UNITY IN DIVERSITY: ECOLOGICAL REFLECTIONS AS A TRIBUTE TO MARGALEF

CHAPTER

The network approach in ecology

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1 Introduction

1.1 Networks as complex systems

Ramon Margalef wrote in 1991 a book chapter entitled "Networks in Ecology". There, he advanced a series of ideas on the network paradigm, a paradigm that has grown popular in the last five years. Specifically, Margalef advocated a multidisciplinary comparison of different network types, something which is now common practice in the field of complex networks. He also envisioned scale-invariant properties of ecological networks, an idea that has been confirmed by the finding that complex networks are very heterogeneous: one can find nodes with numbers of links spanning several scales. In this chapter, we describe the network approach in ecology by reviewing recent discoveries in this field. These discoveries have been initiated by the study of non-biological networks such as the Internet, extended to biological networks such as gene expression networks or metabolic networks, and also applied to describe the complexity of ecological communities. Here, we will focus on the implications for ecology.

During the twentieth century, graph theory (see Harary 1969; Bollobás 1998) has developed into a substantial body of knowledge. In the last few years and in spite of a long tradition of network analysis in sociology (see Watts 2004 for a recent review), an increasing number of complex systems have been described and represented as networks (i.e., a set of nodes connected by links; see Fig. 1). The network approach pervades all scientific fields (Strogatz 2001) as a metaphor or description of the real world complexity. Physical, social, and more recently, biological systems have benefited from the mathematical framework of graph theory that underlies the network paradigm. In this way, the World Wide Web (Albert, Jeong, & Barabási 1999; Huberman & Adami 1999), the Internet (Doyle *et al.* 2005), the worldwide air transportation network (Guimerá & Amaral, 2004; Guimerá *et al.* 2005), social networks of acquaintance or other connections between individuals (Newman, Watts, & Strogatz 2002; Liben-Nowell *et al.* 2005), scientific collaboration networks (Newman 2001; Barabási *et al.*, 2002), the network of human sexual contacts (Liljeros *et al.* 2001), metabolic networks (Jeong *et al.* 2000; Ravasz *et al.* 2002), protein networks (Jeong *et al.* 2001), gene regulatory networks (Davidson 2002; Luscombe, 2004), food webs (Paine 1966; Cohen 1978; Pimm 1982), plant-animal mutualistic networks (Bascompte *et al.* 2003; Jordano *et al.* 2003), and many others, are examples of different systems studied under this common framework. This represents a really multidisciplinary research agenda, where concepts and tools applied to one field have been successfully imported to other fields in a very synthetic, Margalefian way.

No other example than molecular biology justifies the network approach as a new research agenda instead of as merely a different representation or diagram. Molecular biology, as particle physics, has had an extremely reductionist approach. Scientists have isolated a few genes and studied their produced proteins or activity patterns. However, gene regulation is eminently a coordinated enterprise where some genes act regulating other genes. Only with the onset of computer capacity, using multidisciplinary approaches combining experimental work in the lab with numerical analysis of simple network models, scientist have started to explore whole networks of genetic activity. One example is the gene network regulating the development of the sea urchin (Davidson *et al.* 2002). Since the publication of that study, molecular biologists have kept describing whole genetic networks in the most influential scientific journals, emphasizing structural properties which largely affect their stability (e.g. the spread of deleterious effects of mutations). Clearly, this is knowledge that could not be obtained by studying isolated genes. Diseases or development, for example, may be more related to the large scale architecture of regulation networks than to the proteins produced by a few such genes.

Ecosystems have been since long ago described as networks. Lindenmayer, Odum, Margalef, and many others have described communities as graphs of energy transfer. Food webs are a common theme in ecology with a long tradition (Cohen 1978; Pimm 1982). Food webs have pervaded ecological research as a way of representing community complexity. However, as with other themes in ecology, the intensity and emphasis has changed through the last decades. Here we will focus on the most recent outbreak of network thinking in ecology, the one using ideas from the recent field of complex networks.

1.2 Network structure and implications for its dynamics

Comparative studies of networks from different branches of science (from the pioneering work by Watts & Strogatz 1998) show common structural properties (Newman 2003 for a review). These comparative studies have used several descriptors of network complexity. In what follows we describe a few of such descriptors and how they have unravel different layers of network complexity.

One of the simplest ways to describe the statistical properties of a network is by plotting its degree (the number of links per node) distribution. Large real-life networks may show several degree distributions reflecting their architecture (e.g., Amaral *et al.* 2000) and robustness (e.g., Albert, Jeong, &

Barabási 2000). Some networks such as the electric power-grid of Southern California (Watts & Strogatz 1998) show an exponential distribution. Other networks such as the World Wide Web (Albert, Jeong, & Barabási 1999) and the worldwide air transportation network (Guimerá *et al.* 2005) show a power-law distribution and a truncated power-law (broad-scale) distribution, respectively. An exponential distribution, characterized by a fast decaying tail, implies that nodes have a well-defined average number of links. This is the reason this distribution is also called single-scale: the average number of links per node define the scale of the degree distribution. A power-law distribution, on the other hand, indicates a much higher variability in the number of links per node. That is, the bulk of nodes have a few links, but a few nodes are much more connected than expected by chance. A power-law distribution is right-skewed, that is, it has flat tails. Now the average number of links per node is not informative at all because the variance is much higher. This is the reason this distribution is also called sale-free: it has no characteristic scale, we can find nodes with a number of connections spanning several scales. An intermediate situation is represented by the broad-scale degree distribution, characterized by a power-law regime followed by a sharp cutoff, like an exponential or Gaussian decay of the tail.

The interest of the degree distribution stems from two facts. First, the degree distribution uncovers that different types of networks have the same architecture, which suggests common organizing principles. Second, the shape of the degree distribution greatly affects the robustness of the network to node deletion (e.g., Albert, Jeong, & Barabási 2000). Scale-free, heterogeneous networks are very robust to random removal of nodes because the few hubs act as the glue bringing together the whole network. Since hubs are uncommon, the likelihood of knocking down by chance such hubs is small. However, hubs are also the Achilles heel of scale-free networks: these networks are very fragile to the removal of the most connected nodes (deliberate attacks on the hubs). This robustness/fragility pattern grows stronger the highest the skewness of the degree distribution.

As noted above, the degree distribution is also informative of potential build-up mechanisms originating the observed network. For example, an exponential degree distribution is the hallmark of a random network. One can envision such a network growing by the following simple rule. Starting with a few randomly connected nodes, at each time step a new node is introduced and interacts with an average number of pre-existing nodes randomly chosen. On the other hand, the basic recipe to build a scale-free network is one in which each new node tends to interact preferentially with the already most connected nodes in a "rich get richer fashion." This is the preferential attachment model proposed by Barabasi & Albert (1999). When there are constraints on such preferential attachment (filtering information), such as an imperfect knowledge of the whole network, a broad scale distribution emerges.

Another structural property shared by some networks is the small-world effect (Watts & Strogatz 1998), characterized by *i*) a high clustering coefficient (i.e., a high probability that two nodes connected to a common node are connected to each other) compared with a random graph, and *ii*) a short path length, meaning that most pairs of nodes are connected by a short path through the network. Specifically, the diameter of the network, quantified by the average shortest distance between all pairs of nodes (i.e., the smallest number of links that must be followed to go from one node to the other), increases logarithmically with the number of nodes (as for random graphs).

The small-world effect has implications for the dynamics of processes taking place on networks. The spread of information or a disease across the network will be fast. If it takes only "six steps" for a rumor to spread from any person to any other (from the earlier empirical study conduced by Milgram 1967), then the rumor will spread much faster than if it takes a hundred steps. This also affects the time it takes for a disease to spread throughout a population (Pastor-Satorras & Vespignani 2001).

Studies of the effects of structure on network dynamics are still in their infancy. Much more progress in this direction must be made to advance in the knowledge of complex systems behavior.

2 Insight from ecological networks

The network approach, as noted above, is a very useful framework to represent many physical, social, and biological systems. But, in spite of its potential, network analysis techniques have only been incorporated in ecology (for a recent review see Proulx, Promislow, & Phillips 2005) to characterize food webs (see e.g., Paine 1966; Pimm 1982; Cohen, Briand, & Newman 1990) and, more recently, plant-animal mutualistic interactions (see e.g., Bascompte *et al.* 2003; Jordano et al. 2003). While in both fields nodes represent species and links depict ecological interactions, incipient studies focus on spatial networks (Urban & Keitt 2001) in which nodes represent discrete habitat patches and links depict movements of individuals, colonizations, or gene and seed dispersal.

In the following sections we summarize the main results derived from applying the network approach to the following fields of ecology: food webs, plant-animal mutualisms, and spatial networks.

2.1 Food webs

Ecology has a long tradition studying the structure of food webs as an important property for understand the dynamical stability of communities (e.g., Paine 1966; Cohen 1978, Pimm 1982). Food webs depict trophic relationships between species, that is, who eats whom. Generally, food webs have a much higher connectance (the fraction of all possible links that are realized) and a much smaller size than other networks studied, which has important implications for network topology (see Dunne, Williams, & Martinez 2002 for a recent review).

Some recent work (e.g., Montoya & Solé 2002; Dunne, Williams, & Martinez 2002) has focussed on the degree distribution shown by real food webs. Dunne, Williams, & Martinez (2002) analyzed a broad range of 16 high-quality food webs from a variety of aquatic and terrestrial ecosystems to investigate whether food webs displayed small-world effect and scale-free structure (i.e., the topology characteristic of many other real world networks). They demonstrated that although some food webs had small-world and scale-free structure (the largest networks with the lowest connectivity; Fig. 2a), most did not. Food webs displayed a variety of functional forms related with connectance and network size, but the bulk of food webs showed distribution tails dropping off fast, as expected for exponential distributions (see Fig. 2b).

The degree distribution uncovers only a first description of structure. It is a statistical description of the probability of a randomly picked species interacting with k other species, but it does not describe the identity of these species. As Ravastz *et al.* (2002) first described for genetic networks, two networks can show the same degree distribution but have different architectural designs (consider for example two species interacting with n and m species: in one case these two subsets of species can be highly overlapping, and in another these two subsets may contain completely distinct species). Parallel studies on food webs looked at a deeper level of structure beyond the one depicted by the degree distribution (Melián & Bascompte 2002, 2004). Melián & Bascompte (2002) applied a measure of correlation between the number of links of each species and the average number of links of the species they interact with. This connectivity correlation measure had previously been applied by physicists studying the Internet (Pastor-Satorras, Vazquez, & Vespignani 2001) and biologists studying protein networks (Jeong *et al.* 2000). Whereas two highly connected nodes are unlike to be connected between each other in protein networks (Jeong *et al.* 2000), the reverse happens in food webs (Melián & Bascompte 2002). On the other hand, Melián & Bascompte (2004) studied how links are distributed within and between subwebs (a k subweb is a subset of species that are connected to at least k species from the same subset, see Fig. 2c). The k subweb frequency distribution decays as a power law. The most dense subweb has the most interactions, despite containing a small number of species (see Fig. 2c). Melián & Bascompte's (2004) results suggest a cohesive organization, that it, a high number of small subwebs highly connected among themselves through the most dense subweb. This cohesive topological organization may decrease the probability of network fragmentation when species are removed (Solé & Montoya 2001; Dunne, Williams, & Martinez 2002).

What implications does food web structure have in relation to the likelihood of trophic cascades? Beyond properties derived from binary food webs in which trophic links are either present or absent, the structure of the strength of species interactions may help bridge the gap between food web structure and dynamics (Berlow *et al.* 2004). In a recent work, Bascompte, Melián, & Sala (2005) show that interaction strengths are structured non-randomly in a large Caribbean food web. In the largest and most resolved food web, the co-occurrence of strong interactions on two consecutive levels of food chains occurs less frequently than expected by chance, and when they occur, these strongly interacting chains are accompanied by strong omnivory more often than expected by chance. The distribution of interaction strength in these trophic modules (or motifs) reduces the likelihood of trophic cascade after the overfishing of top predators.

2.2 Plant-animal mutualistic networks

The bulk of mutualistic studies have focused on a single plant-single animal interaction, i.e. pairwise coevolution. There are, however, some community-level studies of mutualisms (e.g., Feisinger 1978; Waser *et al.* 1996), which have recently benefited from a network perspective (Olesen & Jordano 2002; Bascompte *et al.* 2003; Jordano, Bascompte, & Olesen 2003; Vázquez & Aizen 2004; Memmott, Waser, & Price 2004; Vázquez 2005; Olesen *et al.* 2006).

Plant-animal mutualistic networks are described by a different type of network than food webs. While in food webs there is only a single type of node and all species can, in principle, be connected to any other, plant-animal networks correspond to the so-called bipartite networks. Bipartite networks are defined by two distinct sets (plants and animals) with interactions between, but not within sets (see Fig. 3e). Other types of bipartite networks are social networks (e.g., linking people to the social events they attend, see Newman, Watts, & Strogatz (2002)). Plant-animal mutualistic networks can be described by two basic structural properties. First, they are very heterogeneous. That is, the bulk of species have a few interactions, but a few species are much more connected than expected by chance (Jordano, Bascompte, & Olesen 2003). Second, mutualistic networks are highly nested, that is, specialists interact with proper subsets of the species interacting with generalists (Bascompte *et al.* 2003).

We can characterize network heterogeneity studying the degree distribution. Because mutualistic networks are bipartite networks, we can represent the degree distribution for both plant and animal species. Jordano, Bascompte, & Olesen (2003) described the topology of 29 plant-pollinator and 24 plant-seed disperser networks in natural communities. They showed that the bulk of mutualistic networks follow a truncated power-law degree distribution, and almost the total of the rest followed a power-law degree distribution. They suggested that constraints in the addition of links such as morphological mismatching or phenological uncoupling between mutualistic partners, restrict the number of interactions established and hence, caused deviations from scale-invariance. Other potential explanations for the truncated distributions deal not with external constraints on the preferential attachment, but on the bipartite nature of this networks: differences on the original core of species, and differences in size between plants and animals (Guimeraes *et al.* 2005). This is a striking difference in relation to food webs which, as noted above, seem to be described by exponential degree distributions. One potential explanation for this difference steams from the fact that plant-animal networks are much more resolved than traditional food webs, although other biological differences could also play a role.

Nestedness in mutualistic networks has been investigated by Bascompte *et al.* (2003) comparing real networks with two different null models. In their first null model, connections are randomized probabilistically keeping only the observed total number of interactions. Their second null model, probabilistically maintains the observed total number of interactions and approximately maintains the number of interactions per species (degree). Bascompte *et al.* showed that in real mutualistic networks there is a tendency for specialist species interact with generalist ones and conversely, beyond random expectation (see Fig. 3d).

What consequences this structure has for the persistence and stability of plan-animal communities? There are a few studies attempting to relate mutualistic network structure with dynamics. For example, Memmott, Waser, & Price (2004) and Jordano, Bascompte, & Olesen (2006) look at the network responses to species deletion. These studies followed early work on network robustness in the Internet (Albert *et al.* 2000) and food webs (Solé & Montoya 2001). However, the first paper exploring dynamical implications of real network structure for the persistence of mutualistic communities is the study by Fortuna & Bascompte (2006). They developed a patch-model of a whole plant-animal mutualistic community and explored the role of network structure for the response of a metacommunity to habitat loss. To assess the role of network structure, Fortuna and Bascompte (2006) built three versions of the metacommunity model. In the first version, they used the exact network of interactions of two real mutualistic communities. In the other versions, they randomized the observed network of interactions using the two different null models described above (the first null model lacks degree and nestedness, and the second null model lacks nestedness but not degree). They showed that the community response to habitat loss is affected by network structure. Real communities started to decay sooner than random communities, but persisted for higher habitat destruction levels, and also there was a destruction threshold at which the community collapsed (Fig. 4).

The above described topological properties of real networks can explain the different rate of species decline. The high heterogeneity in species degree imply that the last few species going extinct are the most generalist species. Since they rely on so many species, some of the few available patches will at least contain one of the species they interact with. Similarly, for the very same reason, some species are less connected than expected by chance. These specialists go extinct first. Nestedness, on the other hand, implies two properties. First, a nested matrix is highly cohesive, because generalist plants and animals interact among themselves. This creates a core in which a small set of species leads the bulk of interactions (Bascompte *et al.* 2003). This dense core is very robust to habitat loss. Second, these matrices embed asymmetric interactions in the sense that specialist species tend to interact with the more generalist species (both for plants and animals; Bascompte *et al.* 2003; Vázquez & Aizen 2004). Network structure has also been recently adduced to explain empirical plant species decline with habitat loss in a plant-pollinator community (Ashworth *et al.* 2004).

What consequences does this structure have for coevolution? (see Bascompte & Jordano 2006). It is well accepted that the interactions between plants and the animals that pollinate them or disperse their seeds have played a major role in the generation of terrestrial biodiversity. Traditionally, studies on coevolution have focussed on highly specific pairwise interactions. The alternative of one-to-one coevolution up to the recent years has been the concept of diffuse coevolution (Janzen 1980) stating that interactions are not species-to-species, but guild-to-guild. If there is no structure, that is, plants and animals interact randomly, then a concept such as diffuse coevolution may be enough to describe coevolutionary interactions in species-rich communities. If there is structure, however, the shape of this structure will certainly lead to an alternative view of coevolution. The nested matrix has a dense core of species that capture the bulk of interactions. The species forming the core are going to highly determine the selective forces exerted on other more specialist species which will become attached to such a core. The network perspective has provided analytic tractability to coevolution in multispecific communities (Thompson 2005).

2.3 Spatial networks

The network approach complements previous levels of spatial description. Spatial processes can be described by means of spatially implicit or spatially explicit models. Spatially implicit models, although allow analytical solutions, are necessarily simple. Spatially explicit models, on the other hand, can account for spatial detail and local dispersal, but have to rely on numerical simulations. The spatial network approach is a spatially explicit landscape description which uses information on network topology. That is, its main advantage is to import concepts and measures from complex network theory.

Previous studies already suggested the suitability of the network approach to the study of spatial ecology (e.g., Cantwell & Forman 1993; Urban & Keitt 2001), but only few attempts incorporate basic properties of graph theory (Bunn et al 2000; Urban & Keitt 2001; Fagan 2002). In some cases, it is convenient to link habitat fragments whenever movement from one to another can be performed by a target species, such as landscape network models (Keitt 2003) and spatially realistic metapopulation models (Hanski 2001).

In a recent study (Fortuna, Gómez-Rodríguez, & Bascompte 2006), a large spatial network of temporary ponds which are used as breeding sites by several amphibian species is identified and analyzed (see Fig. 5a). The authors investigated how the structural properties of the spatial network change as a function of the amphibian dispersal distance as drought increases (Fig. 5b-d). Using measures of graph theory to characterize the network topology, Fortuna, Gómez-Rodríguez, & Bascompte (2006) suggested that the alteration by drought of this undisturbed network not only reduced the total number of ponds where amphibians could reproduce and successfully recruited metamorphosing juveniles. It also changed the structural properties of the remaining pond network, with implications for amphibian persistence. The observed spatial structure of temporary ponds was robust to drought compared with similar random structures. This allows the movement of amphibians to and between flooded ponds, thus increasing the probability of reproduction even in dry seasons (Fig. 6).

Analysis of network topology provide a new and straightforward way to quantify the robustness of a patchy population to habitat loss and the identification of "keystone" patches that are critical to landscape connectivity and hence population persistence (Urban & Keitt 2001; Keitt 2003). The application of existing network approaches to spatial processes can yield valuable insight. Network analysis is a powerful tool for analyzing real landscapes and can also be used as a basis for building more complex population viability models. Optimization techniques to select a subset of available habitats that maximize species persistence can be based on a network approach (see Cabeza & Moilanen 2001 and references therein). We think that detailed spatial network structure can also form a basis for constructing new metapopulation models. Future progress, however, will depend on a synergistic interplay between the network structure of the landscape and the underlying biological processes.

3 Unity in diversity: towards ecological networks

We have seen briefly the main issues concerning food webs, plant-animal mutualistic networks, and spatial networks. Structural implications for dynamics have been explored separately for each community level. But ecological systems are more complex, combining different type of interactions and so composed networks. When available data allows us to integrate multiple interaction types in species-rich communities, we will be ready to study ecological networks in a broader context.

A pretty recent study has incorporated trophic and mutualistic interactions in a simple module. Knight *et al.* (2005) have showed that fish indirectly facilitate terrestrial plant reproduction through cascading trophic interactions across ecosystems boundaries. The abundance of larval dragonfly in ponds was reduced by fish, leading to fewer adult dragonflies that consume insect pollinator nearby. As a result, the authors showed that plants near ponds with fish received more pollinator visits and were less pollen limited that plants near fish-free ponds.

Melián, Bascompte, & Jordano (submitted) have synthesized and analyzed the trophic and mutualism plant community (plant-herbivore, plant-pollinator, and plant-seed disperser interactions) from Doñana National Park (Southern Spain). Their results suggest that a plant exposed to pollinators is visited significantly by herbivores, and this structure alters the persistence of the community. This type of studies can address questions as whether communities with different types of interactions are randomly assembled, and what implications this structure has for the dynamics of the whole community. Traditionally, studies on community stability have focussed on a single interaction type. Combining different interaction types can serve to explore to what extend community stability has more to do with how different interaction types are combined than on patterns from a single interaction type. This can also balance the bias of community-wide competition and predation studies. If plant-animal mutualistic interactions are so important for biodiversity maintenance, it is worth incorporating such mutualistic interactions into community criteria for persistence.

There is one more aspect we will like to emphasize in relation to the current status of studies on ecological networks. Traditionally, the wide majority of ecological processes have been studied without any consideration of the spatial dimension. As we have showed above, the network approach can also be a useful tool for the study of spatial processes. Because interactions among species take place in a spatial dimension (and in a time), the framework of ecological networks can only be complete if we take into account the spatial network in which ecological interactions occur (Fig. 7). In this way, we will be moving towards a more realistic description (networks of networks).

In summary, this chapter has emphasized recent work on the field of complex networks with implications in ecology. The network perspective, as many others, was long ago envisioned by Margalef. He saw the potential of networks, and some of his views have been confirmed in the last few years. He also emphasized aspects of ecological networks which need still to be developed. Specifically, he advocated to unify what he saw as the two main approaches in networks, one focussing on the nodes and the other focussing on the flows. Margalef's approach was more dynamic, and he emphasized the need to quantify networks, that is, to use interaction strength measures. More importantly, Margalef also saw the limitations of the network approach, and would be a nice tribute to his immense wisdom to recall his critic view in here. Margalef (1991) writes "The concept of network has been imposed on ecology from outside and 'sold' as a necessary reference to construct models. Is it worthwhile, therefore, to spend time on networks? Perhaps only to learn not to care about nets that are too simple. Maybe just to have some fun". With his unique self-criticism, Margalef advanced points of view so innovative that touched us in ways we could not fully grasp until years after.

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6 Figure legends

Fig-1. Map of protein-protein interactions (modified from Jeong *et al.* 2001) showing the complex arquitecture of biological networks.

Fig-2. Cumulative degree distribution of the Ythan esturary (a) and the Silwood Park food-webs (b). n is the number of species, and C is the connectance (the number of links in the web divided by the maximun number of possible links including cannibalism and mutual predation). c) Graph depicting k subwebs (i.e., subwebs where each species has at least k interactions within that subset) in the Ythan estuary food web (modified from Melián & Bascompte 2004). The most dense k subweb (in the middle of the graph) has the most interactions, despite containing a small number of species.

Fig-3. (a-d) Plant-animal mutualistic interaction matrices (modified from Bascompte *et al.* 2003). Numbers label plant and animal species (which are ranked in decreasing number of interactions per species). A filled square indicates an observed interaction between plant i and animal j. a) Perfectly nested matrix. b) Random matrix. c) Compartimentalized matrix. d) Real plant-pollinator mutualistic matrix (data compiled by J. M. Olesen and H. Elberling). e) Bipartite graph depicting a real plant-seed disperser mutualistic network (data compiled by P. Jordano). Species are represented by nodes arranged along the vertical lines (plants (25) on the left and animals (33) on the right) and shown in decreasing number of interactions per species. A plant and an animal interact if they are linked by a line.

Fig-4. Effect of habitat loss (d) on the fraction of species surviving for the real network (solid line; average of 10 replicates), and the randomizations using two null models (dotted line and broken line, respectively; average of 10 replicates), for both the plant-pollinator network (a), and the plant-seed disperser network (b). Inset names indicate the taxa represented (modified from Fortuna & Bascompte 2006).

Fig-5. a) Spatial location of the ponds (circles; size is proportional to area on a logarithmic scale) in Doñana National Park. b-d) Schematic representation of a subset of ponds linked by different dispersal distances d of three hypothetical amphibian groups (b, $d = 100$ m; c, $d = 500$ m; and d, $d = 1000$ m). Black nodes and white nodes represent flooded and dry ponds, respectively. Solid lines indicate directed links between dry and flooded ponds. Broken lines represent undirected links between flooded ponds. Note that we can identify network components (i.e., groups of interlinked flooded ponds) at different scales (modified from Fortuna, Gómez-Rodríguez & Bascompte 2006).

Fig-6. Probability to move from a dry to a flooded pond for three dispersal distances along all the gradient of drought intensity. Solid line, broken line, and dotted line represent real data, null model 1 (randomizing the spatial locations of the ponds), and null model 2 (randomly allocating the sizes of the ponds but keeping their spatial locations), respectively (modified of Fortuna, Gómez-Rodríguez & Bascompte 2006).

Fig-7. Schematic framework depicting different levels of ecological study. On one hand, at local patch scale (on the left, from up to down), studies can focus on single species, pairwise interacting species, multispecies with a single type of interaction, and multispecies with more than one type of interactions (ecological communities). On the other hand, at spatial network scale (on the right, from up to down), there are less studies considering the spatial dimension in which the former ecological systems are embedded. Beyond pairwise spatial interactions, food web studies and, more recently, plant-animal mutualistic networks (both considering one single type of interaction), should be integrated within the spatial network in which they are inhabited.

7 Figures

Fig. 1

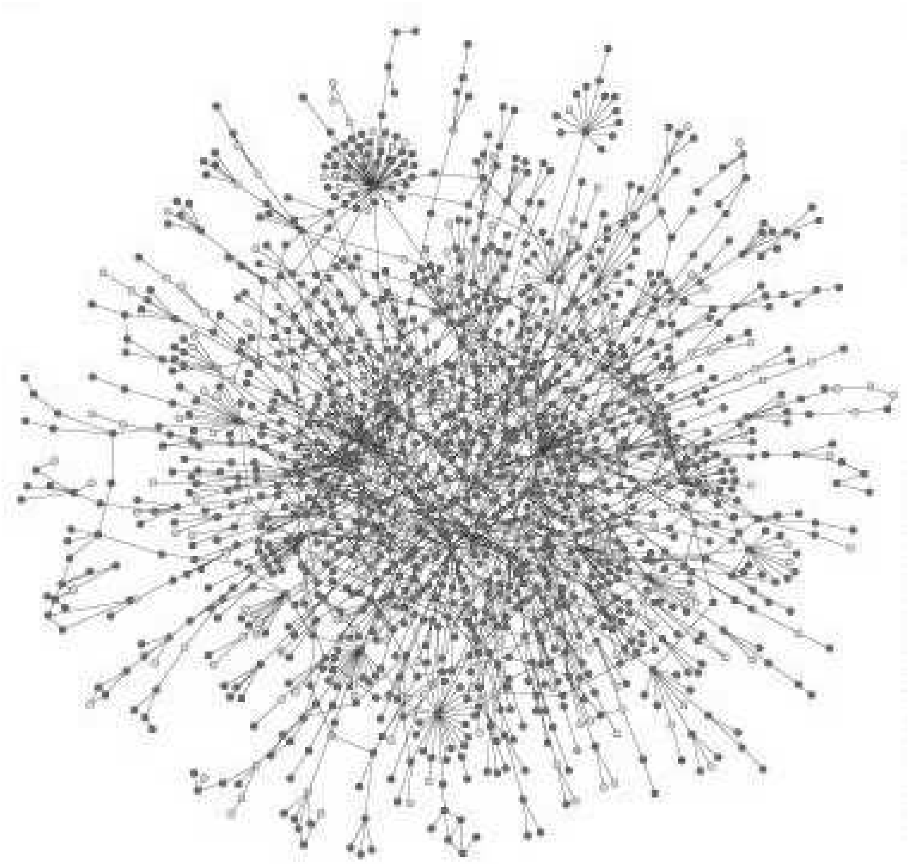


Fig. 2

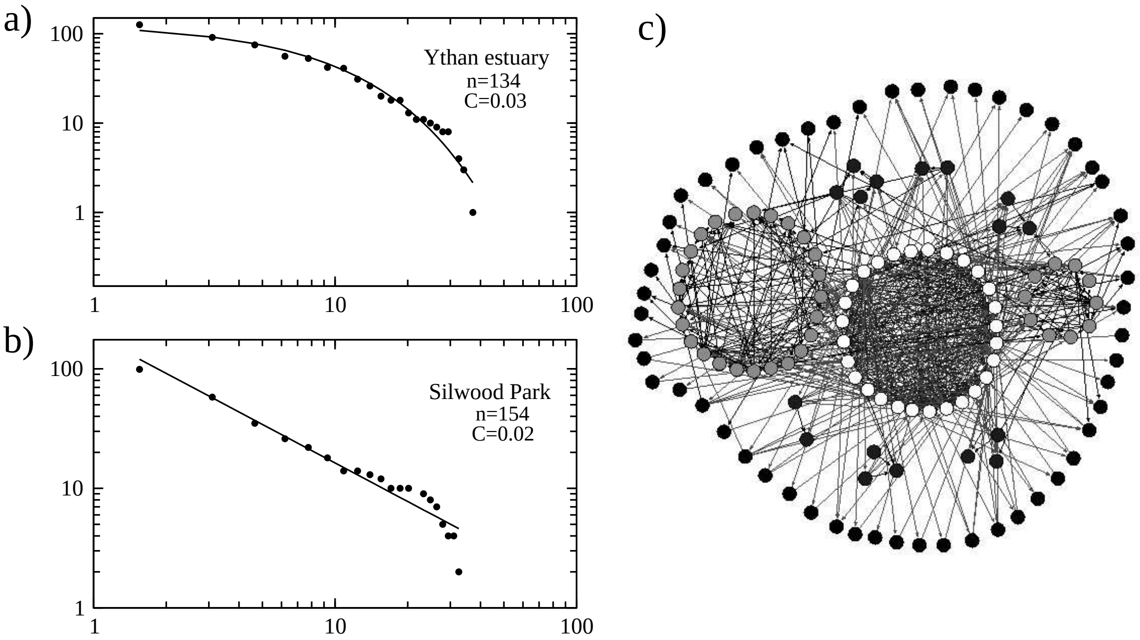

a)
Ythan estuary
n=134
C=0.03
100
10
1
1
10
100
b)
Silwood Park
n=154
C=0.02
100
10
1
1
10
100
c)

Fig. 3

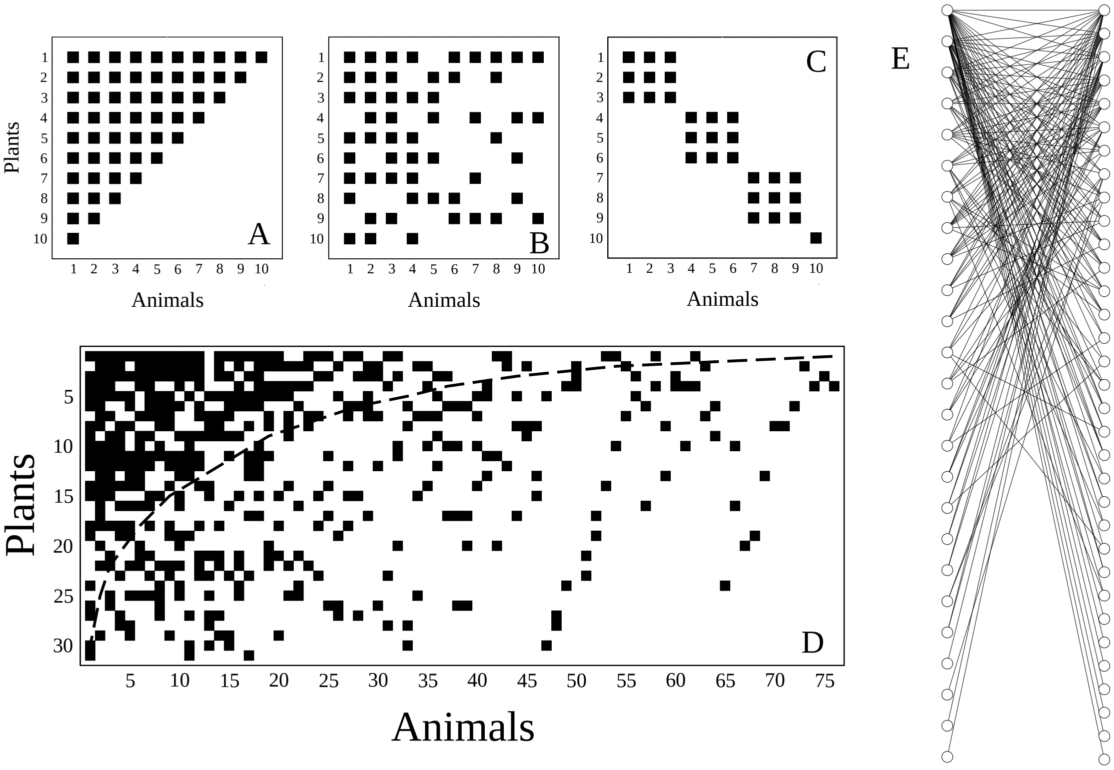
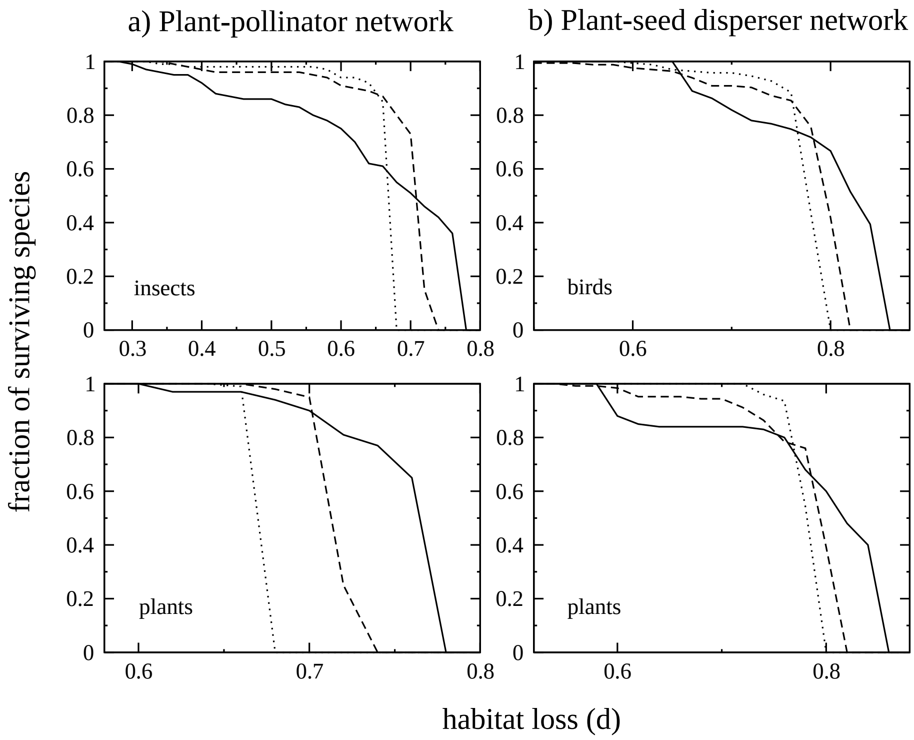

Plants
Animals
1 2 3 4 5 6 7 8 9 10
A
B
C
D
E
5 10 15 20 25 30
5 10 15 20 25 30 35 40 45 50 55 60 65 70 75

Fig. 4



a) Plant-pollinator network
b) Plant-seed disperser network
fraction of surviving species
habitat loss (d)
insects
birds
plants
plants
0
0.2
0.4
0.6
0.8
1
0.3
0.4
0.5
0.6
0.7
0.8

Fig. 5

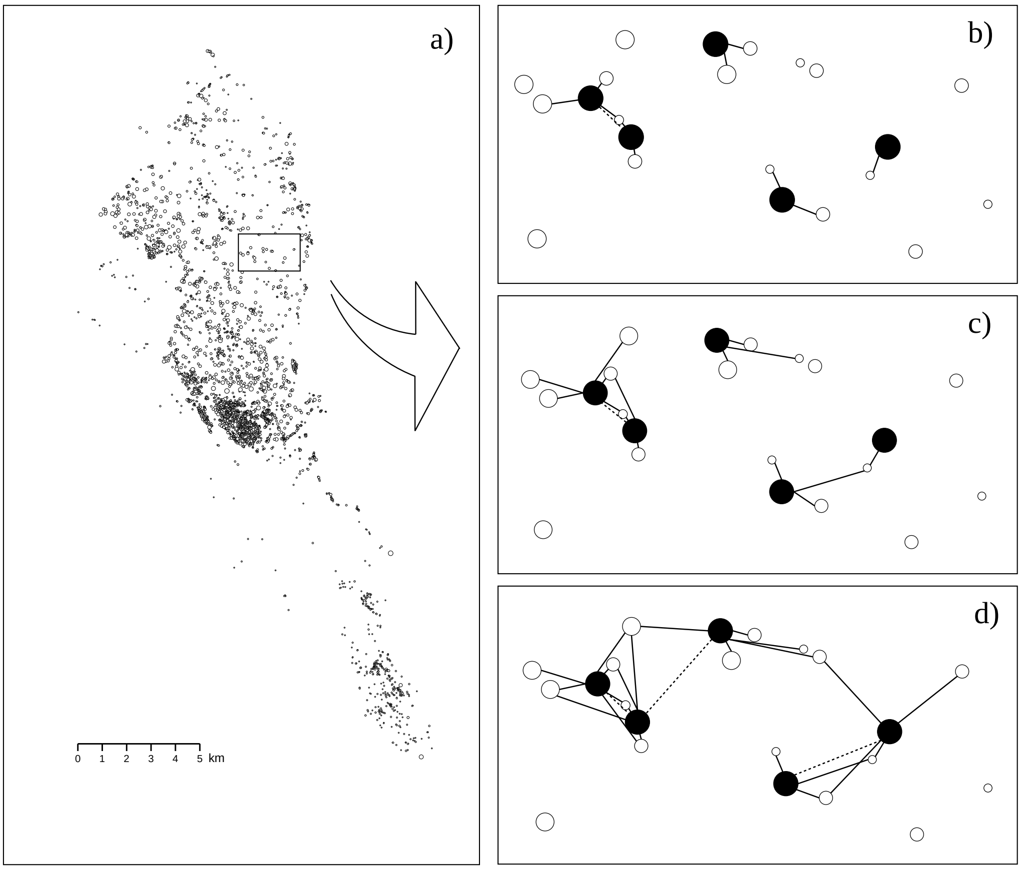


Fig. 6

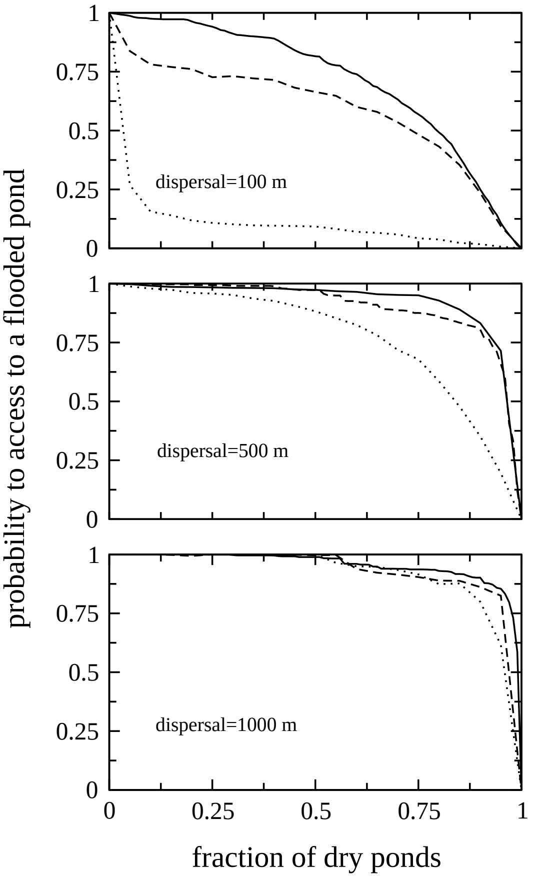
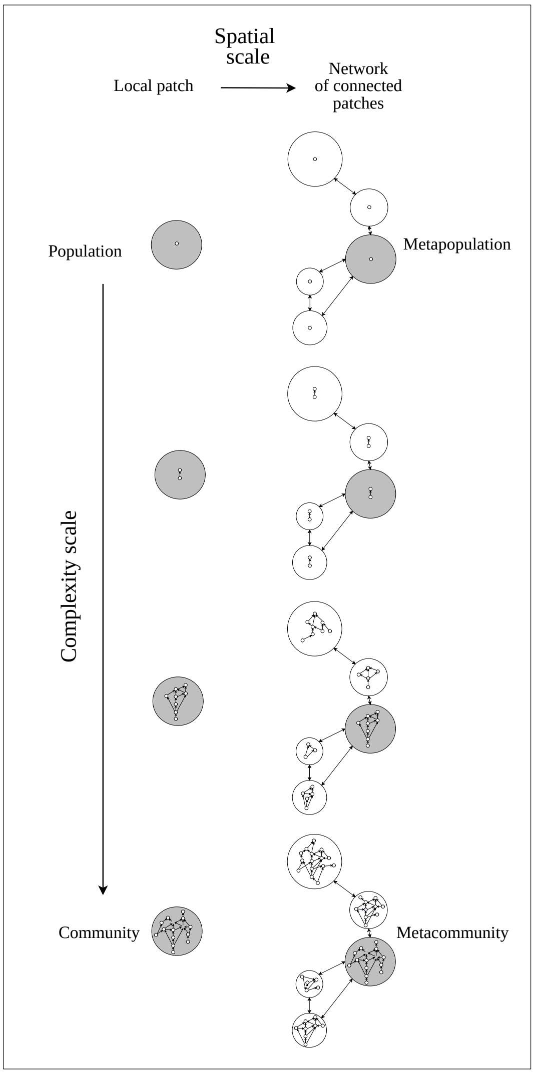

probability to access to a flooded pond
1
0.75
0.5
0.25
0
dispersal=100 m
1
0.75
0.5
0.25
0
dispersal=500 m
1
0.75
0.5
0.25
0
dispersal=1000 m
0
0.25
0.5
0.75
1
fraction of dry ponds

Fig. 7


Spatial scale
Local patch
Network of connected patches
Population
Metapopulation
Complexity scale
Community
Metacommunity