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Para Patricia, por ensinar a beleza da palavra contingência.

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RESUMO

INTRODUÇÃO: mutualismos são interações entre espécies diferentes que beneficiam os indivíduos envolvidos. Em uma comunidade ecológica, mutualismos tais como interações entre plantas e polinizadores e entre plantas e dispersores de sementes podem ser descritas como uma rede. O estudo dessas redes de interações levou à descrição de duas propriedades estruturais gerais: (1) a probabilidade de se encontrar uma espécie com *k* interações decai seguindo uma lei de potência com truncamento exponencial e (2) aninhamento. Essas duas propriedades estão, aparentemente, ausentes em interações entre predadores e presas, as chamadas teias tróficas.

OBJETIVOS: contribuir para a compreensão dos processos subjacentes aos padrões observados em redes mutualísticas e investigar o grau de generalização desses padrões.

PRINCIPAIS RESULTADOS:

- A lei de potência truncada que caracteriza a distribuição do grau de redes mutualísticas pode ser explicada por condições iniciais aleatórias e por processos associados à diferença de riqueza entre plantas e animais.
- A estrutura aninhada de uma rede mutualística é parcialmente explicada por diferenças entre as abundâncias das espécies.
- Problemas de resolução taxonômica característicos de estudos sobre teias tróficas, mas pouco comuns no estudo de mutualismos, explicam as diferenças nas distribuições do grau desses dois tipos de redes ecológicas. A ausência de aninhamento, todavia, não é explicada por este problema de resolução.
- As redes que descrevem outros dois mutualismos, as interações entre limpadores e clientes em recifes de corais e entre formigas e plantas produtoras de néctar extrafloral, são aninhadas.

PRINCIPAIS CONCLUSÕES: a forma da distribuição do grau observada em mutualismos é esperada por processos simples e gerais. O aninhamento é uma propriedade geral de mutualismos em comunidades ricas de espécies.

INTRODUÇÃO

“It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us”

Charles Darwin

“All the effects of Nature are only the mathematical consequences of a small number of immutable laws”

Pierre Simon Laplace

Mutualismos são interações entre indivíduos de espécies diferentes que trazem benefícios para os envolvidos (Begon et al. 1996). Interações mutualísticas são observadas em todos os ecossistemas, das florestas tropicais aos recifes de corais, envolvendo de organismos unicelulares a grandes árvores e vertebrados, e estão entre os principais processos subjacentes à evolução e organização da biodiversidade (Thompson 1994). De fato, a maioria das espécies depende de outras espécies para se alimentar, se reproduzir e se defender contra parasitas e outros inimigos naturais (Bronstein et al. 2004; Côte 2000; Thompson 2005; Figura 1).

Um exemplo clássico de mutualismo é a polinização das figueiras do gênero *Ficus* pelas vespas-do-figo (Chalcidoidea, Hymenoptera). Cada espécie de figueira é polinizada por apenas uma ou poucas espécies de vespas-do-figo (Bronstein et al. 2004). Nessa interação, a figueira é beneficiada pela polinização promovida pelas vespas-do-figo, enquanto as vespas obtêm recurso alimentar e proteção para a sua prole (Bronstein et al. 2004). Todavia, grande parte das interações mutualísticas não é tão específica. Em uma localidade, muitas espécies de plantas são polinizadas por dezenas de espécies de polinizadores, enquanto uma mesma espécie de polinizador contribui para a reprodução de muitas espécies de plantas (Vazquez & Aizen 2003). De forma similar, uma mesma espécie de ave pode consumir frutos e dispersar sementes de dezenas de espécies de plantas (Herrera 2002). Por conseguinte, mutualismos podem ser vistos como interações ecológicas que conectam diferentes espécies em uma localidade, formando uma teia de interações (Jordano et al. 2003; Memmott 1999).

Os padrões de interação observados em teias de interações mutualísticas são um aspecto fundamental da biodiversidade, uma vez que descrevem a interdependência entre as espécies (Montoya et al. 2006; Thompson 2006). Nesse sentido, os padrões macroscópicos de interações entre espécies mutualistas podem conter informação sobre a importância de diferentes processos ecológicos e evolutivos para a organização da biodiversidade (Bascompte et al. 2003; Lewinsohn et al. 2006; Thompson 2005). Conseqüentemente, métodos que descrevam a estrutura interconectada dos mutualismos podem contribuir para entender a origem, evolução e manutenção dessas interações.

FIGURA 1. Mutualismos investigados neste estudo. Quadro superior esquerdo: polinização de *Cirsium* sp. pela borboleta *Pandoriana pandora* (Foto: Pedro Jordano). Quadro superior direito: dispersão de sementes do jatobá *Hymenaea courbaril* por uma cutia *Dasyprocta leporina* (Foto: Rafael L. Fonseca). Quadro inferior esquerdo: proteção das vagens de *Crotalaria pallida* pela formiga *Ectatomma quadridens* (Foto: Rafael L. Fonseca). Quadro inferior direito: limpeza de ectoparasitas e tecidos danificados do peixe *Cephalopholis fulva* pelo peixe *Elacantinus randalli* (Foto: Ivan Sazima).

A estrutura interconectada da teia de interações mutualísticas pode ser descrita através de uma rede (ou grafo), isto é, um conjunto de pontos (ou vértices) que podem ou não estar conectados através de linhas (ou arestas) (Harary 1969, Figura 2a). Em uma rede mutualística os pontos representam as espécies de uma localidade e as linhas representam interações mutualísticas entre as espécies (Jordano et al. 2003). A estrutura da rede que descreve as interações mutualísticas em uma localidade pode então ser descrita através de diferentes métricas que capturam alguns aspectos de interesse.

Atualmente, redes são utilizadas para descrever uma grande variedade de sistemas naturais (Strogatz 2001). A maior descoberta relacionada à aplicação de redes em diferentes áreas do conhecimento foi a generalidade de certos padrões estruturais, que foram encontrados em sistemas aparentemente não relacionados, tais como a Internet, as interações sociais entre seres humanos e as vias metabólicas no interior das células (Albert & Barabasi 2002). Essa generalidade indica que parte da estrutura dessas redes é determinada não por características particulares do sistema, mas por processos análogos atuando em diferentes sistemas (Albert & Barabasi 2002). Dessa forma, a abordagem de redes permite estudar problemas aparentemente bem diferrentes e explicar processos fundamentais como derivados de princípios comuns (Amaral & Ottino 2004).

Apesar dos recentes avanços teóricos, o estudo da estrutura das redes mutualísticas ainda está em uma fase essencialmente descritiva (Bascompte & Jordano 2006; Bascompte et al. 2003; Jordano et al. 2003; Lewinsohn et al. 2006; Memmott 1999; Olesen & Jordano 2002; Vazquez & Aizen 2004). Nesse contexto, dois padrões estruturais caracterizam as redes que descrevem a polinização por animais e dispersão de sementes por vertebrados:

(1) A distribuição do grau, isto é, a probabilidade de uma espécie interagir com k outras espécies, decai seguindo uma lei de potência com truncamento exponencial (Jordano et al. 2003, Figura 2b), como o observado em certas redes sociais (Amaral et al. 2000). Dessa forma, mutualismos estão em uma posição intermediária entre redes nas quais todos os elementos apresentam aproximadamente o mesmo número de interações (ex. redes aleatórias) e sistemas nos quais há muitos elementos com poucas interações e alguns poucos elementos com um número muito grande de interações (ex. a Internet).

(2) As redes mutualísticas são aninhadas (Bascompte et al. 2003, Figura 2a), isto é, apresentam três propriedades estruturais relacionadas: (i) plantas com muitas interações

interagem com animais com muitas interações; (ii) plantas e animais com poucas interações raramente interagem entre si; (iii) espécies com poucas interações geralmente interagem com as espécies com mais interações.

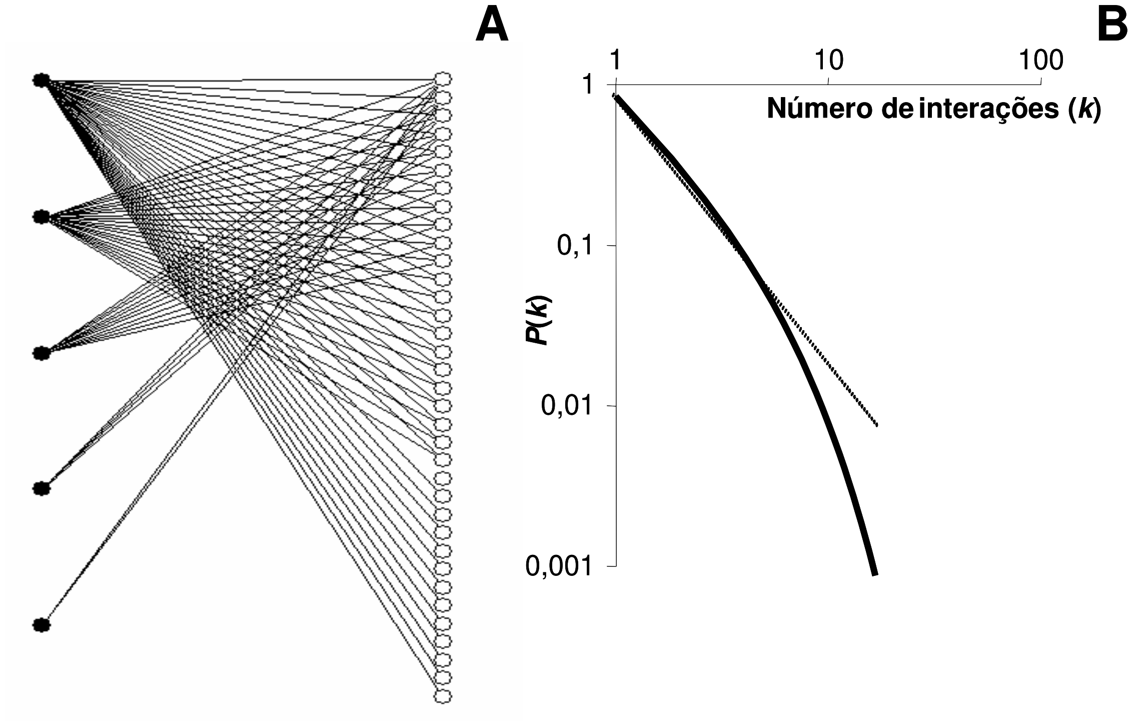

FIGURA 2. Mutualismos como redes e suas propriedades. (a) Interações hipotéticas entre limpadores e clientes em recifes de corais (veja capítulo 6). As espécies de limpadores estão representadas por pontos pretos e os clientes por pontos brancos. Esta rede é perfeitamente aninhada, uma vez que (i) clientes com muitas interações interagem com limpadores com muitas interações; (ii) espécies com poucas interações raramente interagem entre si; (iii) espécies com poucas interações geralmente interagem com as espécies com mais interações. (b) Freqüência de interações por espécies decaindo como uma lei de potência com truncamento exponencial (a curva que decai mais rápido). Note que para valores altos de número de interações (*k*) a freqüência de pontos é muito mais baixa que o esperado por uma lei de potência (reta).

Poucos mecanismos foram propostos como possíveis explicações para os padrões observados em redes mutualísticas. Além disso, a própria caracterização dos padrões observados em redes mutualísticas está limitada a estudos descritivos de redes de polinizadores e dispersores de sementes. Dessa forma, este estudo teve como objetivos (i) contribuir para a compreensão dos processos subjacentes aos padrões observados em redes mutualísticas e (ii) investigar o grau de generalização dos padrões descritos acima.

Nos **Capítulos 1** e **2**, hipóteses alternativas para a origem do truncamento exponencial são exploradas através da modelagem estatístico-matemática. Demonstra-se que o pequeno número de elementos (ex. espécies) pode levar ao truncamento exponencial, especialmente se associado (i) a condições iniciais aleatórias (**Capítulo 1**) e (ii) a processos ecológicos responsáveis por diferenças na riqueza de animais e plantas (**Capítulo 2**). No **Capítulo 3** é investigada a hipótese de que diferenças nas abundâncias de espécies explicariam, pelo menos em parte, o padrão aninhado observado em redes mutualísticas (Lewinsohn et al. 2006). Os resultados apóiam a hipótese, mas sugerem que quase 40% da estrutura aninhada não podem ser explicados por diferenças de abundâncias entre as espécies.

As redes que descrevem as interações entre presas e predadores, as chamadas teias tróficas, não são aninhadas e apresentam uma freqüência de interações por espécie que, em geral, não segue uma lei de potência truncada. O **Capítulo 4** investiga se essas diferenças entre as redes mutualísticas e teias tróficas estão relacionadas à representação de diferentes espécies por um único ponto, um problema de resolução taxonômica típico de teias tróficas, mas pouco comum em redes mutualísticas. Os resultados mostram que as diferenças na forma da freqüência de interações por espécie podem ser explicadas pela representação de espécies por um único pronto. Entretanto, essa representação não explica a ausência de aninhamento em teias tróficas.

Os **Capítulos 5** e **6** testam a generalidade da estrutura aninhada entre os diferentes tipos de mutualismos. Até o momento, apenas a estrutura de dois mutualismos (polinização e dispersão de sementes) foi investigada, sendo caracterizada por um alto grau de aninhamento (Bascompte et al. 2003). Os resultados obtidos aqui apóiam a idéia de generalidade, uma vez que o aninhamento caracteriza as redes que descrevem outras interações mutualísticas, como as interações entre formigas e plantas que produzem néctar extrafloral (**Capítulo 5**) e entre peixes e crustáceos limpadores de parasitas e peixes clientes em recifes de corais (**Capítulo 6**).

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Capítulo 1

Random initial condition in small Barabasi-Albert networks and deviations from the scale-free behavior

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Random initial condition in small Barabasi-Albert networks and deviations from the scale-free behavior

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Barabasi-Albert networks are constructed by adding nodes via preferential attachment to an initial core of nodes. We study the topology of small scale-free networks as a function of the size and average connectivity of their initial random core. We show that these two parameters may strongly affect the tail of the degree distribution, by consistently leading to broad-scale or single-scale networks. In particular, we argue that the size of the initial network core and its density of connections may be the main responsible for the exponential truncation of the power-law behavior observed in some small scale-free networks.

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I. INTRODUCTION

Complex networks describe a large number of social, physical, and biological systems [1–9]. The very basic organizing principles of complex networks are encoded, in some level, in network topology [1,3,9,10]. For example, their degree distribution, which is the cumulative probability distribution of the number of edges per node, captures in quantitative terms some rules that govern the connection of nodes in growing networks [1,5,11]. The Barabasi-Albert (BA) model for growing networks proposes that the two main organizing principles acting during the buildup of complex network are growth and "preferential attachment." Under this mechanism there is a nonuniform probability with which a new node connects to an existing node of the network, which increases with the number of connections of that node [11]. The BA model generates a degree distribution that decays as a power law, implying that the system does not have a particular scale (scale-free networks) [11]. Although several physical and biological systems are indeed scale free [3,11,12], there are several examples of complex networks, such as the small mutualistic networks of interactions among plants and animals [7], in which an exponential truncation of the power-law behavior predominates for large degrees [1,5]. These networks are called broad-scale networks and are more homogeneous than scale-free networks (Fig. 1). This observed truncation in power-law behavior can be explained by the small size of these networks [10,13] or by mechanisms such as the addition of links limited by aging or connection costs [1], forbidden links [7], and information filtering [1,5]. These mechanisms suggest that, in broad-scale networks, preferential attachment is constrained by node characteristics operating during the network evolution.

However, size effects and growth constraints might not be the sole responsibility for the exponential tail of the degree distribution. In this paper we argue that, for relatively small networks, the initial set of nodes over which the network evolves has strong effects on the tail of the degree distribution. To understand why this is so we recall that the BA network is constructed from a small number of nodes which we call the "initial core." Then, at each step a new node is added and connected to the already existing ones following the preferential attachment rule [11]. Although the original model does not say anything about connections between the initial nodes, later work has assumed that the initial core is totally connected [5,14], totally disconnected [15], or randomly connected [16]. In this paper we demonstrate that, for small networks, a randomly connected initial core in BA networks consistently generates a truncation of the degree distribution and that the truncation depends on the relative size of this random initial core. Moreover, we show that highly connected large initial cores generate degree distributions that markedly deviate from the power-law regime. This indicates that the tail of the degree distribution might contain information about the genesis of the network. We note that the characterization of small networks has been pointed as one of the leading questions in network research [17]. This work aims at contributing in this direction.

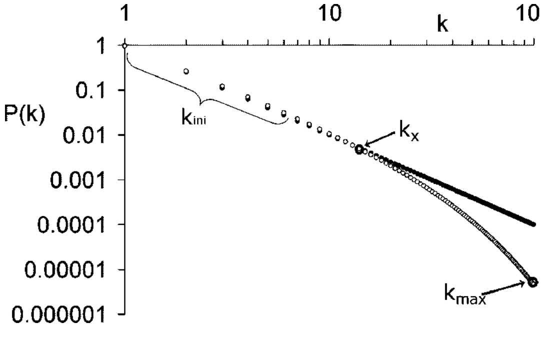

FIG. 1. Illustration of the exponential truncation of the power-law behavior of degree distributions. Open circles are recorded values for $P(k)$ for a hypothetical degree distribution. Solid circles are values of $P(k)$ predicted by a power-law distribution, computed using the first k_{ini} values of k. k_x indicates the lowest value where the "observed" $P(k)$ departs from the predicted power-law behavior. k_{max} is maximum recorded degree.

II. BA MODEL WITH A RANDOM INITIAL CORE

The network's random initial core is defined as follows: at time $t=0$, one creates m_0 nodes and connects each pair of nodes with constant probability p. Thus, this initial core of nodes is an Erdos-Renyi (ER) random graph [3]. Then, at each time step, a new node with $m \leqslant m_0$ edges is added to the network. To incorporate preferential attachment, we assume that the probability Π that a new node will be connected to node i depends on the degree k of that node, so that

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

To test numerically the effect of the size of the ER initial core on the degree distribution, we simulate the evolution of different networks with fixed final size $S=100$ nodes and $m=5$ links, but with different initial connection probabilities p ($p=0.1$ and $p=0.8$) and different sizes of ER initial cores. To reduce fluctuations in the degree distribution related to the small network size [1,2], we calculated the cumulative degree distribution $P(k)$.

Preliminary simulations suggest that, even for small values of m_0, the cumulative degree distribution $P(k)$ shows an exponential truncation for large values of k. To reduce the effects of this truncation on the estimate of the exponent of power-law behavior for the degree distribution, we only used the first five recorded values of k to compute the power law exponent of $P(k)$, as illustrated in Fig. 1.

For the less connected ER core ($p=0.1$), we used the following measures to characterize the effects of m_0 on the $P(k)$ (see Fig. 1): (1) the cutoff degree k_x, in which the observed $P(k)$ departs from the predicted power-law behavior, decreasing exponentially; (2) the maximum recorded degree k_{max}; (3) the proportion of nodes with $k_i > k_x$; and (4) the strength of truncation t, which describes the rate of decrease of $P(k)$ with k, following e^{-tk} for $k > k_x$. For the highly connected ER core ($p=0.8$) we only show how the degree distribution departs from the predicted power-law behavior.

III. RESULTS

Our results show that the scale-free nature of small BA networks is strongly affected by the size of ER initial core. For $p=0.1$, the strength of the exponential truncation of the power-law behavior of the degree distribution is enhanced by ER initial core size, as shown in Fig. 2. Figure 2(a) shows that increasing the ER initial core results in a linear decrease in k_x. Moreover, the exponent t increases linearly with the size of the ER initial core, for $k \geqslant k_x$, as shown in Fig. 2(b). The earlier truncation of the power-law behavior and the increase of t with m_0 imply that the homogeneity of the BA networks (i.e., similarity of the degree k between different nodes) increases with ER core size. In fact, the increase in ER core size generates a linear reduction in the maximum recorded degree, Fig. 2(c), and a logarithmic increase in the proportion of nodes in which $k_i > k_x$, Fig. 2(d).

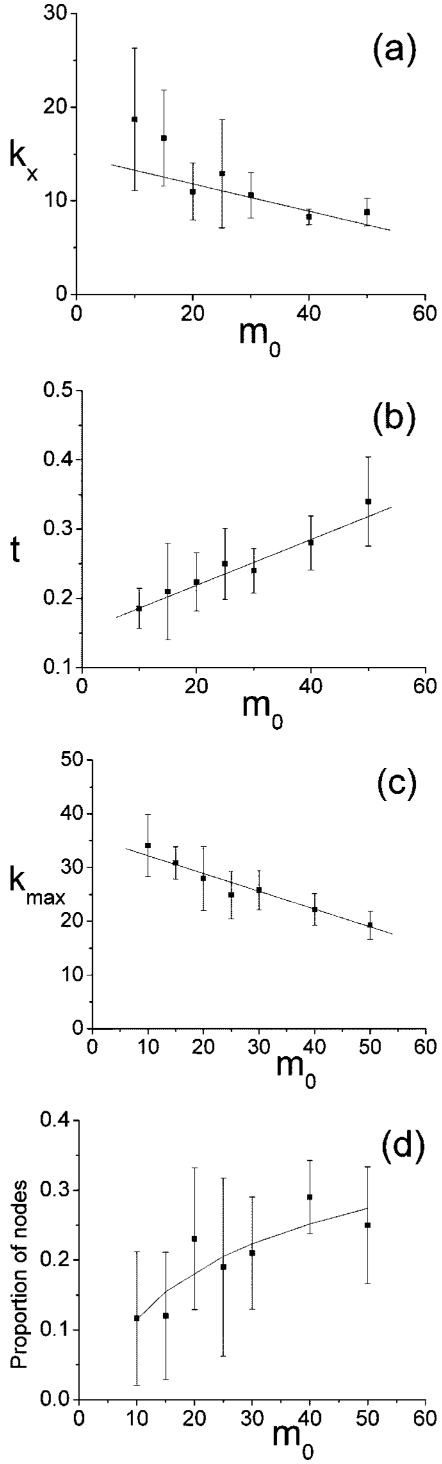

FIG. 2. Effects of the ER initial core size m_0 for $p=0.1$ on (a) the cutoff degree; (b) the strength of exponential truncation, t (see text for further details); (c) the maximum recorded degree, k_{max}; and (d) the proportion of nodes of the network with $k_i > k_x$. The network size has been fixed to 100 nodes.

The degree distribution in BA network with less-connected ER initial cores, including 15%–30% of all nodes of the network, behaves as a power law for $k_i < k_x$ and as an exponential for $k_i > k_x$. Thus, these networks are broad-scale networks. For larger initial cores ($m_0=30$), the degree distribution $P(k)$ departs from the expected by the power law even earlier ($k_x < 10$). In fact, these networks cannot be character-

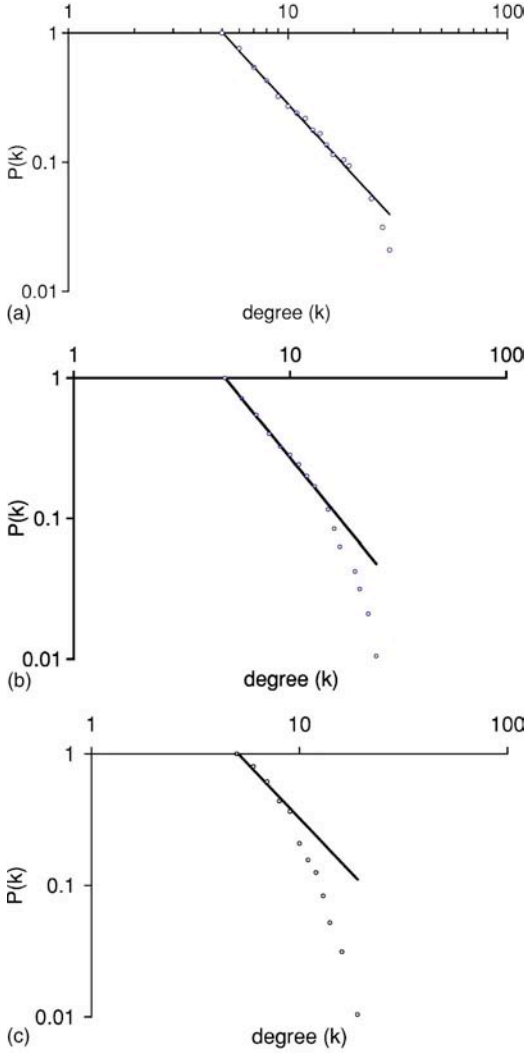

FIG. 3. Different classes of complex networks are generated by varying the size of the ER initial core m_0 for $p=0.1$. The network size has been fixed to 100 nodes. (a) scale-free networks ($m_0=15$), (b) broad-scale networks ($m_0=25$) and (c) single-scale networks ($m_0=50$).

ized as scale-free or broad-scale networks, being essentially exponential or single-scale networks [1]. Therefore, by simply changing the ER core size we are able to reproduce the main classes of complex networks [5], as shown in Fig. 3.

Figure 4 displays the degree distribution for $p=0.8$, showing that it markedly departs from the expected by power-law behavior. A gap in the range of k values appears and linearly increases with ER core size. These networks can therefore be divided into two subnetworks: (1) before the gap, a group of nodes that attached preferentially to nodes in the ER core, generating a power-law degree distribution, and (2) after the gap, a highly connected group of nodes, the ER core, in which the degree distribution is exponential.

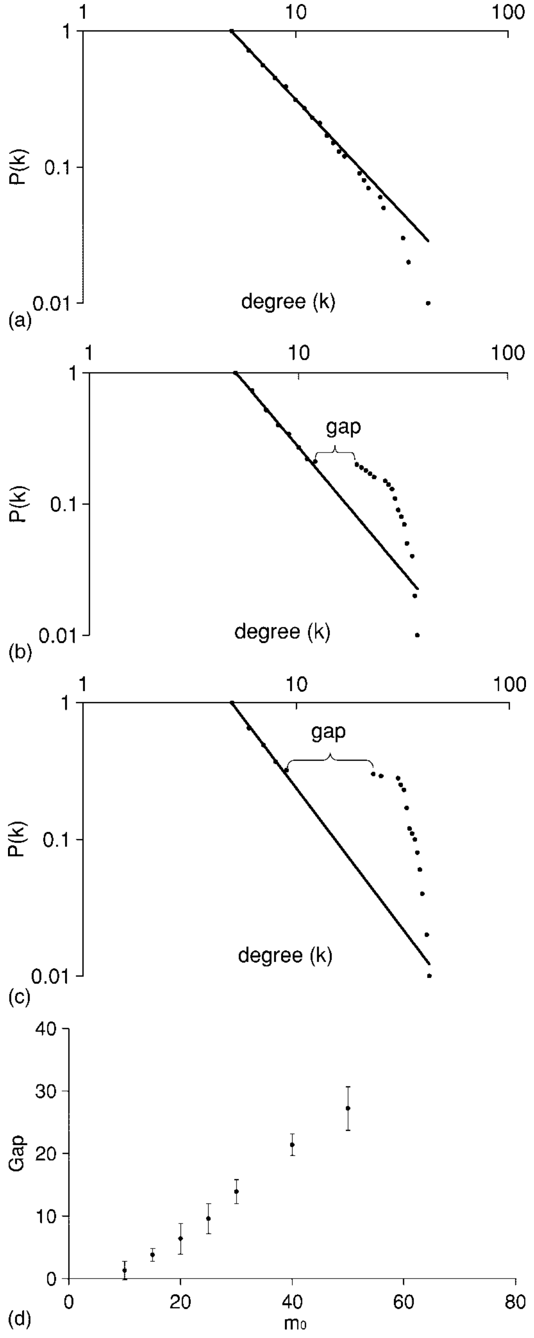

FIG. 4. Effects of the size of the ER initial core m_0 on the degree distribution for highly connected cores ($p=0.8$). The network size has been fixed to 100 nodes. (a) $m_0=10$, (b) $m_0=20$, and (c) $m_0=30$. Panel (d) shows that the gap indicated in parts (b) and (c) increases linearly with m_0 (see text for further details).

IV. SUMMARY AND DISCUSSION

Complex networks, both biotic and abiotic, often show exponential truncation in scale-invariant topology [1,5,7]. Previous works suggest that this truncation may be a result of constraints on addition of links. Some different classes of such constraints have been proposed, such as information filtering [5], aging, or connection costs [1]. In ecology, the truncation of power-law behavior was observed in food webs [19] and in coevolutionary bipartite networks of plant-animal interactions [7]. Jordano *et al.* [7] suggested that these truncations are generated by biological constraints that limit the possible links formed when species add up to the net, a phenomenon called forbidden interactions. Our results enlarge the catalog of mechanisms that could give rise to broad-scale networks, by adding the ER initial core as a new candidate. It is important to realize, however, that this new mechanism implies in a qualitatively new scenario. Assuming that there is a randomly connected initial core of nodes before preferential attachment starts to act in the network, there is no need to resort to additional constraints operating during network evolution; the truncation of power-law behavior is solely, or largely, a consequence of the system's initial condition. We expect that ER core hypothesis will be especially useful for systems in which it is possible to recognize the nodes that participated at the birth of the network from the nodes that appeared after a certain time period (e.g., species invading a food web or those occurring along a seasonal sequence).

The hypothesis of the ER initial core can be used to explain the buildup of all three main classes of networks [1]. As the size of the initial core is negatively related with the value of the cutoff in which the degree distribution departs from the predicted by the power-law behavior, it is possible to generate networks that are essentially scale free (small ER cores), broad-scale (intermediate ER cores) and essentially single-scale (large ER cores). The similarity of the pattern generated by two distinct, highly different mechanisms—namely, initial conditions and growth constraints—implies that alternative measures are necessary before arguing that constraints are limiting the network evolution in physical or biological systems best described as small networks. A simple way to distinguish between the two mechanisms is to measure the preferential attachment probability during network growth [18]. Mechanisms of constraints predict a reduction of preferential attachment during network growth while the ER core hypothesis predicts that, once preferential attachment starts, it is no longer affected by network growth. In several natural systems, however, the addition of new nodes (e.g., species in food webs) occurs over long time periods and it becomes impossible to measure the attachment probability. As a consequence, the development of new topological measures is central to allow an adequate distinction between the effects of constraints and those of the ER initial condition on real networks.

Finally we notice that the effects of the ER core on network topology will vary depending on how densely connected it is. While a less-connected ER core generates a size-dependent exponential truncation of the degree distribution, highly connected cores will affect differently the degree distribution: as the ER core size increases the network will be more clearly structured in two sets of nodes. In the first set of nodes, the ER core, the $\langle k \rangle$ is large and the degree distribution follows an exponential decay. In the second set, the nodes in which preferential attachment is operating, the degree distribution follows a power law. The distance in the degree between the two sets, measured by the gap in k values, increases linearly with ER core size. Recently, Melián and Bascompte [20] described food webs in which there is one or more cohesive, central subnets with the remaining nodes connected to them. The initial highly dense ER core is a possible mechanism to explain this pattern, by generating a central, densely connected core of nodes.

ACKNOWLEDGMENTS

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Capítulo 2

Build-up mechanisms determining the topology of mutualistic networks

Build-up mechanisms determining the topology of mutualistic networks

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Summary

The frequency distribution of interactions per species (i.e., degree distribution) within plant-animal mutualistic assemblages often decays as 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 similar 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 small 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 degree distributions of mutualistic networks.

*Key-word*s: complex networks, finite-size fluctuations, plant-animal networks, small networks, species richness

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 & Dunne 2006) and of other interespecific interactions (Guimarães et al. 2006; Jordano 1987; Memmott 1999; Vazquez et al. 2005). In network formalism, species are represented by nodes and interactions between species are described by links (Pimm 2002). The network approach is helping to describe consistent patterns at the community-level structure of interespecific interactions (Bascompte et al. 2003; Bascompte et al. 2006; Guimarães et al. 2006; Jordano et al. 2003; Lewinsohn et al. 2006; Montoya et al. 2006; Prado & 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. In this context, community-level patterns of specialization are likely to uncover the importance of different ecological factors and coevolutionary processes (Lewinsohn et al. 2006; Olesen & Jordano 2002; Thompson 2005; Thompson 2006).

Previous studies demonstrated that the degree distribution, that is, the frequency distribution of the number of interactions per species within a ecological community, decays as a power-law with an exponential truncation in the majority of plant-animal mutualisms (Jordano et al. 2003). Power-law distributions are expected by preferential attachment (Barabasi & Albert 1999) because recently arrived species are likely to interact with most generalist and usually more abundant 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 a 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 no interactions between species within the same set (Harary 1969; Jordano et al. 2003; Figure 1). 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 between animal and plant richness (high richness ratio, see Table 1). If high richness ratio is not generated by sampling bias, it is a result 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 through preferential attachment (Barabasi & Albert 1999). We use analytical predictions and numerical simulations to explore the relationship between exponential truncations and ecological processes that lead to a high richness ratio. Our aim is contribute to the study of community-level patterns of interactions in plant-animal mutualisms exploring the importance of simple build-up mechanisms to the observed network structure.

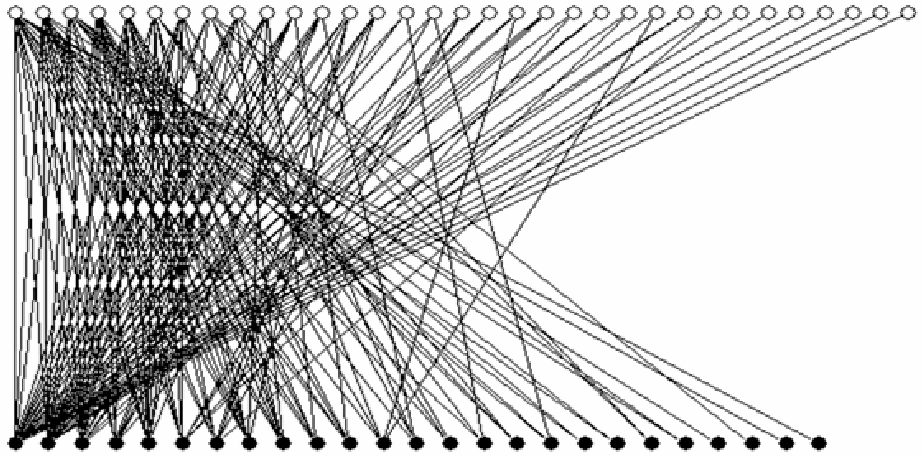

Figure 1. The network describing community-level patterns of interactions among frugivore birds (black nodes) and plants (white nodes) in Correhuelas, Spain (P. Jordano, unpublished data).

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

Mutualistic interactions	n	Median network size	Median S_A / S_B ratio	% 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

The model

In this paper, we incorporate bipartivity and mechanisms that lead to high richness ratios into one of simplest models generating power-law degree distributions, the Barabási-Albert (BA) model (Barabasi & 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 to the highly connected nodes in the network, which constitutes the so-called preferential attachment or 'the rich gets richer' phenomenon (Barabasi & Albert 1999). The BA model is defined by the following algorithm: (1) at time $t = 0$, one creates m_0 disconnected nodes (Albert & Barabasi 2000); (2) at each time step, a new node with $m \leq m_0$ edges is added to the network and connected to a node with probability Π; (3) the probability Π that a new node will be connected to node i depends on the degree k of that node, so that

$$\Pi(k_i) = (k_i + 1) / \sum_j (k_j + 1) \qquad (1)$$

Here we propose a model that incorporates the intrinsic bipartivity of plant-animal mutualisms into the BA model: (1) at time $t = 0$, one creates m_0 disconnected nodes; (2) 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}; (3) at each time step, a new node with *m* edges is added to the network; (4) the new node belongs to the first set, hereafter set *A*, with probability $(1-p)$, or to the second set (*B*) with probability p; (5) 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 (1.2) with the sum over *j* restricted to the set A.

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 $p = 1$ after S_A has been reached. Therefore, for simplifying proposes, we may assume that differential limiting size is an especial 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 the preferential attachment (hereafter PA). Thus, the proposed mechanisms *per se* 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 that constraint the PA process (Amaral et al. 2000; Jordano et al. 2003; Mossa et al. 2002).

Analytic predictions and numerical results

We explore the differences between analytic predictions considering large and small networks. A reasonable analytic prediction for the structure of large networks may be derived by generalizing previous studies with unipartite networks. Barabási and Albert (1999) applied continuum theory to obtain the analytical predictions for degree distribution in unipartite BA networks. The BA model predicts that, for large networks, the degree (k) of the node i varies with time following the dynamical equation:

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

The solution of the above equation is:

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

in which $\beta = 1/2$. The degree distribution could be interpreted as the probability of a node show k links and the prediction derived from (3) is

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

It is important to note that the above analytic predictions assume that the network is unipartite and, more importantly, that the number of elements of the network is virtually infinite. In contrast, plant-animal mutualisms often form small networks (< 10^3 species) (Bascompte et al. 2003). Therefore, the predictions derived from models that assume large network size may not be valid for small networks (Amaral et al. 2004; Guimarães et al. 2006). In fact, data from real networks often show exponential truncations (Jordano et al. 2003). Additionally, numerical simulations suggest that finite-size fluctuations may lead to truncations in small unipartite networks and animal aggregation models (Guimarães et al. 2005; Keitt & Stanley 1998). However, no previous study investigates if under finite-size fluctuations some build-up mechanisms will be more likely in generate truncated power-laws. We introduced an additional analytic approach to explore under what conditions finite-size effects lead to exponential truncation. The introduced approach demonstrates that truncated power-laws observed in plant-animal mutualisms are expected if high richness ratio is present due to some build-up mechanisms.

We recall that the degree of a node *i* may increase in time events where a node enters in the other set (set *B*). As a consequence, the time events in which a node enters in the set *B* can be described by a random variable, *T*, the number of time steps in which nodes enter in set *B*. Additionally, we define *Ti* as the time step in which node *i* appears in set A; *Ti* and *T* are random variables sampled from a binomial distribution with parameters *t* and *p*. Therefore, the degree of node *i* will increase following $k_i(t) = m(T/T_i)^{\beta}$, similarly to the analytic prediction for large networks (3), and the degree distribution can be described as $P(k_i(t) < k) = P(T_i > m^{1/\beta}T/k^{1/\beta})$. As *T* is a random variable sampled from a binomial distribution, the probability for a node *i* to have $k_i < k$ follows:

$$P(k_i(T) < k) = 1 - P(T \geq k) + \sum_{\tau=k} \frac{m^{1/\beta}\tau}{k^{1/\beta}(m_{0A} + \tau)} \binom{t}{\tau} p^{\tau}(1-p)^{t-\tau} \quad (5),$$

in which τ is an arbitrary *T*. If *t* is sufficiently large, the binomial in (5) can be approximated by a normal distribution:

$$P(k_i(T) < k) = 1 + \frac{m^{1/\beta}}{k^{1/\beta}}(1 - m_{0A})\left[1 - \Phi\left(\frac{k - tp}{\sqrt{tp(1-p)}}\right)\right] \quad (6),$$

where Φ is the cumulative normal distribution function. For small values of $\left|(k - tp)/\sqrt{tp(1-p)}\right|$ (6) can be approximated by (4), i.e., the degree distribution will have the same asymptotic behavior predicted for large networks. If, however, $\left|(k-tp)/\sqrt{tp(1-p)}\right|$ is large (large normal deviates), (6) can be approximated by

$$P(k_i(T)<k)\sim 1+\frac{m^{1/\beta}}{k^{1/\beta}}(1-m_{0A})\left[1-\left(\frac{k-tp}{\sqrt{tp(1-p)}}\right)^{-1}e^{-\frac{1}{2}\left(\frac{k-tp}{\sqrt{tp(1-p)}}\right)^{2}}\right] \quad (7).$$

Therefore, the degree distribution will have an exponential behavior.

We used numerical simulations to investigate if the analytic approach qualitatively reproduces the behavior of degree distributions. Except when explicitly stated the simulations were performed using $m_{0A}=m_{0B}=10$, $p=0.5$, and $m=3$. The simulations ended when one of the set sizes reached $S_i=5.0\times 10^2$. We plot the $P(k)$ 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 varied the initial core of set *A*, m_{0A}, keeping the initial core of set *B* as $m_{0B}=10$. In figure 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 the functional form of $P(k)$ predicted by BA model even in small networks.

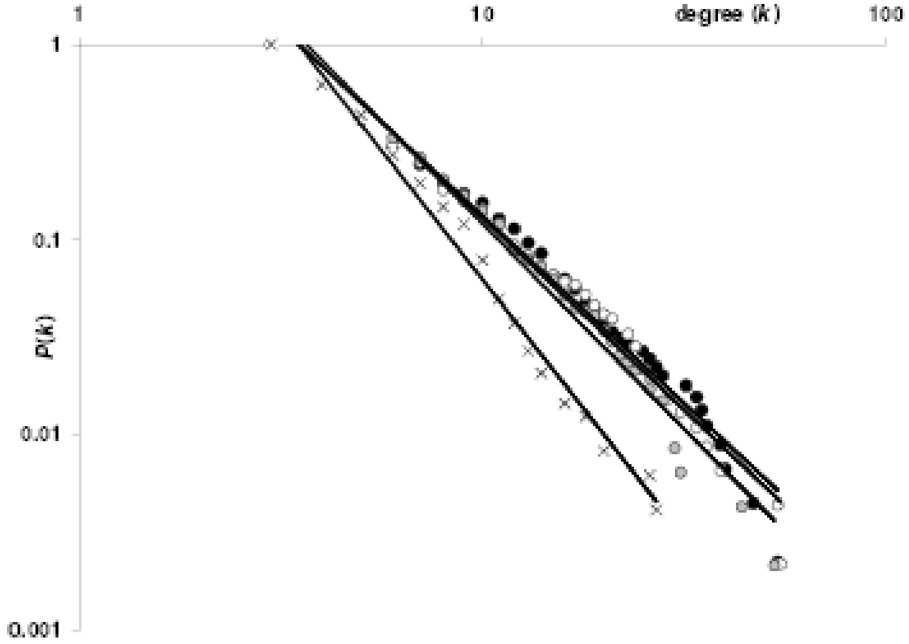

Fig. 2. Effects of differential starting size $(m_{0A} > m_{0B})$ on degree distribution. Log-log plot of the cumulative $P(k_A)$ for distinct differential starting sizes (in all cases, $m_{0B} = 10$): $m_{0A} = 10$ (closed circles), $m_{0A} = 15$ (open circles), $m_{0A} = 30$ (grey circles), and $m_{0A}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

To test the effect of "differential growth rate" on $P(k)$ we varied p , the probability of a new node being assigned to set *B*, maintaining the initial size of the sets equal. We used $m_{0A} = m_{0B} = 50$ 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 affects markedly the functional form of $P(k_A)$. The power-law behavior of $P(k_A)$ is preserved for $p \leq 0.5$, that is, when the size of set *A* increases faster or at the same rate than set *B* (Figure 3a). However, if $p > 0.5$, 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 (Figure 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 $P(k) \sim e^{-k\gamma}$ (Figure 3a). Therefore, in small bipartite networks in which $p \approx 1$, preferential attachment generates slow-decaying exponential curves and not power-law degree distribution, as usually expected (Barabasi & 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 & Barabasi 2002). However, it is noteworthy that the exponential distribution generated by p =1 decays slower than the distribution predicted by random attachment (Figure 3b).

In the last simulation, aimed to test the effect of "differential limiting size" on $P(k)$, we varied the final size of set A, S_A, and kept the final size of set B, S_B, constant ($S_B = 1.0 \times 10^3$). If we let the simulation stop when one of the sets reached the previously established limiting size, we find that the scale-free behavior is preserved for both $P(k_A)$ and $P(k_B)$ (Figure 4). However, if $S_A << S_B$ and the simulation stops solely when both sets reach the previously established limiting size we find that $P(k_A)$ behaves as a slow-decaying exponential function (Figure 4).

The results of numerical simulations are in agreement with the analytic prediction assuming small network size. The absence of effects of "differential start size" on $P(k)$ is not surprising, since $P(k)$ is independent of the ratio m_{0A}/m_{0B} even in the finite-size situation. The exponential tails observed under some conditions of "differential growth rate" and "differential limiting size" is also explained by the fact that values of p close to 1 – the set did not grow or grew slowly compared to the other set – imply in large values of $\left|(k - tp)/\sqrt{tp(1-p)}\right|$ and, consequently, leading to degree distributions with a markedly exponential tail.

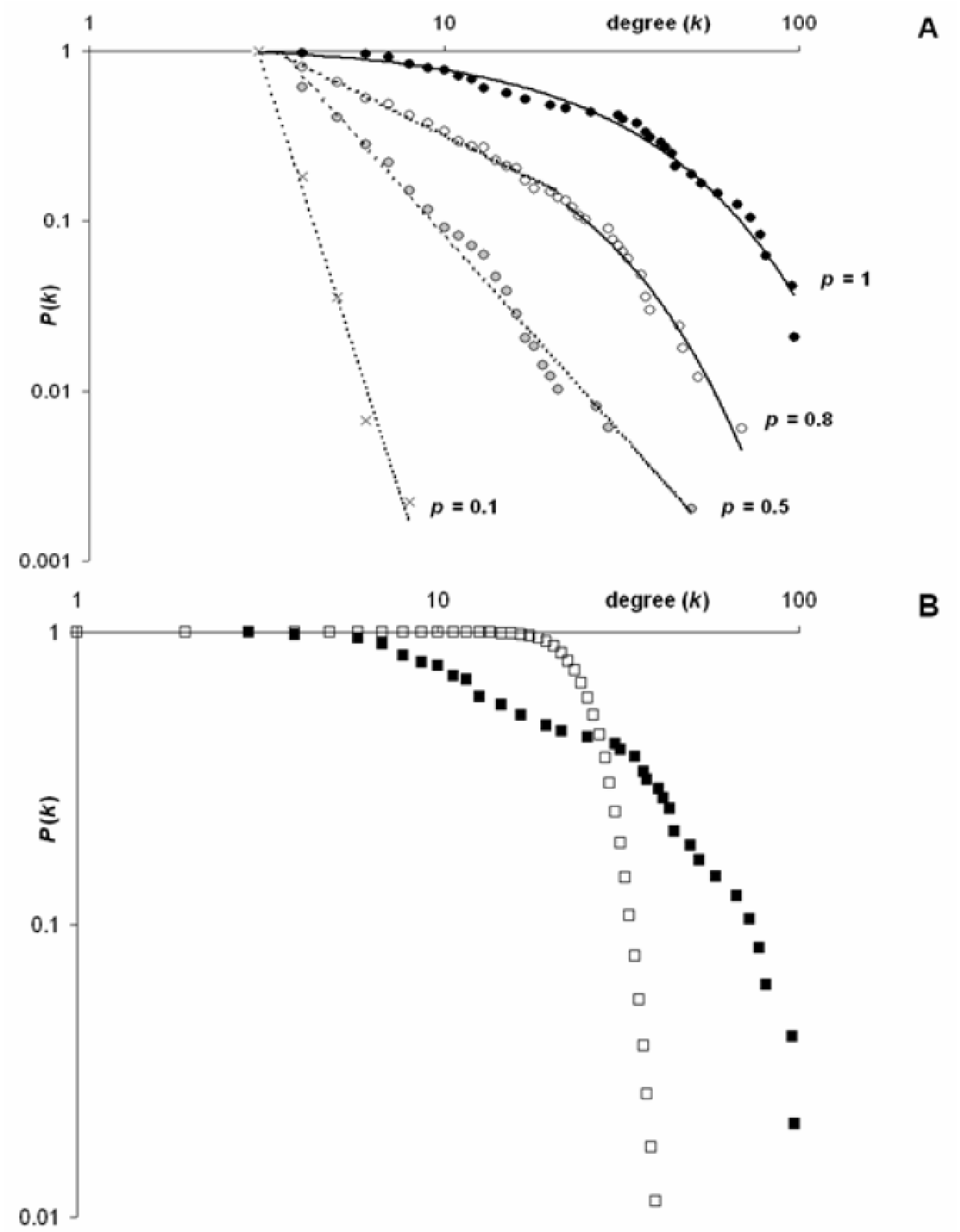

Figure 3. Effects of the rate of increase of a set size (number of nodes), p , on its $P(k)$. (a) Log-log plot of the cumulative $P(k)$ for different values of p . Dashed lines indicate the fit to a power-law distribution whereas continuous lines indicate exponential deviations. Note that for $p=1$, $P(k)$ is described solely by the exponential function. (b) The slow-decaying, exponential $P(k)$ for $p=1$ (black squares) and the Binomial $P(k)$ predicted by a random network (empty squares).

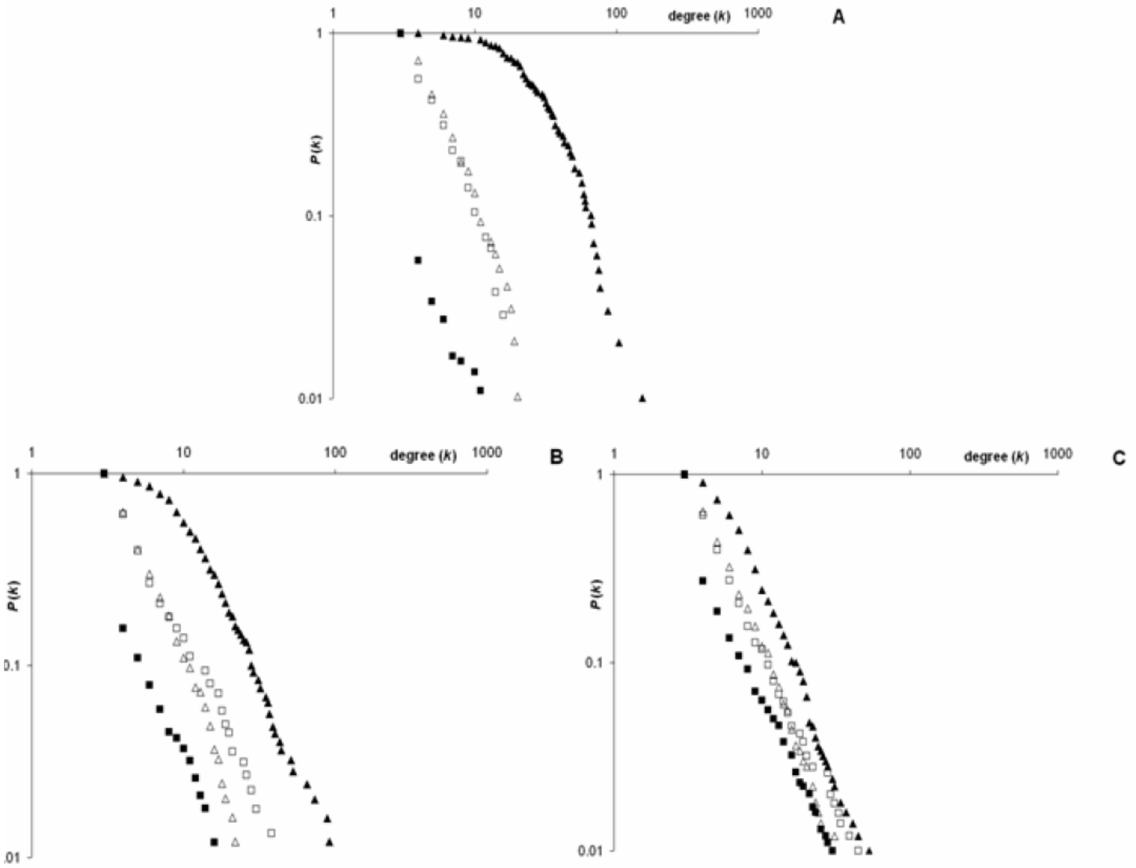

Figure 4. Effects of differences of set size limits, S_A and S_B on $P(k_A)$ and $P(k_B)$. Each figure has four degree distributions: $P(k_A)$ and $P(k_B)$ for a simulation in which network growth stops when the smaller size limit was reached (empty symbols) and $P(k_A)$ and $P(k_B)$ for a simulation 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) $S_A = 5.0 \times 10^2$.

Implications for plant-animal networks

Complex networks in both ecological and non-ecological systems usually show deviations from a power law degree distribution such as exponential truncations. This exponential truncation is often 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 the majority of bipartite networks of plant-animal interactions. 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. Forbidden links do occur and limit the number of interactions in biological systems (Bascompte & Jordano 2006) as, for example, when a given bird species is unable to interact to a fraction of plant species simply because biological constraints prevent the interaction from occurring. However, we clearly demonstrate here that exponential truncations can also emerge from processes associated to differences in species richness among plants and animals.

As stated before, it is a general feature of mutualistic networks to have high richness ratio (see Table 1) and we show that “differential growth rate” and “differential limiting size” do promote deviations of the power-law distribution predicted by a minimal model that generate power-laws through preferential attachment. In fact, the association between preferential attachment and power-law distributions, widely reported for unipartite networks (Albert & Barabasi 2002), is expected for finite bipartite networks only when two conditions are satisfied: the set of interest growths at the same rate or faster than the other set $\left(p \leq 0.5\right)$and has a similar or higher limiting size $\left(S_A \geq S_B\right)$.

Our results indicate the importance of exploring the finite-size fluctuations to the characterization of predictions of network models (Amaral et al. 2004; Guimarães et al. 2005, 2006). Additionally, our results suggest that processes determining the differences of species richness among plants and animals may affect the organization of ecological bipartite networks. Examples of differential growth rate and differential limiting sizes are widespread in nature. In evolutionary time, for instance, the diversity of insect herbivores and host plants seldom increase at similar rates (Thompson 1994). In ecological time, the dispersal rates of plants and animals (e.g., pollinators or seed dispersers) to recently created habitats, may differ (e.g., Shanahan et al. 2001) – both examples of “differential growth rate”. 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 abovementioned plant-animal networks even if preferential attachment is occurring without forbidden links.

In conclusion, together with random initial conditions (Guimarães et al. 2005) and constraints to preferential attachment (Jordano et al. 2003), processes affecting species richness are an alternative explanation to the existence of broad-scale ecological bipartite networks. Future work should investigate how to differentiate between these alternative processes.

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Capítulo 3

Investigating the importance of abundance for nestedness in a plant-frugivore network

Investigating the importance of abundance for nestedness in a plant-frugivore network

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Summary

At the community level, mutualistic interactions form webs of interacting species that can be described as networks, in which species are nodes and links are interespecific interactions. Mutualistic networks often exhibit a particular type of asymmetrical specialization called nestedness and different evolutionary and ecological factors were hypothesized to explain this community-level pattern. However, computational limitations prevent direct tests of the importance of ecological factors to nestedness. Here, we introduce a new approach that allows exploring the relation between ecological factors and nestedness. We illustrated the introduced approach testing the hypothesis that variation in abundance among species explains the nested structure of one of the best studied plant-animal networks. We show that abundance patterns explain about 60% of the observed nested structure. Our study shows that abundance is an essential but not exclusive ecological factor underlying nestedness. The introduced approach will be useful to study the ecological basis of nestedness in plant-animal networks and in other ecological systems, such as biogeographic patterns in species distributions.

*Key-word*s: asymmetrical specialization, bi-clustering algorithms, community structure, ecological networks

Introduction

In a given ecological community, each species interacts with a few to dozens of mutualistic partners (Jordano 1987). Therefore, at the community level, mutualistic interactions often emerge as networks of highly diversified, and low-specificity relations among free-living species (Guimarães et al. 2006; Jordano et al. 2003; Memmott 1999). Analyses of network structure are helping to detect and explain patterns of specialization (i.e. number of interaction per species) across communities and among different types of interactions (Bascompte & Jordano 2006; Memmott 1999; Olesen & Jordano 2002; Ollerton & Cranmer 2002; Vazquez & Aizen 2004; Vazquez et al. 2005). In this context, one of the central problems to solve is: what is the ecological and evolutionary basis of the observed community-level structure (Thompson 2005; 2006)?

Recent studies suggested that networks describing species-rich, mutualistic interactions between animals and plants show a specific type of asymmetrical interaction called nestedness (Bascompte et al. 2003). Nested networks are characterized by (1) species with many interactions ("generalists") that interact with each other, forming a core of interacting species; (2) species with few interactions ("specialists") that commonly interact only with generalists; (3) and by the near complete absence of specialist-specialist interactions (Figure 1a). Several authors have suggested that nestedness is a consequence of simple ecological and evolutionary processes that affect the interactions among species, including variation in abundance of species (Bascompte et al. 2003; Jordano 1987; Lewinsohn et al. 2006) and convergence of traits among interacting species (Guimarães et al. 2006; Thompson 2005; 2006). Understanding nestedness therefore entails quantifying the contribution of ecological and evolutionary factors to the observed pattern.

Although different metrics have been proposed to quantify nestedness (Brualdi & Sanderson 1999; Cutler 1994; 1998; Wright et al. 1998), the matrix's temperature, *T*, which allows comparisons of nestedness among different networks (Atmar & Patterson 1993), has become established as the standard measurement of the degree of nestedness in ecological interaction networks (Bascompte et al. 2003). The matrix's temperature has advantages in relation to alternative nestedness metrics, in that it is less sensitive to effects of species richness, richness ratio among plants and animals, and number of interactions (see Wright et al. 1998 in the context of patterns of species distribution). However, computational limitations prevent the direct test of the importance of a given ecological factor to the observed values of *T*. Although usual statistical methods such as correlations that indirectly relate nestedness to ecological factors might circumvent this problem (e.g., McAbendroth et al. 2005), they do not allow estimates, in terms of *T*, of how much of the nested pattern is related to a given ecological factor. Moreover, these methods assume that the nestedness varies monotonically with the ecological factor.

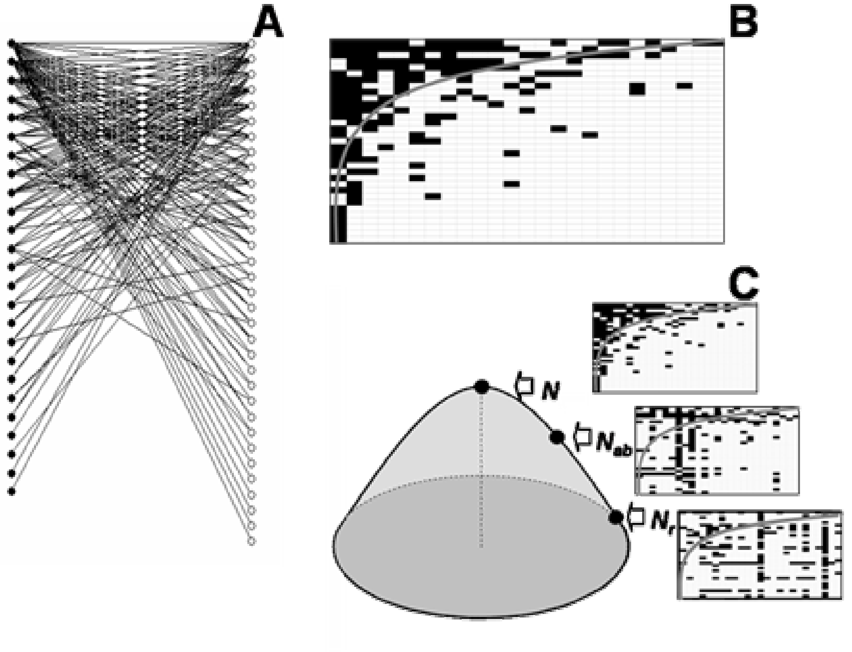

Figure 1. (a) The network describing community-level patterns of interactions among frugivore birds (black nodes) and plants (white nodes) in Correhuelas, Spain. Both birds and plants are organized in decreasing number of interactions to evidence nested structure (see text for further details). (b) Matrix descrybing Correhuelas network. Again, both birds (rows) and plants (columns) are organized in decreasing number of interactions (filled elements) to evidence nested structure. The degree of nestedness (*N*) would be maximum (*N* = 1) if all interactions were located on the left side of the isocline of perfect nestedness (in grey). (c) We can compute N_i for any arrange of rows and columns, generating a distribution of N_i values (the bell-shaped figure). In this context, the *N* often reported in nested studies is the N_i recorded in the arrangement that maximizes nestedness. The hypothesis that abundance (or other ecological factor) at least partially explains nestedness is supported if the degree of nestedness for the matrix in which species were arranged following their abundances (N_{ab}) is higher than expected by the random arrangement of rows and columns (N_r). Additionally, the ratio N_{ab}/N is a measure of how much abundance explains of the total nested pattern.

Here, we explore a possible solution for the study of the relation between nestedness and ecological factors, using as a reference system one of best documented plant-animal networks, that depicting the interactions between frugivores and plants in a SE Spanish locality. We propose an approach that allows a direct test of putative effects of ecological factors to nested structure and also provides an estimation of the extent of the nested pattern that is explained by the analyzed ecological factor. We illustrated our approach by testing the hypothesis that nested structure is at least partly explained by differences in abundance among interacting species (Lewinsohn et al. 2006).

Methods

(a) Dataset

The studied mutualistic community corresponds to the plant–frugivore network of a high elevation Mediterranean forest (Nava de las Correhuelas, Sierra de Cazorla, southeastern Spain). The Correhuelas network is composed of 33 frugivorous bird species and 25 fruiting plant species. This network was specially suitable to illustrate the introduced approach for three reasons: (1) the described network resulted from long-term fieldwork by one of us (P. Jordano, unpublished data) is one of most nested networks described so far (Bascompte et al. 2003) and (2) the annual density data of both frugivorous birds (individual birds/area) and fruiting trees (fruits/area) were estimated independently of the census of actual plant-frugivore interactions, as reported in previous studies (Jordano 1988; 1994; 1995). The dataset contains records from >200 km line transect census of frugivore abundance and >4000 feeding records of frugivores visiting fruiting plants. A feeding record entails the observation of a frugivore handling and, eventually, ingesting a fruit (see Snow & Snow 1988).

(b) Network description and nestedness analyses

A bipartite network was described by an incidence matrix **R**, in which rows were bird species, columns were plant species and the element r_{ij} was equal to one if the bird species i was observed eating the fruits of the plant species j and zero otherwise (Jordano et al. 2003). The matrix **R** is perfectly nested if it shows a progression of inclusive subsets after ordering rows and columns in decreasing totals (Lewinsohn et al. 2006, Figure 1b). The degree of nestedness (N) can be quantified as $N = (100 - T)/100$ (Bascompte et al. 2003), in which T is a measure of how much the interaction patterns described by **R** departs from perfect nestedness, values ranging from zero (perfectly nestedness) to 100 (perfectly non-nestedness) (Atmar & Patterson 1993). In figure 1, we illustrate nestedness using the highly nested Correhuelas network (N = 0.94, Bascompte et al. 2003). Although the available computer programs calculate T rather than N (e.g., Atmar & Patterson 1993; Guimarães & Guimarães 2006; Rodríguez-Gironés & Santamaría 2006), we will refer to N to emphasize our focus on the degree of nestedness.

The calculation of N involves three steps: (1) an isocline of perfect nestedness is calculated based on the number of plant and animal species and the number of interactions (Figure 1b); (2) for a particular arrangement of matrices, the deviations from this isocline (i.e. unexpected interactions and absences of interactions) are standardized and recorded, computing N_i, (3) a bi-clustering algorithm (usually called "packing" in nestedness analysis (Atmar & Patterson 1993; Guimarães & Guimarães 2006; Rodríguez-Gironés & Santamaría 2006) is used to change the indexes of rows and columns, maximizing N_i. It is assumed that after the packing process, N value is the highest possible. Indeed, the N values often reported in nestedness studies is the N_i recorded in the arrangement that maximizes nestedness (Figure 1c).

2.2. Relating abundance with nestedness

Traditionally, the approach used to investigate how ecological variables are related with N is the use of correlations between a given ecological variable and the index (or order) of each species in the packed matrix (e.g., McAbendroth et al. 2005). This approach has two drawbacks: (1) it does not provide an estimate of the fraction of total nestedness that is explained by the ecological variable, and (2) it assumes that nestedness varies monotonically with ecological factor, and will not necessarily detect some possible effects of an ecological factor on nestedness. For example, if all generalist species are among the most abundant species, but specialist species are not necessarily rare. To circumvent these drawbacks, we propose the following approach (Figure 1c): first, we note that if a given ecological factor, such as abundance, totally explains nestedness, we should expect that if we organize both animal and plant species from most to least abundant the recorded value for N_i (hereafter N_{ab}) would equal the value resulting after the packing procedure (N). Therefore, the ratio N_{ab}/N would vary from zero (abundance did not explain any aspect of the nestedness structure) to one (abundance totally explains nestedness). Thus, N_{ab}/N can be used as an estimate of the degree to which observed nestedness is explained by the analyzed ecological factor.

If the contribution of abundance to the degree of nestedness is statistically significant, N_{ab} is expected to be higher than a given N_r resulting from random organization of the matrix. Therefore, we tested N_{ab} by comparing it with an empirical null distribution of N_i obtained from an ensemble of matrices in which the organization of rows and columns was randomly determined.

We investigated the effect of the factor 'abundance' on the nested structure of the Correhuelas network using the introduced approach. Some plant species have equal abundance estimates, so we calculated the average N_{ab} for all matrices in which species with the same abundance are randomly organized (n = 24 matrices). All nestedness analyses were performed using ANINHADO (Guimarães & Guimarães 2006), a C-language software based on the original code of the widely used Nestedness Temperature Calculator (Atmar & Patterson 1993). ANINHADO allows the calculation of the matrices without using the packing algorithm, allowing the calculation of N_i for any given organization of the matrix. The program is available for download at www.guimaraes.bio.br.

Results

The 24 abundance-arranged matrices showed very similar degrees of nestedness ($N_{ab} = 0.56 \pm 0.01$, minimum = 0.55 and maximum = 0.57). These values for N_{ab} are almost two fold higher than expected by randomly arranged matrices

($N_r = 0.24 \pm 0.13; P = 0.003; n = 1000$ replicates), suggesting that patterns of variation in abundance of birds and plants explain a substantial fraction of the degree of nestedness observed in the Correhuelas network.

The abundance patterns observed in bird and plant species explain more than half of the observed degree of nestedness ($N_{ab}/N = 0.60$). That is, the core of generalist species observed in plant-animal mutualistic networks is usually formed by both abundant frugivorous birds (e.g., *Phoenicurus ochruros*, *Turdus merula, T. viscivorus*) and plants (e.g., *Prunus mahaleb*, *Crataegus monogyna*, *Berberis vulgaris*), but there are some generalists that are not among the most abundant species (e.g., the bird *Turdus iliacus* and the plant *Rubus ulmifolius*). Accordingly, several birds (e.g., *Corvus corax* and *Pica pica*) and plants (e.g., *Paeonia officinalis* and *Polygonatum odoratum*) with few interactions are among the less abundant species in the community, but there are a few ecological specialists that are not rare (e.g., the bird *Sylvia communis* and the plant *Rhamnus saxatilis*).

Discussion

The approach used here allows the estimation of the extent to which the nested structure of a given plant-animal mutualistic network is explained by a particular ecological or evolutionary factor. Therefore, it can be a useful approach to test hypotheses on the relative importance of distinct ecological and evolutionary factors to the organization of mutualistic interactions. In the context of the interactions of frugivores and fruiting plants studied here, the introduced approach provided support to the notion that nestedness is at least partially determined by variations in the abundance of interacting species (Bascompte et al. 2003; Jordano 1987; Lewinsohn et al. 2006). In our study we use truly independent data for the abundance estimates and the actual records of interactions. The abundance estimates from frugivores were derived from line transect counts involving monitoring of all the avifauna. The plant abundance data were obtained from transect counts of fruit production that actually indicate the availability of fruits of different species to the frugivore consumers. The interaction data were obtained along independent feeding records by direct watch of the fruiting plants. These types of independent estimates of the ecological variable being tested and the interaction matrix aimed to explain are difficult to obtain, but are needed for a robust test that attempts to avoid circularity arising from abundance estimates derived directly from interaction frequency (Vazquez & Aizen 2004). Such type of information might be more difficult to obtain for interaction matrices involving invertebrate consumers (e.g., pollination and herbivory networks, or host-parasitoid networks) for which a direct estimation of abundance might be difficult. In a more general context, our study corroborates the idea that many patterns observed in ecological networks are the result of differences in abundance among interacting species (Bascompte et al. 2003; Jordano 1987; Lewinsohn et al. 2006; Vazquez & Aizen 2004), but also emphasizes that other ecological factors influence the structure of these complex networks.

Although abundance patterns explains a large part of the nestedness structure, it is important to emphasize that a not negligible amount of the nested structure (up to 40%) is not explained by this ecological factor. Some very abundant species show few interactions while some rare species are part of the core of generalist species. Different ecological and evolutionary processes may explain the observed pattern. One possible explanation for these patterns include variation in the importance of fruits on the diet of a given species, i.e., abundant but not highly frugivorous species might establish few interactions while rare but highly frugivorous species may consume several plant species. Alternatively, morphological and phenological constraints may limit the possible interactions of abundant species (“forbidden links” sensu Jordano et al. 2003; also see Stang et al. 2006). Examples of constraints include fruit size and short fruiting seasons for plants and gap width and migratory behavior for birds. Additionally, coevolutionary processes that led to life strategies in which species interact with one or many generalist species may contribute to nestedness (Thompson 2005), without be necessarily related with abundance patterns. Future studies should focus on testing these and additional ecological and evolutionary factors that may explain nestedness. By now, our study demonstrates the importance of abundance to nested structure and provides a direct approach to quantify the importance of specific factors on nestedness, based on a rigorous computational formalism and the requirement of independent data for ecological variables and for the observed interaction matrix.

We emphasize that the usefulness of the approach described here is not restricted to test differences in abundances among interacting species. Rather, the introduced approach can be applied to investigate any ecological, evolutionary or behavioral factor that may explain nestedness in plant-mutualistic networks. Additionally, nestedness is not an exclusive property of mutualistic networks, but is also observed in the distribution of parasite species among individual hosts (Rohde et al. 1998) and in the biogeographic patterns of species distributions (Atmar & Patterson 1993; McAbendroth et al. 2005). Therefore, the introduced approach may be useful in the characterization of the biological basis of nestedness in different ecological systems.

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Capítulo 4

Structural differences in ecological networks: a matter of lumping?

Structural differences among ecological networks: a matter of lumping

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Summary

Recent studies suggest that food webs and plant-animal mutualistic networks differ in at least two aspects of their structure. First, the degree distribution (i.e., the probability of finding a species with a given number of interactions) decays exponentially for food webs and as truncated power-laws for mutualistic networks. Second, mutualistic networks often show a specific pattern of asymmetrical specialization called nestedness, whereas food webs are often non-nested. Here we investigated if lumping of species, a methodological procedure frequently used in food webs studies but rarely employed in mutualistic networks, can explain the observed differences in network topology. We simulate lumping of species in two well-studied ecological networks (a food web and a plant-animal interaction network) and in theoretical networks. Our simulations show that species lumping in networks in which the degree distribution decays as truncated power-laws often leads to exponential distributions, suggesting that bias introduced by lumping of species explain differences in the heterogeneity of interactions between both types of ecological networks. In contrast, lumping of species did not reduce nestedness, suggesting that structural differences are a result of different ecological and evolutionary processes operating in both types of ecological networks.

Key-words: complex networks, degree distribution, food webs, lumping, nestedness, plant-animal mutualistic networks

Introduction

Complex networks describe a large number of social, physical and biological systems (Albert & Barabasi 2002; Amaral & Ottino 2004) and its use to describe ecological systems, such as food webs (consumer-resource networks) and plant-animal mutualistic networks, has increased markedly in the last years (Pascual & Dunne 2006). These studies have revealed two main topological differences between the structure of food webs and that of plant-animal mutualistic networks in terms of two metrics: the distribution of the number of interactions (k) per species, the so-called degree distribution (Jordano et al. 2003), and the presence of nestedness, a specific pattern of asymmetrical specialization in which the more specialist species interact only with subsets of those species interacting with the more generalists and specialist-specialist interactions are almost absent (Bascompte et al. 2003; Guimarães et al. 2006; Vazquez & Aizen 2004).

The degree distribution varies widely among food webs, but in the majority of food webs examined so far the degree distributions decay exponentially (Dunne et al. 2002, Figure 1), indicating that there is few variation in the level of specialization among the interacting species. In contrast, the bulk of mutualistic networks are broad-scale, in which the degree distribution mainly follows a truncated power-law (Figure 1), characterized by a number of species with few interactions and by a low but significant probability of finding species with many interactions (“supergeneralists”) (Jordano et al. 2003). Regarding to nested patterns, food webs are usually not significantly nested, whereas plant animal mutualistic networks are in general highly nested (Bascompte et al. 2003; Guimarães et al. 2006, Figure 1).

Structural differences between these two types of networks may be an indicative of different ecological and evolutionary processes acting on different types of interespecific interactions (Lewinsohn et al. 2006; Proulx et al. 2005; Thompson 2005; 2006). However, before assuming that the structural differences in food webs and mutualistic networks are the result of different ecological and evolutionary processes, we must rule out the possibility that the observed differences are a consequence of the poor taxonomic resolution in food webs, a sampling issue that has been addressed by many authors for other metrics (e.g., Sugihara et al. 1997).

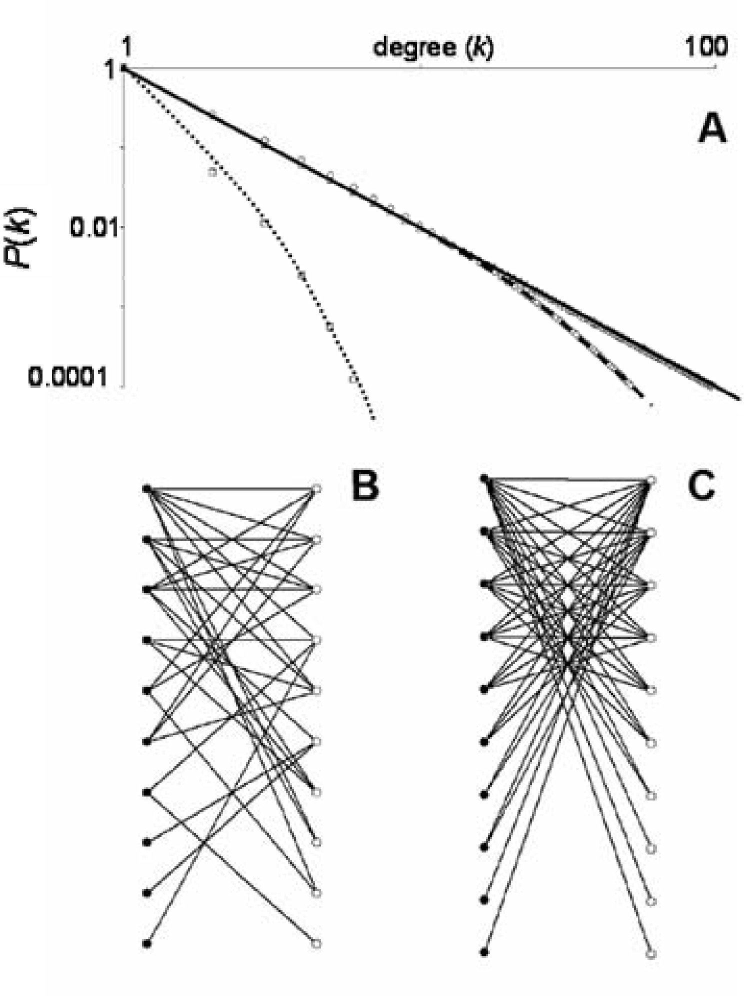

Figure 1. Structural patterns in ecological networks: (a) differences in degree distribution (see text for further details): scale-free networks, in which degree distribution decays as a power-law (solid line), broad-scale networks, in which degree distribution decays as a power-law with an exponential truncation for a large value of *k* (dashed curve), and single-scale networks, characterized by a degree distribution that decays exponentially (dotted line), (b-c) differences in nestedness (see text for further details): (b) non-nested networks and (c) significantly nested networks. Both examples are hypothetical networks draw using the software Pajek (Batagelj & Mrvar 1998). Empty nodes represent plants, solid nodes represent animals.

Food webs analyzed in the literature tend to show a poorer taxonomic resolution than mutualistic networks (Olesen & Jordano 2002), because species are sometimes difficult to segregate taxonomically and are lumped into more inclusive categories (e.g. genera, families or even orders). There are also cases in which species are assumed to be trophically identical, i.e., they share the same set of predators and prey, and are also lumped into what has been termed trophic species (e.g., carnivorous lizards). In contrast, in plant-animal mutualistic networks nodes are often resolved to the species level (see dataset of Bascompte et al. 2003; Jordano et al. 2003).

Species lumping may not be a problem or may be even desirable for studies focusing community fragility or stability (Fonseca & Ganade 2001). However, if one is interested in patterns of specialization within communities (Olesen & Jordano 2002), species lumping may introduce serious bias. For example, if in a given community most of species interacts with few species (Thompson 1994; 2005) but there is a few species with many interactions (Jordano et al. 2003), we should expect that lumping will usually aggregate species with few interactions and increase the number of moderately-connected "species". Therefore, species lumping will lead to fast-decaying degree distributions, which more closely resemble exponential functions. In contrast, nestedness is characterized by generalist-generalist and generalist-specialist interactions and the almost complete absence of specialist-specialist interactions (Guimarães et al. 2006) and would only be decreased by the addition of specialist-specialist interactions. As species lumping does not create new interactions, we should expect that nestedness is not affected by species lumping.

Here, we test the above predictions about the effects of species lumping on the degree distribution and nestedness of ecological networks. We believe that our results may shed light on the important question of whether the reported structural differences between food webs and mutualistic networks are really a reflection of different ecological and evolutionary factors or are indeed the result of methodological issues. We report quantitative analysis of the effects of different procedures of species lumping on two well-solved ecological networks (a food web and a plant-frugivore network) and as well as on theoretical networks.

Methods

(a) Studied networks

Two types of networks are used to describe ecological systems. Food webs are usually represented as unipartite networks, in which the network size, S , is not divided into subsets. In contrast, plant-animal mutualistic interactions are usually represented as bipartite networks, in which the original set S can be divided into two subsets, S_A and S_B , and there are no edges connecting nodes in the same set (Harary 1969). It is important to notice that, while the degree distribution can be used to characterize both unipartite and bipartite networks (Jordano et al. 2003), nestedness analysis is restricted to bipartite networks. Thus, for nestedness analysis of food webs, bipartite networks must be extracted from the original unipartite network, such as interactions between producers and herbivores (see Bascompte et al. 2003). To test whether species lumping is the sole responsible to the observed differences between food webs and mutualistic networks, we used two different approaches.

First, we analyzed two real ecological networks: the predator-prey interactions among fish species in the Caribbean Food Web (S = 209 species, Bascompte et al. 2005), and the Correhuelas Plant-Frugivore Network (S = 58 species, P. Jordano, unpublished data). These are among the largest and best resolved ecological networks compiled so far. To perform nestedness analysis in the Caribbean food web, we extracted a bipartite network (including 98.5% species of the fishes in the original network) in which one set was composed of fish species that are prey but did not prey upon any fish species and the other was composed by fish predators of the first set. Second, we investigated the effects of lumping of nodes in theoretical networks to assess if the conclusions obtained with real networks can be generalized for a broad class of networks.

(b) Lumping of species

We simulated two different processes of lumping of species: taxonomic and trophic lumping. In the taxonomic lumping, all species with the same genera or family were lumped together and represented as a single node with all edges of the lumped species. In the trophic lumping, two species were selected based on their topological similarity and interchanged by a new “species”. The algorithm for trophic lumping was:

1. The first species was randomly selected.
2. We calculated the similarities between the first, randomly-selected species selected and all the remaining species using Jaccard’s index (J)

$$J = \frac{a}{k_i + k_j - a} \qquad (1),$$

in which a is the number of partners that both species interact with, k_i is the degree of the first species, and k_j is the degree of the second species.

3. A second species was selected with probability proportional to his *J*.
4. The two selected species were lumped and represented as single node with the same edges of both selected species.
5. This steps (1-4) was repeated until achieving the desired number of nodes, S'.

Both processes of lumping were performed in the two real networks. Trophic lumping, with arbitrary final sizes for lumped networks, was also performed in theoretical networks.

(c) Degree distribution

The degree distribution, $P(k)$, is often used to classify a network as one of the following three different classes: (1) scale-free network, in which the probability of finding a node with $k > \langle k \rangle$, $\langle k \rangle$ being the average degree, decays as a power-law, $P(k) \sim k^{-\gamma}$; (2) broad-scale network, in which the probability of finding a node with $k > \langle k \rangle$ decays as a truncated power-law, $P(k) \sim k^{-\gamma} e^{-k/k_x}$; k_x is a cut-off value and the degree distribution decays as an exponential for $k > \langle k \rangle$; (3) single-scale network, in which the probability of finding a node with $k > \langle k \rangle$ decays as an exponential, $P(k) \sim e^{-k\gamma}$.We used the cut-off value, k_x, to track changes in the degree distribution due to the species lumping (Figure 2a). Preliminary simulations demonstrated that the average degree, $\langle k \rangle$, increased with lumping of species (results not shown). As k_x is a function of $\langle k \rangle$, we used a standardized

k_x, $k_x/\langle k\rangle$ to investigate if there is an increase in exponentially with lumping of species. The cut-off value, k_x, was estimated using an adapted version of a recently described approach to characterize the $P(k)$ of small networks (Guimarães et al. 2005).

We calculated the cumulative $P(k)$ (i.e, the probability of interacting with k or more species) to reduce fluctuations in the $P(k)$ related to small network size (Strogatz 2001). The five lower recorded values of k for which $k > \langle k\rangle$ were used to compute the predicted distribution of $P(k)$, $P(k)_{PRED}$, assuming that $P(k)$ decays as a power-law. The use of the five lower values prevents the effects of eventual exponential decays on power-law fit. We defined k_x as the largest value of k for which $P(k)_{OBS} \geq P(k)_{PRED}$, in which $P(k)_{OBS}$ is the observed $P(k)$. If $k_x/\langle k\rangle$ is small, $P(k)$ is essentially exponential and if $k_x/\langle k\rangle$ is large, $P(k)$ is essentially a power-law, creating a gradient from single-scale to broad-scale and to scale-free networks. In the theoretical simulations, we used a very popular and minimal theoretical model, the BA model proposed by Barabási and Albert (1999), to create theoretical networks. The BA model simulates two general processes that act in real networks: (i) network grows in time by adding new elements, and (ii) new nodes tend to interact preferentially with the highly connected elements in the systems, which constitutes the so-called preferential attachment (Barabasi & Albert 1999). The BA model was defined by the following network growth rules:

1. at time $t = 0$, one creates m_0 connected nodes (e.g., Melian & Bascompte 2002),
2. at each time step, a new node with $m \leq m_0$ links is added to the network and connected to a node with probability Π;
3. the probability Π that a new node will be connected to node i depends on the degree k of that node, so that $\Pi(k_i) = k_i / \sum_j k_j$,

For a sufficiently large network $(S \to \infty)$ generated by a BA model (hereafter BA network), $P(k)$ follows the power-law $P(k) \sim k^{-\gamma}$. Truncated power-laws emerge in BA model networks under certain specific circumstances (Amaral et al. 2000; Guimarães et al. 2005; Jordano et al. 2003; Mossa et al. 2002) and are expected due to small network size.

Exponential distributions are associated to random networks in which preferential attachment is severely limited (Amaral et al. 2000) or do not even occur (Albert & Barabasi 2002). We simulated BA networks using the above steps and then we start trophically lumping species exactly as done with the real networks. We repeated this procedure 1000 times and obtained the average value for $k_x / \langle k \rangle$ and its 95% confidence interval.

In principle, lumping of species may cause two different effects on networks. First, there can be a size-based effect, in which changes on $k_x / \langle k \rangle$ would be a byproduct of the reduction in network size. Second, there can be a lumping-based effect, in which changes in $k_x / \langle k \rangle$ cannot be explained by the simple reduction in network size. Each ensemble of lumped BA networks was compared with an ensemble of one thousand BA networks generated with similar k and equal S'. The $\langle k \rangle$ is not identical to those of the lumped networks because in BA networks $\langle k \rangle \sim 2m$, and m is an integer. If the effect of lumping of species on the degree distribution is solely size-based, we would expect that both lumped BA networks and BA networks have similar values for $k_x / \langle k \rangle$. However, if the effects of lumping on the degree distribution were not restricted to size-effects, we would expect $k_x / \langle k \rangle$ will be lower for lumped networks than for non-lumped networks.

(d) Nestedness

As previously stated, nestedness is a measure of asymmetry in a bipartite network. The ANINHADO (Guimarães & Guimarães 2006) was used to calculate an index of nestedness for the original real networks. The program is available for download at www.guimaraes.bio.br. First, nodes were represented by columns (nodes of set 1) and rows (nodes of set 2) in an adjacent matrix in which edges between nodes were represented as "1s" and absence of edges as zeros. Each adjacency matrix was maximally packed, that is, the matrix was reorganized in a way that maximizes nestedness (Atmar & Patterson 1993). Given the structure of the adjacency matrix (the number of species in each set and the number of edges), an isocline of perfect nestedness was calculated for the adjacency matrix (Atmar & Patterson 1993; Bascompte et al. 2003). Then, it was possible to calculate an average measure of the unexpectedness in the presence and absence of edges, the so-called temperature, T, with values ranging from 0º (perfectly nested) to 100º (perfectly non-nested). As we are interested in the degree of nestedness and not on the degree of disorder, we calculate nestedness, N, in which $N = (100 - T)/100$ (following Bascompte et al. 2003).

Monte-Carlo simulations were used to assess nestedness significance. The simulations generated random adjacency matrices assuming that an edge between any randomly selected pair of nodes of different sets had an equal probability of occurrence. An empirical distribution of *N*-values was generated using the Monte-Carlo simulations (*n* = 1000 simulations). The average nestedness for the random population, N_R, was used to calculate the value of relative nestedness, that is $N^* = \left(N_O - N_R\right)/N_R$, in which N_O is the observed nestedness. N^* is a measure of how nested is a network with respect to the degree of nestedness expected for a random network with the same number of species in both sets and the same number of interactions (Bascompte et al. 2003). If N^* is not statistically different from zero, the degree of observed nestedness is expected by a random network and the network is called non-nested. We computed N^* for original and lumped networks.

In the theoretical simulations, we used a very simple model: a highly nested network $\left(N = 1\right)$ in which set sizes were defined as $S_1 = S_2 = 100$ and the proportion of edges actually established is 5%. We used the following algorithm to explore the effects of species lumping on nestedness:

1. Two species of set 1 were selected and deleted in the same way as in the simulations with real networks. A new species with the same links of both the original species was introduced in set 1.
2. Step (1) was repeated until S_1 was equal to a previous determined final value S'. The final values of used in these analyses were $S_1 = \{90,80,70,60,50,40,30\}$.
3. Two species of set 2 were selected and deleted in the same way as in the simulations with real networks. A new species with the same links of both the original species was introduced in set 2.

4. Step (3) was repeated until S_2 was equal to a previous determined final value, $S_2' = S_1'$.

For each lumped network, we recorded the average value of N^* and its 95% confidence interval. If lumping of species leads to non-nested networks, we would expect the relative nestedness to decrease towards zero (non-significant nestedness) by lumping.

Results

Lumping species to genus level reduced the number of species by 41.8% in the Caribbean Food Web and by 39.7% in the Correhuelas Plant-Frugivore Network. At family level, network size decreased by 71.1% in the Caribbean Food Web and by 62.1% in the Correhuelas Plant-Frugivore Network. This taxonomic lumping reduced $k_x / \langle k \rangle$ in relation to the original networks at both genus and family level (Figure 2b-d). The trophic lumping of species, however, did only reduce $k_x / \langle k \rangle$ at the level of lumping equivalent to the family level (Figure 2b-d). At genus-level, no effect of trophic lumping of species on $k_x / \langle k \rangle$ was recorded.

In the simulations using theoretical networks, although the BA model predicts a huge variation in $k_x / \langle k \rangle$, trophic lumping markedly reduced the average ratio $k_x / \langle k \rangle$ for the ensemble of BA networks (Figure 2e). The reduction of $k_x / \langle k \rangle$ is partly a result of the simple reduction of network size (Figure 2e). However, lumped networks showed lower values of $k_x / \langle k \rangle$ than similar-sized BA networks though, especially for the initial levels of lumping (Figure 2f). Thus, our results show that lumping of species can actually transform scale-free or broad-scale networks in single-scale networks by both size- and lumped-based effects.

Both ecological real networks were extremely nested: N = 0.93 for the Caribbean Food Web and N = 0.94 for the Correhuelas Plant-Frugivore Network. Species lumping did not reduce nestedness in neither of the two ecological networks. Indeed, it actually increased relative nestedness in some cases (Figure 3a-b). Accordingly, increase of relative nestedness was also recorded for the theoretical network (Figure 3c).

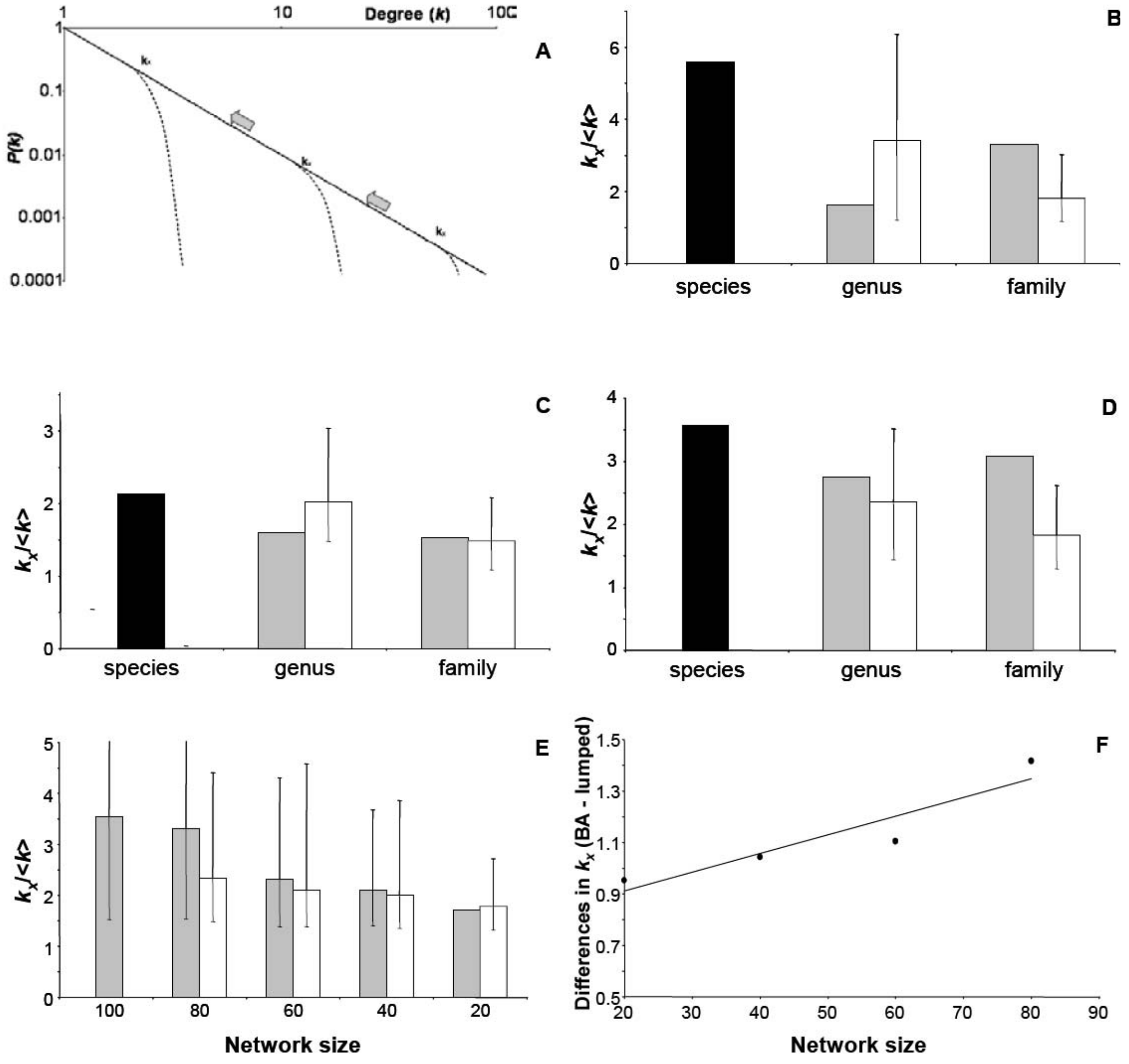

Figure 2. Species lumping and degree distribution. (a) The decrease in $k_x/\langle k\rangle$ (grey arrows) represents changes from power-law distributions to exponential distributions. (b-d) $k_x/\langle k\rangle$ for original networks (black columns), taxonomic-lumped networks (grey), and trophic-lumped networks (white): (b) Caribbean Food Web, (c) animal species in Correhuelas Network, and (d) plant species in Correhuelas Network. (e) trophic lumping and $k_x/\langle k\rangle$ for BA networks (grey columns) and lumped BA networks (white). (f) The relationship between the $k_x/\langle k\rangle$ of non-lumped and lumped BA networks and network size. In all graphs, bars indicate 95% confidence interval.

The analyses of nestedness values (*N*) for lumped versions of theoretical networks and their Monte Carlo counterparts showed that the increase in the relative nestedness was not a result of the reduction of *N* with lumping. Rather, lumping of species in a given matrix led to no clear changes in *N* (Figure 3d). However, there was a strong decrease in *N* for the Monte Carlo matrices. Therefore, the relative nestedness, that is, the difference in nestedness between real matrix and their Monte Carlo counterparts, increased (Figure 3d). In conclusion, our results indicate that the lumping of species cannot transform nested networks in non-nested networks. Rather, lumped networks may actually show higher relative nestedness than non-lumped networks, leading to false conclusions that a given lumped network is significantly nested.

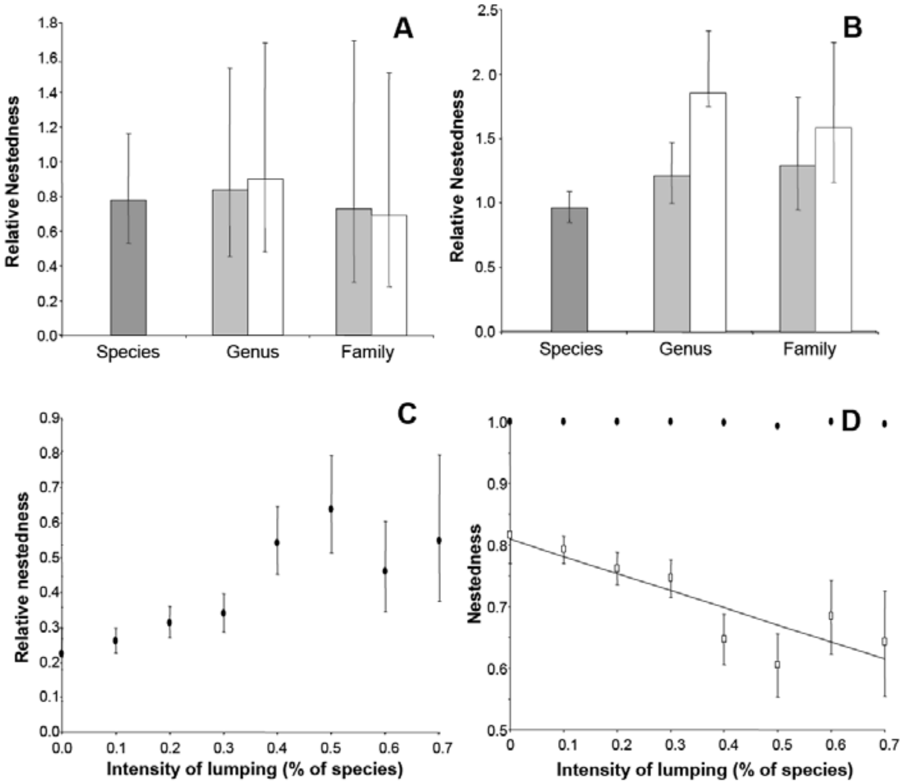

Figure 3. Effects of the lumping of species on nestedness: (a-b) The relative nestedness for real networks (dark grey columns), taxonomic-lumped networks (grey), and trophic-lumped networks (white). (a) The original Caribbean Food Web. (b) the Correhuelas Network. (c) Relationship between relative nestedness of theoretical networks and intensity of lumping (see text for further details). Note that the relative nestedness increases with lumping. (d) Relationship between nestedness and intensity of lumping for theoretical networks (black circles) and their random counterparts (open squares). In all graphs, bars indicate 95% confidence interval.

Discussion

Ideally, complex networks should be applied to the analysis of the interactions between well-defined elements in a given natural system (Proulx et al. 2005). However, this is not always possible, because it might be difficult to (i) record and identify all elements involved or (ii) record all the interactions between elements. This problem is especially serious in food web analyses, in which taxonomic and trophic lumping of species is commonplace (Pimm 2002; Sugihara et al. 1997). In this context, the aim of our study was to contribute to a better understanding of the effects of the aggregation of species on two important properties of networks, namely, the degree distribution and nestedness.

We demonstrated that the observed differences in the functional form of the degree distribution between food webs and plant-animal networks can emerge simply as a result of lumping procedures. Sampling biases are already known to affect the shape of the degree distributions of scale-free networks (Stumpf et al. 2005), but not to generate exponential truncations for large degrees. Our results show that the lumping of nodes can strongly alter scale-free networks and broad-scale networks by turning them into single-scale networks. Moreover, the effects of lumping cannot be interpreted as simple small-size effects, at least for small levels of lumping. At higher levels of lumping, the network size is probably so small that we cannot distinguish the effects of lumping from effects of network size.

These findings may have important implications to both the understanding of the principles of organization of food webs and their vulnerability to the loss of species. For instance, exponential distributions are often interpreted as the absence or severe limitation of preferential attachment (Amaral et al. 2000). This in turn has been interpreted as evidence of different processes shaping food webs and mutualistic networks (Dunne et al. 2002; Jordano et al. 2003). Here, we suggest an alternative and more parsimonious view, in which both types of networks may be indeed generated by preferential attachment, but the usual poor resolution of food webs falsely creates the exponential distributions observed in the literature. It is important to notice that even best resolved food webs actually show lumping of species (e.g., nodes representing ‘plankton’, ‘carrion’ or ‘seeds’ – see Table 1 from Dunne et al. 2002). The degree distributions of networks have also been commonly interpreted in terms of their fragility to random or directed removal of species. Single-scale networks are more vulnerable to random removal of nodes. In contrast, broad-scale and scale-free networks are far more resistant to the random removal of nodes, yet much more sensitive to the directed removal of high-connected nodes (Albert et al. 2000). Thus, if nodes are to be interpreted as the species of food webs, by erroneously describing food webs as single-scale networks, we may be overlooking the importance of highly connected species for their stability.

With respect to nestedness, Bascompte et al. (2003) demonstrated that plant-animal pollination and seed dispersal networks were usually more nested than food webs. The proportions of significantly nested networks found by these authors were 0.70 (19 in 27 networks) for seed dispersal networks, 0.80 (20 in 25) for pollination networks, but only 0.29 (4 in 14) for food webs. Other studies demonstrated that ant-plant mutualistic networks are also nested (Guimarães et al. 2006). Our results demonstrate that the low frequency of significantly nested food webs is not a result of lumping of species, which further supports previously described patterns in ecological networks (Bascompte et al. 2003). A relevant point is that lumping actually increases relative nestedness in the simulated and real, nested networks. It seems that not only are food webs not usually nested, by they are structured in a way that somehow prevents nesting by lumping of species.

What topological features of food webs are responsible for this anti-nestedness is an open question that should be pursued in future studies. One possible explanation may rely on the fact that food webs and mutualistic networks may really be a result of different ecological and evolutionary processes (Thompson 2005). For example, a few bipartite host-parasitoid and parasitoid-hyperparasitoid food webs were significantly less nested than expected by chance, which may describe its organization in compartments (Bascompte & Jordano 2006). Nestedness may emerge in mutualistic networks because natural selection on mutualisms often specifically favors the development of non-specific and asymmetrical interactions through the convergence of traits in interacting species (Thompson 2005). In contrast, in food webs, coevolution of defenses and counterdefenses may have led to the emergence of non-nested macroscopic structures, such as compartments (Prado & Lewinsohn 2004). In conclusion, although differences in degree distribution can be explained by differences in sampling detail, the results for nestedness suggest that deeper, biological explanations should not be ruled out.

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Capítulo 5

Asymmetries in specialization in ant-plant mutualistic networks

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Asymmetries in specialization in ant–plant mutualistic networks

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Mutualistic networks involving plants and their pollinators or frugivores have been shown recently to exhibit a particular asymmetrical organization of interactions among species called nestedness: a core of reciprocal generalists accompanied by specialist species that interact almost exclusively with generalists. This structure contrasts with compartmentalized assemblage structures that have been verified in antagonistic food webs. Here we evaluated whether nestedness is a property of another type of mutualism—the interactions between ants and extrafloral nectary-bearing plants—and whether species richness may lead to differences in degree of nestedness among biological communities. We investigated network structure in four communities in Mexico. Nested patterns in ant–plant networks were very similar to those previously reported for pollination and frugivore systems, indicating that this form of asymmetry in specialization is a common feature of mutualisms between free-living species, but not always present in species-poor systems. Other ecological factors also appeared to contribute to the nested asymmetry in specialization, because some assemblages showed more extreme asymmetry than others even when species richness was held constant. Our results support a promising approach for the development of multispecies coevolutionary theory, leading to the idea that specialization may coevolve in different but simple ways in antagonistic and mutualistic assemblages.

Keywords: asymmetric specialization; complex networks; extrafloral nectaries; geographic mosaic; nestedness

1. INTRODUCTION

Species interact within communities as networks, with each species connected to one or more other species (Pascual & Dunne 2006; Waser & Ollerton 2006). Analyses of network structure are allowing prediction of the consequences of species extinction and environmental perturbation to the whole community (Pascual & Dunne 2006). Additionally, comparative studies of network structure are helping to explain variation in patterns of specialization across communities (Olesen & Jordano 2002; Waser & Ollerton 2006). In this context, one of the central problems to solve in community ecology is whether different forms of interaction favour alternative structures in these networks of interacting species (Bascompte *et al.* 2003; Jordano *et al.* 2003).

A network of interacting species may have a small number of links among species, indicating an assemblage of ecological specialists, or many links, indicating ecological generalists. Mutualisms between free-living species often form multispecies networks apparently similar to the food webs commonly described for antagonistic interactions (Jordano 1987). Recent studies of pollinator–plant and seed disperser–plant interactions, however, have suggested that mutualistic and antagonistic webs of free-living species may differ fundamentally in the structure of how specialization is distributed among interacting species (Bascompte *et al.* 2003; Jordano *et al.* 2003; Vazquez & Aizen 2004). Bascompte *et al.* (2003) found that pollination and seed dispersal networks often show a specific type of asymmetrical specialization called nested. Nested networks are characterized by (i) generalists that all interact with each other, forming a core of interacting species; (ii) specialist species that commonly interact only with generalists and (iii) the absence of specialists that interact only with other specialists (figure 1*a*). In contrast, antagonistic networks (e.g. predator–prey, herbivore–plant), tend to be more compartmentalized, i.e. characterized by cohesive groups of interacting species (compartments) with relatively few interactions among groups (Prado & Lewinsohn 2004; Bascompte & Jordano 2006; figure 1*b*).

Nested patterns of asymmetrical specialization may be more likely to develop in mutualistic interactions among free-living species than in antagonistic interactions,

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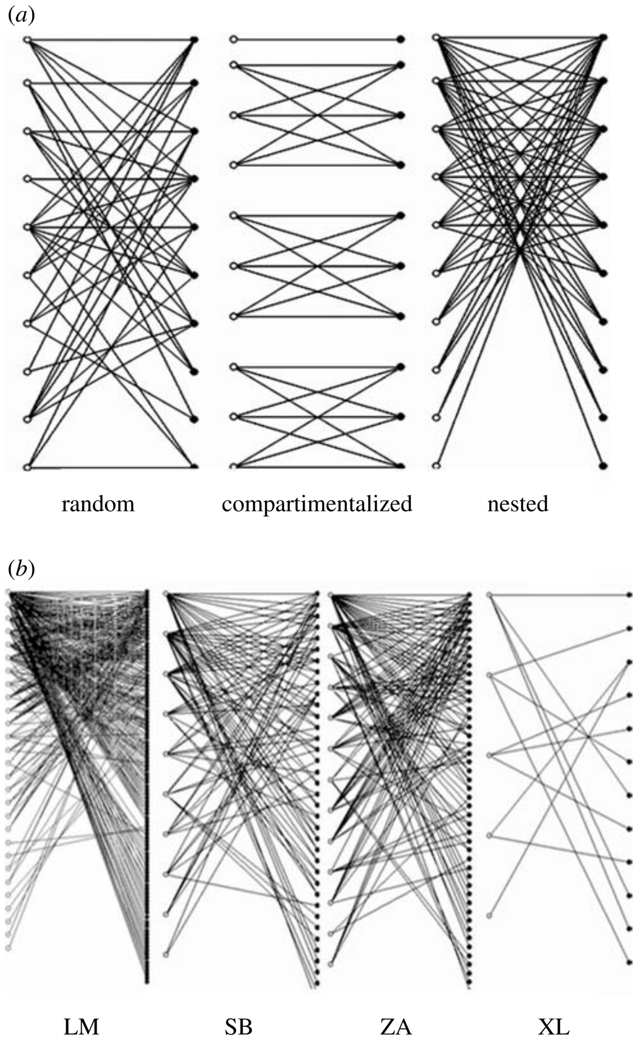

Figure 1. (*a*) Different types of hypothetical plant–animal networks: random networks, in which there is no community-level patterns of specialization; compartmentalized networks, in which there is symmetrical specialization; and nested networks in which there is asymmetrical specialization, i.e. specialists interact with the core of generalist species. (*b*) EFN networks: LM, La Mancha; SB, San Benito; ZA, Zapotitlán; XL, Xalapa. Open nodes are ant species and closed nodes are extrafloral nectary-bearing plant species. Only the first three networks (LM, SB and ZA) show high degree of nestedness. Networks were drawn in Pajek (http://vlado.fmf.uni-lj.si/pub/networks/pajek/).

because natural selection on mutualisms often specifically favours the development of multispecies networks through convergence and complementarity of traits in interacting species (see Thompson 1994, 2005). In contrast, antagonistic interactions may favour greater compartmentalization through the continual coevolution of defences and counter defences that generates greater specificity (see Thompson 2005). If nested asymmetries in specialization are indeed generated by simple coevolutionary processes such as convergence and complementarity of traits, it should be a common feature of mutualisms, spanning multiple forms of interaction beyond those investigated so far for plants and their pollinators and frugivores.

Nevertheless, we currently do not know whether the nested pattern of asymmetries in specialization is common in other forms of mutualism or how different ecological conditions may shape the extent of asymmetry (i.e. the degree of nestedness). We already know from past studies of mutualism that species commonly differ geographically in the species with which they interact (Anderson *et al.* 2004; Rudgers & Strauss 2004) and that some interactions coevolve as a geographic mosaic in which populations differ across landscapes in their adaptation and specialization to other species (Thompson 1994, 2005). Hence, the problem to solve is whether interaction networks show similar patterns of specialization in different communities regardless of the particular species involved. By exploring variation in community-level patterns of mutualistic networks, we will be able to bridge the two main approaches to explore the organization of multispecies mutualisms: geographic mosaic theory and complex network theory (Bascompte & Jordano 2006).

Here, we take a first step towards filling these gaps, by exploring whether interactions between plants with extrafloral nectaries (EFN) and ants (hereafter EFN networks), which are among the most commonly studied types of plant–animal mutualisms (Bronstein 1998), show predictable patterns of asymmetry in specialization and whether those patterns vary with ecological conditions. In a given tropical community, dozens of nectar-producing plant species may interact with ants (Díaz-Castelazo *et al.* 2004). These interactions are often defensive mutualisms, in which the ants protect plants against their natural enemies and plants reward ants with nectar (Rico-Gray *et al.* 1998*b*). We studied nested patterns and their variation in four EFN networks, each from a different site in Mexico, to address the following questions: do ant–plant networks show a predictable pattern of specialization within and among communities? To what extent is the pattern of specialization similar to that found in studies of other forms of interaction?

2. MATERIAL AND METHODS

(a) *Study areas*

We constructed networks using previously published data from interactions between ants and EFN-bearing plants in four different communities (Rico-Gray 1993; Díaz-Castelazo & Rico-Gray 1998; Rico-Gray *et al.* 1998*a*,*b*) and compared those with patterns found in previous studies of nestedness in pollinator–plant and seed disperser–plant networks (Bascompte *et al.* 2003). For the ant–plant networks, we evaluated four habitats with a similar number of flowering plant species (about 250–300) but with contrasting environmental characteristics: lowland tropical dry forest (La Mancha, Veracruz), coastal tropical sand dune matorral (San Benito, Yucatán), highland semiarid vegetation (Zapotitlán, Puebla), and lower montane humid forest (Xalapa, Veracruz). The vegetation in Xalapa, a mixture of tropical and temperate floristic elements (Williams-Linera & Tolome 1996), constrains the development of species-rich EFN networks because relatively few plants have EFN (Díaz-Castelazo & Rico-Gray 1998). In contrast, the other three habitats have tropical floristic elements (e.g. Leguminosae, Bignoniaceae, Cactaceae) that are abundant and frequently have nectar-producing structures (Elias 1983; Schupp & Feener 1991). See electronic supplementary material for detailed description of study sites.

(b) *Nestedness in EFN networks*

Typically, plant–animal interactions can be depicted as networks consisting of two sets of nodes (plants and animals;

Jordano *et al.* 2003; figure 1) and links among them that depict the interactions between any species pair. An EFN network is defined by an adjacency matrix $\boldsymbol{R}$ describing trophic interactions between E extrafloral nectary-bearing plant species and A visiting ants within a well-defined ecological community, where $r_{ij}=1$ if the plant i is visited and its extrafloral nectar harvested by the ant j and zero otherwise. Thus, this matrix has non-zero r elements wherever ants visit the EFN of a plant. It is important to emphasize that visitation by ants does not necessarily imply that ants are protecting the plant. Rather, certain ant species may only explore the resource without protecting the plants or only protecting under certain ecological conditions. Therefore, only a subset of recorded interactions in these networks is unambiguously mutualistic. Future studies should focus on the importance of exploiters of mutualistic interactions to network structure. In this study, we follow the approach already used in other interactions and considering that all interacting species are part of the mutualistic network (see Jordano *et al.* 2003).

Our discussion about nested asymmetrical specialization is based on the ecological concepts of specialist and generalist (see Olesen & Jordano 2002), in which the level of generalization of a given species is equal to the number of recorded interactions. In this context, specialists and generalists are terms used to describe the endpoints of a continuum varying from species that interact with only one partner (extreme specialists) to species that interact with near all possible partners (extreme generalists). Ecological specialization may emerge as a consequence of coevolutionary processes between the plants and ants, differences in species abundance and competitive interactions among the plants or the ants.

We follow Bascompte *et al.* (2003) and define nestedness, N, as $N=(100-T/100)$, in which T is the matrix temperature, a measure of matrix disorder with values ranging from 0° (perfectly nested) to 100° (perfectly non-nested). Values of N close to one therefore indicate strong asymmetrical patterns in specialization (same as high degree of nestedness), intermediate values are usually produced assuming random interactions among species, and low values of N may indicate compartmentalization (Bascompte & Jordano 2006). Thus, by calculating nestedness we are able to investigate if a given ecological interaction can be described as one of the three main classes of networks (figure 1*a*). In effect, we are testing three alternative hypotheses on the structure of specialization in these assemblages.

To calculate T, the adjacency matrix $\boldsymbol{R}$ is maximally packed (see Atmar & Patterson 1993 for further details). Then, an isocline of perfect nestedness is calculated and deviations from this isocline (i.e. unexpected recorded presences and absences of interactions that deviate from a perfectly nested pattern) are standardized and recorded. The average degree of deviation from this isocline is T. All nestedness analyses were performed using ANINHADO v. 1.0, C-language software based on the original code of the widely used nestedness temperature software (hereafter NTC) that allows rapid analyses of thousands of replicates (Guimarães & Guimarães 2005).

We assessed the significance of nestedness, using two null models. The first null model was based on NTC's null model and tested if the observed nested pattern is expected by the average level of generalization. Null model I assumes that each randomly assigned pair of ants and plants interacts with constant probability, p. This probability is related to the average level of generalization observed in the network and was estimated as $\hat{p}=E/AP$, in which E is the number of observed interactions and AP is the maximum possible number of interactions in a network with A ant and P plant species. This model generates networks in which differences in the number of interactions among species of the same assemblage is small. Different nested patterns, in turn, may result from differences in the number of interactions among species. In pollination and seed dispersal networks, however, the degree of nestedness is often higher than expected by the heterogeneity of number of interactions (Bascompte *et al.* 2003). As we are interested in whether EFN networks show patterns of nestedness similar to those recorded in other mutualistic networks, we also used null model II from Bascompte *et al.* (2003), which assumes that the probability that a plant i interacts with an ant j depends on the observed number of interactions of both species, such that

$$p(r_{ij}=1)=\left(\frac{k_i}{A}+\frac{k_j}{E}\right)\frac{1}{2}, \tag{2.1}$$

in which k is the observed number of interactions for the species. As k is correlated with species abundance in plant–animal interactions (Jordano 1987; Jordano *et al.* 2003), this model also controls for potential sampling bias, in which asymmetrical patterns of interactions are generated only by differences in species abundance.

We compared the proportion of networks that show significant values of N with those recorded for pollination ($n=25$), seed dispersal networks ($n=27$) and with a set of antagonistic networks that include predator–prey, consumer–producer and herbivore–plant interactions ($n=14$, all values recorded from Bascompte *et al.* 2003).

(c) *Comparisons among communities*

We also investigated how ecological variables affect nestedness patterns. The degree of nestedness is thought to be a measure independent of matrix properties (Atmar & Patterson 1993). For pollination and seed dispersal networks, however, the degree of nestedness increases with species richness (Bascompte *et al.* 2003), indicating a biological pattern. Thus, we investigated whether the degree of nestedness is related to species richness in EFN networks. Then, we contrasted our four EFN networks to investigate how ecological variables affect nestedness. We assessed whether the four EFN networks showed differences in nested pattern after controlling for total number of species (network size) and the ratio between the number of ant and plant species (network form). We predicted that, if network size and form were solely responsible for the nested pattern, then the observed nestedness of a small EFN network would be equal to the nested pattern of a sub-network with equal size and form randomly sampled from a larger network. We tested this hypothesis using the following algorithm to compare pairs of networks in which L is the larger network and l is the smaller network: (i) assuming that the probability of a plant species being removed is equal in all plant species, randomly remove plant species of L until $E_L=E_l$; (ii) assuming that the probability of an ant species being removed is equal in all ant species, randomly remove ant species of L until $A_L=A_l$; (iii) record nestedness of the rarefied L network; (iv) repeat (i–iii) for 999 times; (v) calculate the probability p that a rarefied L shows a degree of nestedness equal to or more extreme than l. We only consider rarefied networks in which all species at the end have at least one interaction, because species without any interaction lack biological meaning. If other factors besides network size and form affect the nestedness pattern of the smaller network, we expect that $p < 0.05$. It is important to note that differences in nestedness may be a result of sampling (Fischer & Lindenmayer 2002). Small networks may indeed be small datasets in which more generalists are recorded, since generalists are usually the most abundant species (Jordano 1987). To investigate if differences in nestedness among communities are a result of simple sampling bias, we used a rarefaction procedure identical to the above one, except for the fact that the probability of a plant or ant species being removed is proportional to $1/k$ in which k is the number of interactions of the species.

3. RESULTS

Extrafloral nectary network showed on average strongly nested patterns of asymmetric specialization among the interacting species (figure 1*b*, $N = 0.71 \pm 0.10$, mean ± s.e.). As a consequence of these community-level patterns, nestedness was very high on average. The three tropical networks showed nestedness values similar to those observed in pollination and seed dispersal networks (figure 2*a*). Indeed, the probability of a given tropical EFN network showing a nested pattern equal to or more extreme than that observed for seed dispersal or pollination network was always non-significant (La Mancha, $N = 0.949$, $p = 0.17$; San Benito, $N = 0.748$, $p = 0.19$; Zapotitlán, $N = 0.706$, $p = 0.13$). These networks were significantly nested whether tested against null model I or II (figure 2*b*). Therefore, the degree of nestedness observed in these ant–plant interactions was higher than expected by random interactions or by differences in the number of interactions among species. In contrast, Xalapa showed the lowest nestedness ever recorded in the literature for a mutualistic plant–animal network ($N = 0.453$; figure 2*a*). Both null models reproduced the nested pattern for Xalapa (figure 2*b*), indicating that the patterns of asymmetrical specialization in this community are expected by random interactions. The proportion of EFN networks that showed significant nestedness was very similar to the other two types of mutualistic networks analysed and very different to the pattern observed for antagonistic networks (figure 3), although our small sample of communities leads to caution when interpreting the results.

Asymmetries in specialization increased with species richness (figure 2*b*). We re-analysed data from Bascompte *et al.* (2003) for plants and their pollinators and seed dispersers and found that for large networks ($S > 40$, $n = 28$), nestedness increased with the logarithm of network size ($N = 0.36 + 0.1 \log(S)$, $F = 12.98$, d.f. $= 27$, $R^2 = 0.33$, $p = 0.01$), indicating that only species-rich systems will show high patterns of nestedness. We used this function to control network size, computing the differences between the nestedness predicted by network size and the observed nestedness for pollination, seed dispersal, and the three significant nested EFN networks. After controlling for network size, all tropical EFN networks showed patterns of nestedness similar to those observed for pollination and seed dispersal networks (La Mancha, $p = 0.29$; San Benito, $p = 0.32$; Zapotitlán, $p = 0.14$).

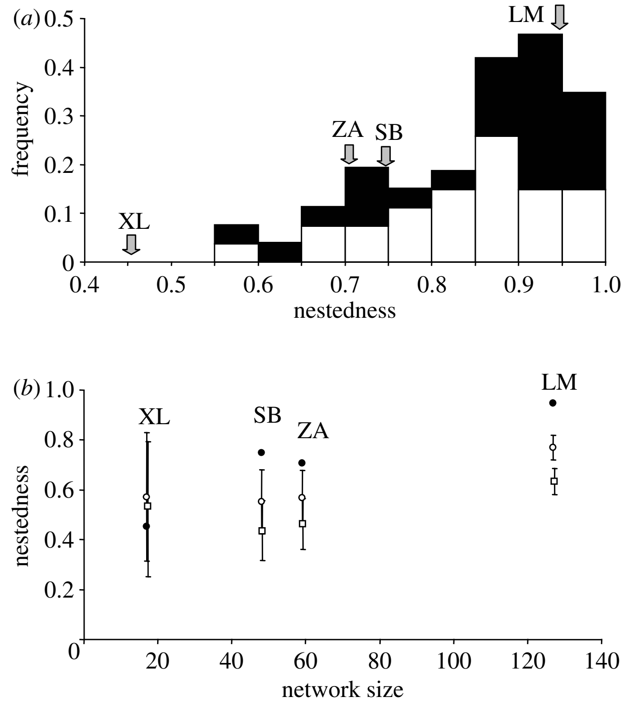

Figure 2. (*a*) Frequency of different degrees of nestedness observed in published studies on pollination, seed dispersal, and analysed EFN networks. Black columns indicate pollination networks, white columns indicate seed dispersal networks, and grey arrows indicate the values for analysed EFN networks (networks labelled as in figure 1). (*b*) The relationship between degree of nestedness and network size (i.e. number of interacting species). Closed circles indicate observed values of nestedness for each EFN network. Open squares indicate the average nested value predicted by null model I and open circles indicate the average value predicted by null model II (see text for further details). Error bars indicate 95% confidence interval (10 000 replicates for each null model).

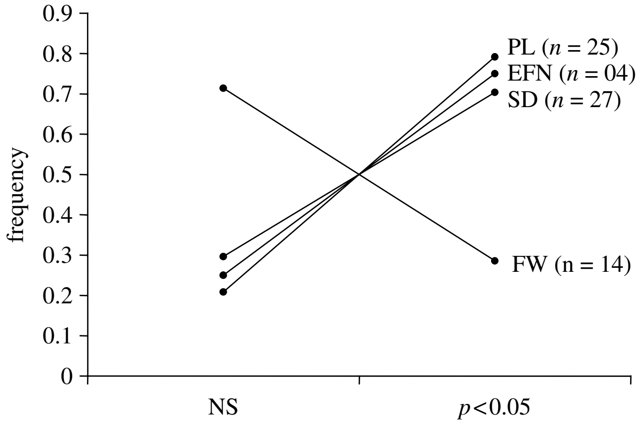

Figure 3. The proportion of significant nestedness found in different types of interaction: EFN, extrafloral nectaries; SD, seed dispersal; PL, pollination; FW, food webs (antagonistic networks). NS, non-significant nestedness; $p < 0.05$ = significant nestedness.

Species richness, however, was not the only factor affecting the degree of asymmetry in specialization. Tropical EFN networks showed larger values of nestedness than Xalapa even after controlling for network size and form (figure 4*a*–*c*), Among the tropical networks, Zapotitlán and San Benito showed a similar degree of

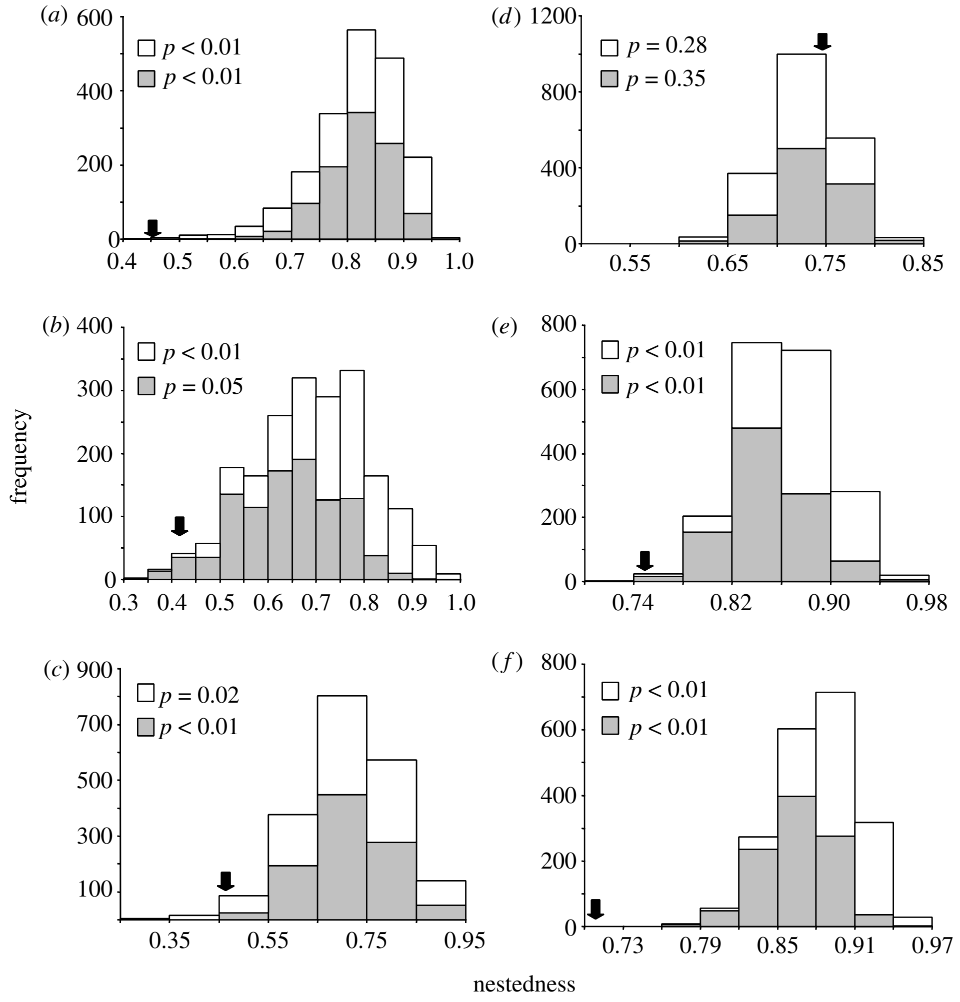

Figure 4. Nestedness for real EFN and rarefied networks. Ensembles of rarefied networks were generated by randomly removing ant and plant species using two different procedures: assuming that each plant or ant species has the same probability of removal (white columns) and assuming that the probability of a species being removed is negatively correlated with the degree of generalism (grey columns). Arrows indicate the actual degree of nestedness of the smaller network. The p indicates the probability of a rarefied network showing nestedness equal to or more extreme than the real, smaller network: Xalapa and (*a*) rarefied La Mancha networks, (*b*) rarefied Zapotitlán and (*c*) rarefied San Benito; San Benito and (*d*) rarefied Zapotitlán, (*e*) rarefied La Mancha and (*f*) Zapotitlán and rarefied La Mancha.

nestedness (figure 4*d*), but La Mancha showed stronger asymmetries than these other sites, even after controlling for network size and form (figure 4*e*,*f*). Hence, ecological factors other than species richness must contribute to geographic variation in the degree of asymmetry in specialization in these mutualisms, but they do not completely override the tendency of large mutualistic networks to be significantly nested.

4. DISCUSSION

The interactions between ants and plants differ in many ways from those involving pollinators and seed dispersers. In ant–EFN plant interactions, the benefit for plants is protection against herbivores. Protection, in turn, is an indirect benefit, because it depends on ants being efficient in deterring a third assemblage of species: the herbivores. In contrast, in pollination and seed dispersal interactions the benefit for plants is reproduction, and the interaction does not involve manipulating the effects of a third group of species. Yet, all these interactions show similar patterns of nestedness, in which specialist–specialist interactions are rare and specialists interact with a core of generalist species.

Our results corroborate and extend the conclusions of recent studies suggesting that interactions among free-living species in species-rich communities show a nested pattern of asymmetrical specialization, when at least some of the interactions have potentially strong mutualistic components (Bascompte *et al.* 2003). Although, it is well known that different processes may lead to similar patterns in ecology (Levin 1992), a parsimonious possibility is that all three types of mutualism may be affected by similar evolutionary processes, such as convergence and complementarity of traits among interacting species (Thompson 2005), that differ from the processes acting on antagonistic networks. Indeed, network theory predicts that these similarities and differences are a result of simple processes (Albert & Barabási 2002). These results therefore provide support for the development of multispecies coevolutionary theory, leading to the notion that specialization may evolve and coevolve in different but simple ways in mutualistic and antagonistic interaction networks. Caution is needed since nested patterns have been explored in only a few types of interaction. Based upon current results, however, we predict that nestedness will be observed in other interactions between free-living mutualists, such as associations between host fish and their cleaners on coral reefs (e.g. Cote 2000).

Additionally, our study highlights the potential importance of species richness and its influence on geographic variation in nested asymmetrical specialization within mutualistic networks. The logarithmic relationship between network size and nestedness suggests that only species-rich systems will be highly nested. Moreover, small networks generally do not show significant nestedness (Bascompte *et al*. 2003; this study). This feature may be a consequence of nestedness being inherently undetectable below a certain threshold of species richness, a typical problem of characterization of small networks (Guimarães *et al*. 2005). Alternatively, it may be that species-poor communities do not have sufficient number of species for the evolution of species specialized in interacting with generalist species. In fact, many mutualistic lifestyles (e.g. nectar and pollen gathering in social bees and near-obligate frugivory in some vertebrates) became possible only after local multispecies mutualistic networks came into existence (Thompson 1982).

The variation in nested asymmetrical specialization among EFN networks, however, is not totally explained by differences in species richness or by differences in the ratio between ants and plants. These differences may be a result of sampling bias, but after we controlled for preferential sampling of generalists, some communities still differed in the level of specialization (figure 4). Thus, other ecological variables may contribute to the particular degree of nestedness in any particular assemblage. Olesen & Jordano (2002) have shown that, beyond species richness, altitude and the biogeographic region affect the average level of specialization within pollination networks. We suggest that future work with mutualistic networks should focus on the role of these factors in driving regional differences in patterns of nested asymmetrical specialization.

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SUPPLEMENTARY MATERIAL

Detailed description of study sites

LOWLAND TROPICAL DRY FOREST (LA MANCHA).--Centro de Investigaciones Costeras La Mancha is located on the coast of the state of Veracruz, México (19°36'N, 96°22'W; elev. < 100 m). The climate is warm and subhumid; a rainy season occurs between June and September, total annual precipitation is *ca* 1500 mm (1800 mm in study year), mean annual temperature is 24°-26°C, and minimum temperature is 15°C. The major vegetation associations in the area are: tropical deciduous forest [with *Brosimum alicastrum* Swartz, *Bursera simaruba* (L.) Sarg., *Cedrela odorata* L., *Enterolobium cyclocarpum* (Jacq.) Griseb., *Ficus cotinifolia* H. B. & K.], tropical dry forest [with *Acacia* spp., *Bursera fagaroides* (H. B. & K.) Engl., *B. simaruba*, *Plumeria rubra* L.], sand dune matorral [with *Acacia macracanta* Humb. & Bonpl., *Diphysa robinoides* Benth., *Randia laetevirens* Standl., *Tecoma stans* (L.) Juss. ex H. B. & K.], mangrove forest, freshwater marsh, freshwater lagoon and surrounding forest, and riparian vegetation (Moreno-Casasola *et al.* 1982, Novelo 1978; Rico-Gray 1993).

COASTAL SAND DUNE MATORRAL (SAN BENITO).--San Benito is located on the central coast of the state of Yucatán, México (21°20'N, 89°10'W; elev. < 3 m). The area is characterized as a narrow well developed calcareous sandy beach. The climate is dry, a rainy season occurs between June and September, total annual precipitation is *ca* 300 mm (320 mm in study year), mean annual temperature is 24°-26°C, and minimum temperature is 15°C. The dominant species are *Agave angustifolia* Haw., *Bravaisia tubiflora* Hemsl., *Bumelia retusa* Swartz, *Coccoloba uvifera* L., *Coccothrinax readii* Quero, *Gossypium hirsutum* L., *Mammillaria gaumeri* Orcutt, *Pithecellobium keyense* Britton ex Coker, *Scaevola plumierii* (L.) Vahl, *Schomburgkia tibicinis* Batem., *Suriana maritima* L., and *Tournefortia gnaphalodes* (L.) R.Br. ex Roem. & Schult. (Rico-Gray *et al*. 1987; Rico-Gray 1989).

SEMIARID HIGHLAND ENVIRONMENT (ZAPOTITLÁN).--The Valle de Zapotitlán is located in the Tehuacán-Cuicatlán valley system, located in the mountainous area in the southeast portion of the state of Puebla, close to the northeastern limits of the state of Oaxaca, México (18°20'N, 97°20'W; elev. 1450-1600 m). The climate is dry, a rainy season occurs between May and August (sometimes September), total annual precipitation is *ca* 300 mm (296 mm in study year), mean annual temperature is *ca* 20°C, and minimum temperature is 8°C (Valiente-Banuet 1991, Zavala 1982). The major vegetation associations, with no clear boundaries in many areas, are: thorny scrub or matorral [with *Acacia cochliacantha* Humb. & Bonpl. ex Willd., *Cercidium praecox* (Ruiz & Pavón) Harms, *Ipomoea pauciflora* Mart. & Gal., *Mimosa luisiana* Brandegee, *Prosopis laevigata* (Humb. & Bonpl. ex Willd.) M. C. Johnston], 'tetechera' [dominated by columnar cacti, like *Neobuxbaumia tetetzo* (F. A. C. Weber) Backeb.], 'cardonal' [dominated by cacti, like *Cephalocereus hoppenstedtii* (F. A. C. Weber) Schumann], 'izotal' (dominated by the Agavaceae *Yucca periculosa* F. Baker and the Nolinaceae *Beaucarnea gracilis* Lem.), and tropical dry forest (with *Bursera* spp., *Ceiba parviflora* Rose, *Lysiloma* spp., *Plumeria rubra*) (Dávila *et al*. 1993; Jaramillo & González-Medrano 1983; Villaseñor *et al*. 1990; Zavala 1982).

LOWER MONTANE HUMID FOREST (XALAPA).--Parque Ecológico Clavijero is located 2.5 km south of Xalapa, Veracruz (19°30'N, 96°57'W; elev. 1250 m). The climate is temperate humid with rain throughout the year, total annual precipitation is *ca* 1800 mm (2100 mm in study year), mean annual temperature is *ca* 19°C, and minimum temperature is 6°C. The vegetation in the park is a fragment of lower montane forest, some dominant tree species are *Liquidambar macrophylla* Oersted, *Carpinus caroliniana* Walter, *Quercus germana* Schlecht. & Cham., *Q. xalapensis* Humb. & Bonpl., *Clethra mexicana* DC., *Ocotea psychotrioides* Kunth, *Turpinia insignis* (H. B. & K.) Tul., and *Eugenia xalapensis* DC. (Williams-Linera & Tolome 1996). Other species present are *Trema micrantha* (L.) Blume, *Meliosma alba* (Schlecht.) Walp., *Persea americana* L., *Oreopanax* spp., *Cnidoscolus aconitifolius* (Mill.) I. M. Johnst., *Piper auritum* H. B. & K., *Solanum* sp., *Cestrum nocturnum* L., and *Baccharis multiflora* H. B. & K. There are also many epiphytes and ferns.

Data collection - Modified from Rico-Gray (1993).

Biweekly field observations (three days per visit) were made for La Mancha, Zapotitlan and Xalapa, and monthly for San Benito along arbitrarily selected but representative 1 km trails that sampled different vegetation associations. We recorded all occurrences of ants collecting liquids from plants. On each visit we noted ant species, plant species, and food source or structure mediating the ant-plant interaction. Once an individual plant was marked as being visited by ants, it was subsequently re-checked throughout the study. Ants were considered to be feeding on nectar when they were immobile, with mouth parts in contact with nectar-secreting tissues, for periods of up to several minutes. Nectar-feeding ants often showed obviously distended gasters.

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Capítulo 6

The nested structure of marine cleaning symbiosis: is it like flowers and bees?

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The nested structure of marine cleaning symbiosis: is it like flowers and bees?

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In a given area, plant–animal mutualistic interactions form complex networks that often display nestedness, a particular type of asymmetry in interactions. Simple ecological and evolutionary factors have been hypothesized to lead to nested networks. Therefore, nestedness is expected to occur in other types of mutualisms as well. We tested the above prediction with the network structure of interactions in cleaning symbiosis at three reef assemblages. In this type of interaction, shrimps and fishes forage on ectoparasites and injured tissues from the body surface of fish species. Cleaning networks show strong patterns of nestedness. In fact, after controlling for species richness, cleaning networks are even more nested than plant–animal mutualisms. Our results support the notion that mutualisms evolve to a predictable community-level structure, be it in terrestrial or marine communities.

Keywords: asymmetrical interactions; coevolutionary networks; coral reefs; null models

1. INTRODUCTION

In ecological communities, each species interacts in different ways with one to several species forming networks of interacting species (Pascual & Dunne 2006). The network approach has been useful for investigating the structure and fragility of ecological interactions, and comparative studies of network structure help to uncover community-level patterns of ecological specialization in different types of interspecific interactions (Jordano *et al.* 2003; Vázquez & Aizen 2004; Vázquez *et al.* 2005; Pascual & Dunne 2006). In this context, recent studies demonstrate that the network structure of species-rich, plant–animal mutualisms is often nested, whereas antagonistic interactions are usually non-nested (Bascompte *et al.* 2003; Guimarães *et al.* 2006). Nestedness is a specific type of asymmetric interactions characterized by (i) species with many interactions form a core of interacting species, (ii) species with few interactions commonly interact only with species with many interactions and (iii) the absence of interactions between species with few interactions (figure 1).

Nestedness is expected to appear in ecological interactions such as mutualisms between free-living species, in which the core of generalist species forms a stable set of resources, allowing the evolution of specialized lifestyles (Thompson 2005). Additionally, it was recently suggested that ecological factors such as differences in abundance among species may explain asymmetric interactions (Vázquez & Aizen 2004; Vázquez *et al.* 2005) and, more specifically, nestedness (Lewinsohn *et al.* 2006). If nestedness is indeed generated by simple coevolutionary and ecological processes such as those mentioned previously, it is expected to characterize mutualistic networks irrespective of the identity of interacting species. In fact, nestedness should be a common feature of other types of mutualisms beyond those investigated so far for plants and animals (Bascompte *et al.* 2003; Guimarães *et al.* 2006).

Here, we investigate for the first time the community-level patterns of interactions observed in cleaning symbiosis in the reef environment. In this type of mutualism, the so-called cleaners (shrimps or fishes) forage on ectoparasites, diseased or injured tissues and mucus from the body surface of fish species called clients, which in their turn get rid of unwanted material (Floeter *et al.* in press). Cleaning is a common and widespread type of foraging association between reef species, recorded for several animal taxa and geographical sites (Floeter *et al.* in press). We studied nested patterns in three cleaning networks. We specifically addressed the following questions: does nestedness characterize cleaning networks; and are the patterns of interactions observed for cleaners and clients similar to those previously observed in plant–animal mutualistic networks?

2. MATERIAL AND METHODS

(a) *Studied communities*

Most studies on cleaning symbiosis between reef animals focus on one or a few species (e.g. Sazima *et al.* 1999) and community-level patterns of these interactions have been largely ignored (but see Floeter *et al.* in press). Here, we use data on cleaners and clients in three different assemblages of reef animals in the Western Atlantic (Johnson & Ruben 1988; Wicksten 1998; Sazima 2002) and compare them with patterns found in studies of nestedness in plant–animal mutualistic networks (Bascompte *et al.* 2003; Guimarães *et al.* 2006). The three above-mentioned studies on cleaning symbiosis deal with the majority of cleaner and client species within the studied assemblages and thus are appropriate for assessing community-level patterns. Moreover, these assemblages have more than three species of cleaners each, allowing the emergence of nestedness. The studied cleaners may be grouped into four broad categories: (i) fishes cleaning through whole life cycle (*Elacatinus*=*Gobiosoma*), (ii) fishes cleaning only or mostly while juveniles (e.g. *Bodianus*, *Pomacanthus*, *Thalassoma*), (iii) fishes cleaning sporadically either as adults or juveniles (e.g. *Chaetodon*), and (iv) shrimps (e.g. *Periclimenes*). The studied assemblages were at (i) Abrolhos Archipelago, Western South Atlantic (hereafter Abrolhos), where five cleaners and 35 client species were examined in a total of 70 h (Sazima 2002), (ii) Bonaire, Netherlands Antilles, Caribbean (Bonaire), where six cleaners and 50 client species were examined in a total of 700 h (Wicksten 1998) and (iii) Saint Croix, US Virgin Islands, Caribbean (St Croix), where four cleaners and 32 client species were examined in a total of 110 h (Johnson & Ruben 1988). The studied areas were composed of coral reefs, and depths of studied cleaning stations varied among the three areas from 3 to 30 m.

(b) *Cleaning networks*

Interspecific interactions can be described as networks in which species are nodes and interactions between any species pair are depicted as links (Jordano *et al.* 2003). A cleaning network is defined by an adjacency matrix $\boldsymbol{R}$ describing interactions between L cleaner species and F client species in a well-defined ecological assemblage, where $r_{ij}=1$ if the client j is cleaned by the species i and zero otherwise. It is important to emphasize that client–cleaner interactions do not necessarily imply mutual benefits for both species. In fact, cleaner species may act as parasites in some ecological communities. Therefore, only a subset of recorded interactions in these networks is unambiguously mutualistic. Future studies should focus on the importance of exploiters of mutualisms to network structure. Here, we follow the approach already used in

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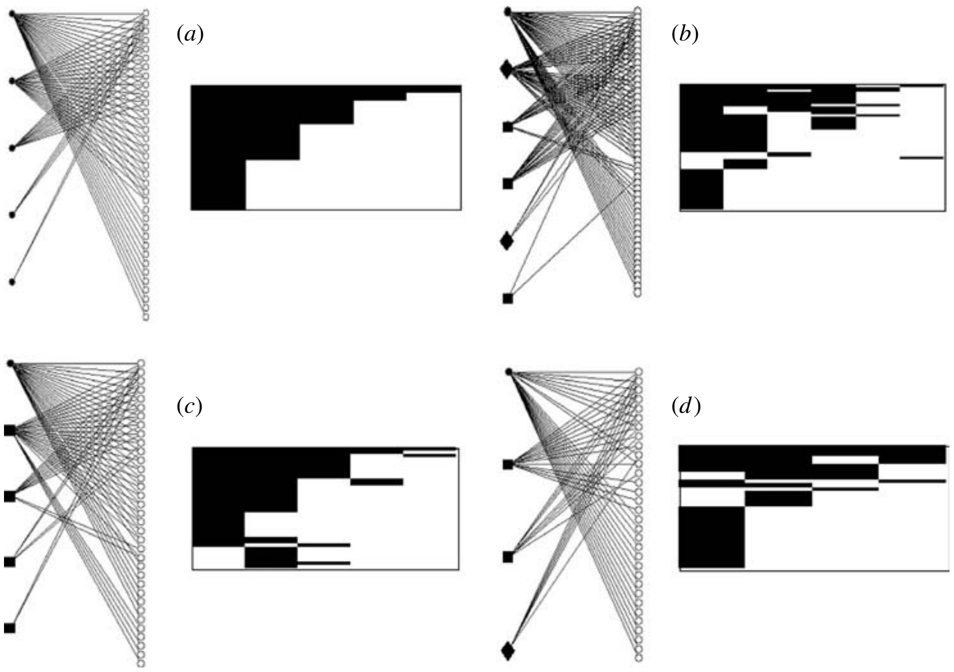

Figure 1. Network and matrix representations of community-level patterns of interactions between cleaners and clients. Lines and black squares represent interactions between cleaners (closed symbols and columns) and clients (open circles and rows). Cleaner fishes are represented by circles (*Elacatinus*) and squares (other genera), and cleaner shrimps are represented by diamonds. (*a*) Hypothetical, perfectly nested network, (*b*) Bonaire, (*c*) Abrolhos and (*d*) St Croix. Networks were drawn in Pajek (http://vlado.fmf.uni-lj.si/pub/networks/pajek/).

other interactions and consider that all interacting species are part of the mutualistic network (Jordano *et al.* 2003), since there is a wide gradient of mutually beneficial effects from pure mutualism to pure antagonism or amensalism, and all them potentially influence network build-up and evolution.

(c) *Nestedness*

The matrix ***R*** is perfectly nested if showing a progression of inclusive subsets after ordering rows and columns in decreasing totals (Lewinsohn *et al.* 2006, figure 1*a*). We follow Bascompte *et al.* (2003) and define the degree of nestedness, N, as $N=(100-T)/100$, in which T is the matrix temperature, with values ranging from 0° (perfectly nested) to 100° (perfectly non-nested). Additional details about T are provided elsewhere (Guimarães & Guimarães 2006). We used two null models to test if the degree of nestedness is expected from basic network features (Bascompte *et al.* 2003). The null model 1 assumes that each randomly assigned pair of cleaner and client interacts with constant probability, C, in which C is the connectance, i.e. the proportion of interactions actually observed in the network. Therefore, it tests if the observed N is higher than expected for random networks with similar number of interactions. The null model 2 assumes that the probability that a cleaner i interacts with a client j depends on the observed number of interactions of both species, such that

$$C(r_{ij}=1)=\left(\frac{k_i}{F}+\frac{k_j}{L}\right)\frac{1}{2}, \qquad (2.1)$$

in which k is the observed number of interactions for the species. Therefore, the null model 2 tests if observed N is higher than expected for random networks with similar heterogeneity of interactions among species (Bascompte *et al.* 2003). Each community was compared with 1000 replicates generated by each null model. We only considered replicates in which all species have at least one interaction, because species without interaction lack biological meaning. All nestedness analyses were performed using ANINHADO (Guimarães & Guimarães 2006).

To assess if the observed patterns of nestedness for cleaning networks are similar to other mutualisms, we compared the values of N recorded for the three cleaning networks with those recorded for pollination ($n=25$), seed dispersal ($n=27$), ant–plant mutualisms ($n=4$; dataset from Bascompte *et al.* 2003; Guimarães *et al.* 2006). To study the basic aspects of network structure, we investigate how the degree of nestedness (N) is related to species richness and the ratio between the richness of two sets (animal, plant, client or cleaner) of interacting species (richness ratio). These two aspects of network structure may affect nestedness (Guimarães *et al.* 2006). We investigate the relationship between nestedness and these variables using multiple regression. The degree of nestedness was angular transformed and species richness and richness ratio (set with higher number of species/set with lower number of species) were log transformed to improve normality and homoscedasticity.

3. RESULTS

The three analysed cleaning networks show strong nested patterns, in which species with few interactions often interact with the core of species with many interactions (Abrolhos, $N=0.92$; Bonaire, $N=0.92$; St Croix, $N=0.84$; figure 1). These networks were significantly more nested than expected from random interactions (null model 1, $p<0.001$ for all networks) or from differences in the number of interactions among species (null model 2, Abrolhos and Bonaire: $p<0.001$ for all networks; St Croix: $p=0.007$).

The ratio between species richness of cleaners and clients was higher than that between animals and plants in terrestrial mutualistic networks (figure 2*a*). In all cases, client richness was sevenfold higher than cleaner richness. However, this aspect of network structure did not affect the degree of nestedness in species-rich (more than 25 species) mutualistic networks ($F=2.18$, $p=0.15$, $n=45$ networks). In contrast, species richness markedly affected the degree of nestedness ($F=24.12$, $p<0.0001$). After controlling for the effects of species richness, cleaning networks show higher residual nestedness when compared with plant–animal mutualisms (figure 2*b*; $p=0.002$, randomization test, 10 000 randomizations). Thus, compared with plant–animal mutualistic networks of similar species richness, cleaning networks show more marked patterns of nested interactions.

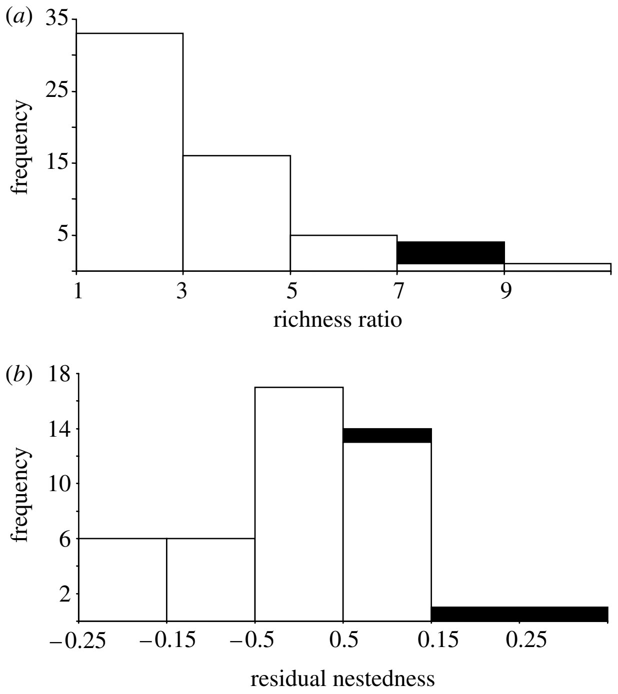

Figure 2. Frequency of networks per (*a*) richness ratio and (*b*) residual nestedness (see text for further details). Plant–animal mutualisms (white columns) and cleaning interactions (black columns).

4. DISCUSSION

Cleaning interactions differ in several ways from terrestrial mutualistic networks analysed so far. For example, previously studied terrestrial mutualisms involve interactions between plants and animals, often birds and insects (Jordano *et al.* 2003). In contrast, the cleaning interactions in the reef environment involve a completely different set of species (fishes and shrimps) in a completely different ecosystem. Additionally, our study demonstrates that the cleaning assemblages are characterized by a few (i.e. four to six) cleaner species that maintain a highly diverse coterie of clients (typically more than 20 species). This difference in richness of cleaner and client assemblages is much higher than those observed for plants and animals in terrestrial mutualisms (Jordano *et al.* 2003; Vázquez & Aizen 2004). Thus, it is expected that the dynamics of cleaning symbiosis is more affected by evolutionary and ecological changes in one assemblage of species (cleaners) than plant–animal mutualisms.

In spite of differences in the component species or in basic properties of interacting assemblages, all these mutualistic interactions show strong patterns of nestedness, in which species with few interactions are linked to a core of species with many interactions. Therefore, our study broadens previous findings for interactions between terrestrial plants and animals (Bascompte *et al.* 2003; Guimarães *et al.* 2006) and indicates that mutualisms evolve to a predictable community-level structure (Thompson 2005; Lewinsohn *et al.* 2006), be it in terrestrial or marine assemblages.

Although caution is needed due to our small sample, our results suggest that cleaning networks may be more nested than terrestrial mutualisms with similar species richness. Thus, cleaning networks are even more asymmetric than plant–animal mutualisms in terms of the specificity of their interactions. Future studies should investigate the relative importance of ecological and evolutionary processes that might lead to the nested pattern. Symmetric interactions (i.e. reciprocal levels of specificity among interacting partner species) in plant–animal networks may be a result of the evolutionary history constraining interactions (Lewinsohn *et al.* 2006). Thus, we hypothesize that cleaning mutualisms may be less affected by phylogenetic constraints than other mutualisms. Consequently, convergence (Thompson 2005) and the variation in local assemblage composition to differences in abundances (Lewinsohn *et al.* 2006) would act more freely to generate a highly nested structure such as that in the present study. Clients and cleaners may select their partners preferring some species or individuals over others (e.g. Sazima *et al.* 1999). In fact, recent macroecological analyses support this idea and indicate that abundance, together with client's diet, size and behaviour, may play a key role on the patterns of interactions among cleaners and clients (Floeter *et al.* in press).

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Conclusões

Este estudo contribui de três formas diferentes para o desenvolvimento de uma teoria de redes ecológicas e, mais especificamente, para a compreensão da origem e da generalidade dos padrões observados em redes de interações mutualísticas:

1. *Quais são os fatores subjacentes à forma da distribuição do grau observada em redes mutualísticas?*

Através de uma abordagem estatístico-matemática demonstrou-se que a distribuição do grau observada em redes mutualísticas poderia ser explicada pelo tamanho pequeno dessas redes, associado a dois processos previamente desconsiderados: a condição inicial da rede e a diferença de riqueza entre plantas e animais. Após este estudo, está disponível na literatura um conjunto de modelos candidatos a explicar a distribuição do grau observada em redes mutualísticas (Guimarães et al. 2005; Jordano et al. 2003) e estudos futuros terão que desenvolver novas métricas capazes de selecionar entre os modelos candidatos (Levin 1992).

2. *Qual a importância da variação de abundância entre espécies para a estrutura de redes mutualísticas?*

Através da introdução de uma nova abordagem computacional e de um estudo de caso, corroborou-se a idéia de que abundância é um fator fundamental subjacente à estrutura de redes mutualísticas (Jordano 1987; Vazquez & Aizen 2003; Vazquez & Aizen 2004) e, especificamente, à estrutura aninhada (Lewinsohn et al. 2006). No entanto, 40% da estrutura aninhada não foram explicados por variações de abundância entre as espécies. Essa porcentagem da estrutura aninhada pode estar associada a outros fatores ecológicos como aspectos da biologia das plantas e animais que impossibilitam as interações entre as espécies (Jordano et al. 2003) ou a processos coevolutivos que restringem o número de interações de espécies (Thompson 2005). Estudos futuros deverão investigar a importância de processos coevolutivos e ecológicos para o aninhamento.

A relação positiva entre número de interações e abundância sugere que a estrutura de redes mutualísticas deve ser bem robusta a perturbações como a extinção de espécies.

Posteriormente, deve-se investigar através de simulações numéricas qual o grau de robustez da estrutura dessas redes a processos de perda de espécies raras.

3. *Qual a generalidade do padrão aninhado em redes ecológicas?*

Ao se demonstrar que a ausência de aninhamento observado em interações predador-presa (teias tróficas) (Bascompte et al. 2003) não é explicada por problemas de resolução taxonômica, este estudo corrobora a idéia de que mutualismos e antagonismos diferem fundamentalmente em sua organização (Guimarães et al. 2006; Thompson 2005).

O estudo das interações entre formigas e plantas produtoras de néctar extrafloral e das interações entre limpadores e clientes em recifes de corais corroborou a idéia de que mutualismos se organizam como redes aninhadas, independentemente da localidade e da natureza do mutualismo (Bascompte et al. 2003). De fato, este estudo generaliza o padrão de aninhamento anteriormente descrito apenas para mutualismos reprodutivos entre plantas e animais (polinização e dispersão de sementes) e sugere que esta estrutura é comum a todos os tipos de mutualismo.

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Anexo

Este anexo contém o manuscrito publicado descrevendo o programa aninhado, utilizado nas análises dos capítulos 3 a 6.

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Improving the analyses of nestedness for large sets of matrices

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Abstract

Nestedness is a property of binary matrices of ecological data and quantified by the matrix's temperature, *T*. The program widely used to calculate *T* is Nestedness Temperature Calculator (NTC). NTC analyses matrices individually, turning the analysis of large sets time-consuming. We introduce ANINHADO, a program developed to perform rapid and automatic calculation of *T* over 10,000 matrices. ANINHADO can be useful to minimize the time spent in analysis and to compare real data against a variety of null models that typically generate a large number of replicates.

Keywords: Biogeography; Community assembly; Ecological networks

Software availability

Name of software: ANINHADO
Developers: Paulo Guimarães and Paulo R. Guimarães Jr.
Platform: MS-DOS under Windows.
Contact address: Instituto de Biologia, UNICAMP, CP 6109, Campinas, SP, Brazil
Telephone: +55 19 97861978
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Availability: http://www.guimaraes.bio.br

Environmental scientists have been studying systems to discover for the patterns of the underlying processes. Many of these patterns are described in binary or presence/absence matrices (Bascompte et al., 2003). Nestedness is a pattern (Fig. 1), which characterizes distributions of species within a habitat (Atmar and Patterson, 1993), parasites among hosts (Worthen and Rohde, 1996), and interactions in ecological networks (Bascompte et al., 2003).

The degree of nestedness of a matrix can be quantified by the matrix's temperature (*T*), a measure of how the presence/absence pattern departs from perfect nestedness (calculated by NESTEDNESS TEMPERATURE CALCULATOR (NTC), see Atmar and Patterson, 1993). Nevertheless, as the studies about nestedness have increased, some analyses cannot be optimally performed using NTC, leading to the necessity of new tools. Here we introduce ANINHADO, a program developed to attend to one of these needs: the rapid, automatic calculation of *T* for many matrices.

NTC is a Visual Basic package downloadable at http://aics-research.com/nestedness/tempcalc.html. It implements a good graphical user interface, intuitive menus, it includes background information about the nestedness theory and it also allows hypothesis testing: the observed value of *T* can be compared with the expected one under the assumption that presences were randomly assigned to any cell within the matrix. The graphical user interface and the supporting documentation about nestedness theory make NTC a convenient tool for users willing to analyze a limited number of matrices. However, the user needs to load and calculate *T* from each matrix individually, making the calculation of *T* time-consuming when there are many matrices to examine.

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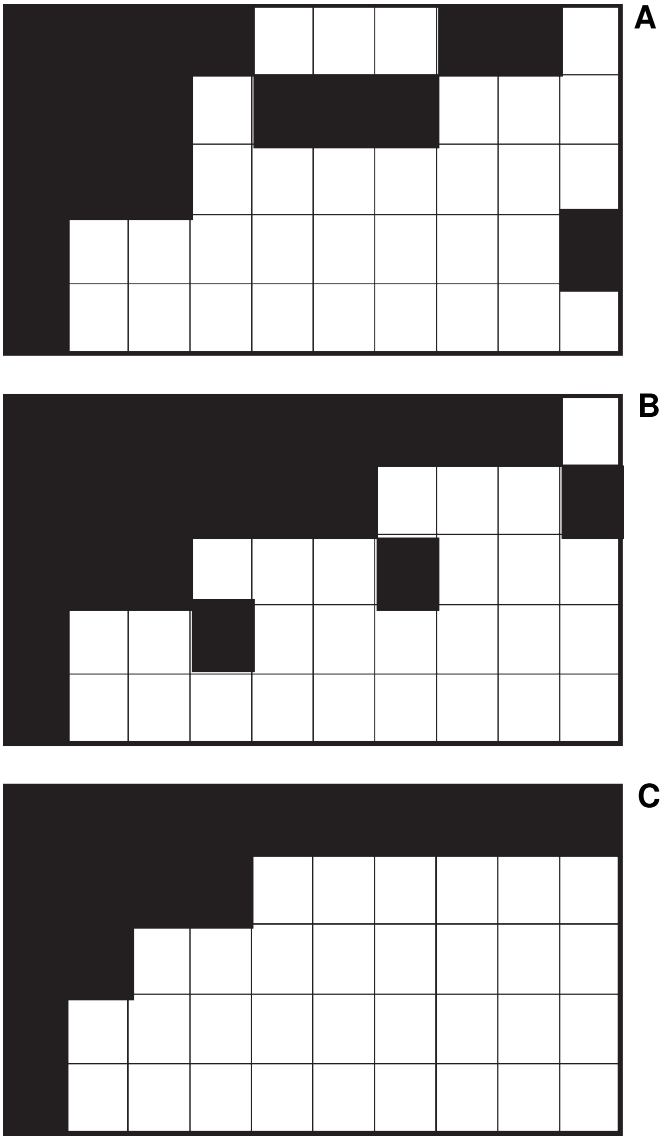

Fig. 1. Hypothetical matrices describing presences (black squares) of species (rows) in locations (columns). Nestedness occurs when presences in a row/column is often a subset of presences recorded in rows/columns with more presences. The matrices vary in their degree of nestedness: low (A), high (B), and perfect (C).

Table 1
Performance of NTC and ANINHADO using a Mobile Intel Pentium 4, 2.8 GHz CPU processor

	NTC	ANINHADO
Matrices/run	One	10,000
Matrices/min	~8	>80
Automatic processing	No	Full

The C++ software ANINHADO was developed to perform rapid, automatic calculation of T of many matrices (Table 1). ANINHADO analyzes a set of user-specified matrices and generates a file containing their names and respective T values. Moreover ANINHADO does not require the user‘s interaction during its execution, and it is therefore possible to perform other tasks in the computer during the analysis.

The automatic processing capabilities and speed of ANINHADO are also an asset when the user is interested in analyzing sets of real matrices or when testing null models other than the one implemented in NTC (Bascompte et al., 2003). The null model approach is based on the comparison of real data with an empirical distribution obtained from the analysis of thousands of algorithm-generated matrices that deliberately exclude an influence (Gotelli and Graves, 1996). As a consequence, the rigorous characterization of the expected T for an alternative null model will consume hours of continuous work in NTC, but only few minutes in ANINHADO. Additionally, ANINHADO generates empirical distributions for four pre-determined null models, allowing users not familiarized with programming to compare their data against alternative hypotheses.

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