richness between plants and animals. We show that high richness ratios associated with “differential growth rate” and “differential limiting size” promote deviations of the power-law distribution predicted by a minimal model that generates power-laws through preferential attachment. Therefore, along with random initial conditions (Guimarães et al., 2005) and constraints to preferential attachment (Jordano et al., 2003), processes affecting species richness are

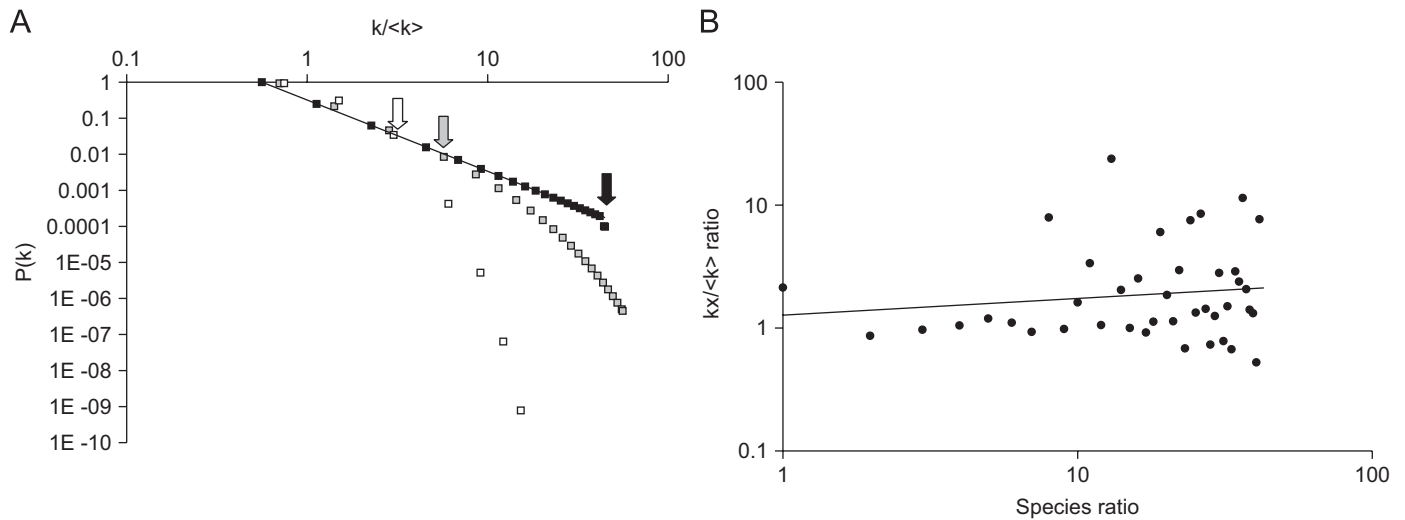


Fig. 5. The use of the standardized cut-off value  $k_x/\langle k \rangle$  (see text for further details) to track the increase of truncation in theoretical and real networks (A) three theoretical degree distributions: almost perfectly power-law (diamonds), truncated power-law (squares) and almost perfectly exponentials (circles). The arrows indicate the different values of  $k_x/\langle k \rangle$  for each distribution. Note that  $k_x/\langle k \rangle$  decreases with the increase of exponential truncation from the power-law (continuous line). (B) The ratio between  $k_x/\langle k \rangle$  of two sets increases with richness ratio (log–log regression,  $F = 4.09$ ;  $R^2 = 0.095$ ;  $p = 0.05$ ).

alternative factors contributing to the existence of exponential truncations in ecological bipartite networks.

Our results point to the importance of exploring finite-size fluctuations for the characterization of small networks (Amaral et al., 2004; Guimarães et al., 2005, 2007a). Additionally, our results suggest that long-term processes of community assembly determining the differences of species richness between plants and animals may affect the organization of ecological bipartite networks. We should expect that other network measurements may be affected by high richness ratios. For example, richness ratio may affect asymmetry in the mutual specialization between species (Vázquez and Aizen, 2004): if there is a high richness ratio and interactions are randomly distributed, the species that form the smaller set will have many interactions (“generalists”). In contrast, species from the larger set will have a lower number of interactions and would be called “specialists”. Similar effects are expected in quantitative measurements of the extent of mutual dependence or interaction strength, which generate dependence asymmetries (Bascompte et al., 2006). Future studies should quantify the importance of richness ratio in the patterns recorded for these measurements (Bascompte et al., 2006; Vázquez and Aizen, 2004). However, asymmetry, dependence and other network metrics such as nestedness are often analyzed using a null model approach (Bascompte et al., 2003; Vázquez and Aizen, 2003), which controls for the effects of high richness ratio. In contrast, the description of degree distribution does not take into account high richness ratio.

Our analytical and numerical results suggest that the association between preferential attachment and power-law distributions, widely reported for unipartite networks (Albert and Barabási, 2002), is expected for finite bipartite

networks only when two conditions are satisfied: the set of interest grows at the same rate or faster than the other set ( $p \leq 0.5$ ) and has a similar or higher limiting size ( $S_A \geq S_B$ ). Examples of differential growth rate and differential limiting sizes are widespread in nature. Differential growth rate occurs over evolutionary time, for instance, because the diversity of insect herbivores and host plants in interacting plant–herbivore assemblages seldom increase at similar rates (Thompson, 1994). In ecological time, differential growth rate occurs when the dispersal rates of plants and animals (e.g., pollinators or seed dispersers) to recently created habitats differ (e.g., Shanahan et al., 2001). On the contrary, “differential limiting sizes” may occur, for example, when the number of species of a given set is limited by metabolic-related processes, or when the species entering the network originate from a depauperate biogeographic pool. As a consequence of these processes, we will not expect to find power-law behavior for the  $P(k)$  of the set that increases at a slower rate in the above-mentioned plant–animal networks, even if preferential attachment is occurring without forbidden links. The more marked truncation of  $P(k)$  in the smaller sets and the positive association between differences in cut-off values and richness ratio in real mutualistic networks corroborates these ideas.

The structure of ecological networks may also have consequences for the robustness of interspecific interactions to local extinctions (Fortuna and Bascompte, 2006; Memmott et al., 2004). Networks characterized by truncated power-laws are more robust to the extinction of keystone, highly connected species than scale-free networks (Jordano et al., 2003). Therefore, we hypothesize those ecological processes that affect species richness may also increase the robustness of interaction networks by generating truncated degree distributions through high



richness ratios. Future theoretical studies should investigate this hypothesis.

### Acknowledgments

We are indebted to P.P. Coltri, M.A. de Menezes, M. Galetti, P. Guimarães T. M. Lewinsohn, J.N. Thompson and two anonymous reviewers for comments on the manuscript. Financial support was provided by the Brazilian agencies FAPESP and CNPq (G.M., M.A.M.A., P.R.G., and S.F.R.), Grant nos. BOS2000-1366-C02, REN2003-00273, and CGL2006-00373 from the Spanish Ministerio de Educación (MEC), Grant no. RNM-305 (Junta de Andalucía, Spain) and CNPq-CSIC bilateral agreement (P.J. and J.B.), European Heads of Research Councils and the European Science Foundation through an EURYI award and Grant no. REN2003-04774 from Spanish Ministerio de Educación y Ciencia (J.B.).

### References

- Albert, R., Barabási, A.L., 2000. Topology of evolving networks: local events and universality. *Phys. Rev. Lett.* 85, 5234–5237.
- Albert, R., Barabási, A.L., 2002. Statistical mechanics of complex networks. *Rev. Mod. Phys.* 74, 47–97.
- Amaral, L.A.N., Scala, A., Barthelemy, M., Stanley, H.E., 2000. Classes of small-world networks. *Proc. Natl. Acad. Sci. USA* 97, 11149–11152.
- Amaral, L.A.N., Barrat, A., Barabási, A.L., Caldarelli, G., De los Rios, P., Erzan, A., Kahng, B., Mantegna, R., Mendes, J.F.F., Pastor-Satorras, R., Vespignani, A., 2004. Virtual round table on ten leading questions for network research. *Eur. Phys. J. B* 38, 143–145.
- Barabási, A.L., Albert, R., 1999. Emergence of scaling in random networks. *Science* 286, 509–512.
- Bascompte, J., Jordano, P., 2006. The structure of plant–animal mutualistic networks. In: Pascual, M., Dunne, J.A. (Eds.), *Food Webs as Complex Adaptive Networks: Linking Structure to Dynamics*. Oxford University Press, Oxford.
- Bascompte, J., Jordano, P., Melian, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* 100, 9383–9387.
- Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci. USA* 99, 12917–12922.
- Ergun, G., 2002. Human sexual contact network as a bipartite graph. *Phys. a-Stat. Mech. Appl.* 308, 483–488.
- Fleming, T.H., 2005. The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemisphere. *Oikos* 111, 556–562.
- Fortuna, M.A., Bascompte, J., 2006. Habitat loss and the structure of plant–animal mutualistic networks. *Ecol. Lett.* 9 (3), 278–283.
- Guimarães, P.R., de Aguiar, M.A.M., Bascompte, J., Jordano, P., dos Reis, S.F., 2005. Random initial condition in small Barabási–Albert networks and deviations from the scale-free behavior. *Phys. Rev. E* 71, 037101.
- Guimarães, P.R., Rico-Gray, V., dos Reis, S.F., Thompson, J.N., 2006. Asymmetries in specialization in ant–plant mutualistic networks. *Proc. R. Soc. London B* 273, 2041–2047.
- Guimarães, P.R., Bonaldo, R.M., Krajewski, J.P., Pinheiro, A., Guimarães, P., Powers, J., dos Reis, S.F., 2007a. Investigating small fish schools: selection of school-formation models by means of general linear models and numerical simulations. *J. Theor. Biol.* 245, 784–789.
- Guimaraes, P.R., Sazima, C., dos Reis, S.F., Sazima, I., 2007b. The nested structure of marine cleaning symbiosis: is it like flowers and bees? *Biol. Lett.* 3, 51–54.
- Harary, F., 1969. *Graph Theory*. Addison-Wesley, Reading.
- Hubbell, S., 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Jordano, P., 1987. Patterns of mutualistic interactions in pollination and seed dispersal—connectance, dependence asymmetries, and coevolution. *Am. Nat.* 129, 657–677.
- Jordano, P., Bascompte, J., Olesen, J.M., 2003. Invariant properties in coevolutionary networks of plant–animal interactions. *Ecol. Lett.* 6, 69–81.
- Keitt, T.H., Stanley, H.E., 1998. Dynamics of North American breeding bird populations. *Nature* 393, 257–260.
- Lewinsohn, T.M., Prado, P.I., Jordano, P., Bascompte, J., Olesen, J.M., 2006. Structure in plant–animal interaction assemblages. *Oikos* 113, 174–184.
- Liljeros, F., Edling, C.R., Amaral, L.A.N., Stanley, H.E., Aberg, Y., 2001. The web of human sexual contacts. *Nature* 411, 907–908.
- Memmott, J., 1999. The structure of a plant–pollinator food web. *Ecol. Lett.* 2, 276–280.
- Memmott, J., Martinez, N.D., Cohen, J.E., 2000. Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web. *J. Anim. Ecol.* 69, 1–15.
- Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B: Biol. Sci.* 271, 2605–2611.
- Montoya, J.M., Pimm, S.L., Sole, R.V., 2006. Ecological networks and their fragility. *Nature* 442.
- Mossa, S., Barthelemy, M., Stanley, H.E., Amaral, L.A.N., 2002. Truncation of power-law behavior in “scale-free” network models due to information filtering. *Phys. Rev. Lett.* 88, 138071.
- Olesen, J.M., Jordano, P., 2002. Geographic patterns in plant–pollinator mutualistic networks. *Ecology* 83, 2416–2424.
- Pascual, M., Dunne, J.A., 2006. *Ecological Networks: Linking Dynamics in Food Webs*. Oxford University Press, Oxford.
- Pimm, S.L., 2002. *Food Webs*. University of Chicago Press, Chicago.
- Prado, P.I., Lewinsohn, T.M., 2004. Compartments in insect–plant associations and their consequences for community structure. *J. Anim. Ecol.* 73, 1168–1178.
- Shanahan, M., Harrison, R.D., Yamuna, R., Boen, W., Thornton, I.W.B., 2001. Colonization of an island volcano, long island, papua new guinea, and an emergent island, motmot, in its caldera lake. V. Colonization by figs (*figus* spp.), their dispersers and pollinators. *J. Biogeogr.* 28, 1365–1378.
- Strogatz, S.H., 2001. Exploring complex networks. *Nature* 410, 268–276.
- Thompson, J.N., 1994. *The Coevolutionary Process*. The University of Chicago Press, Chicago.
- Thompson, J.N., 2005. *The Geographic Mosaic of Coevolution*. The University of Chicago Press, Chicago.
- Thompson, J.N., 2006. Mutualistic web of species. *Science*, 372–373.
- Vazquez, D.P., 2005. Degree distribution in plant–animal mutualistic networks: forbidden links or random interactions? *Oikos* 108, 421–426.
- Vázquez, D.P., Aizen, M.A., 2003. Null model analyses of specialization in plant–pollinator interactions. *Ecology* 84, 2493–2501.
- Vázquez, D.P., Aizen, M.A., 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. *Ecology* 85, 1251–1257.
- Vazquez, D.P., Poulin, R., Krasnov, B.R., Shenbrot, G.I., 2005. Species abundance and the distribution of specialization in host–parasite interaction networks. *J. Anim. Ecol.* 74, 946–955.