



INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

Networks in ecology

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Abstract

Recently, ecology has shown a strong interest in network theory. The question, as with any other emerging field, is to what extent we are making real progress in understanding ecological and evolutionary processes or just telling the same stories with fancy new words. I first present a biased overview of the development of network theory, focusing on its search for common patterns across seemingly different systems. I then proceed by discussing some applications of network theory in ecology, namely, species interactions, spatial ecology, epidemiology, and evolution in social groups. Finally, I suggest important contributions of the network approach such as identifying the consequences of heterogeneity for population and community dynamics, potential pitfalls, and future directions.

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Zusammenfassung

In jüngerer Zeit hat die Ökologie ein starkes Interesse an der Netzwerktheorie gezeigt. Wie bei jedem neu auftauchenden Feld stellt sich die Frage, in welchem Maße wir echte Fortschritte im Verständnis ökologischer und evolutionärer Prozesse machen oder nur dieselben alten Geschichten mit neuen Phantasiebegriffen erzählen. Ich beginne

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mit einem nicht unparteiischen Überblick über die Entwicklung der Netzwerktheorie, wobei ich mich besonders auf ihre Suche nach den gemeinsamen Mustern von scheinbar unähnlichen Systemen konzentriere. Ich diskutiere dann einige Anwendungen der Netzwerktheorie in der Ökologie, namentlich die Interaktionen zwischen Arten, räumliche Ökologie, Epidemiologie und Evolution in sozialen Gruppen. Schließlich weise ich hin auf bedeutende Beiträge des Netzwerkansatzes, wie die Identifizierung der Folgen von Heterogenität für Populations- und Gemeinschaftsdynamik, auf mögliche Fallstricke und zukünftige Entwicklungsrichtungen.

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Introduction

One can argue that complex networks represent the fourth strike of the science of complexity into ecology. First, deterministic chaos showed that simple non-linear deterministic models can produce complex time series, and so we can no longer assume that knowledge implies prediction, a long-standing tenet of Newtonian physics. Later, spatial models of local, non-linear growth, and long-range dispersal have been seen as an easy recipe for generating a myriad of complex spatio-temporal patterns that emerge in otherwise homogeneous landscapes. As a consequence, complex spatiotemporal patterns do not necessarily reflect complex mechanisms. Self-organized criticality, with the sandpile as its paradigmatic example, illustrated that some systems spontaneously evolve towards a critical state where small perturbations lead generally to small consequences, but can also be amplified and affect the whole system. Simple perturbations do not have necessarily simple consequences.

Network theory is the new flag of the complexity sciences (see [Amaral, Scala, Barthelemy, & Stanley, 2000](#) and [Albert & Barabasi, 2002](#) for general introductions to complex networks and [Proulx, Promislow, & Phillips, 2005](#), [May, 2006](#), and [Montoya, Pimm, & Solé, 2006](#) for applications in ecology). In the last few years, many systems have been described as networks (protein networks, genetic networks, food webs, etc.). These networks are defined by nodes (species, genes, computers, etc.) that are connected through links (trophic interactions, gene regulation, information transfer, etc.). But, are we really making progress by having ecological papers talking about genes, the Internet or proteins? Let me first revisit deterministic chaos as an illustrative example of what can happen with the network approach.

Chaos

In the mid-1980s and early 1990s, deterministic chaos was a hot area in ecology, with large numbers of both empirical and theoretical papers. It is now hard

to see any paper on the subject, which of course is part of the fad component of any such appealing label. One could be tempted to conclude that no long-standing achievement was brought by work on chaos. I think that claim would be false and unfair. It certainly is not that everything around us is chaos. But it is also probably true that we have a few text book examples of chaotic systems in ecology. Even if we did not have any, I would claim that chaos theory has been a very valuable intellectual contribution. It brought a new way to look at complex time series. It also put emphasis on non-linear dynamics, and led to more recent work on the joint effect of stochasticity and non-linear, deterministic dynamics ([Solé & Bascompte, 2006](#)). Thus, we have learned a lot from the experience. One can have a similar feeling about the future of network theory. There are now many papers proudly waving the words “complex networks” in the title, and skeptics may claim this will vanish in a few years. But, what can remain of all this excitement?

Networks

Network thinking is by no means new to ecology. Great ecologists such as [Lindenman](#) and [Odum](#) pioneered the use of networks as a way to represent and describe food webs ([Lindenman, 1942](#); [Odum, 1956](#)). Interestingly enough, food webs have been an important field in ecology for several decades, although with periodic waves of interest. The most recent one echoes similar work on complex networks and characterizes the architecture of food webs and its implications for network robustness. This is, however, a long-standing question that has been previously addressed with other tools and ideas. [Ramon Margalef](#), for example, entitled a book chapter “Ecological Networks” ([Margalef, 1991](#)). It is not only that he thought about networks as a way to describe ecological systems, but he also advocated a multidisciplinary comparison of different network types, something that is now common practice in the field of complex networks. He also envisaged 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. Networks thus have been around for a long time, and we have to be aware of this previous (sometimes even classic) work. One should integrate this with new concepts and tools and critically apply them to interesting ecological questions to try to advance not just the network agenda, but whenever possible, the ecological agenda.

Looking at commonalities across apparently different systems may bring new insights. For example, the fact that different networks have similar statistical properties is useful for at least two reasons. First, it can point towards similar mechanisms of network build up. Second, it may suggest that regardless of the identity of nodes real world networks have to be stable in the face of perturbations, which may impose some architectural constraints. In relation to the search for common mechanisms of network formation, physicists have a simple toy model of network formation that explains some statistical properties of complex networks including food webs. This model follows the path of the pioneering work by the mathematicians Paul Erdős and Alfred Rényi, who built the pillars of random graphs (Albert & Barabasi, 2002). They envisaged a series of nodes and an increasing fraction of links built as follows: select randomly two nodes and establish a link between them. After a series of iterations one gets a random network. Unfortunately, its statistical properties do not match some of the properties of real complex networks. Specifically, complex networks are very heterogeneous in the sense that the bulk of nodes have a small number of interactions, but a few nodes are much more connected than expected by chance. Trying to address this mismatch, Barabasi and Albert (1999) popularized a model they named preferential attachment. The idea is very simple. New nodes tend to interact with existing nodes with a probability proportional to their number of links. It is a kind of “rich gets richer” process. This simple mechanism predicts the heterogeneity observed in complex networks. The concept of this model as a way to generate skewed distributions, however, goes back to Simon (1955). This mechanistic approach is not new in ecology either. Several food web models parallel theoretical progress in physics. One of the first such models in food webs is an equivalent to the random model of Erdős and Rényi (Cohen, 1978). Essentially, each pair of species can be linked with the same probability estimated as the global connectance. This was followed by a more elaborate version, the cascade model (Cohen, Briand, & Newman, 1990) where species are arranged on an axis (e.g. body size) and allowed to prey only on smaller species. More recently, Williams and Martinez (2000) proposed the niche model, where species are allowed only to prey

on species within a certain size range. Cattin, Bersier, Banasek-Richter, Baltensperger, and Gabriel's (2004) addition of phylogenetic information and adaptation, have added biological layers on top of this. In summary, this global effort has shown how very simple rules can yield complex food webs. These models are important in the sense of providing a bridge between food web structure and dynamics.

A strict interpretation of the preferential attachment mechanisms (or any similar) is viewed with difficulty by ecologists. Part of this may be that the model is not good enough to describe linkage in ecological systems; part is just that the metaphor has to be interpreted in ecological terms. For example, even if the preferential attachment model is at work in ecosystems, one does not need to assume literally that the number of links is the primary variable. Here, one has to translate the metaphor into ecological terms. Species may respond not to the number of interactions of other species, but to other variables correlated with the former, such as species abundance. Generalist species can be more abundant, and so other species may tend to interact with them.

However, in the assessment of common mechanisms of network construction we encounter a familiar problem, namely, inferring process from pattern. That preferential attachment or any other model produces statistical properties such as scale-free distributions in the probability distributions of the number of links per node does not necessarily mean the reverse is true. That is, highly heterogeneous distributions of interactions per species do not necessarily imply a particular mechanism. This is the same mistake that was often made in relation to self-organized criticality. People tended to infer self-organized criticality (process) from the basis of scale-free distributions of the frequency of perturbations (e.g. avalanches in the sand pile) (pattern).

The second potential benefit of looking at common properties across seemingly different network types is that a common structure may suggest the existence of constraints on network robustness. The relationship between network structure and robustness has been a recurrent topic in food web research (Cohen et al., 1990; May, 1974; Pascual & Dunne, 2006; Pimm, 2002). What is useful from this new approximation is to focus on new structural properties such as the distribution of the number of interactions per species. For someone seeing a half-filled glass, network research brings new ideas to integrate with older ones that can advance our understanding of how fragile food webs are. Again, exploring the metaphor in the ecological realm would, for example, use this information to better understand the community-wide consequences of perturbations. What are the consequences of the loss of one species?

Will these changes remain local, affecting only a few other species, or will they cascade through the whole food web? These are interesting ecological questions that can benefit from a network approach. One risk here, however, is to assume that if a particular network architecture confers stability, this structure has been selected for that particular reason. This is a familiar debate in relation to adaptation versus exaptation (Gould & Vrba, 1982).

Examples

Let me now briefly describe four examples of applications of network theory in ecology. First, let us consider networks of species interactions. Food webs, as noted in the few examples above, are the paradigmatic example of a network in ecology. There has been much progress in recent decades, and I will not review this here (see Cohen et al., 1990; May, 1974; Pascual & Dunne, 2006; Pimm, 2002 for general reviews). Other types of species interactions, such as those between plants and their animal pollinators and seed dispersers, have more recently also benefited from the network approach (Jordano, Bascompte & Olesen, 2003). Much progress has been made in the last two decades or so in understanding how specific pairwise interactions between a plant and an animal are shaped by a community context, either in a single locality, or geographically (see Thompson, 2005 and Waser & Ollerton, 2006 for general reviews). Networks are a useful tool to tackle full communities of mutualisms, and so to go a step further into addressing how networks of species, rather than pairs of species, coevolve (Bascompte et al., 2003). Whenever coevolution truly happens, that is, there are reciprocal selective forces between a plant and an animal, this takes place in the topology of an interaction network. The shape of this network can certainly constrain the coevolutionary process. At the very least, there is a tool to represent and describe species-rich mutualistic interactions, and hopefully a way to explore dynamic implications (Bascompte, Jordano & Olesen, 2006). Thus, with the geographic mosaic of coevolution, network theory has provided a rich framework to tackle coevolution in species-rich communities. Again, the likelihood of real progress will be determined by a blend of statistical tools and a good understanding of natural history. This requires understanding the metaphor, using it for what it is good, but cautiously. It would not be important if the metaphor were replaced in the near future, if it only had improved our understanding of coevolution at the community level.

A second application of networks in ecology can be named spatial networks. Graph theory was brought into landscape ecology as a way to

generalize the consequences of habitat loss for patch connectivity and its implications for metapopulations. Urban and Keitt (2001) is a classic work spurring this subfield. However, not much followed for a while until in the last 2 years there has been a rapid increase of papers on spatial networks. But again, one could claim that new wording is used to describe what is well known. Metapopulation theory has described networks of patches, and a large body of work has been produced in the last two decades (Hanski, 1999). One thus should make an effort to relate new theory to previous work, and critically think about what is new or complementary. Once more, for an optimist there is always something to be gained. For example, because of the influence of network theory, one now has better ways to characterize landscapes and can use previous settings of node removal simulations to look at the relationship between landscape structure and robustness (Fortuna, Gómez-Rodríguez, & Bascompte, 2006). Network theory can describe the physical substrate on which a metapopulation may evolve. More recently, Fagan (2002) has extended the graph theoretical perspective by Urban and Keitt to describe dendritic networks such as the river-creek systems. This excellent work has clearly showed to what extent the topology and dimensionality of the underlying network affects metapopulation processes such as time to extinction (Fagan, 2002). This is improving our understanding of the relationship between network structure and dynamics.

My third example of the application of networks in ecology is epidemiology. Classic epidemiological models, as other areas in ecology, were based on mean field equations. That is, spatially implicit settings where all individuals had the same probability of interacting with each other. SIR and SEIR models, named after classes susceptible, exposed, infected, and resistant, are classic examples (Anderson & May, 1982). The next step, as in spatial ecology, was to use spatially explicit landscapes in which only neighboring individuals interact (it is normally assumed that a lattice cell interacts with only its four or eight nearest neighbours). In these cases, networks are regular, that is, all individuals have the same number of interactions. The rise of complex networks, and in particular, the discovery of their high heterogeneity and its implications for robustness lead to a growing interest in similar epidemiological models running on networks. Two combined papers illustrate perfectly the importance of the network approach. First, Liljeros, Edling, Nunes Amaral, Stanley, and Åberg (2001) showed the highly heterogeneous network of human sexual contacts; a homogeneous setting is not a good frame

for understanding sexually transmitted diseases. Second, [Pastor-Satorras and Vespignani \(2001\)](#) challenged a classic concept in epidemiological theory, that of eradication thresholds. The eradication threshold indicates that it is not necessary to vaccinate all hosts in a population. After a critical fraction of hosts is vaccinated, the disease disappears. [Pastor-Satorras and Vespignani \(2001\)](#) showed that the eradication threshold vanishes in complex networks with very heterogeneous distributions of links per node. The disease never disappears. This is bad news. However, the good news is that a few nodes have an incredibly important role in maintaining the disease, and so vaccination campaigns can focus on these hubs. This has important implications for disease control, and this is an important result not anticipated from previous work assuming homogeneous settings: a real advance due to network thinking.

My final example is evolutionary dynamics on social networks. Evolutionary dynamics, like epidemiology, were traditionally studied in homogeneous settings. Nowak and colleagues introduced evolutionary dynamics on graphs where each node is now an individual, and links indicate how often individuals place offspring in other nodes. Interestingly, the outcome of the evolutionary dynamics depends very much on the topology of these networks. Some networks amplify selection, whereas others reduce it or fix any advantageous mutations ([Lieberman, Hauert, & Nowak, 2005](#)). As in the epidemiological context, predictions from theory based on homogeneous settings do not work in heterogeneous systems. A particular example of an evolutionary game is that determining the evolution of cooperation in social networks. [Santos, Rodrigues, and Pacheco \(2006\)](#) applied a well-known game theoretical model, the Prisoner's Dilemma, to social networks of contrasting topology. Specifically, they explored heterogeneous networks where a few individuals have a huge number of interactions, the type of network resulting from the preferential attachment rule described above. Since this network topology seems pervasive, it is worth asking about the consequences for the evolution of behavior. The conclusion of this study is that scale-free social networks are very prone to cooperation. Cooperation is much more common than expected for regular or random networks ([Santos et al., 2006](#)). This is an important result relating network structure to dynamics.

Outlook

As for future applications of network theory, exploring their role in conservation biology can certainly increase the appeal of networks for

empirical ecologists. A few papers have analyzed species invasions in mutualistic networks ([Memmott & Waser, 2002](#)). Biological invasions occur in the context of a network. Thus, it seems that the properties of this network, not only the list of species, may contribute to the likelihood of a successful invasion. This is a promising area. If biologically sound work is done here, this will certainly help establish networks in ecology and conservation. This is also true for human-induced habitat alteration. One usually measures the consequences of this destructive process as the consequent decrease in species richness. However, habitat alteration may have profound consequences on food web structure even in the absence of a reduction in species richness ([Fortuna and Bascompte, 2006](#); [Tyllianakis, Tschardtke, & Lewis, 2007](#)). These previously unnoticed changes are important because they may affect ecosystem services such as pollination or pest control. Here networks have a clearly applied side. The likelihood of trophic cascades also depends on the structure of the network, and particularly on the combination of strong interactions ([Bascompte, Melián, & Sala, 2005](#)). Better expanding the bridge between food web structure and dynamics may demonstrate the usefulness of the network approach in conservation and management. Of course, some technical challenges remain: it is much simpler to study models of simple trophic modules involving three or four species than models of entire food webs. Another interesting direction for future research is the integration of several network types: for example, how networks of species interactions evolve within spatial networks, or how social networks are shaped by food webs (and vice versa). Thus, network theory is developing strongly. As with all new successful areas there is a component of reinventing old ideas, but some progress has certainly been made. Specifically, I would like to emphasize three main lessons. First, the network approach has provided a way to describe complex communities. This has brought a community context into coevolution, and has allowed to explore the community-wide consequences of human-induced perturbations. Second, scientists have found commonalities among seemingly different systems. This may reflect similar processes of network formation, selection of robust structures, or just a simpler statistical consequence of large sets of interconnected elements. Third, the network approach has improved our understanding of the consequences of heterogeneity for population and community dynamics, which has led to important results on, e.g. the persistence of diseases. These are certainly exciting results, but the best are probably yet to come.

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