Meeting Report

Ecological networks: Delving into the architecture of biodiversity

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Summary

In recent years, the analysis of interaction networks has grown popular as a framework to explore ecological processes and the relationships between community structure and its functioning. The field has rapidly moved from its infancy to a vibrant youth, as reflected in the variety and quality of the discussions held at the 1st international symposium on Ecological Networks in Coimbra – Portugal (23-25 October). The meeting gathered 170 scientists from 22 countries, who presented data from a broad geographical range, and covering all stages of network analyses, from sampling strategies, to effective ways of communicating results, presenting new analytical tools, incorporation of temporal and spatial dynamics, new applications and visualization tools[1]. The meeting revealed that while many of the caveats diagnosed in early ecological networks are successively being tackled, new challenges arise, attesting to the health of the discipline.

Keywords: Community ecology, Food-webs, Interaction matrix, Interactome, Spatio-temporal network dynamics

1. Introduction

"All life is connected" was one of Avatar's[2] main headlines, but it also encapsulates the central tenet of ecology and clearly shows why network theory offers such a great potential for advancing our understanding of ecological processes, or as Charles Darwin put it: "*I am tempted to give one more instance showing how plants and animals, most remote in the scale of nature, are bound together by a web of complex relations*."[3]. Networks are constructions of inter–linked nodes delimited by either link-poor space or other methodological decisions of the researcher. In nature, networks are spatio-temporally dynamic structures organized hierarchically from interlinked atoms, molecules, cell organelles, organs, individuals, populations, species, communities, ecosystems, and ultimately the biosphere. On the ecological realm, interactions play a determinant role in population dynamics, species coevolution and community structure, affecting the functions performed by ecosystems and the services they deliver to humans. Networks are particularly attractive to ecologists for providing a dynamic viewpoint from where scientists can simultaneously "see the forest and the trees", *i.e.* evaluate emergent network-level properties and at the same time consider the behavior and functional role of nodes. In other words, the “network thinking” in ecology not only offers an expanded way to look at biodiversity but also a mechanistic approach to assess the processes that underpin the complex patterns we observe in nature.

Since the 70s, when networks were imported from physics and social sciences into ecology, they have grown increasingly popular among ecologists (Fig. 1). During the construction of the *status quo* of complex network analysis, promising avenues of research have been frequently listed as ways to advance the field[4, 5]. It has been encouraging to see in this meeting that we are now making very significant progress into exploring many of these “dark corners”, such as: moving from static to temporally dynamic networks, building networks of networks, mapping individual-based networks, identifying drivers of general link patterns such as modularity, framing coevolution on a network context, and increasingly using network science as a practical conservation tool.

2. Improving ecological networks

Regardless of the proclaimed potential of networks to advance ecological theory and practice, broader generalizations and practical applications of this approach are still relatively modest. During the symposium, we identified some general challenges that networks need to overcome in order to meet their full potential. We grouped these challenges into three broad categories, which we discuss here:

a. Increasingly realistic

The accuracy of the insights gained from analyzing interaction networks is primarily limited by the quality of the data. Networks are simplified representations of reality, which is necessary in order to extract the overall patterns from what seems an “infinitely wonderful and complex World[6]. However, the lower limits for this simplification have to be based on solid scientific criteria, such as taxa resolution, natural habitat borders, and clearly delimited processes, and not by researchers’ “comfort zones”. Similarly, this “simplification” cannot be a justification for poor sampling. In this regard, it has become evident that in the same way that ecologists have built a solid body of theory for sampling individuals and species, a theory for sampling interactions still needs to be developed, e.g. guidelines for defining minimum acceptable effort, or better ways to deal with incomplete datasets. Such a step will be important for addressing one of the most persistent problems in the field: the *a posteriori* comparison of networks assembled by different researchers for different ends and which vary greatly in their sampling protocols and effort[7].

The difficulty in quantifying the effectiveness of the processes being studied, e.g. pollination or seed-dispersal, often leads researchers to focus on related processes and use these as proxies, e.g. flower-visitation and frugivory as surrogates for pollination and seed-dispersal networks. While these proxies hold valuable information, it is important to be clear about what is the actual ecological process expressed by the data, i.e. what kind of "information" flows through the links of the network and what is its ecological meaning. A correct quantification of the outcome and effectiveness of the real ecological process of interest will be invaluable in leading to relevant conclusions.

Ultimately, the realism of a network, i.e. how close it mirrors real phenomena, depends on the layers of information that it holds. For example, all nodes within a trophic level are frequently considered to be equal and each of these nodes, formed by an assemblage of "replicated" individuals (regardless of their age, sex, size, social status, etc.). An interesting avenue in order to explore the importance of the nature of the network building blocks is to explore if species-based and individual-based networks offer complementary or diverging information.

b) Increasingly informative

The first generation of ecological networks mapped observed links between nodes without trying to estimate their relative importance. These qualitative network studies are the foundation of a second generation of quantitative/weighted networks in which the weight of all observed links are scored in a common currency, e.g. interaction frequency or biomass. The incorporation of link weight into interaction matrices represents an enormous increase in informative value. Other much less frequent sources of information are independent estimates of species abundance, node traits (discussed above), and spatially and temporally resolved network data.

As networks continue incorporating more detailed information (*e.g.* time and space data, type of interaction), classic graphical representations will most likely become less efficient at visualizing such information. The possibility of depicting the complexity of interactions into relatively simple and attractive diagrams has been one of the biggest advancements of network ecology. Therefore, we envisage that new visualization tools that incorporate new layers of information, such as detailed characterization of nodes and links may require the development of new graphing routines, such as interactive interfaces, improved zooming capabilities, and interaction with geo-referenced visual tools (e.g. Google Earth, GIS).

As network ecology is pushed forward and increasingly used to explore community dynamics and mechanistic processes driving ecosystem functions, the choice of the most appropriate descriptors and indices of the behaviour of systems needs to be made carefully. Rather than using the myriad of metrics produced by specific software, it is important to carefully decide which network variables have most heuristic value to a given study. While non-biological network literature will continue to have a great guidance potential for our choice of metrics, it is important to keep in mind the specificities of ecological data/problems. For example, null models are important tools to deal with incomplete datasets, however, there are no completely "fool-proof" null models (e.g. for nestedness or modularity), and accepting certain assumptions will likely inflate either type-I or type-II error rates. And as useful as network analysis is, it will not always, of course, be the best approach to a specific ecological question.

c. Increasingly useful

The advantages of a network approach for conservation planning and as a monitoring tool are frequently listed but much less often translated into a significant contribution for conservation managers. This can be partly explained by the deficit of complete datasets that can provide a solid basis for conservation planning, and also by the frequent lack of communication between scientists and practitioners and the difficulty in establishing good and long-term mutualistic collaborations. Yet, such cooperation between scientists, practitioners and politicians, is invaluable, in order to make the analysis of network complexity useful for *in situ* conservation. In this regard, a most desirable output is the formulation of rules of thumb that can be easily communicated to broad audiences. Positive signs of a more applied role for networks were presented at the Coimbra meeting and include the implementation of network analysis as *a priori* planning tool in biological control, urban planning, control of invasive species, and identification of priority areas for conservation.

3. Conclusions

During this meeting it became evident that “webbers” still have much to gain from continuously scanning for advances on partially overlapping fields, such as evolutionary biology, landscape genetics, behavioral ecology and phylogeography, and also from other formal disciplines, including physics, social sciences and mathematics (particularly graph theory). For example, recent analyses and developments in the fields of statistical mechanics (physics) and socioeconomics may provide new tools to approach problems related to highly dynamic networks in time, or the fractal structure of “networks of networks”. Thus we envision that cross disciplinary insights will continue to be extremely beneficial to the application of complex network tools in ecology.

Experimental studies are crucial to increase the predictive power of ecological networks, particularly for assessing community robustness and resilience. Given the logistic and ethical limitations of manipulating whole communities, this can be done either using a mesocosm approach or by taking advantage of large-scale ecological changes, e.g. intense fires, emergence of new islands, massive changes in land use. These data will be highly valuable to construct more realistic models that incorporate the rewiring potential of generalized interactions.

Network theory provides ecologists with an important tool to explore nature’s complex web of interactions; however, the network tool-kit still needs to be much improved in order to extract the most out of this promising approach. While it is not always easy to distinguish patterns from noise when comparing community data, we have renewed confidence that network analysis is a valuable tool when trying to understand the complexity of natures’ entangled bank[3]. The first meeting nurtured the general feeling that we soon should get together again, and therefore a second symposium is planned to be hosted at the University of Bristol, UK in 2015.

“Although many fads have come and gone in complexity, one thing is increasingly clear: interconnectivity is so fundamental to the behavior of complex systems that networks are here to stay.”[8]

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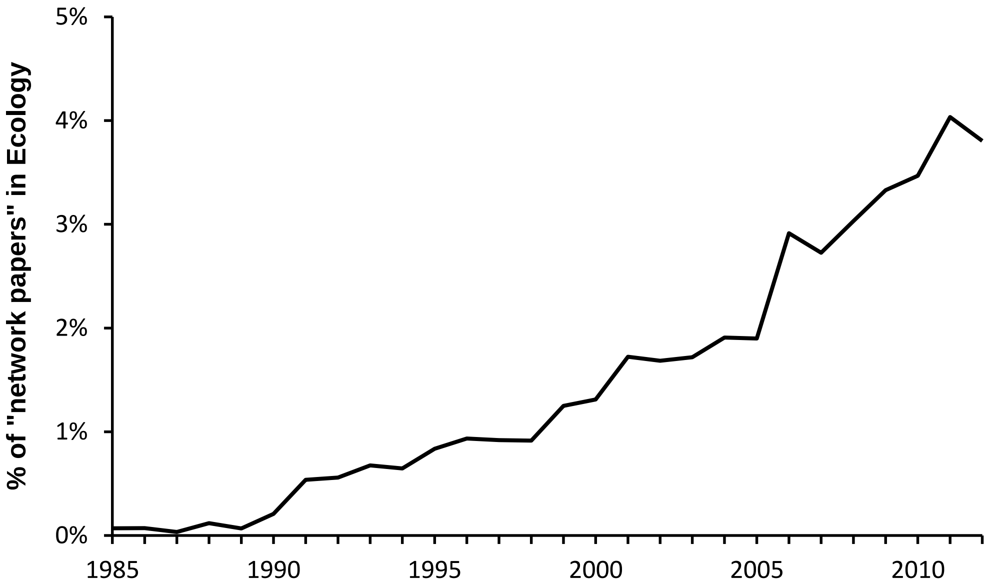

Figure 1. Proportion of the bulk of ecological papers published since 1985 that include the term "network(s)" in their title, keywords or abstract. Data extracted from the Web of Science®, accessed in October 2013. Search terms: Topic=(network*) and Year Published=(1985-2012) and Category=(Ecology).

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