Plant-Animal Mutualistic Networks: The Architecture of Biodiversity

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coevolution, complex networks, mutualism, pollination, seed dispersal

Abstract

The mutually beneficial interactions between plants and their animal pollinators and seed dispersers have been paramount in the generation of Earth's biodiversity. These mutualistic interactions often involve dozens or even hundreds of species that form complex networks of interdependences. Understanding how coevolution proceeds in these highly diversified mutualisms among free-living species presents a conceptual challenge. Recent work has led to the unambiguous conclusion that mutualistic networks are very heterogeneous (the bulk of the species have a few interactions, but a few species are much more connected than expected by chance), nested (specialists interact with subsets of the species with which generalists interact), and built on weak and asymmetric links among species. Both ecological variables (e.g., phenology, local abundance, and geographic range) and past evolutionary history may explain such network patterns. Network structure has important implications for the coexistence and stability of species as well as for the coevolutionary process. Mutualistic networks can thus be regarded as the architecture of biodiversity.

1. INTRODUCTION

Network: a set of nodes (e.g., species) connected through links (e.g., trophic or mutualistic interactions)

Charles Darwin was fascinated by the almost perfect match between the morphology of some orchids and that of the insects that pollinate them (Darwin 1862). Darwin realized that the reproduction of these plants was intimately linked to their interaction with the insects, and even predicted that the extinction of one of the partners would lead to the extinction of the other [p. 202: "If such great moths were to become extinct in Madagascar, assuredly the *Angraecum* would become extinct" (Darwin 1862)]. Since then, a myriad of scientific papers have described the mutually beneficial (mutualistic) interactions between plants and their animal pollinators or seed dispersers.

The classic paper by Ehrlich & Raven (1964) advocated that plant-animal interactions have played a very important role in the generation of Earth's biodiversity. As a matter of fact, flowering plants and insects are two of the major groups of living beings. The origin of flowering plants opened new niches for insect diversification, which in turn may have driven plant speciation. Alternatively, one group may have tracked the previous diversification of the other group without affecting it (Ehrlich & Raven 1964, Pellmyr 1992). In any case, animal-pollinated angiosperm families are more diverse than their abiotically pollinated sister clades (Dodd et al. 1999). These plant-animal interactions are found widely from the mid-Cretaceous period, more than 100 million years ago (Mya), but some preliminary adaptations to mutually beneficial pollination can be tracked as early as approximately the mid-Mesozoic era, almost 200 Mya (Labandeira 2002). Similarly, interactions with animal frugivores also played a central role in the diversification of plant fruit structures and dispersal devices. The early evolution of animal-dispersed fruits in the Pennsylvanian period, together with the diversification of small mammals and birds in the Tertiary period, allowed the widespread occurrence of biotic dispersal in higher plants (Tiffney 2004).

The current importance of mutualisms for biodiversity maintenance is supported by the fact that more than 90% of tropical plant species rely on animals for the dispersal of their seeds (Jordano 2000). Similar figures can be adduced for pollination (Bawa 1990). If these animals disappear, their plant partners may follow. The cascading consequences of the disappearance of large seed dispersers due to hunting or habitat loss, experienced through a reduction in seed dispersal or pollination, is an important threat to biodiversity (Dirzo & Miranda 1990, Kearns et al. 1998, Wright 2003). Information from the fossil record shows clearly that major extinctions of flowering plants resulted from episodes of insect diversity decline, for example during the Middle to Late Pennsylvanian extinction, during the Permian event, and at the Cretaceous/Tertiary boundary (Labandeira 2002, Labandeira et al. 2002). To assess the likelihood and magnitude of these coextinction cascades, we need a network approach to plant-animal mutualistic interactions.

Early studies on mutualistic interactions dealt mainly with species-specific patterns of interactions or reduced subsets of the whole community (Johnson & Steiner 1997, Nilsson 1988). Although examples of these highly specific pairwise interactions exist, such as Darwin's moth and the *Angraecum* (Darwin 1862, Johnson & Steiner 1997, Nilsson 1988), fig wasps and figs (Cook & Rasplus 2003), and yucca moths and yuccas (Pellmyr 2003), their strong emphasis in evolutionary studies probably reflects the aesthetics of such almost perfect matching, more than their frequency in nature (Schemske 1983, Waser et al. 1996). As a consequence, several researchers advocated a community context to address mutualistic interactions (Bronstein 1995, Feinsinger 1978, Fox 1988, Herrera 1982, Inouye & Stinchcombe 2001, Iwao & Rausher 1997, Janzen 1980, Jordano 1987, Petanidou & Ellis 1993, Waser et al. 1996). This opened the path for significant progress in the past two decades in the analysis of how pairwise interactions are shaped within small groups of species across time and space (Parchman & Benkman 2002, Thompson 1994, Thompson & Pellmyr 1992). The next frontier is the extension of these multispecific systems to embrace whole networks, to address the organization of these large assemblages of species by ecological and evolutionary processes, and to infer the consequences of network architecture for the persistence of biodiversity. This is the goal of this review. The rationale for this endeavor is that some questions can be only addressed using a network approach. For example, What are the community-wide consequences of a mutualism disruption or a species invasion? How does coevolution proceed in species-rich communities? Before trying to address these questions we need some tools and concepts that come from the study of other types of networks.

Erdös-Rényi random network: a set of nodes with a probability p that any two nodes chosen at random are connected by a link

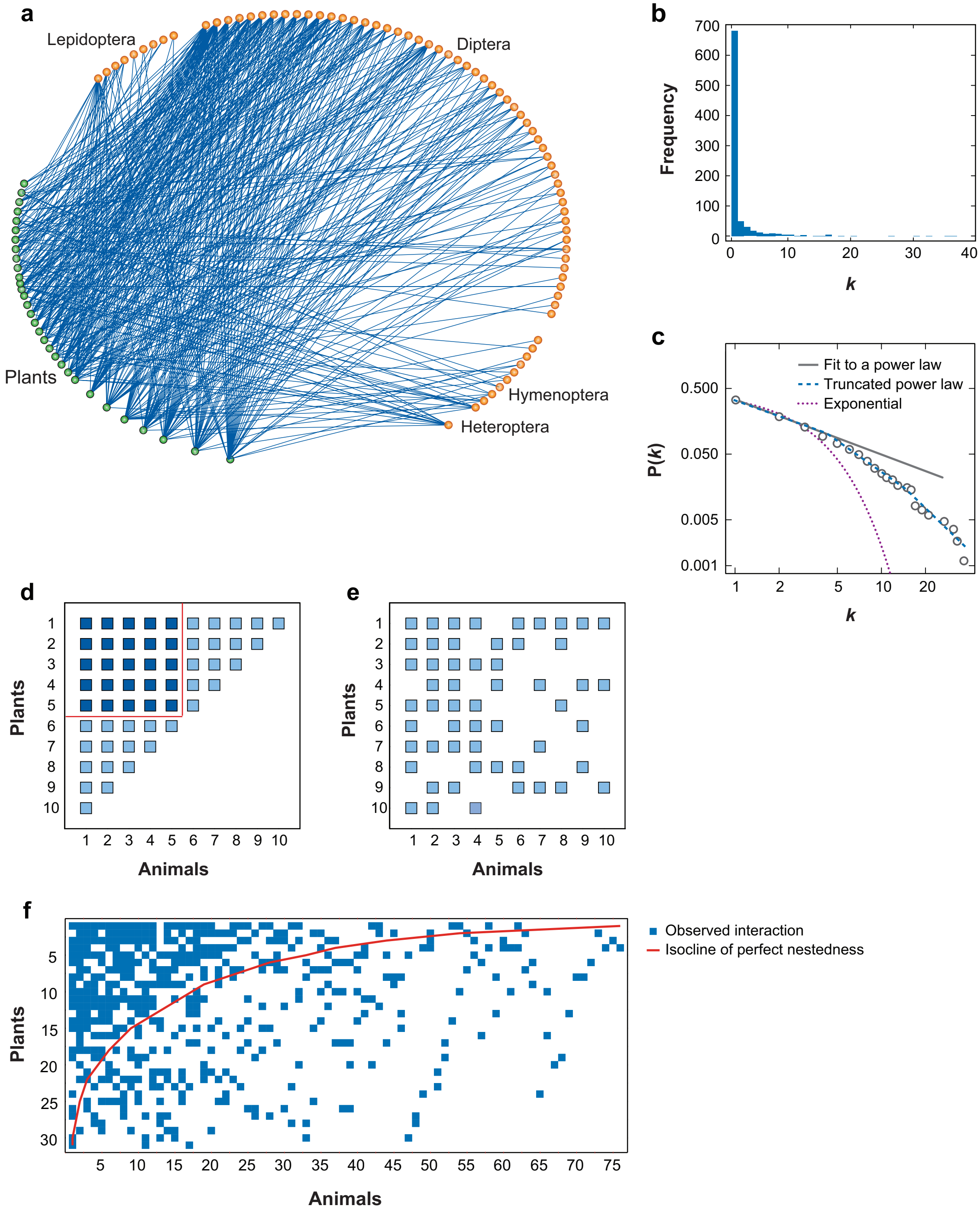
2. COMPLEX NETWORKS

2.1. A Network Approach to Complex Systems

The field of complex networks has grown extraordinarily in the last few years (Albert & Barabasi 2002, Amaral et al. 2000, Dorogovtsev & Mendes 2002, Newman 2003, 2004, Newman et al. 2006, Solé & Bascompte 2006, Strogatz 2001). Several systems that range from genetic networks to societies and the Internet have been described with a common framework in which elements (genes, proteins, or ecological species) are nodes connected by links. These links can take the form of gene activation, protein interaction, or species interactions such as predator-prey or mutualism (Albert & Barabasi 2002, Amaral et al. 2000, Dorogovtsev & Mendes 2002, May 2006, Montoya et al. 2006, Newman 2003, Proulx et al. 2005, Strogatz 2001, Watts 2003) (**Figure 1*a***). Historically, these networks have been described and analyzed by graph theory, an important field in mathematics.

The great mathematician Paul Erdös, together with Alfred Rényi, built graph theory by studying the simplest network: a random graph (Erdös & Rényi 1959). This random graph is defined by a set of nodes and a probability p that two such nodes chosen at random are connected by a link. Many mathematical theorems on these random graphs have been produced since then. For example, one can derive analytically the probability of finding a node with a specific number of links. The Erdös-Rényi model established a theoretical approach to complex networks. However, as we discuss below, it has limited applications to the real world because the majority of complex networks are much more heterogeneous, i.e., they show a huge variability in the number of links per node.

One of the most interesting contributions from recent research on complex networks is the recognition that several networks, despite differences in the nature of


a
Lepidoptera
Diptera
Plants
Hymenoptera
Heteroptera
b
Frequency
700
600
500
400
300
200
100
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20
30
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Fit to a power law
Truncated power law
Exponential
P(k)
0.500
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Observed interaction
Isocline of perfect nestedness

their nodes, exhibit similar statistical properties. This is important for at least two reasons: First, a common architecture may be related to common patterns of network formation. Second, structure greatly influences network robustness, which is measured as the fraction of the species that must become extinct for the resulting network to fragment into several disjointed pieces (Albert et al. 2000). Network theory has certainly led to a new approach in many different fields. For example, molecular biologists used to be limited to the study of a few genes at a time, but they can now develop extensive maps that describe how many such genes depend on each other for genetic control such as gene activation (Luscombe et al. 2004).

Ecology has a long tradition in the study of networks such as food webs (Cohen 1978, Cohen et al. 1990, May 1973, Pimm 1982) and other types of network-related processes (May 2006, Proulx et al. 2005). These studies mainly focused on global descriptors such as connectance (i.e., the fraction of realized links), compartments, fraction of top predators, and similar variables. Researchers recently revisited this area with new tools that illuminate community organization using a new generation of larger, more resolved food webs (Bascompte & Melián 2005, Belgrano et al. 2005, Montoya et al. 2006, Pascual & Dunne 2006).

Species degree: the number of different species a certain species interacts with; also known as generalization level

Degree distribution: the frequency distribution of the number of interactions per species

Scale-free network: a heterogeneous network in which the bulk of the nodes have a few links, but a few nodes are much more connected than expected by chance

2.2. Scale-Free Networks

A node is characterized by its degree, which is defined as the number of links to other nodes. A first measure of network structure is based on the concept of degree distribution, i.e., the frequency distribution of the number of links per node (**Figure 1*b***). Erdös-Rényi's random graphs are characterized by a degree distribution that follows a Poisson distribution (or an exponential one if the number of nodes keeps growing). The tail of this distribution is narrow: All nodes have a similar number of links, and the probability of a node having a number of links larger than the average drops very fast. In sum, random graphs are very homogeneous.

Conversely, complex networks such as the Internet are much more heterogeneous; the bulk of the nodes have a few interactions, but a few nodes are much more connected than would be expected by chance. These highly connected nodes are hubs that act as the glue to bring the network together. The average degree is not a good

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Figure 1

The architecture of plant-animal interaction networks. (*a*) A plant-pollinator network in Zackenberg Arctic tundra, Greenland that illustrates the pattern of interactions among insects (*orange dots*) and plants (*green dots*) (H. Elberling and J.M. Olesen, unpublished data). (*b*) Frequency distribution of the number of interactions per species, *k*, for pollinators in a temperate forest community in Kibune forest, Kyoto, Japan (Inoue et al. 1990). (*c*) Degree distribution is defined as the probability of one species interacting with *k* species. The lines illustrate the fit to a power-law (*gray line*), truncated power-law (*dotted blue line*), and exponential (*dashed purple line*) distributions. (*d–f*) Interaction matrices illustrate the situation of perfect nestedness (*d*), with a core of interactions among generalist species (*dark blue*), a random interaction pattern (*e*), and a real interaction network (*f*) [*f* corresponds to the graph in *a*]. A filled square indicates an observed interaction between plant species *i* in a row and animal species *j* in a column, and the line represents the isocline of perfect nestedness.

descriptor of such networks, because the variance is much higher. Mathematically, this heterogeneous distribution of degree is described by a power-law function:

Weighted networks: networks that include information on the intensity or weight of the interactions among nodes

$$p(k) \propto k^{-\gamma}, \qquad 1.$$

where $p(k)$ is the probability of a node having k links and γ is a critical exponent. This distribution is called scale-free because the relationship between k and $p(k)$ is not defined on a particular scale (Schroeder 1991). In a log-log plot, this relationship is given by a straight line of slope $-\gamma$ for the entire range of k values (**Figure 1*c***). This is not true for a distribution with an exponential tail that has a specific scale, the average number of links per node. In that case, the relationship between $\log k$ and $\log p(k)$ changes as one moves along the x-axis (Schroeder 1991).

2.3. Weighted Networks

Up to this point we have considered binary links. A next step is to characterize the intensity or weight of these interactions. A quantitative extension of degree is that of a node's strength, i.e., the sum of the weights of all its interactions (Barrat et al. 2004). In the case of world-wide air traffic, for example, we would consider the total number of passengers flying from one airport to another airport. The strength of an airport would be defined by the sum of such values, and would give us the quantitative importance of each airport (Barrat et al. 2004). Analogous to the degree distribution, one could also plot the strength distribution, that is, how many airports serve a certain range of passengers (Barrat et al. 2004).

2.4. Mechanisms of Network Buildup

We showed that Erdös-Rényi's random graphs do not reproduce some properties of the architecture of real networks. This finding called for the generation of new models of network formation. Specifically, the discovery that complex networks, such as the Internet and protein networks, have skewed connectivity distributions, and so do not fit the exponential decay expected for random networks, led to research on the simplest mechanism of network formation compatible with such a pattern. The answer was first provided by Simon (1955) and Price (1965), and later by Barabasi and colleagues (Barabasi & Albert 1999). Their model is called preferential attachment. Imagine a core of randomly connected initial nodes. Then, at each time step a new node is introduced and the new node tends to interact with an existing node with a probability proportional to its degree. That is, new nodes tend to interact preferentially with the most-connected nodes, leading to a kind of rich-gets-richer process. This simple self-organizing model generates power-law connectivity distributions as observed in real-world complex networks (Barabasi & Albert 1999).

2.5. One-Mode and Two-Mode Networks

Two main types of networks exist: one-mode and two-mode webs. In one-mode networks nodes belong to a single category, such as airports or genes. In principle, any node may be connected to another node. In two-mode networks there are two well-defined types of nodes, and interactions occur between but not within node types. Examples of two-node networks include social networks in which people are linked to a set of social events (Borgatti & Everett 1997). Two-mode networks are represented by bipartite graphs. Plant-animal mutualistic networks are by definition two-mode networks: Plants (green nodes in **Figure 1*a***) are pollinated or dispersed by animals (orange nodes in **Figure 1*a***). The bipartite representation of mutualistic networks illustrates explicitly the reciprocity involved in the interaction and helps in the understanding of the complex patterns that arise in highly diversified mutualisms (Bascompte et al. 2003, 2006b; Jordano 1987; Jordano et al. 2003, 2006).

Bipartite graph: the graphical representation of a two-mode network, consists of two sets of nodes with interactions between (but not within) sets

A bipartite graph is defined by an adjacency matrix whose elements a_{ij} will be 1 if plant i and animal j interact, and will be zero otherwise (**Figure 1*d*,*e***). In weighted networks, there are two such adjacency matrices: one for plants (P) and the other for animals (A). $d_{ij}{}^{P}$ represents the mutualism strength or dependence of the plant species i on the animal species j, and $d_{ji}{}^{A}$ depicts the dependence of animal species j on plant species i (**Figure 2*b***).

3. THE STRUCTURE OF PLANT-ANIMAL MUTUALISTIC NETWORKS

The concepts from network theory described above allow the visualization of interactions in highly diverse communities, and provide ways to quantify and compare network patterns across communities statistically. The first comparative study of mutualistic interactions from a network perspective is arguably the study by Jordano (1987). The past five years have seen a tremendous explosion of studies on mutualistic networks (Bascompte et al. 2003, 2006b; Jordano et al. 2003; Memmott 1999; Memmott & Waser 2002; Thompson 2006; Vázquez & Aizen 2004). These first papers described the structure of mutualistic networks. We describe briefly the results on network structure in this section. Below, we discuss the potential mechanisms that led to the observed network structure and its implications.

3.1. Degree Distribution

Motivated by the discovery of scale-free networks in the Internet (Albert et al. 2000), and simultaneous to their search in food webs (Camacho et al. 2002, Dunne et al. 2002a, Solé & Montoya 2001), Jordano and colleagues (2003) explored the degree distribution of 29 plant-pollinator networks and 24 plant-frugivore networks in natural communities. The bulk of the cases for both plants and animals (65.6%) showed degree distributions with a power-law regime but decaying as a marked cut-off (i.e., truncated power-laws or broad-scale networks); a few cases (22.2%) showed scale-invariance. The remaining networks either best fit an exponential distribution or showed no fit at all. The truncation of the degree distribution is described by the following equation:

$$p(k) \propto k^{-\gamma} e^{-k/k_c}, \qquad 2.$$

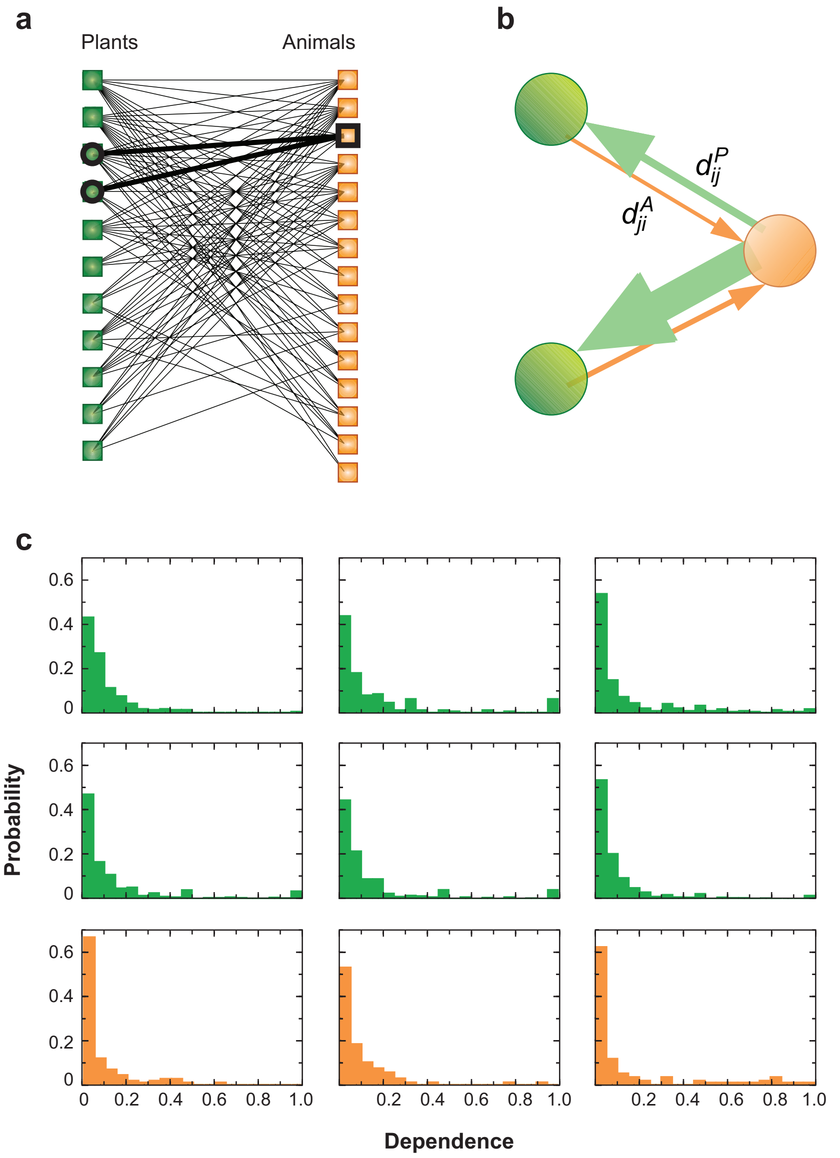


Figure 2

Weighted networks of plant-animal interactions. In an interaction web (*a*), we can represent the strength of mutual dependences between interacting species by the variable thickness of the links, shown in (*b*). For each pairwise interaction, two values of mutual dependence are obtained: $d_{ji}{}^{A}$ for the dependence of the animal species *j* on plant species *i* (*orange arrow*), and $d_{ij}{}^{P}$ for the dependence of plant species *i* on animal species *j* (*green arrow*). (*c*) Examples of the frequency distributions of dependence values for animals and plants in several communities, which illustrates the marked skew in interaction strength. Histograms in green represent dependences of plants on pollinators; orange represents dependences of animal frugivores on plants. Modified from Bascompte et al. (2006b).

where the new term in relation to Equation 1 is e^{-k/k_c}, which defines the exponential cut-off. Mutualistic networks are still much more heterogeneous than expected by chance (i.e., the bulk of the species have a few interactions and a few species have a very large number of interactions), although not as heterogeneous as scale-free networks. The exponential truncation in Equation 2 signifies that as the number of interactions reaches the critical k_c value, the probability of finding more connected species drops faster than expected for a power-law (**Figure 1*c***). Both plant-pollinator and plant–seed disperser networks show the same degree distribution: The data for different communities collapse to a simple scaling function when the scaled cumulative distributions of links per species, $k^{-\gamma} P(k)$ are plotted versus the scaled links per species (k/k_c) (p. 74, Jordano et al. 2003). This result reveals a shared pattern of internal topology that is independent of scaling considerations (Bersier et al. 1999, Sugihara et al. 1989), which is evident only upon examination of the whole network of interactions, not just isolated species (Jordano et al. 2003). Regardless of the differences in latitude, ecosystem properties, and species composition, mutualistic networks display a common and well-defined connectivity distribution (Jordano et al. 2003).

Nestedness: a pattern of interaction in which specialists interact with species that form perfect subsets of the species with which generalists interact

3.2. Nestedness

This concept of network structure originated in the field of island biogeography and describes the pattern of species presences across islands (Atmar & Patterson 1993, Patterson & Atmar 1986). In the previous section we looked at the number of interactions per species without noticing the identity of the partners. Nestedness relates the set of animals that interact with one plant species, for example, with the set of animals that interact with another plant species (**Figure 1*d*,*e***). Bascompte and colleagues (Bascompte et al. 2003) studied 27 plant-frugivore networks and 25 plant-pollinator networks and concluded that these networks are neither randomly assembled nor organized in compartments arising from tight, reciprocal specialization. Plant-animal mutualistic networks are highly nested (**Figure 1*f***). That is, specialists interact with species that form well-defined subsets of the species with which generalists interact. In other words, if we rank plants from the most specialized to the least specialized, we find that the set of animals a plant interacts with are contained in a larger set, which in turn is contained in a larger set, and so on, as in nested Chinese boxes (Bascompte et al. 2003).

Two properties arise from a nested matrix (**Figure 1*d***). First, there is a core of generalist plants and animals that interact among themselves. Therefore, a few species may be involved in a large number of interactions, which introduces functional redundancy and the possibility for alternative routes for system persistence if some of these interactions disappear. Thus, all species are very close to each other, which is also noted by the small path lengths or the average minimum number of intermediate species that separate two given species (Olesen et al. 2006). A few species in the core may drive the selective forces experienced by species that are subsequently attached to this network (Thompson 1994). Second, asymmetries exist in the level of specialization. That is, specialists tend to interact with the most generalist species (**Figure 1*d***), as noted independently by Vázquez & Aizen (2004). Generalists tend to be more abundant, less-fluctuating species compared with specialists because generalists rely on so many other species. Thus, other things being equal, this asymmetrical structure provides pathways for the persistence of specialists (Bascompte et al. 2003). Essentially, nestedness means that mutualistic networks are very cohesive. As for the connectivity distribution, regardless of the type of mutualism and the ecological details, all communities are organized similarly (**Figure 1*f***).

Researchers recently looked for nestedness in other types of mutualisms and different interactions (Guimarães et al. 2007b, Lafferty et al. 2006, Ollerton et al. 2003, Selva & Fortuna 2007). For example, Guimarães et al. (2006) analyzed ants and extrafloral nectary-bearing plants and found that nestedness values are very similar to the values reported previously for pollination and seed dispersal (Bascompte et al. 2003). Nestedness is found in fish parasites (Poulin & Valtonen 2001), marine cleaning mutualisms (Guimarães et al. 2007b), and scavenger communities (Selva & Fortuna 2007). In relation to food webs, analogous two-mode networks such as plants and herbivores or herbivores and carnivores are significantly less nested than mutualistic networks (Bascompte et al. 2003). This result is in agreement with the finding of a larger propensity for compartments in plant-herbivore networks (Lewinsohn et al. 2006). Finally, the consideration of parasites increases the level of nestedness of the food web, which may increase the cohesion and robustness of the whole network (Lafferty et al. 2006). Other properties of food webs, such as their organization in subwebs (Melián & Bascompte 2004) and the correlation between the degree of a species and the average degree of the species with which it interacts (Melián & Bascompte 2002), also show a cohesive core of generalists.

3.3. Dependences and Asymmetries

The network properties discussed above are based on qualitative data. Mutualism strength or the dependence of a plant species on an animal species has been estimated as the relative frequency of floral visits or the relative frequency of fruits consumed by that particular animal species (Bascompte et al. 2006b, Jordano 1987) (**Figure 2*a*,*b***). Similarly, the dependence of an animal species on a plant species has been estimated as the relative frequency of fruits consumed that come from that particular plant species. Pairwise dependence seems to be a good surrogate for the total effects of a pairwise interaction in most networks (Vázquez et al. 2005).

As noted in the examples plotted in **Figure 2*c***, the frequency distribution of dependence values is highly skewed, with many weak values and a few strong dependences (Bascompte et al. 2006b, Jordano 1987). This abundance of weak interactions has been reported also in food webs (Bascompte et al. 2005, Fagan & Hurd 1994, Paine 1980, 1992; Raffaelli & Hall 1995, Ulanowicz & Wolff 1991, Wootton 1997) and nonbiological networks (Barrat et al. 2004). Interestingly enough, mounting evidence suggests that the dominance of weak interactions in food webs promotes community persistence and stability by buffering the transmission of perturbation through the whole community (Bascompte et al. 2005, Kokkoris et al. 1999, May 1973, McCann et al. 1998). Researchers compiled weighted interaction networks for host-parasitoid interactions (Müller et al. 1999, van Veen et al. 2006), which led to a community-wide quantification of parasitism rates and the role of indirect interactions (Müller et al. 1999).

The combination of the two dependence values within a plant-animal pair (**Figure2*b***) is highly asymmetric (Bascompte et al. 2006b, Jordano 1987) but not more asymmetric than expected on the basis of the skewed distribution of dependence values (Bascompte et al. 2006b). However, in the few cases in which a plant species, for example, is highly dependent on an animal species, then that animal tends to rely significantly less on the plant (Bascompte et al. 2006b). Brazil's manduvi tree, for example, depends almost entirely on the Toco toucan to disperse its seeds, but this is not an exclusive relationship: The toucan also depends on a large, diverse group of other fruiting species. This asymmetry may help interdependent groups of species coexist, because if both plant and animal depend strongly on each other, a decrease in plant abundance will be followed by a similar decrease in the animal abundance, which in turn will feed back on its partner. This kind of downward loop is less common in uneven relationships because the plant could recover by relying on a generalist partner that depends on many other species. This verbal argument is shown mathematically as reviewed in section 5.2. Similar constraints in the combination of interaction strength values in food chains (e.g., avoiding strong interactions in long loops or in successive levels of tri-trophic food chains) also enhances food-web stability (Bascompte et al. 2005, Neutel et al. 2002).

Species strength: the sum of dependences or interaction strengths of the animals on a specific plant species, or the sum of dependences of the plants on a specific animal species

3.4. Species Strength

To explore how the weak, asymmetric dependences described in the previous section shape the whole network, we now consider the frequency distribution of species strength. A quantitative extension of species degree, species strength can be defined as the sum of dependences of the animals on a specific plant, or the sum of dependences of the plants on a specific animal. Species strength represents a measure of the quantitative importance of a species for the other set. Species strength increases faster than species degree (Bascompte et al. 2006b). Thus, mutualistic networks are even more heterogeneous when quantitative information is used.

Nestedness can partially explain this higher-than-expected strength of generalists in plant-animal assemblages. Owing to the nested structure, species with high degree interact with specialists. Because specialists by definition interact exclusively with these generalists, specialists contribute largely to increase the strength of generalists. When we described nestedness, we focused on asymmetry at the level of species. In this section we focus on asymmetry at the level of links, which certainly builds on the previous asymmetry. Further work should quantify what component of asymmetry at the link level is explained by asymmetry at the species level.

3.5. Network Structure and Sampling Effort

To conclude this section on network structure, we now briefly consider how robust these patterns are in terms of resolution and sampling effort. Some of the network patterns described here, such as degree distribution or nestedness, are defined using binary data, i.e., assuming that all links are the same. To what degree do these results stand up when quantitative information is used? As noted above, weighted extensions of both species degree (strength) and asymmetry of generalization (link asymmetry), confirm and expand on results obtained by the analysis of binary data. Once more, these networks seem to be very heterogeneous and asymmetric. Thus, the previous results are not an artifact of using binary data. In relation to sampling effort, the only study to our knowledge that addressed the issue of sampling effort on network structure explicitly concluded that nestedness is quite robust. Even when the number of species and, especially, the number of interactions grow with sampling intensity (both in time and space), the value of nestedness converges when a minimum sampling effort is reached (Nielsen & Bascompte 2007).

Forbidden links: pairwise interactions that are impossible to occur, for example, owing to phenological or size mismatch

4. ECOLOGICAL AND EVOLUTIONARY PROCESSES

Once network patterns are described, we may investigate the suite of ecological and evolutionary mechanisms that are responsible for generating such patterns. We saw above that physicists studied preferential attachment to generate some network patterns such as power-law degree distributions. One avenue is to explore to what degree several modifications of these basic mechanisms produce most network patterns. For example, which mechanisms lead to truncated power-law connectivity distributions? The most basic explanation is small size effects, i.e., the truncation of a power-law owing to the fact that the network is not large enough to accommodate extremely connected species (Guimarães et al. 2005, Jordano et al. 2003, Keitt & Stanley 1998, Mossa et al. 2002). However, Jordano and colleagues (2003) found that the frequency of truncated power-laws was not larger among the smallest communities, which suggests that other explanations are at work. Knowledge of the natural history of the mutualisms gives rise to a related explanation, the concept of forbidden links (Jordano et al. 2003, 2006). This refers to the fact that, in opposition to other nonbiological networks, some connections are not currently possible (at least over ecological time scales, e.g., one assumes no adaptation occurs) because of phenological or size constraints. A plant, for example, would not interact with a pollinator that is a late season migrant arriving at the community after the flowering period. A small bird, for example, would not be able to disperse the seeds of a species producing very large fruits. In one of the communities studied by Jordano and coworkers (2003), 51% of the nonobserved interactions were due to phenological uncoupling, and 24% were due to size restrictions.

Conversely, Vázquez (2005) proposed a neutral explanation in which network patterns can be explained on the basis of species abundance and random interactions. Researchers have claimed that abundance is a major factor in the explanation of network patterns, although most recent papers tend to shift the explanation back to the role of forbidden links (Santamaría & Rodríguez-Gironés 2007) or to a combination of abundance and forbidden links (Blüthgen et al. 2006, Stang et al. 2007). Santamaría and Rodríguez-Gironés (2007) discuss three reasons why neutrality should be rejected as the most parsimonious explanation of network topology in favor of forbidden links. First, it is not clear whether generalist species are generalists because they are more abundant or vice versa (Stang et al. 2007). Second, recent work by Blüthgen and coworkers (2006) has challenged the tenet that species abundance determines the frequency of interaction. Third, neutral theory assumes that the phenotypic characteristics of interacting species are irrelevant for network patterns, which contradicts strong confirmations for forbidden links (Jordano et al. 2003).

Forbidden links operate as constraints on the preferential attachment mechanism. Other mechanisms can explain truncations without such constraints. For example, when the initial core of species over which the preferential attachment operates is large enough, power-laws become truncated (Guimarães et al. 2005) without the need to adduce any further explanations. Also, the two-mode nature of these networks imposes truncations that would not be observed in one-mode networks if, for example, one of the sets (plants or animals) is much larger than the other (Guimarães et al. 2007a).

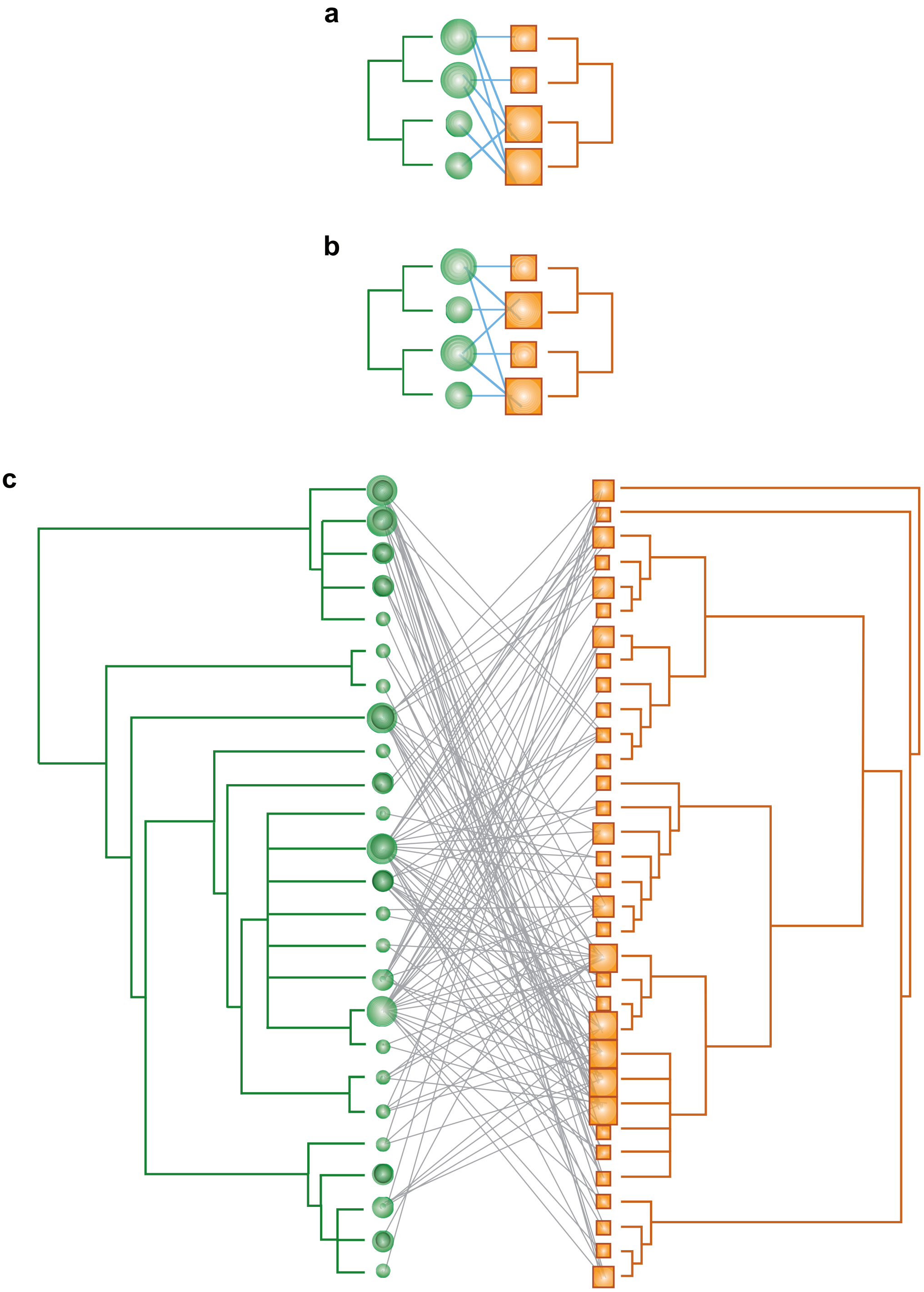
Phylogenetic signal: tendency of phylogenetically similar species to have similar phenotipic attributes

How are these basic mechanisms of network build-up mediated in ecological networks? For example, preferential attachment may be at work, but it may not necessarily act through species degree. If degree is correlated with any other ecological property, such as local abundance or geographic distribution, a new species may tend to become attached to the most abundant or more widely distributed species. Also, species are not independent entities but related to a common evolutionary history. Thus, we must first determine the magnitude of the phylogenetic signal in a species position (e.g., number of interactions, or with whom it interacts) in the network. In sum, we must look at the details of the species forming the network.

4.1. Phylogenetic and Ecological Correlates

Understanding interaction patterns from a biological perspective requires a combination of phylogenetic information and information on species' ecological traits to estimate effects on associations (Ives & Godfray 2006). Phylogenetic signal is the tendency of species closer in the phylogeny to have similar network properties (Blomberg et al. 2003, Freckleton et al. 2002, Garland et al. 2005, Ives & Godfray 2006, Lewinsohn et al. 2005). For example, **Figure 3*a*** illustrates a case where phylogenetically related species tend to have the same number of interactions, whereas **Figure 3*b*** shows a scenario with no relationship between phylogenetic proximity and the number of interactions. Finding a phylogenetic signal informs us about the extent to which past evolutionary history determines both the position of species in the network (e.g., their degree and with whom they interact) and the global network architecture. The role of past evolutionary history in explaining network patterns highlights the limitations of explanations based exclusively on ultimate ecological factors (Herrera 1992; Ives & Godfray 2006; P. Jordano & J. Bascompte, submitted; Rezende et al. 2007a,b).

4.1.1. Phylogenies and species positions. In a study on phylogenetic signal on a species position in the network, Rezende and colleagues (2007b) built a large data set with 36 plant pollinator and 23 plant-frugivore mutualistic networks and compiled the phylogenies for each plant and animal community (**Figure 3*c***). These researchers found a significant phylogenetic signal in species degree (i.e., number of interactions per species) in approximately half of the largest phylogenies. Therefore, there is a tendency of species close in the phylogeny to have a similar number of interactions. However, species strength, the quantitative importance of a species for the other set, is only significant in 1 of the 38 phylogenies that correspond to weighted networks. The reason for this difference between degree and strength may lie in the fact that


a
b
c

abundance affects species strength strongly and abundance may respond to more proximate, local factors.

The second property of a species position in the network analyzed by Rezende and coworkers (2007b) is with whom each species interacts. One can create a matrix of ecological dissimilarity between species in which two plants, for example, are very distant if they are visited by different pollinator species. Similarly, one can construct a matrix of phylogenetic distance. Rezende and coworkers analyzed the correlation between these two distance matrices and found a significant correlation between ecological and phylogenetic distance in approximately one-half of the 103 available phylogenies. This means that two phylogenetically similar species tend to interact with the same subset of species. Also, ecological and phylogenetic distances correlate better among animals than among plants (more than half the correlations were significant for animals whereas one-third were significant for plants). One potential explanation involves evolutionary differences linked to mobility: By playing a more active role, animals can search and select with whom they interact, which promotes selection for specific floral or fruit phenotypes (Rezende et al. 2007b).

In summary, there is significant phylogenetic signal in both the number of interactions per species and with whom they interact.

4.1.2. Ecological correlates of species positions. P. Jordano and J. Bascompte (submitted) performed phylogenetically independent contrasts between the ecological traits of a species and two measures of its position in the network: degree and eigenvector centrality. Eigenvector centrality is defined as the connectance of a node measured as the number of interactions of the node in question and the number of interactions of the nodes to which it is connected (Borgatti & Everett 1997, Jordano et al. 2006). Their goal was to see to what extent variation in degree and centrality across species correlates with local abundance, body or fruit size, geographic range, and phenological spread after accounting for phylogenetic effects. Jordano and Bascompte used network, phylogenetic, and ecological information from two Mediterranean communities in Southern Spain, and found the following results: Geographic range is significantly correlated with species degree both for plants and animals in the two communities; phenological spread is significantly correlated with species degree in both plants and animals in one community, and only with plants in the second community; and abundance is significantly correlated with species degree only for animals in both communities.

←

Figure 3

A phylogenetic approach to mutualistic networks. (*a*) A scenario with a strong phylogenetic signal in species degree, so that phylogenetically related species tend to have a similar number of interactions. Green circles represent plants and orange squares represent animals. The size of the node is proportional to its degree. (*b*) A similar case without phylogenetic signal. The phylogenetic information can be incorporated in the analysis of complex webs of interaction as shown in (*c*); this example corresponds to a plant-frugivore community in southeastern Spain. Plant phylogenies in this community are shown in green and animal phylogenies are shown in orange. Modified from Rezende et al. (2007b).

Ecological factors such as abundance are certainly involved in shaping mutualistic networks (Jordano 1987, Jordano et al. 2003, Olesen et al. 2002, Vázquez & Aizen 2004). However, the magnitude and even direction of the correlation between species degree and abundance may change across species and communities (Blüthgen et al. 2006). Also, more explanatory power may exist in the interaction between two such factors, such as abundance and morphological constraints (Jordano et al. 2003, Stang et al. 2007, Santamaría & Rodríguez-Gironés 2007).

4.1.3. Phylogenies and global network patterns. We turn now to phylogenetic effects on global network patterns. P. Jordano and J. Bascompte (submitted) tested the effect of plant and animal phylogenies in the explanation of the global structure of interactions via the use of the statistical methods recently developed by Ives & Godfray (2006). Phylogenetic covariation patterns explain a significant fraction of the total variance of the interaction pattern at the whole-network level (P. Jordano & J. Bascompte, submitted). In this case, as opposed to the findings for a species position in the network, there is a more marked effect of phylogeny for plants. This suggests that the overall pattern of interaction is influenced markedly by the evolutionary history of the plants and is more labile when mapped against the phylogeny of frugivores.

In summary, the results of this explicit use of phylogenetic data in the study of mutualistic networks provide insights into the ongoing assembly process. Both ultimate ecological factors and the evolutionary history conveyed in the phylogenies explain network patterns. The phylogenetic patterns of shared ancestry play a key role in the explanation of both species positions in the network and the overall pattern of mutualistic associations between the two sets of species.

5. IMPLICATIONS OF NETWORK STRUCTURE

5.1. Coevolutionary Implications

Plant-animal mutualistic networks form the physical template on which coevolution may proceed. Heterogeneous, nested networks built on weak and asymmetric interactions confer a predictable pattern of links among species that can both be generated by and affect coevolution. Two coevolutionary forces in combination can potentially generate a nested network: coevolutionary complementarity and coevolutionary convergence (Thompson 2005, 2006). Pairwise interactions build up on traits that are complementary between a plant and an animal, such as the length of the pollinator's tongue and the length of the corolla. This complementarity is key for the success of the pairwise interaction, and it is based on phenotypic traits that play a role in the fitness outcome of the interaction for the two partners. Once this pairwise interaction is defined, other species can become attached to the network through convergence of traits. One example is the syndromes or convergence in fruit shape and color among species that are dispersed by mammals as opposed to birds. Support for the role of coevolutionary complementarity comes from simulations that indicate that phenotypic complementarity, particularly when several traits are involved, produces highly nested networks (Rezende et al. 2007a, Santamaría & Rodríguez-Gironés 2007).

The identity of the species in the core of a nested network, with the potential to drive the coevolution of the whole network, can change geographically. Local communities vary in species composition relative to regional pools of species, which results in different local assemblages of mutualists. This phenomenon provides a link between the two major theories that bring tractability to multispecific coevolutionary studies: network theory and the geographic mosaic theory (Bascompte & Jordano 2006, Thompson 1994, 2005). For example, to what extent is local network structure explained by properties at the landscape level? As we discussed in the previous section, a species degree is correlated with its geographic distribution. The most generalized species, those that form the core of the matrix, will probably be present across communities, whereas specialists may be more variable across communities (Bascompte & Jordano 2006).

5.2. Implications for Network Robustness

The architecture of mutualistic networks may have profound implications for robustness, which is defined as network resistance to species loss (**Figure 4**). Albert and coworkers (2000) illustrated that random networks with exponential degree distributions are very fragile: The network suddenly fragments after the removal of a small fraction of nodes. Conversely, a network with a scale-free degree distribution is very robust to the random loss of nodes, but very fragile to the extinction of the most generalist species (Albert et al. 2000). Similar species-deletion experiments in food webs provided information on the fragility of ecological networks (Dunne et al. 2002b, Pimm 1979, Solé & Montoya 2001) (**Figure 4**).

More recently, Memmott and coworkers (2004) simulated the progressive extinction of pollinators and explored the cumulative secondary extinction of the plants that depend on them (Jordano et al. 2006, Memmott et al. 2004, Morris 2003). Memmott and coworkers (2004) concluded that mutualistic networks are very robust and referred both to the truncated power-law degree distribution and to the nested structure as combined explanations for such robustness. On theoretical grounds, networks with truncated power-law distributions of the species degree (broad-scale, as opposed to the scale-free distribution) are less fragile to the loss of the most-connected nodes (Albert et al. 2000).

A second approach to network robustness is a dynamic approach. This approach describes whether small fluctuations around a steady state will amplify or die out (Bronstein et al. 2004, May 1973, Solé & Bascompte 2006). The analysis of a simple model of multispecies facultative mutualisms revealed that as community size increases, the average product of pair-wise mutualistic effects must decrease for the community to remain stable (Bascompte et al. 2006b). This is in agreement with two network patterns reported above, namely, the high frequency of weak dependence values, and their asymmetry when one dependence is large (Bascompte et al. 2006b). However, as with any analytic results, a number of strong assumptions are required to generate such a clear, straightforward expression (Bascompte et al. 2006a, Holland et al. 2006). One such assumption is that all animals interact with all plants, i.e., the model does not incorporate network structure. Fortuna & Bascompte (2006) took a

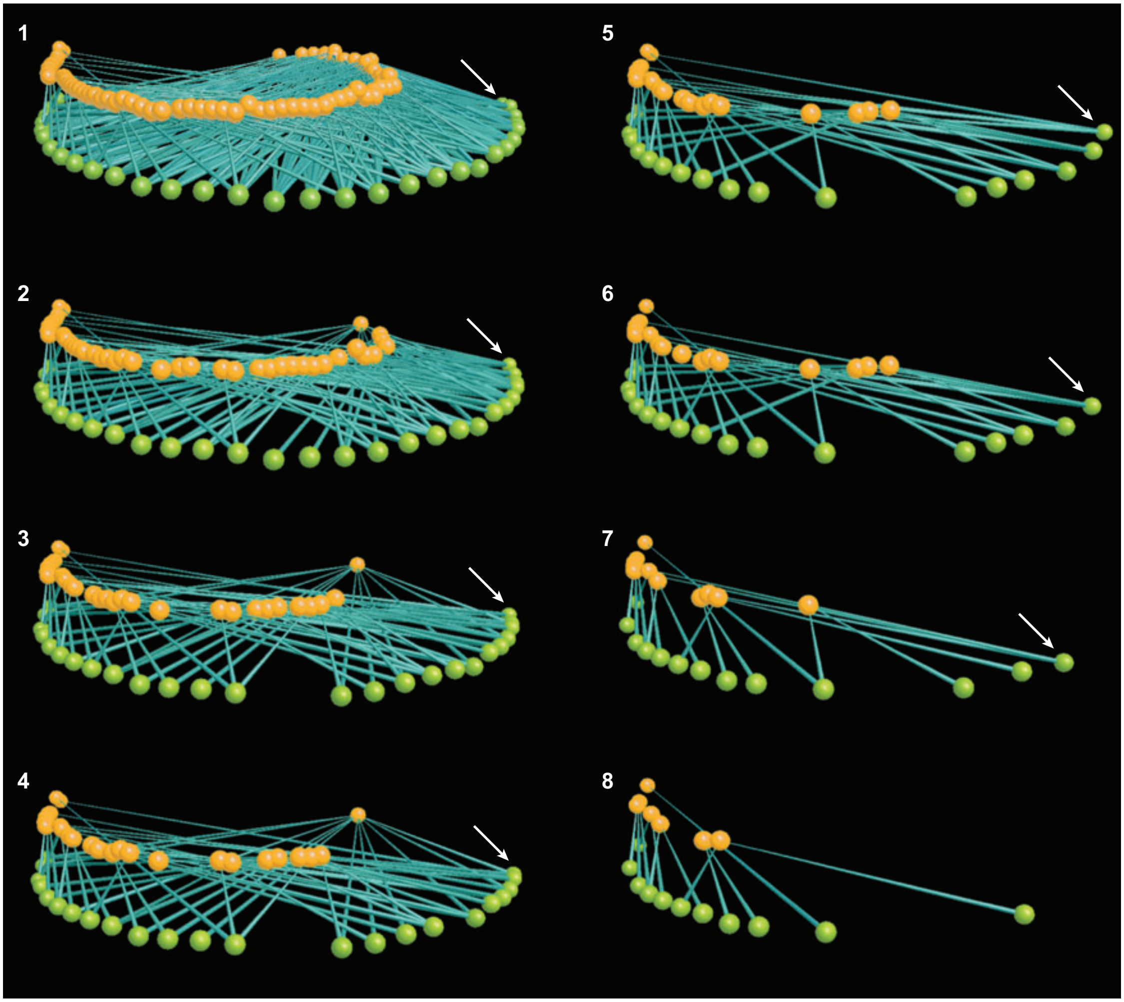


Figure 4

Consequences of species extinction on mutualistic networks. A single plant species is deleted at each step, from (*1*) to (*8*), starting from the most generalist species and proceeding toward the most specialist species. All species that become isolated undergo coextinction. In this case, the network is very fragile, as shown by the large number of secondary extinctions. However, the same network would be very robust (almost all species would persist) if the first species to go extinct were the specialists, or the loss of species was at random. The structure of the network, as described by its degree distribution (**Figure 1*b***) and nestedness (**Figure 1*f***), highly conditions network robustness to species extinctions. Image produced with FoodWeb3D, written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab (**http://www.foodwebs.org**).

first step toward introducing network structure in dynamical models by studying a metacommunity model in which species interact exactly as in two real mutualistic networks. Real networks, as compared with randomizations, start losing species sooner, but the community as a whole persists for higher values of habitat loss (Fortuna & Bascompte 2006). This robustness is again explained by both the heterogeneous degree distribution and the cohesive organization in nested systems.

5.3. Implications for Conservation Biology

The fact that mutualistic networks form well-defined and predictable patterns of interdependences provides a community-wide perspective for species conservation. For example, because of the asymmetry in specialization, both specialist and generalist plant species exhibit similar reproductive susceptibility to habitat loss: Although specialists depend on a single resource, they tend to interact with the most generalist animal species. Other things being equal, generalist animals tend to be more abundant (Ashworth et al. 2004).

The invasion of exotic species is a leading factor in mutualism disruptions (Bronstein et al. 2004, Traveset & Richardson 2006). At least three papers explored how network structure affects the likelihood of invasions (Memmott & Waser 2002, Morales & Aizen 2006, Olesen et al. 2002). All three studies concluded that invasive species become well integrated into the existing pollination network. Memmott & Waser (2002), for example, conclude that a lower number of pollinator species visited flowers of alien plants compared with native plants, but these insects were extremely generalist (Memmott & Waser 2002). This asymmetry in specialization is in agreement with the predictions of a nested community as noted above. Thus, network architecture provides alien species with more abundant and reliable resources. However, disagreement exists regarding the likelihood of invader complexes, groups of plant and animal invaders that rely more on each other than on native species (Olesen et al. 2002). These invader complexes are important because they can increase invasion speed and establishment success greatly. Whereas Olesen and colleagues (2002) found that introduced plants and pollinators do not interact as much as expected by chance, and so there is no evidence of invader complexes (Olesen et al. 2002), Morales & Aizen (2006) found that alien flower visitors were more closely associated with alien than with native species.

Another issue in conservation biology that requires a network approach is defaunation, which is an increasing problem in tropical ecosystems and has far-reaching consequences for biotic interactions (Dirzo & Miranda 1990). Hunting preferentially targets large species of mammals and birds that play a paramount role in seed dispersal because they are highly mobile and contribute disproportionately to connectivity in fragmented landscapes. The community-wide effects of the extinction of such large species depends on the structure of mutualistic networks and their ecological correlates (see above). For example, are large-bodied frugivores randomly scattered through the matrix of interactions, or are they more likely the generalists forming the core? In the latter case, the nested structure of mutualistic networks implies that losing these few species may induce a collapse of the whole network, which is defined as the fragmentation of a previous single-connected cluster into a set of disconnected subsets.

SUMMARY POINTS

1. Mutually beneficial interactions such as pollination and seed dispersal form heterogeneous, nested networks built on weak and asymmetric links among animal and plant species.
2. Researchers find a common, well-defined network architecture regardless of the type of mutualism, species composition, latitude, and other variables.
3. Mutualistic networks can be approached neither as collections of pair-wise, highly specific interactions nor as diffuse, random assemblages.
4. The above network patterns may facilitate species persistence; mutualistic networks can thus be regarded as the architecture of biodiversity.
5. Several ecological factors and evolutionary history contribute to create the observed network patterns.

FUTURE ISSUES

1. The field requires an exploration of how mutualistic networks change in time and space.
2. Also needed is the development of a mathematical theory for mutualistic networks that is aimed at linking network structure and dynamics.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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RELATED RESOURCES

Software packages for the analysis of complex networks:

Aninhado **http://www.guimaraes.bio.br/sof.html**

A software package for estimation of nestedness using NTC algorithm but including new null models.

Guimarães PR Jr, Guimarães PR. 2006. Improving the analyses of nestedness for large sets of matrices. *Environ. Model. Softw.* 21:1512–13

Binmatnest **http://www.eeza.csic.es/eeza/personales/rgirones.aspx**

Another package calculating the nestedness temperature of binary presence-absence matrices in a different way than the NTC.

Rodríguez-Gironés MA, Santamaría L. 2006. A new algorithm to calculate the nestedness temperature of presence-absence matrices. *J. Biogeogr.* 33:924–35

FoodWeb3D **http://www.foodwebs.org/index_page/wow2.html**

Written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Lab (**http://www.foodwebs.org**).

Libraries sna, network, nettheory in R package **http://www.r-project.org/**

NTC **http://www.aics-research.com/nestedness/tempcalc.html**

The Nestedness Calculator measures the extent of the order present in nested presence-absence matrices.

Atmar W, Patterson BD. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96:373–82

Pajek **http://vlado.fmf.uni-lj.si/pub/networks/pajek/**

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