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Mutualistic networks

Jordi Bascompte

The mutually beneficial interactions between plants and their animal pollinators and seed dispersers form complex networks of species interdependence. Until very recently, the complexity of these networks precluded a community-wide approach to mutualism. However, recent studies using tools and concepts from physics and sociology have allowed the exploration of this complexity within a rational framework. Regardless of differences across sites or species composition, networks of mutual benefit have a similar structure. Describing these network patterns is important for understanding both the generation of biodiversity and its responses to anthropogenic disturbances, such as habitat loss and species extinctions. This network approach is currently being applied to restoration ecology, biological invasions, and the conservation of endangered species.

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Up to 90% of tree species in the tropics depend on interactions with animals to complete their life cycles, either through pollination of flowers or dispersal of seeds (Jordano 2000). Pollination and seed dispersal are mutually beneficial interactions: plants obtain the dispersing services of the animals, and the animals, in turn, obtain food or other benefits in exchange for their services (Figure 1). The role of these mutualisms in the diversification of life on Earth has now been recognized by several authors.

The importance of mutualistic interactions did not escape the trained eye of Charles Darwin, who was fascinated by the morphological match between orchids and their insect pollinators. Only 3 years after the publication of *On the origin of species*, Darwin published a book entirely devoted to the various contrivances by which orchids are fertilized (Darwin 1862). Since then, there has been an intense program of research on plant–animal mutualistic interactions. Until a few decades ago, the bulk of this research agenda revolved around a single plant or a single pollinator species, and highly specialized one-on-one interactions seemed to be accepted as a common feature of coevolution. However, these examples of extreme, pairwise specialization may more often be the exception than the rule. Waser *et al.* (1996) argued that many mutualistic (pollination) interactions are generalized. Other authors had already acknowledged the community context of mutualistic interactions (Feinsinger 1978; Petanidou and Ellis 1993; Bronstein 1995). For example, recent work on the geographic mosaic of coevolution has analyzed how the type of a plant–animal interaction (mutualism versus antagonism) and its magnitude are shaped by the community context, both in time and space (Thompson 2005). The next step was to scale all the way up from these small groups of species to study entire networks of interactions. Here, I aim to assess the importance of taking a network approach to coevolution.

In a nutshell:

- Interactions of mutual benefit between plants and animals have molded much of Earth's biodiversity
- Such mutualistic interactions involve dozens, even hundreds, of species shaping complex networks of interdependence
- Mutualistic networks have a well-defined architecture that may have a considerable effect on the the coevolutionary process and the response of these networks to anthropogenic disturbances

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Darwin's "entangled bank"?

An example of a mutualistic network is illustrated in Figure 2. At a first glance, this may seem a diffuse object, difficult to characterize. We are tempted to infer that there is no pattern at all, but the alternative approach is to find ways to tackle the complexity of mutualistic networks. However, first let us consider whether it is worth thinking in terms of networks at all.

A network approach would be unnecessary for understanding ecological, evolutionary, and coevolutionary dynamics if the properties of the whole network could be deduced from the properties of the pairs of interacting species. To some extent, this question touches a major scientific theme of the past few centuries: the so-called reductionist approach. Studying the apparent complexity underlying Figure 2 has been a constant challenge for various disciplines. Take, for example, the brain, with its enormous number of neurons and interactions, or the genome, with hundreds of thousands of genes. The classical approach to dealing with this sort of complexity has been to break down complex systems into smaller components, to isolate these basic blocks, and to study them as much as possible. The problem, as noted by the late Nobel laureate Ilya Prigogine, is that we often do not know how to reassemble the pieces (Prigogine and Stengers 1984). To assess the limitations of this approach,

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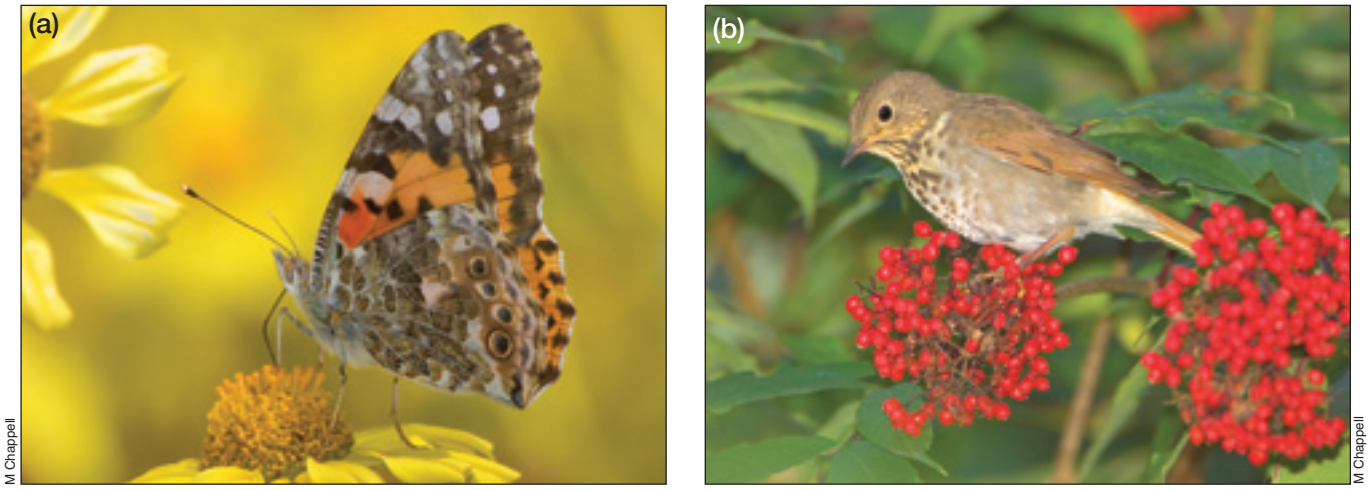

Figure 1. *The interactions of mutual benefit between plants and (a) pollinators or (b) seed dispersers have played a very important role in the generation of biodiversity.*

consider how limiting it would be if we were to try to understand human consciousness by studying the chemical reactions in single neurons, or to understand development by studying the sequence of the genetic code. One can then argue that the bulk of ecological and evolutionary problems take place at the scale of whole networks and cannot be deduced from their basic elements. I believe that this is the case for coevolutionary networks. This by no means undervalues the wonderful advances made using a reductionist approach. It just suggests that these advances should be complemented by a system-wide approximation. Several properties of mutualistic networks that greatly affect their stability and the coevolution of species are defined at the scale of the whole network. Furthermore, growing concerns about human impacts on the biosphere require a community-wide approach to assess how local changes cascade, or are buffered, through the web of life (Levin 1999). We can no longer consider isolated species.

Having concluded that we need to study networks, our next question becomes: how do we do so? Research on mutualistic networks highlights the value of an interdisciplinary approach. In this case, we can see through the apparent complexity of Figure 2 by means of tools used by physicists working on other types of complex networks, such as the internet or air transportation, and by sociologists working on social networks, such as the ones formed by groups of individuals participating in similar events (eg CEOs and the boards they sit on). Let us then briefly define some of the tools that will help us to describe the architecture of mutualistic networks.

Tales from the internet

In the past few years, there has been great excitement about complex networks, such as the internet. Research has been motivated by the belief that the structure of a network will greatly affect its robustness, and by the possibility that such an architecture can inform us about the mechanisms of network formation. Understanding the extent to which, for example, the internet is robust to node failure and attack is certainly important, and it is a question that must be addressed at the network level. That is, robustness is not so much a property of each of the servers, but of the overall network of relationships. A first description of network architecture is provided by the frequency distribution of the number of interactions per node. This tells us the probability of a randomly selected node being connected to one or more other nodes (Figure 3). The expectation, based on previous work on random graphs by the mathematician Paul Erdös (Erdös and Rényi 1959), was for a homogeneous network in which all nodes are equally important – a democratic network well des-

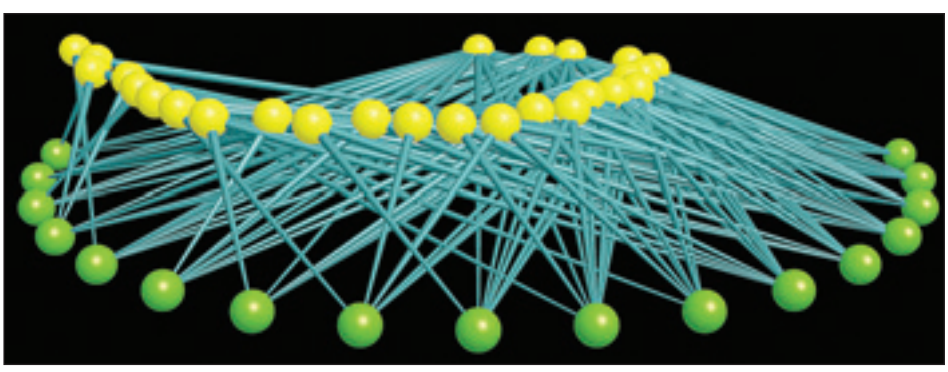

Figure 2. *Plant–animal pollination network. Green and yellow nodes represent plant and insect species, respectively. A link between one plant and one animal indicates that the former is pollinated by the latter (such as in Figure 1a). Data correspond to the Zackenberg field station in Greenland and were compiled by J Olesen. Figure plotted using FoodWeb3D (www.foodwebs.org).*

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cribed by the average number of interactions per node. Instead, Albert *et al.* (2000) found that the internet is much more heterogeneous. The bulk of nodes have a small number of interactions, but a few nodes are much more connected than would be expected by chance. This is a heterogeneous distribution, similar to wealth distribution in human societies. The average number of interactions per node is no longer a good descriptor of this sort of network, because the variance is too large.

What are the consequences of this heterogeneous structure? Albert *et al.* (2000) performed computer simulations, progressively removing an increasing fraction of nodes to find the critical point at which the network becomes fragmented. They compared homogeneous networks, such as the ones studied by graph theory, with heterogeneous networks like the internet. In the first case, networks were quite fragile. At moderate levels of node removal, the network collapsed. However, the situation was quite different for heterogeneous networks. These were much more robust to the random loss of nodes. The reason for this robustness has to do with the role of those few, extremely connected nodes, also known as hubs. They acted as the "glue" bringing cohesion to the whole network. However, these hubs are also the network's Achilles' heel. If the simulated removal experiment begins by targeting the most connected node, as a hacker might, the network collapses very quickly (Albert *et al.* 2000).

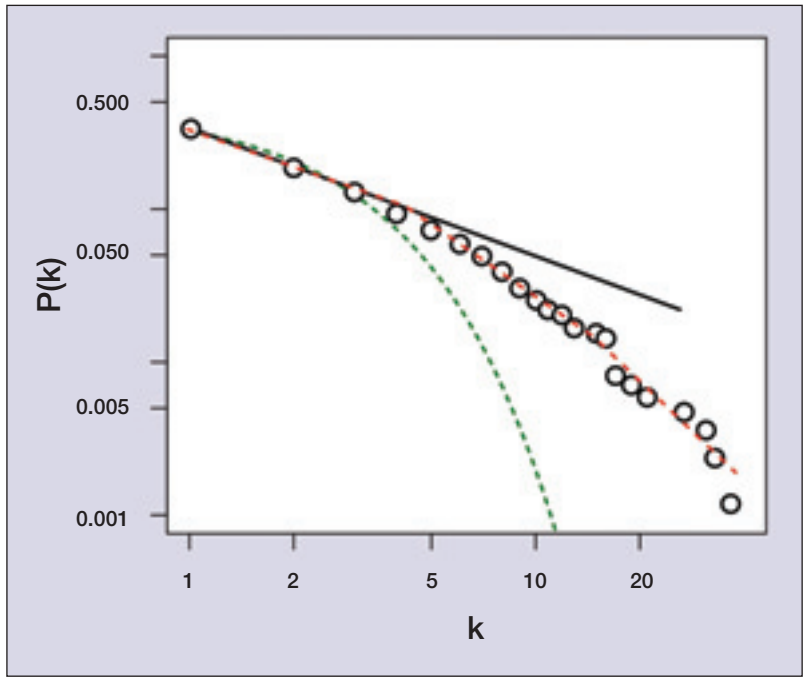

Figure 3. *Mutualistic networks are very heterogeneous: although the bulk of species interact only with a few other species, some are much more connected than would be expected by chance. The figure represents the connectivity distribution for pollinators in a pollination network in Kyoto (Inoue* et al. *1990), showing the probability of an insect interacting with* k *plants (dots). The three lines are the best fit to a power-law (the distribution of complex networks showing scale invariance; continuous black line), truncated power-law (as before, but with a decay in the probability of the most connected species due, for example, to forbidden links or size effects; broken red), and exponential (the distribution for a random, homogeneous network; broken green).*

In summary, heterogeneous networks, such as the internet, are very robust to random failure, but very sensitive to deliberate attack. The implications for information transfer are obvious, and this example clearly illustrates why understanding the architecture of networks is so important for assessing their robustness. Similar lessons can be learned from the study of other complex networks, such as global airport traffic (Barrat *et al.* 2004; Guimerà *et al.* 2005). Once we have absorbed this lesson, it is time to go back to the coevolved web of life. With these new tools, we will be able to see beyond the apparent entangled bank, and will instead see repeated, simple patterns.

The architecture of biodiversity

Mutualistic networks are heterogeneous

Jordano *et al.* (2003) applied the analysis of connectivity distribution to mutualistic networks in much the same way as others had applied it to food webs (Solé and Montoya 2001; Camacho *et al.* 2002; Dunne *et al.* 2002). Again, mutualistic networks are much more heterogeneous than would be expected by chance (Vázquez and Aizen 2003); the bulk of plants and animals interact with only one or a few other species, but a few species are super-generalists, interacting with many other species (Figure 3). The frequency distributions that describe numbers of links per species are very broad, but, in contrast to the internet, for example, the frequency distribution is truncated before reaching nodes with many interactions (ie hubs; Figure 3). There are various non-exclusive explanations for such a truncation of the distribution, such as forbidden links (ie interactions that cannot occur due, for example, to constraints of morphology or of phenology – plants and animals active in different seasons cannot interact; Jordano *et al.* 2003). Thus, this merger of quantitative approaches and natural history can increase our understanding of the causes of network patterns.

This heterogeneous distribution is a first description of mutualistic networks, but it is a limited one. Although it tells us the probability of a randomly selected plant species interacting with any number of other animal species, it does not provide any clue as to the identity of these species. Let us consider two plant species, each of which interacts with five and 12 animal species, respectively. Will these five animal species be part of the 12 species interacting with the second plant species? To answer this type of question, we have to go a step further

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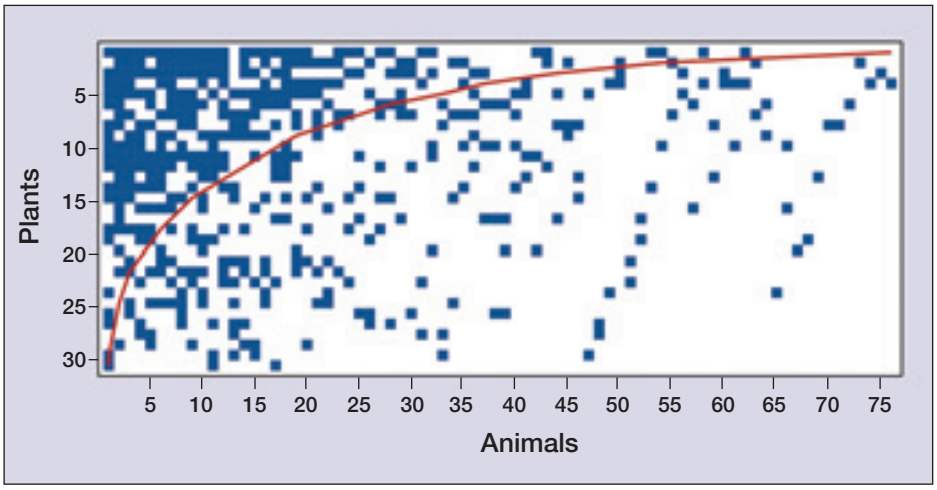

Figure 4. *Mutualistic networks are nested: species interacting with the specialists form well-defined subsets of the species that generalists interact with. This results in a cohesive network (generalist plants and animals interact among themselves) with asymmetric specialization (specialists interact with the most generalist species). Rows represent plants, columns represent animals, and a blue square indicates that the plant in the row and the animal in the column interact. This matrix representation is equivalent to a network representation. Community is the same as that depicted in Figure 2.*

in our description of network structure. This question is very much related to a classical question in food web research: namely, whether food webs are organized into compartments, where species within a compartment interact together to a high degree, while there are almost no interactions between species belonging to different compartments (May 1973; Pimm 1979). We will next address this issue by turning to island biogeography (Atmar and Patterson 1993).

Mutualistic networks are nested

Let us make an analogy between physical islands and plants "hosting" several animal species. A mutualistic network can be described as a matrix, with plants in rows and animals in columns (Bascompte *et al.* 2003). A cell in this matrix will have a value of "1" if the plant in that row is pollinated or dispersed by the animal in that column. Up to this point, we are considering qualitative data; if we use quantitative data, then this value would measure the strength of the interaction, as we will see in the next subsection. If rows and columns are properly arranged from the most generalist to the most specialist species, we can define the degree of nestedness of the matrix. Such a matrix will be perfectly nested if specialists interact with species that form perfect subsets of the species with which generalists interact. That is, if we move from the most specialist to the most generalist plants, we will see that the animals interacting with the former are contained in the larger list of animals interacting with the latter. This is a structure similar to that of nested Russian dolls, with smaller dolls within larger ones. Mutualistic networks have been found to be highly nested (Figure 4).

There are two properties that originate from a nested network. First, these networks are organized around a cohesive core of species. Generalist plants and generalist animals interact with each other. This makes the system more redundant, in the sense that, even if some interactions are lost, the system may generate alternative interactions that limit the damage from such a perturbation. Second, there is asymmetric specialization, such that the most specialist species tend to interact with the most generalist ones. All things being equal, the abundance of a generalist species is higher and less prone to fluctuation because it relies on a broader range of resources. Thus, asymmetric specialization may provide a mechanism for the persistence of rare, specialist species.

Mutualistic networks are built upon weak and asymmetric links

The two previous measures of network structure are based on qualitative data (ie on whether a plant and an animal interact or not). But how robust are these results when considering the strength of interactions? Two examples of weighted networks studied by physicists are global airport traffic and the network of scientific collaborations (Barrat *et al.* 2004). In the first case, the weight or intensity of a link between any two airports is proportional to the number of passengers going from one to the other, while in the second example, link weight is defined by the number of papers two scientists have coauthored (Barrat *et al.* 2004). In our mutualistic networks, the ideal weight would be the per capita effect or dependence of one partner on the fitness of the other. Normally, one uses a proxy of such pair-wise dependence, such as the relative frequency of fruits consumed or relative frequency of flower visits by each animal species. It is certainly a simplified measure, because it misses the fact that the quality of the dispersal service may vary across animal species. However, it is a good surrogate of the per capita effects of one species on another (Vázquez *et al.* 2005), because the variability in relative frequencies of visits is so high that it overcomes qualitative differences.

The frequency distribution of dependence values, estimated according to the relative frequencies of interactions between specific plants and animals, is very heterogeneous. The bulk of dependences between two species is very weak, but a few are quite strong. In these few cases, in which, for example, a plant depends heavily on an ani-

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mal, the animal tends to depend substantially less than expected on that plant. This shows that the property of asymmetry, previously defined at the generalization level, stands when considering weighted data. The quantitative equivalent of the number of interactions per species is the concept of species strength (Barrat *et al.* 2004), a measure of the quantitative importance of one species for the species of the other set. The strength of a plant species, for example, would be the sum of dependences or mutualistic strength of the animals on that plant. Bascompte *et al.* (2006) found that species strength varies hugely across species, as shown for the distribution of the number of interactions per species. Once more, mutualistic networks are very heterogeneous: the bulk of species are not very important from the point of view of the architecture of the network, but a few species are extraordinarily well connected both in qualitative and quantitative terms.

Figure 5. *The simple building blocks of mutualistic networks. The figure illustrates the different modules in a pollination network from the Andes. Each module is composed of a small group of strongly interacting plants and insects that have only loose interactions with species from other modules. These modules represent the coevolutionary units. Size of modules and links is proportional to the number of species and between-module interactions. Figure modified from Olesen* et al. *(2007).*

The basic building blocks of mutualistic networks

Another property of network structure beyond the distribution of the interactions per species is based on the concept of compartmentalization (also called modularity in the physics literature). A module is a group of species that interact strongly among themselves, but very little with species belonging to other modules. Olesen *et al.* (2007) analyzed a large dataset of qualitative pollination networks and showed that they are strongly modular. They were also able to characterize the composition of some of these modules. For example, one module in a pollination network in the Andes described by Arroyo *et al.* (1982) is formed by one plant species of the genus *Oxalis* and several butterfly species (blue module in Figure 5); another is composed of several plants with white flowers and several dipteran species (black module in Figure 5). As discussed by Olesen *et al.* (2007), these modules can be seen as coevolutionary units. From an architectural point of view, they define the basic building blocks of complex networks.

One important aspect of all these network patterns is that they are very general; these general network patterns are what physicists would call invariant properties. Regardless of the type of mutualism (eg pollination, seed dispersal), of the region in which the community was studied (eg Mediterranean, tropics, Arctic), and of species composition, insularity, and other variables, there is a constant architectural pattern. However, just because a general and robust network architecture exists does not mean that these networks are static over time. Two recent studies have reached the same conclusion: there is a high turnover in species and interactions from year to year, and yet network structure (eg level of nestedness) seems to remain relatively constant (Olesen *et al.* 2008; Petanidou *et al.* 2008).

To fully answer our initial question of whether it is necessary to take a network approach to coevolution, we must not only show that the existence of the above architectural patterns cannot be anticipated from the study of pairs of species, but also that these patterns are important for coevolution and conservation. I will attempt to do this in the following section.

■ Implications for the conservation of biodiversity

To what extent does network architecture affect its stability in the face of global change? Theoretical evidence concludes that heterogeneous, nested, mutualistic networks

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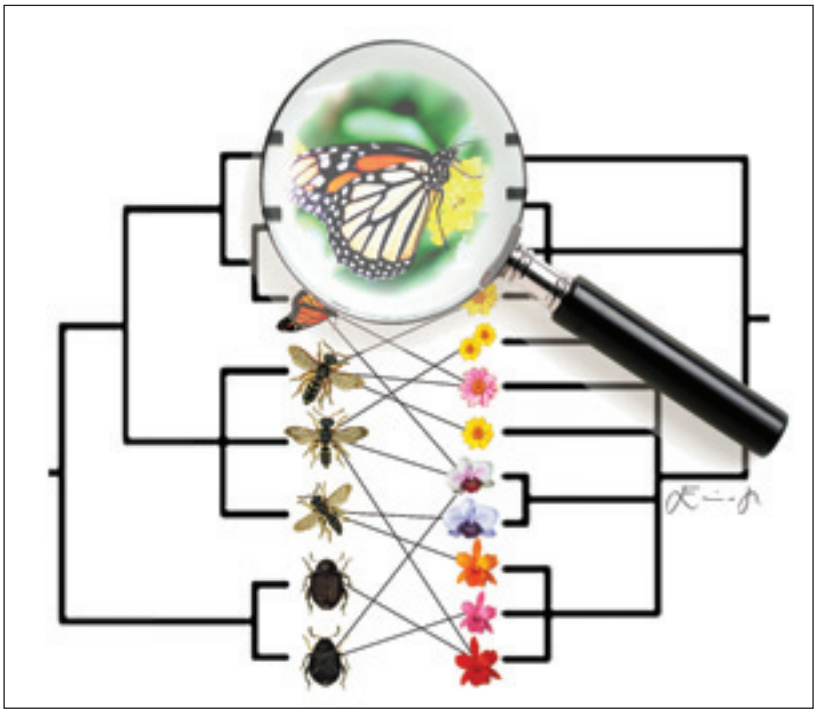

E Rezende

Figure 6. *Whereas phylogenies describe the evolutionary relationships between plants and animals, the magnification glass highlights the interaction between two such species. The simultaneous consideration of phylogenetic structure and network architecture determines to what extent evolutionary history explains the architecture of mutualistic networks, and the rate at which such evolutionary history is lost through co-extinction cascades.*

confer network robustness to species loss and habitat fragmentation (Memmott *et al.* 2004; Fortuna and Bascompte 2006; Burgos *et al.* 2007). This overall robustness in the face of random species losses, however, is partly explained by the role of the few highly connected species that are in the core of the network and with which specialists interact. Thus, the robustness of the entire network is dependent on these species, in the same way that we previously observed for the internet and food webs (Albert *et al.* 2000; Solé and Montoya 2001; Dunne *et al.* 2002).

Besides the importance of these generalist species, the modularity analysis also identifies species that, although they do not have a large number of interactions, do interact with species from different modules (Guimerà *et al.* 2005; Olesen *et al.* 2007). The removal of these connectors can lead to a profound change in the organization of the whole network.

The consequence of species extinctions for biodiversity loss is not only key in terms of the size of co-extinction cascades. Species are part of a historical process and their importance can also be assessed by the millions of years of history behind them. In a recent paper, Rezende *et al.* (2007) brought evolutionary history into the study of mutualistic networks. They first quantified the role of the phylogenies of plants and animals in explaining network patterns. There is an important phylogenetic signal in the number of interactions per species in more than one-third of the networks, and in the identity of the species with which they interact in about half of the networks. This means that phylogenetically similar species tend to play similar roles in the network of interactions (Figure 6). As a consequence of this phylogenetic signal, co-extinction avalanches affect closely related species, further eroding taxonomic diversity.

Conclusions

In summary, recent studies on mutualistic networks have shown that there is more to coevolution than just pairs of highly interacting species. Mutualistic interactions shape webs with a well-defined architecture. Biodiversity is more than the collection of species, because these species interact in well-defined ways. These network-wide patterns are important for our understanding of biodiversity organization and persistence. Finally, it is worth asking what implications, if any, there may be for policy, resource management, and science in general. Below, I present a preliminary overview of the potential impacts.

Policy implications

Major government and non-governmental agencies are currently developing policies to address global change. For example, the UK Department for Environment, Food, and Rural Affairs (Defra; www.defra.gov.uk) has developed an *Introductory guide to valuing ecosystem services*. Its aim is to "provide an introduction to the valuation of ecosystem services...taking...a more systematic approach to the assessment of impacts on the natural environment". Similarly, the Millennium Ecosystem Assessment (www.millenniumassessment.org) brought together a large panel of experts on the consequences of ecosystem change for human well-being, explicitly considering changes in ecosystem services such as pollination. Insect-mediated pollination provides a very important service for crops everywhere, and there is growing concern about a pollination crisis with potential implications for the economy (Biesmeijer *et al.* 2006; Vamosi *et al.* 2006). If the robustness of this ecosystem service depends on the architecture of mutualistic networks, network architecture is to some extent of concern to policy makers.

Similarly, it is now becoming clear that, besides changes in species abundance and geographic distributions, global change can also disrupt interactions, and so change the structure of these networks, with potential changes in network robustness (Tylianakis *et al.* 2007, in press; Memmott *et al.* 2007). We may be losing the "glue" that holds the coevolved web together, changing its topological properties without losing species. In short, we should complement a species-based policy with a network-based policy.

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Resource management

It is becoming more evident that resource management will benefit from ecological networks. For example, basic work on the structure and robustness of mutualistic networks has recently been applied to restoration ecology (Forup *et al.* 2008), to impacts of alien species (Memmott and Waser 2002; Olesen *et al.* 2002; Morales and Aizen 2006; Aizen *et al.* 2008; Bartomeus *et al.* 2008), and the conservation of rare species (Gibson *et al.* 2006). It is still too early to properly assess the benefits of this approach for resource management, but, at the very least, it is good news that a more systemic approach is being developed. It is already clear that, due to asymmetrical specialization, rare plants depend largely on generalist pollinators that, in turn, rely on common plants. Thus, protection of rare plants requires the management of more common plant species (Gibson *et al.* 2006). Similarly, the structure of mutualistic networks favors the integration of alien mutualists (Memmott and Waser 2002; Olesen *et al.* 2002; Aizen *et al.* 2008; Bartomeus *et al.* 2008). After an invasion, links are transferred from generalist native species to super-generalist alien species, so that the whole network depends largely on these alien species (Aizen *et al.* 2008; Bartomeus *et al.* 2008). Also, alien integration decreases mutualism strength, with implications for network stability (Aizen *et al.* 2008).

Scientific implications

The above results are of interest in ecology and beyond. Within ecology, the change of emphasis from studying pairwise interactions or small groups of species to whole networks has been important. Similarly, the study of modules – as defined in Olesen *et al.* (2007) as the basic building blocks of mutualistic networks – may serve to integrate the two major research agendas in coevolution (ie the one focusing on small groups of strongly coevolving species [Thompson 2005] and the one focusing on entire networks of interactions). Beyond ecology, I am advocating for an interdisciplinary approach to complex problems, borrowing and developing tools from computer science, physics, and mathematics, and integrating across different research fields. Research on mutualistic networks has clearly benefited from previous work on other complex networks such as the internet or gene-regulation networks, but can also, in turn, benefit other fields. For example, research on mutualistic networks has stimulated thinking on systemic risk in finance: the daily transactions among banks can also be represented as a network that shares some structural properties with the mutualistic networks reviewed here (May *et al.* 2008).

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