
Mutualistic networks

Jordi Bascompte and Jens M. Olesen

11.1 A historical perspective on network thinking in mutualism

Plant–animal mutualisms such as those between flowering plants and their pollinators or seed dispersers have played a major role in the generation of biodiversity on earth. Beyond early notes and some predecessors of ideas, it is fair to say that studies of mutualistic interactions among free-living species began with the work of J.G. Kölreuter (1733–1806; Waser 2006), later followed by C.K. Sprengel (1793), who became a direct inspiration of Charles Darwin.

Darwin himself is often cited as one of the founders of research on mutualisms. His book *On the Various Contrivances by Which British and Foreign Orchids are Fertilised by Insects, and on the Good Effects of Intercrossing* (Darwin 1862) was very important in advancing the idea that one cannot understand the evolution of floral morphology without taking into account the evolution of insect morphology. That is, the evolution of plants and animals are not independent of each other.

With the development of the modern evolutionary synthesis in the 1930s, mutualisms began to be viewed from a population and evolutionary perspective. This involved formulation of systems of trait “syndromes” and studies of pairwise interactions (Baker 1983). Indeed, most early studies of plant–animal mutualisms focused on single pairs of species. This set up a research agenda organized around highly specific interactions. Paradigmatic examples of these specific interactions are fig wasps and figs (Cook and Rasplus 2003) and yucca moths and yuccas (Pellmyr 2003).

At the same time, however, there are early predecessors of community studies, some of them resulting in the compilation of large datasets of interactions later used in network research. One classic subject of discussion in these community-wide mutualistic studies was whether the majority of interactions are specialized or generalized. In this context, specialist species are those interacting with only one or a few other species. An important contribution here is the classic paper by Waser et al. (1996). This paper made the point that previous studies had overemphasized the prevalence of specific, one-on-one interactions, and that when viewed at a community level, most species interact with a large set of other species.

In another significant contribution, Daniel Janzen wrote a highly influential paper that significantly contrasted with the above dominant focus on the one-species-to-one-species approach (Janzen 1980). He introduced the idea that mutualisms occur in species-rich communities. That is, the interaction is not between one plant species and one animal species, but between one set of plants and one set of animals. The catch-all term “diffuse coevolution” was coined to refer to this situation. Several papers subsequently elaborated upon this concept, emphasizing the high variability of mutualistic interactions (Herrera, 1982). One drawback of this approximation, however, is that it seems to preclude any analytical tractability to community-wide mutualism (Thompson 2005). As a consequence, the theoretical framework in mutualistic studies seems to predict that these interactions have to lead to either highly specific or highly diffuse assemblages.

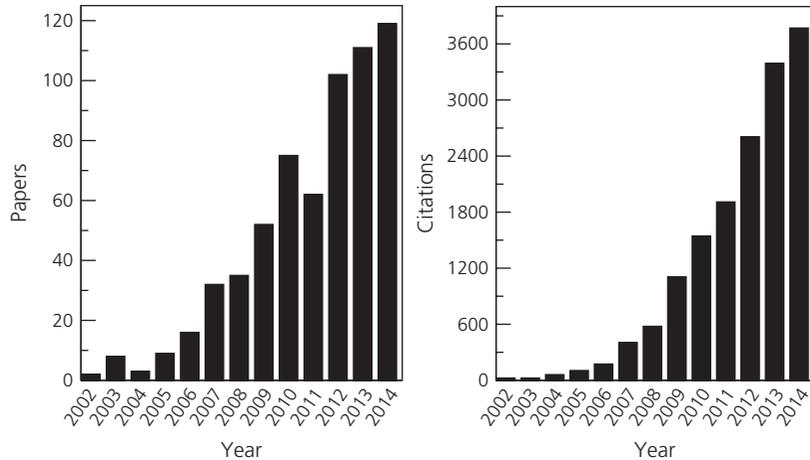


Figure 11.1 Temporal increase in the number of papers (left) and citations to papers (right) on mutualistic networks. Search performed on the Web of Science on 29 January 2015 (topic: *mutualistic networks*).

Several exceptions that brought tractability to the understanding of multispecific mutualism (in terms of allowing the search of repeated patterns) are worth mentioning. For example, the geographic mosaic theory of coevolution (Thompson 2005) described predictable patterns in the geographic distribution of mutualistic interactions involving small groups of species. Thus, the sign and strength of a mutualistic interaction may vary across the landscape. In some patches, the interaction is mutually beneficial, while it becomes antagonistic in other patches. Whether the net effect is positive or negative depends on the presence of other mutualists and antagonists. The geographic mosaic theory has represented a major advance in our understanding of how coevolution proceeds in complex natural settings (see Chapter 7).

The second major approach to community-wide mutualism has been brought by network analysis. The first papers introducing a network approach to mutualism mainly used concepts from food-web theory and looked at global properties such as connectance (Jordano 1987, Memmott 1999, Elberling and Olesen 1999). Several years later, there was a resurgence of interest in mutualistic networks (Bascompte and Jordano 2007, Bascompte and Jordano 2014). These foundational papers applied a new generation of tools and models to large and detailed datasets, facilitating a search for invariant principles or regularities across mutualistic networks despite obvious differences in latitude, habitat,

species richness, and so on. The number of papers on mutualistic networks, and the citations these papers have gathered, have risen exponentially in the last few years (Figure 11.1).

The first studies on mutualistic networks focused on plant–pollinator and plant–seed disperser mutualisms, due to the main interests of the initial core of authors who introduced this approach. Thus, this reflects historical contingency rather than implying that other types of mutualisms cannot be seen as networks. Indeed, in subsequent years, network analysis has been applied to the study of plant–ant mutualisms, cleaning mutualisms, and several other systems, including cooperative interactions in socioeconomic systems (see Bascompte and Jordano 2014 for a review). Network theory has provided a framework that can be used to characterize all mutualisms. Through this chapter, however, we will mainly focus on pollination and seed dispersal mutualisms for illustrative purposes.

11.2 Rationale for a network approach to mutualism

Despite several recent claims and the early predecessors noted above, many coevolutionary researchers still think in a pairwise way. The reason is rooted in the reductionistic tradition of breaking down complex systems into their basic elements in the hope

that their study can be scaled up to understand entire communities. Indeed, we have lacked a conceptual framework to address multispecies interactions. Network theory provides this conceptual framework. This approach treats species as nodes, and mutualistic interactions as links between two such nodes. Technically, the type of network that fits these systems is called a bipartite network, that is, a network formed by two sets of nodes (here, plants and animals) with interactions between, but not within, sets.

Network studies can bring insight in three important ways. First, network theory can unveil complex patterns; that is, it can help us to visualize the structure of highly diverse mutualisms. Second, network tools help us to analyze this complexity and to test hypotheses about its origins. Third, network theory emphasizes the relationship between network structure and dynamics, which may help us evaluate the community-wide effects of species extinctions and other drivers of global change.

Network theory has rapidly become a popular approach in community ecology in general, and in the study of mutualism in particular. As with any new paradigm, there is the risk that it can become a fancy new way of stating what we already knew, or a quantitative exercise poorly rooted in the ecological and evolutionary realities of the system being studied. Another potential problem with the application of network theory is that—as with any other approach—there are trade-offs between simplicity and realism. Treating all species as nodes necessarily masks plenty of very interesting natural history details. The underlying logic of the network approach is not to assume that these details are irrelevant, but rather to consider that for certain questions at certain scales, one can obtain a good global view of these systems without them.

With the above caveats in mind, one can ask whether studies of mutualistic networks have led to significant and novel understanding of the ecology and evolutionary biology of mutualisms. Our goal in this chapter is to focus on that question. We do not aim to provide another review of research on mutualistic networks (Bascompte and Jordano 2007). Rather, we discuss the ecological and evolutionary implications of network studies. We begin by describing an example of the potential of network research at the level of the entire network.

This relates to classic work on specialization versus generalization in mutualistic communities. We devote the rest of this chapter to the study of a particular organization of mutualistic networks that allows linking the scale of the entire network to that of a small subgroup of species.

11.2.1 The example of asymmetric specialization

The network approach has introduced two advances in our understanding of the level of generalization of mutualistic interactions. First, it describes the specific form of the continuum between the frequency of specialists and that of generalists within a community. Second, it has made the point that specialists do not typically interact with specialists, as once believed.

Regarding the first point, network theory has established the concept of connectivity distributions, which describe the cumulative probability of a species interacting with one, two, . . . , k other species. Mutualistic networks have been found to be heterogeneous: while the majority of species have one or a few interactions with other species, a few species are super-generalists, acting like hubs in technological networks. Technically, the connectivity distribution in these networks is best described by a broad scale distribution (Jordano et al. 2003). This naturally leads to a situation in which “specialists” or “generalists” are not discrete entities, but extremes of a continuum. Network theory describes the mathematical function of this continuum. An analogy would be the scale-free distribution describing the frequency of earthquakes releasing a certain amount of energy. One does not need a different theory for small earthquakes than for large ones; these are just extremes of a continuum.

Second, network theory has addressed the novel question of whether specialization is symmetric or asymmetric, that is, whether specialist species interact with specialist species or with generalist ones. Note that we cannot address this sort of question by considering species and their interactions isolated from the community. Now we are looking at how these species and their interactions are embedded within the community; that is, we are now looking at a network level. This result was shown simultaneously by Bascompte et al. (2003) and Vázquez

and Aizen (2004). Both sets of authors described a situation in which specialists tend to interact with generalist species, a pattern that has been proven quite robust when re-analyzed with more conservative null models (Joppa et al. 2009).

Does this network-like description of interactions bring new insight into mutualistic systems? We think so. All else being equal, a specialist interacting with a generalist has more chances to persist

in variable environments, since it relies on a more abundant, relatively less fluctuating species. This concept was first advanced verbally by Bascompte et al. (2003), and later confirmed empirically by Ashworth et al. (2004) and analytically by Bastolla et al. (2009) and Rohr et al. (2014). This is the sort of insight we think is useful in the context of mutualism conservation, an idea developed by Jason Tylianakis in Box 11.1 (see also Chapter 14).

Box 11.1 Conservation and restoration implications of network studies

Jason Tylianakis

There has been growing recognition that the study of ecological networks has applied relevance, by linking persistence of one group of organisms (e.g., birds) with other species (e.g., plants), and by combining biodiversity with ecosystem processes (Tylianakis et al. 2010). Therefore, network studies clearly overlap with the interests of conservation, and their relevance in this regard is only just beginning to be understood (Tylianakis et al. 2010).

Understanding how environmental changes alter networks

Mutualistic networks can inform conservation by providing a context within which to understand how environmental changes affect the stability and functioning of entire communities. Networks can be altered via additions and/or deletions of species (e.g., via invasions, range shifts, or extinctions), or via changes in the strength of interactions (e.g., due to spatial or phenological mismatching or altered search efficiency; Tylianakis et al. 2008). Recent work has begun to illuminate both the community-wide impacts of these changes and some generalities that may inform conservation efforts.

One area that has received particular attention is the impact of invasive species on mutualist networks. Invaders are often "super-generalists," interacting with numerous other species throughout the network (Vilà et al. 2009). This increases overall network connectivity, and it may alter topological aspects of the network. For example, by interacting preferentially with the most generalist species, alien pollinators were found to enhance the nestedness of pollination networks on the Galapagos Islands (Traveset et al. 2013). Combined with previous findings that alien species may engage in highly asymmetric interactions (reviewed in Tylianakis et al. 2010), these results suggest that invaded communities may be more robust to species losses.

However, Traveset et al. (2013) also found that these highly connected invaders tended to act as connectors, both within their own subnetworks and across the different islands that comprised distinct modules within the archipelago network. This may make invaded networks more susceptible to perturbations (e.g., diseases, contaminants) that may spread via interactions.

Mutualist networks have also provided significant insights into the effects of habitat fragmentation. For example, network structure is a key determinant of how pollination and seed-dispersal communities respond to fragmentation, with the nestedness and heterogeneous degree distribution of real networks causing them to decay sooner than random communities, but persist longer as habitat fragmentation continues (Fortuna and Bascompte 2006). In fact, the loss of particular interactions with decreasing fragment size is non-random, and can be predicted based on characteristics such as the rarity of the interaction or the connectedness of the species involved (Aizen et al. 2012).

Translating understanding into restoration practice

Given these and other findings, we can begin to derive recommendations for conservation practices such as restoration of habitat or removal of invaders. For instance, particular species could be targeted for reinstatement (e.g., by replanting) or removal to achieve a certain goal. Generalist species tend to play a central role in structuring the network and connecting modules, so these species could be targeted to generate the most rapid changes in network structure. However, several studies from the group of Jane Memmott have demonstrated potentially harmful indirect effects of removing invasive plants. For example, removal of a flowering invader may reduce the overall attractiveness of the plant community to pollinators, thereby reducing pollination of rare native plants that depend on a diverse, abundant pollinator community

Box 11.1 *Continued*

(Carvalho et al. 2008). Furthermore, by coupling separate modules (e.g., the networks of different habitats), invaders may play an important role in maintaining spatial stability in ecosystem functioning, again suggesting that knowledge of their role in networks could inform the costs or benefits of their removal. Even in the absence of local knowledge regarding the role of each species in the network, the general enhancement of plant diversity can generate more connected pollination networks that are more temporally stable in their pollination services (Ebeling et al. 2011).

Knowledge of network structure may also inform restoration planning. For example, knowing which components of a network occur in which type of habitat allows managers to determine how the loss of certain habitats from the landscape will affect different components of the local interaction network (Evans et al. 2013). Similarly, it can allow computer simulations of plantings of certain species to compare their effects on network structure (Devoto et al. 2012). This can be aimed at generating networks with emergent properties, such as pollination networks with high functional complementarity (to maximize pollination rates) or redundancy (to maximize resilience of the network in the face of extinctions; Devoto et al. 2012). Finally, by incorporating so much information on biodiversity and species interactions, mutualist networks can be a useful yardstick for measuring the success of previous restoration actions (Forup et al. 2008).

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Having introduced the sort of insight that a network approach can provide for our understanding of mutualistic communities, we now expand on one particular way in which a property of a mutualistic network can be further tied to the natural history of its interactions. Specifically, we consider small groups of strongly interacting species that occupy an intermediate scale between a pairwise interaction and the entire network.

11.3 Syndromes, modularity, and coevolutionary units

While the scope of this chapter—like that of this entire volume—addresses mutualism in general, in this section we use pollination mutualisms for illustrative purposes. Similar historical accounts could be drawn for other types of mutualisms.

The first serious attempts to organize lists of visitors to the flowers of particular plant species were

made by the Italian botanist F. Delpino in writings from 1868 to 1875 (Waser 2006). Delpino's classification of flower types was modified by several later pollination biologists, such as P. Knuth in his monumental *Handbook of Flower Biology*, published from 1898 on. These early schemes attempted to sort flowering plants into groups according to floral morphology and rewards in relation to their pollinators.

The concept of pollination syndromes was introduced in the 1960s by L. van der Pijl, K. Faegri, and H.G. Baker (see Faegri and van der Pijl 1971, Vogel 1996, Waser 2006). Syndromes are defined as co-occurring sets of flower (or fruit) traits matched to the morphology of different pollinators or seed dispersers (van der Pijl 1969, Jordano 1995, Ollerton et al. 2009, Lomáscolo et al. 2010). These groups of plants and their animal mutualists exhibit a complex of shared traits and are adduced to be the consequence of coevolutionary convergence. Throughout this chapter, we refer to these strongly interacting groups of species as coevolutionary units.

One problem with syndromes is that they are top-down creations. That is, it is the scientist who defines them on the basis of a somewhat subjective classification. Although syndromes have had a long tradition in shaping coevolutionary thinking about mutualisms, demonstrating their existence has been more elusive. Some notable exceptions are Lomáscolo et al. (2010), who found strong evidence

of syndromes in a detailed study that explicitly considers the phylogenetic non-independence of species.

The identification of the groups of plant and animal species showing the complex of shared traits involved in syndromes is very much related to the problem of scale, which is at the core of ecological and evolutionary thinking (Levin 1992, Chave 2013). One might think that the relevant scale in a network is that of a node. It may also be that the relevant scale is that of the entire network. Finally, it is also possible that the relevant scale lies between the node and the entire network. Modularity analysis generates the best partition of a mutualistic network into modules, resulting in a bottom-up classification based on the patterning of interactions (Box 11.2; Figure 11.2). These modules are groups of strongly interacting nodes that can be a surrogate of the coevolutionary units arising from syndromes. As an example, Figure 11.3 illustrates five distinct modules, such as the one formed by plants whose seeds are dispersed by fishes. In the context of mutualism, modularity can help identifying relevant highly interacting units. Whether or not coevolution plays a role in the structure of these modules is a question that cannot be answered with static patterns. The point, however, is that should coevolution play a role at all in these multispecific systems, the process would take place under the template of these modules.

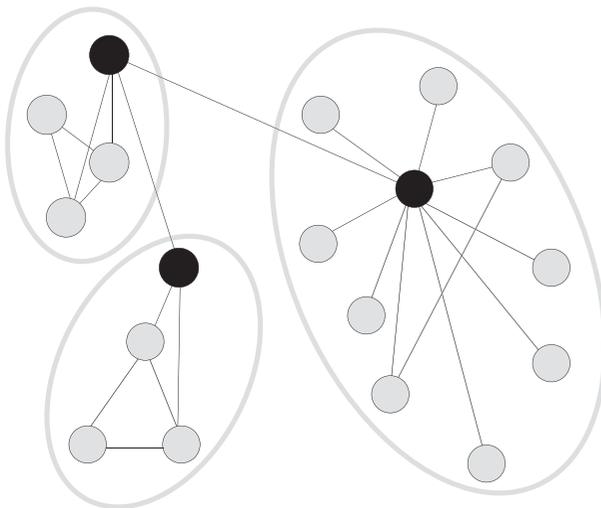


Figure 11.2 A module is a subset of nodes more densely connected among themselves than they are with nodes from other modules. The figure illustrates three modules highlighted by the ellipses. Within a modular network, different nodes have different roles. For example, the three black nodes serve as connectors of different modules. Modified from Bascompte and Jordano (2014).

Box 11.2 Definition and measure of modularity

Roger Guimerà

In nature, complex networks are modular. This means that, rather than being uniform objects whose nodes are all equally likely to connect to each other, real networks have groups, or modules, with high intra-group and low inter-group connectivity (Girvan and Newman 2002, Guimerà et al. 2007, Fortunato 2010, Newman 2011).

Modularity is important for at least two reasons. First, modules define an intermediate scale between the micro-scale of single nodes and the macro-scale of the whole network. This intermediate scale is the most relevant one for dynamical processes in the network because, in general, time scales for processes within modules are much shorter than the time scales for processes between modules (Arenas et al. 2006). In other words, when we consider a dynamical process within a network, we see modules evolving as units with only rapid fluctuations within them. Second, modules provide a convenient way to describe networks, and nodes in a module usually also share other properties (Guimerà et al. 2007). In the context of the subject of this book, modules define groups of species strongly interacting among themselves. If (co)evolution happens in these networks, then a module would be a good candidate for a (co)evolutionary unit.

Unfortunately, identifying modules within complex networks is challenging. The first challenge is how to precisely define what a module is. Indeed, the broad idea of “groups of nodes with higher within-group connectivity than between-group connectivity” is too general to be operational. Is a group of four fully connected nodes a module? Is the whole network a single module, given that if we have a single module all links are then within-module? The second challenge is that, even with a precise definition, there is a combinatorially large number of ways in which one can partition a network into modules. For example, a network with only 20 nodes can be partitioned in more than 5×10^{13} different ways.

A widespread approach to solving the first challenge is to use a modularity function M that quantifies the deviation of a partition from the null expectation of uniform connectivity between modules (Girvan and Newman 2002). Specifically, in the absence of connection bias, the expected number of links between two modules is $d_i d_j / 2L$, where d_i and d_j are the sum of the degrees of the nodes in modules i and j , respectively, and L is the total number of links in the network. Therefore, if we denote by l_i the actual

number of links between nodes in module i , the modularity function is

$$M = \sum_i \left[\frac{l_i}{L} - \left(\frac{d_i}{2L} \right)^2 \right], \quad (1)$$

where l_i/L is the fraction of all links inside module i , and $(d_i/2L)^2$ is the random expectation for the fraction of links within i . Defined in this way, M is close to one when intra-module connectivity is much higher than inter-module connectivity, and close to zero when the modules are random, when all nodes are placed in a single module, or when each node is placed in a separate module (Girvan and Newman 2002).

One then needs to address the second challenge—finding, among all possible partitions, the one with maximum modularity. This is a combinatorial optimization problem for which it is not possible to find the exact solution in “reasonable” time. Therefore, it is necessary to resort to heuristic algorithms (Fortunato 2010). The simplest one would be to start from an arbitrary partition of the network into modules, and then repeatedly choose a random node and move it to a random new module if that increases the modularity of the partition. However, this approach leads to partitions that, while being locally optimal (in the sense that no single node move can increase the modularity), are not even close to the most modular partition.

One way to address this problem is to use simulated annealing (Kirkpatrick et al. 1983, Guimerà and Amaral 2005), a technique designed precisely to avoid local optima in combinatorial optimization problems. In simulated annealing, one attempts random moves of nodes and accepts those that increase modularity, just as in the simple approach above. Unlike there, moves that decrease modularity are also accepted with some small (and decreasing) probability.

This approach (modularity function optimization using simulated annealing) has the advantage that it is accurate, and that it can be generalized to weighted and bipartite networks (Guimerà et al. 2010). It also has limitations, such as the inability to detect certain small groups (Fortunato and Barthélemy 2007) or hierarchically nested modular structures (Sales-Pardo et al. 2007). Many other algorithms have also been developed in the last ten years, some of which address these problems, although often at the price of being less accurate in other situations (Fortunato 2010).

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Box 11.2 *Continued***References**

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Figure 11.3 Modules in a seed-disperser network in the Pantanal, Brazil. Circles and squares indicate animal and plant species, respectively. The size of the nodes represents animal body mass and fruit diameter, respectively. This mutualistic network is organized in five distinct modules highlighted by the different shades of gray. Specifically, there are two bird modules (top), each with 22 species; two mammal-dominated modules (bottom) with 25 and 18 species, respectively; and a fish module with 4 species. Based on Donatti et al. (2011).

In ecology, the concept of modularity has been at the forefront of important research on food webs. The classic paper by Robert May on stability and complexity in model ecosystems not only made the claim that food-web structure is related to stability, but actually suggested that an organization of trophic interactions in modules can increase the persistence of the food web (May 1972). This spurred a rich search for this relationship between structure and stability using other models and real food webs (May 1972, Pimm 1979, Raffaelli and Hall 1992, Melián and Bascompte 2004, Olesen et al. 2007, Guimerà et al. 2010). A recent paper, for example, has proven that the tendency of a food web to be organized in compartments increases its persistence in the sense of buffering the transmission of perturbations across the entire food web (Stouffer and Bascompte 2011).

Olesen et al. (2007) first introduced the concept of modularity in the context of mutualistic networks. These authors analyzed a large dataset of 51 pollination networks including almost 10,000 species and 20,000 interactions. Networks larger than a certain threshold were found to be significantly modular. As described in Olesen et al. (2007), the majority of

modules involved a few species with convergent traits. In a pollination network from the Andes (Arroyo et al. 1982), for example, distinct modules include various Diptera species and many plant species with white flowers or large flies and small, yellow umbellifer flowers (see Figure 11.4).

The pollination modules described by Olesen et al. (2007) consist mainly of two broad types. The first one is formed by one or a few very abundant plant species with open flowers and easily accessible rewards, visited by many animal species, either simultaneously or in a temporal sequence. The second broad type is made up of tightly linked subsets of plants and animals, with their links organized in a nested fashion. Seed-dispersal networks, in turn, tend to consist of one or a few birds, bats, or reptiles (lizards, tortoises) visiting a suite of fleshy-fruited plants, with fruits being ripe simultaneously or in a temporal sequence.

Overall, analyzing the 29 significantly modular pollination networks, and the resulting 254 different modules, Olesen et al. (2007) found that the average number of modules per network was close to nine, with a minimum of five in a temperate forest meadow and a maximum of 19 in a network in the Amami Islands. The specific number of modules

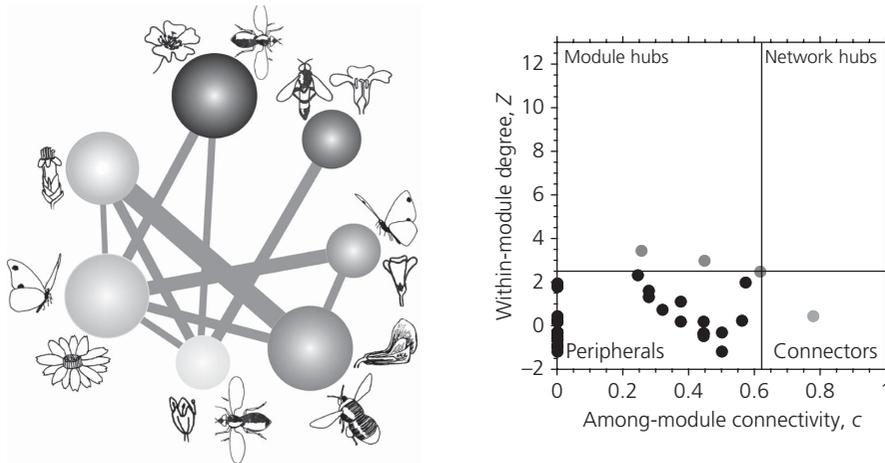


Figure 11.4 The figure at the left illustrates the different modules found in a plant–pollinator network in the Andes (Arroyo et al. 1982). The links between modules are weighted by both number of species links between modules and number of species in modules. The vignettes show dominant pollinator and flower types. From top and clockwise, the first module consists of a Diptera sp. and mainly white flowers; second module: small–medium-sized beetles, flies, an ant, and small, white/yellow flowers; third module: butterflies and one plant species, *Oxalis* sp.; fourth module: bees, birds, and large, mainly yellow flowers with a closed morphology; fifth module: large flies and small, yellow umbellifer flowers; sixth module: butterflies, a large fly, and white/yellow/pink/purple flowers; and seventh module: large flies and mainly small, white flowers. Right: classification of species roles both within their module and between modules, with three module hubs and one connector, but no network hub. From Olesen et al. (2007).

of a network was related to its number of species. As plot size grows or as species density (number of species per unit area) increases, the number of modules increases as well. In Olesen et al. (2007), small networks were shown to be non-modular, i.e., such networks could, in fact, be understood as one module.

Each one of these modules can be thought of as a potential coevolutionary unit. They represent groups of plants and animals that interact more frequently among themselves than they do with other species in the network. Therefore, if there is coevolution (Chapter 7), there are more chances that this occurs within these modules than between modules.

Next, we will consider how these modules combine to form a complex network of mutualistic

interactions, and how this constrains other patterns at the network scale.

11.4 Modularity and the basic building blocks of mutualistic networks

The idea of modularity also helps bridge small groups of mutualisms to entire mutualistic networks. One could see a module as a basic building block of these networks. The way different modules are linked will determine other network properties such as nestedness. In a nested network, specialists interact with species that form perfect subsets of the species with which generalists interact (Figure 11.5). This gives rise to an organization as in Russian dolls, with smaller dolls within larger ones. Olesen et al. (2007) reported a positive correlation between

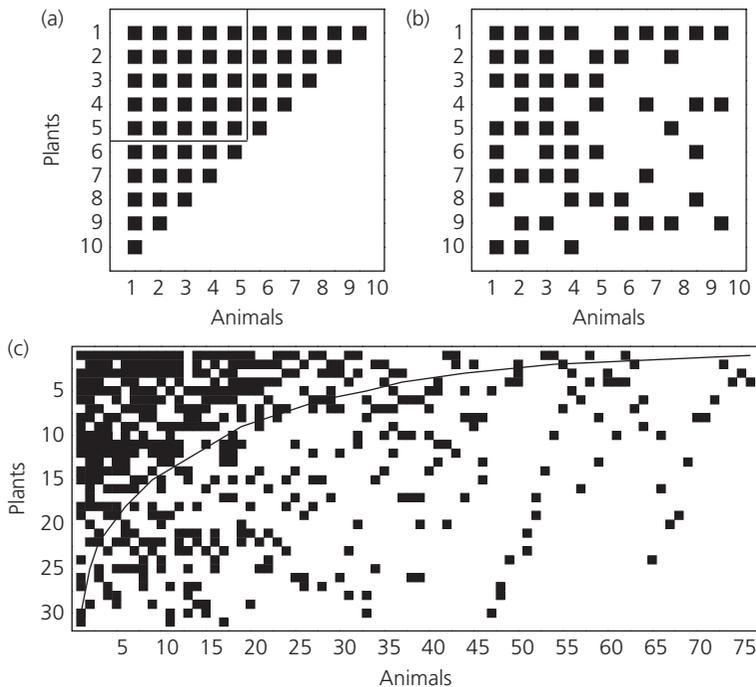


Figure 11.5 Plant–animal mutualistic networks show a nested structure when represented as a matrix. Here, each row and column represents a plant and animal species, respectively, and a square indicates an observed interaction between such a plant and animal. In a nested arrangement (a), specialists interact with species that form well-defined subsets of the species interacting with more generalist ones. (b) Represents a different matrix organization for the same network, which has been obtained by randomizing the distribution of interactions from the previous matrix. (c) Represents the actual arrangement of one plant–pollinator network. From Bascompte et al. (2003).

modularity and nestedness in pollination networks. This overall pattern was explored by Fortuna et al. (2010) in a wider range of ecological networks, using randomization schemes and measures that permit direct comparisons between these two network properties. They essentially confirmed the Olesen et al. (2007) results for low-connectance networks. At low connectivities, significantly nested matrices tend also to be significantly modular (Figure 11.6); as connectivity increases, the correlation between these two network patterns decreases in magnitude and sign. Highly connected matrices are either modular or nested. Put another way, at low connectivity values the modules are glued together in a way that creates a nested structure (Figure 11.6), but as connectivity is increased, the number of degrees

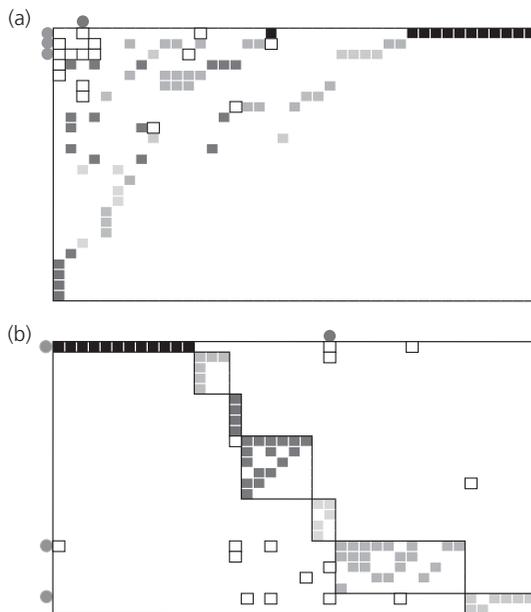


Figure 11.6 Two matrix representations of the pollination network displayed in Figure 11.4. (a) represents the matrix with rows and columns arranged to maximize nestedness, while in (b) they are sorted to maximize similarity in patterns of interaction and module affiliation. The network is organized in seven distinct modules, indicated with different shades of gray. Small squares indicate observed pairwise interactions; four species (three animals, in rows, and one plant, in columns) are highlighted as bullets to illustrate species that have interactions with species in different modules. These species are hubs, and in the nested representation of the network are part of the core. Based on Olesen et al. (2007).

of freedom in combining these basic blocks is very much reduced. One can no longer combine modules into a nested network.

Given the above description, it would be interesting to know how different modules are combined as networks assemble over evolutionary time. Unfortunately, there is a scarcity of information on the build-up of mutualistic networks. One indirect evidence of the evolutionary trace left by this assembly can be obtained by looking at the phylogenetic signal of species within and between modules. The comparative method, or phylogenetic independent contrasts, allows us to study the evolutionary history of mutualistic networks in general, and of modularity in particular. For example, in modules dominated by competition and limited resources, species may become incorporated into modules if they have traits that cause increased phylogenetic overdispersion, such that new species have traits that make them able to harvest resources in novel ways. Alternatively, in modules dominated by convergent traits we may see phylogenetic aggregation, i.e., species becoming attached to the modules if they have traits already present in the modules. This would result in increased phylogenetic aggregation. We turn to this topic next.

11.5 Phylogenetic signal of modularity

Phylogenetic approaches to mutualistic network structure were introduced by Rezende et al. (2007). These authors found that past evolutionary history embedded in the phylogenies are important in understanding the architecture of mutualistic networks. Specifically, closely related species tend to have a similar number of interactions and tend to interact with the same subset of species (see Figure 11.7). Finding such a phylogenetic signal is not only important in terms of assessing the suite of mechanisms generating network structure, but also illuminates the potential community-wide consequences of species extinctions. Coextinction cascades following simulated species extinctions tend to involve phylogenetically close species. This results in a higher loss of taxonomic diversity and a non-random pruning of the evolutionary tree (Rezende et al. 2007).

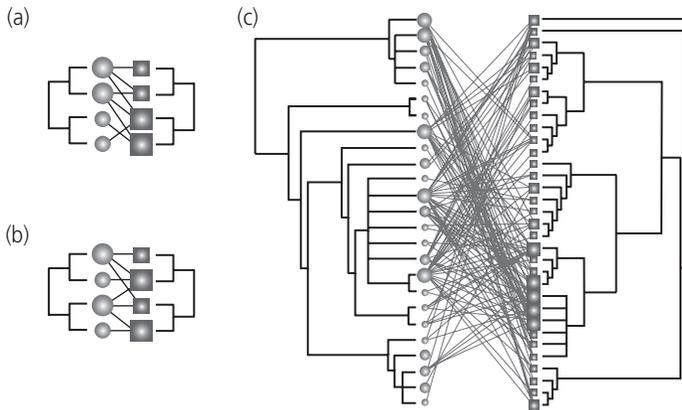


Figure 11.7 Phylogenetic patterns in the architecture of mutualistic networks. A significant phylogenetic signal indicates that past evolutionary history is important for understanding network structure. This is illustrated in panel (a), where phylogeny predicts the number of interactions a species has. In contrast, panel (b) illustrates a case without such a phylogenetic signal. Panel (c) represents a significant phylogenetic signal in the number of interactions a species has for a real plant–frugivore network. A similar significant phylogenetic signal was found in more than one-third of the mutualistic networks studied by Rezende et al. (2007).

A similar phylogenetic approach to mutualistic networks was undertaken by Donatti et al. (2011). These authors studied a seed-dispersal network in the Brazilian Pantanal that includes several taxonomic groups. They first characterized the modular structure of this network, organized around five modules. Of these modules, two are represented by bird species and their host plants, two others by mammal species and their host plants, and the last by fish species and their host plants (see Figure 11.3). Donatti et al. then explored a suite of mechanisms correlated with this modular organization. Overall, these modules were significantly associated with a combination of phylogenetic constraints and trait convergences among unrelated species. Phylogeny was found to explain the association of species within modules dominated by birds, but not by mammals. This points toward the interesting result that finding a phylogenetic signal may be a scale-dependent problem. Different modules correspond to different large taxonomic groups at a coarse scale. At a lower scale, some modules have phylogenetically close species, while this is not the case in other modules. A combination of network and evolutionary approaches is a profitable way to shed light on the nature of syndromes and coevolutionary units.

Donatti et al. (2011) also found that plants within all modules differed from each other significantly in fruit and seed traits. The trait that varied the most among modules was fruit mass, followed by fruit length. Regarding dispersers, their body mass was significantly correlated with module assignment.

This result is consistent with studies of Rezende et al. (2009) on a marine food web. In the Rezende et al. (2009) food web, body size, phylogeny, and spatial structure were jointly associated with the compartmentalized structure. Interestingly, the phylogenetic signal was positive for bony fishes, meaning that related bony fishes tended to be in the same module. However, the phylogenetic signal was negative in the case of sharks; that is, closely related shark species tend to be segregated in different modules (Rezende et al. 2009).

Analyses of phylogenetic signals in network architecture are still quite preliminary in the sense that they have only looked at one component of network structure, such as modularity. Thus, they have left unanswered the question of whether other components of network structure (e.g., nestedness) are equally phylogenetically constrained. Rohr and Bascompte (2014) attempt to fill this gap by building a unified framework in which phylogenetic signal can be quantified in a standardized, comparative way across different network types, species roles, and architectural components. Interestingly, both in mutualistic and antagonistic interactions, phylogenetic signal in the modular component of network structure was higher than the equivalent for nestedness (Rohr and Bascompte 2014).

So far we have revealed a phylogenetic signal of modularity, which means that past evolutionary history embedded in the phylogenies may structure networks into a modular structure. Modules are a mix of species varying in their ecological and evolutionary history. Modules may certainly

be the product of coevolution, but they may also result from ecological fitting (*sensu* Janzen 1985) and coincidental sampling of species. At present, it is not clear how one could tease apart these potential mechanisms. An overview of the few studies that have searched for ecological traits that correlate with modularity helps us to construct a list of the potential causes of modularity. Besides evolutionary history encapsulated in the phylogenetic signal, one can list the following potential mechanisms:

1. Local abiotic heterogeneity, i.e., divergent selection regimes (Pimm and Lawton 1980, Rezende et al. 2009, Hagen et al. 2012). Local sites may impose unique selection regimes, leading to unique subgroups of species that interact more strongly among themselves than with species from other sites.
2. Regional/geographical heterogeneity (Dupont and Olesen 2009, Dupont et al. 2009, Dalsgaard et al. 2013, Trøjelsgaard et al. 2013, Trøjelsgaard and Olesen 2013). This would act similarly to the above, but at a larger spatial scale.
3. Variation in abundance (Montesinos-Navarro et al. 2012). Different subgroups of species that happen to be more abundant may interact more strongly among themselves than with other, less abundant species, thus forming a module.
4. Variation in life-history traits, e.g., body size (Rezende et al. 2009, Bellisario et al. 2012, Martín et al. 2012). Species with life-history traits that facilitate their interaction (e.g., through coevolutionary convergence) may interact more strongly than with other species, and thus will form a module.
5. Sociality (Fortuna et al. 2009). Intraspecific social bonds create subgroups of strongly interacting individuals. Contrary to the other mechanisms from this list, this applies to social networks where nodes are individuals instead of species.
6. Impact of alien species (Valdovinos et al. 2009, Traveset et al. 2013). If an invasive species interacts strongly with a small group of local species, this may create a module within the overall network.
7. Human management (Macfadyen et al. 2011). Human intervention in an ecosystem may favor

a small group of species, increasing the intensity of their interactions.

8. Influence from community assembly history. History may have led an initial subgroup of species to have interacted strongly, leaving a signal in the final network as this initial subgroup forms a module.
9. Seasonality. Only species that overlap in time can interact. Strong seasonality may create subgroups of interacting species that cannot interact with species present at another time.

Needless to say, the above list of causes is neither exhaustive, nor mutually exclusive, since several mechanisms may be correlated. Further research will undoubtedly shed light on the most common mechanisms leading to modularity. We now review evidence for two of the above mechanisms, variation in abundance and strong seasonality.

Regarding the former, abundance of both animals and plants is an important driver of modularity in some but not all mutualistic networks. For example, in the pollination network studied by Martín et al. (2012), abundance was not a significant driver of modularity. In other types of mutualisms, interaction frequency is best explained by abundance, but in combination with phylogenetic distance (Montesinos-Navarro et al. 2012). Thus, generalized, abundant species interact both with other abundant species, but also with distantly related specialist species, resulting in a nested pattern. For example, in a host plant–arbuscular mycorrhizal fungus (AMF) network, modules either contained one or a few common, generalized plants interacting with many rare specialized AMFs, or vice versa for fungi (Montesinos-Navarro et al. 2012), revealing a nested structure.

Seasonality can be a very important driver of modularity (Bosch et al. 2009). Species with relatively long phenophases, such as bumblebees, act as the backbone of pollination modules in which they interact with a series of shorter-phenophase flowering plant species (Olesen et al. 2008, Petanidou et al. 2008, Martín et al. 2012). Both plant and pollinator phenologies have been found to be drivers of modularity in pollination networks (Olesen et al. 2008, Petanidou et al. 2008, Martín et al. 2012). Thus, a seasonal series of modules was distinguished with

a spring module of plants and their dipteran and bee pollinators, and mid- and late-season modules dominated by peaking beetle populations. A few bee species act as the glue joining different modules (see section on species roles below). These bees interact with seasonal series of flowering plants, each with a short flowering season. The same temporal structure of modularity was observed by Dupont and Olesen (2012) in a temperate heathland.

Having reviewed a suite of causes for the overall level of modularity of a network, we now focus on the shape of individual modules.

11.6 Types of modules

In addition to the level of modularity, other factors shape the topological structure of the individual modules. One common type of plant–pollinator module is the “star” (Olesen et al. 2007). It most often consists of 1–2 hub plants linked to many specialized pollinator species. However, the star “flickers in time,” i.e., its links come and go (Olesen et al. 2008, Dupont and Olesen 2012). At any given point in time, only between one-fourth and three-fourths of all links may be present. Stars are assembled through very strong preferential attachment, i.e., all new species are only linked to the hub(s). That is, there is complete hub attraction. These star modules may consist of an abundant and/or widespread plant species with a large and long-lasting floral display visited by many rare and specialized animals. Similarly, in parasitic networks, such stars may be constituted by an abundant host with a stable population infected by a range of specialized parasites (Anderson and Sukhdeo 2011). A stable host makes it possible for parasites to complete their life cycles and even to evolve more complex life cycles.

Another type of plant–pollinator module is composed by compact sets of partners that are organized with high levels of connectance (20%–50%) and nestedness.

Pollination modules are linked together by connectors (see Section 11.7) such as large bees (Olesen et al. 2007) or plants varying in floral morphology (Kratochwil et al. 2009). Some modules are modular at different scales of resolution, revealing a hierarchical structure of nature (Bezerra et al. 2009, Olesen

et al. 2010). A few modules, however, are satellites, unlinked to other modules (Fonseca and Ganade 1996, Cagnolo et al. 2011). These may in some cases be formed by tightly coevolved species groups displaying a high interaction intimacy.

Some modules in a network may deviate considerably in their taxonomic or functional content from the network they belong to, and are only weakly—or not at all—linked to other modules. This could be the result of a particularly strong specificity among the members of a module or the coevolution of specific trait combinations. Around 360 species of Apidae and Melittidae bees are floral oil collectors (Mello et al. 2013). They obtain the oil from specialized flowers and use it for larval provision. Thus, oil bees and oil flowers have both a high specificity and very complicated trait combinations, such as floral oil glands and elaborated bee leg combs involved in the harvesting of oil (Bezerra et al. 2009). These bees and their flowers make up distinct modules in the Brazilian rainforest.

So far we have reviewed the modular structure of an entire network and the shape of individual modules. Next, we zoom in to a single module to characterize the roles of specific species within it.

11.7 Species roles within modular networks

Once we have detected the partitioning of a network into well-defined modules, modularity analysis allows the ranking of nodes as a function of their topological importance, that is, their relative importance from the point of view of network architecture. Here, one must consider two dimensions, the importance of a node within its module and its importance at the level of the entire network (see Box 11.2 by Roger Guimerà for quantitative details, and Figures 11.4 and 11.8 for specific examples). The importance of a node within its module is quantified as the within-module degree, i.e., the normalized number of interactions that any particular node has with the other nodes of its module. Biologically, this would be a surrogate for the generalization level of the species. The importance of a node in the network as a whole is quantified through its participation coefficient, which describes how spread out the interactions of that

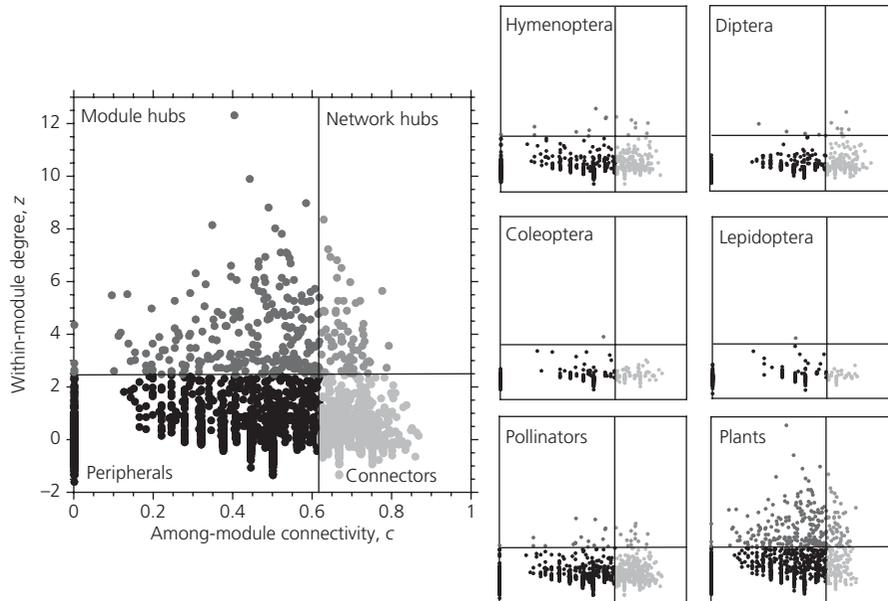


Figure 11.8 Species roles in a dataset of plant–pollinator networks. In all panels, each dot indicates a species. The large panel contains all cumulative data for the 29 modular networks. It comprises 8233 species. Small panels show the same information for given taxonomic groups. From Olesen et al. (2007).

node are across different modules. For a specific number of interactions, the node interacting with nodes from a larger number of different modules is the one with the highest participation coefficient. Nodes with high participation coefficients can be thought of as the glue that keeps the different modules well connected (Figure 11.2). In a strongly modular network, the effect of losing a species varies according to their participation coefficients. For example, the extinction of a module connector should be of huge consequence to the entire network, since it can result in the fragmentation of the original network in several, disjoint subnetworks. This is another illustration of the potential of network studies to inform conservation biology (see Box 11.1 and Chapter 14).

Olesen et al. (2007) classified species in their pollination network dataset in terms of their topological importance. Only about 15% of the almost 10,000 species in these networks were important either at the module level, the network level, or both (Figure 11.8). Species that were important at both the module and entire network were mainly

social bees, especially *Apis* spp. Module connectors included beetles and small flies. These are species whose extinction can have implications at the level of the entire network, not only for the species with which they directly interact. Other things being equal and assuming there is no reorganization of the community, their disappearance could induce the fragmentation of the mutualistic network in the different modules or clusters of modules.

What would be the consequences? One could argue that as long as all the species would be present, this would not make a difference, or could even be positive in terms of strengthening the tendency of a modular structure to buffer the effects of a perturbation now entirely confined within the subnetwork. However, Melián and Bascompte (2002) have discussed the dual nature of robustness; this fragmentation, indeed, could also have negative consequences. For example, the isolation of subnetworks would reduce the number of alternative paths for system response to perturbations and affect the co-evolutionary process. This is particularly relevant

if, as argued by John Thompson (2006), networks need to reach a critical size for some mutualistic life histories to appear. An example of this scenario suggested by Thompson would be that some bee species require an unbroken seasonal succession of flowering plants in order to persist. Thus, if network size is strongly reduced after human alteration, the resulting network may not be large enough to harbor all the previously existing life histories.

The modular description of a network and the consequent classification of species according to their roles, have been traditionally represented as snapshots fixed in time. More recently, we have started adding a temporal dimension to this portrait. Preliminary results in Brazilian pollination networks already suggest that the species' roles may be highly dynamic. The same species do not always play the same network topological role in the different habitats where they occur. For example, the oil flower *Byrsonima sericea* (Malpighiaceae) varied from being a peripheral species in some networks to being a highly connected hub in others (Mello et al. 2013). Among bees, species of the genus *Centris* are more often hubs than are members of other genera. They may, in general, play a central role in module build-up and evolution. Such modules have a long coevolutionary history and function relatively independent of the general pollination network in their habitat.

11.8 Conclusions

The study of mutualistic networks has provided a community-wide framework to understand mutualistic interactions in species-rich communities. It has helped to dispel the assumption that mutualism between free-living species has to lead to either highly specific one-on-one interactions, or to highly diffuse assemblages intractable to study. Studies of mutualistic networks have illustrated that despite the apparent complexity of these interactions, there are repeated patterns in network structure. In particular, the study of modularity has identified units midway between pairwise interactions and full networks. These structures are candidates to be understood as coevolutionary units in cases where coevolution is likely to be an important force shaping these networks. Within a modular network, species play distinct roles related to their topological

positions both within their module and within the entire network. These contrasting positions help us to identify subsets of species that are likely to play keystone roles in communities, and hence that should be the focus for conservation efforts.

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