



Seeing networks for what they are in mycorrhizal ecology



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ABSTRACT

Networks tools are being increasingly used in the study of plant-fungus interactions and likely to provide new insights in the way plant-fungus interactions are structured. At the same time, they raise new questions and challenges. Here, I highlight the most important problems and outline how network tools can be effectively used in mycorrhizal ecology. Network-based tools can be used to explore and visualize mycorrhizal interaction patterns: this can pave the way towards further empirical work and hypothesis testing. However, network-based tools cannot, by themselves alone, provide much insight about the ecological mechanisms driving the establishment of mycorrhizal interactions, because many mechanisms can yield a given network-level pattern. They also cannot help predicting the future dynamics of mycorrhizal communities, because modelling studies need to be conducted using parameters and rules that are relevant to the mycorrhizal symbiosis, which is not currently done. Also, drawing analogies between mycorrhizal networks and other types of networks must be made with caution, taking into account *all* the potential similarities, but also discrepancies, between these kinds of unrelated networks. I think that keeping the above issues in mind will be critical to keep the network-based approach viable and useful in mycorrhizal ecology.

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Network theory is deeply rooted within the ecological literature. A quick scan of the literature reveals that the number of scientific papers containing the search terms “*ecol**” and “*network**” in their title, abstract or keywords has increased from 239 per year in 2000, to 2031 per year in 2015 (Fig. 1). Researchers are interested in better understanding how the structural patterns displayed by natural, ecological networks can inform us about (1) their stability (Dakos and Bascompte, 2014; Lever et al., 2014; Tang et al., 2014), and (2) the ecological rules driving their assembly (e.g., species traits: Chamberlain et al., 2014; Kaiser-Bunbury et al., 2014; Maglianesi et al., 2014/species abundances: Canard et al., 2014; Dáttilo et al., 2014). This enthusiasm in using network-based tools also transpires to the mycorrhizal ecology literature: multiple groups have characterized plant-fungal communities as networks (e.g., Jacquemyn et al., 2011; Chagnon et al., 2012; Montesinos-Navarro et al., 2012, Taudiere et al., 2015, Encinas-Viso et al. 2016). This wealth of network-based studies in mycorrhizal ecology shows that there is an increased use of this approach.

Specifically, this paper aims at outlining how network theory can be used to study the interactions between plants and

mycorrhizal fungi and what kind of insights it can (or cannot) provide. Having a clearer grasp of this issue will be key to avoiding over-extrapolating empirical results, and to identify more easily research areas likely to be more (or less) productive. Throughout the text, I will refer to a mycorrhizal network as a community of interacting host plants and mycorrhizal fungal taxa (although it should be noted that some authors used a network-based approach to analyze mycorrhizal interactions collected at broad spatial scales, thus not representing a community per se (e.g., Jacquemyn et al., 2011; Taudiere et al., 2015)). Such a network can be intuitively drawn as a matrix (with plants as rows and fungi as columns, or vice versa), whereby each cell depicts either the presence/absence, or the frequency of the interaction between the corresponding plant and fungus (Fig. 2). There has been some debate over the formal definitions of fungal taxa in such matrices, and over the baseline to determine when an interaction is indeed occurring (Caruso et al., 2012). In my opinion, these issues pertain to any molecular study of mycorrhizal communities, and are not unique to the network-based approach. Here, I focus on issues that are specific to mycorrhizal networks. I first present promises offered by a network-based approach, and then I present both the pitfalls of such an approach, and perspectives to guide future work.

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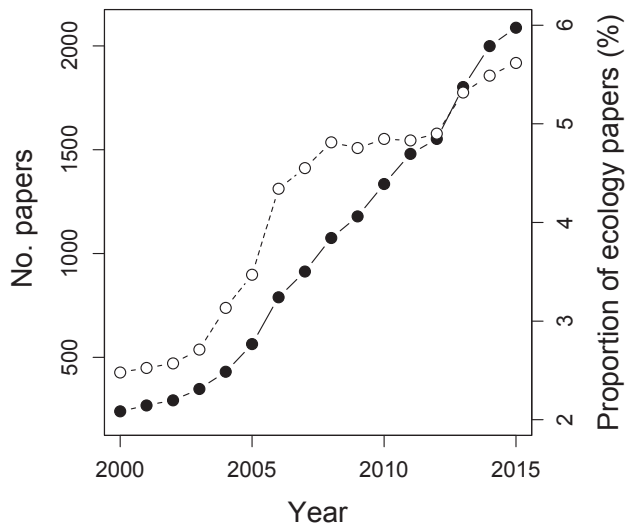


Fig. 1. Number of scientific papers per year containing the terms “ecol” and “network” in their title, abstract, or keywords since 2000 (closed symbols and solid line). The open symbols and dashed line represent the proportion that these papers represent among all ecology papers (here estimated as the number of papers containing the term “ecol” in their title, abstract or keywords). Data was gathered by inquiring the SCOPUS database on February 23rd, 2016.

1. What networks are: a route towards patterns

At the simplest level, many network-based tools can be viewed as just additional ways to describe matrices of mycorrhizal interactions. Having new tools to describe new patterns, may stimulate research on mycorrhizal community assembly, by generating a breadth of testable hypotheses on how those network-level patterns arise in nature. For example, some mycorrhizal networks have been shown to be significantly nested (i.e. a tendency for specialist taxa to interact preferentially with generalists) and it was speculated that this pattern may have been driven by various mechanisms including species abundance distributions (Chagnon et al., 2012), interspecific competition (Montesinos-Navarro et al., 2012), or attraction of the community towards a stable state (Haug et al., 2013). Such exploratory routes pave the way for more intensive field samplings that will uncover the biological mechanisms leading to this network-level pattern (Chagnon et al., 2014). This is just one example of how a novel pattern can stimulate

discussions and further hypothesis testing in the study of mycorrhizal communities, or networks. One danger of bringing in new tools, however, is to bring *false* novelty. For example, many studies have characterized the level of modularity in mycorrhizal networks, that is, the tendency of the community to subdivide in subgroups of species that preferentially interact together (e.g., Martos et al., 2012; Bahram et al., 2015; Chagnon et al., 2015; Jacquemyn et al., 2015). These increasingly popular modularity analyses can be viewed as just another way of clustering a dataset into subgroups, as do other methods from ‘classic’ community ecology, such as hierarchical or flat (e.g., k-means) clustering (thus being redundant to tools that we already had). However, the theoretical redundancy among clustering tools remains unclear: various clustering approaches can provide contradictory results (e.g., Martín González et al., 2012; Leger et al., 2015), making it useful to combine multiple seemingly redundant tools to cross-validate biological conclusions.

Moreover, if we see network-based tools as simple ways to calculate some matrix-level properties, then there is no reason to consider them as apart from other tools to characterize matrices, such as meta-communities (i.e. sites \times species matrices, Leibold and Mikkelsen, 2002; Mihaljevic, 2012). In fact, nestedness, which arose as a popular metric to characterize mycorrhizal network structure, has its roots in biogeography (e.g., Patterson and Atmar, 1986; Ulrich et al., 2009 and references therein), not in the literature on ecological networks. Another good example well-used by fungal ecologists is the C-score (Stone and Roberts, 1990), commonly used to infer competitive interactions (or at least negative associations) between species (e.g., Gorzelak et al., 2012; Pickles et al., 2012; Kennedy et al., 2014). In a nutshell, this metric measures the frequency of species segregation (i.e. when species A is present from site x and absent from site y , and species B presents the exact opposite pattern). While this tool has mostly been restricted to sites \times species matrices in fungal ecology, it can be equally informative when applied to ecological networks (e.g., Gotelli and Rohde, 2002), where one might ask whether mycorrhizal fungal taxa are segregated among different hosts. In this view, numerical tools can not only be borrowed from theory on meta-communities, but from many other disparate areas. I illustrate this point below using the problem of matrix seriation (i.e. ordering rows and columns of a matrix to evidence a dominant gradient).

Determining the gradients shaping mycorrhizal networks is a major challenge. Some have suggested that plant traits may be one

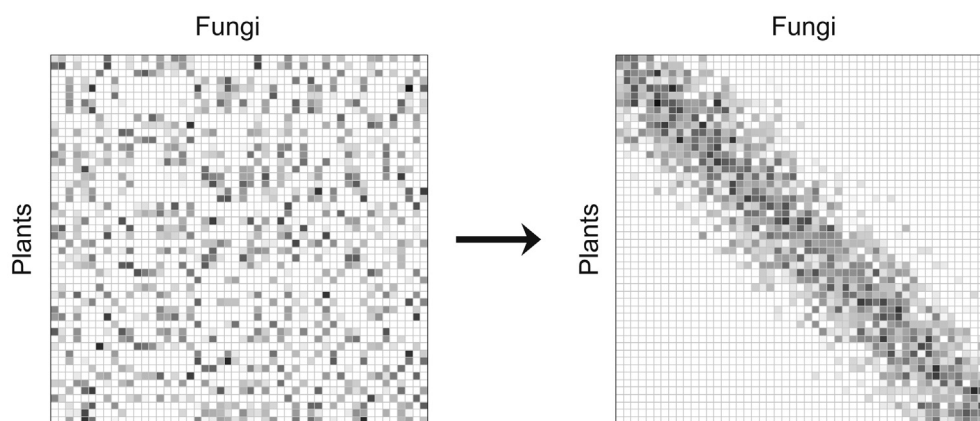


Fig. 2. Illustrative example to show how matrix seriation can evidence network-level patterns. In the left panel, we see a mycorrhizal network (i.e. a plant \times fungi matrix, where each cell is colored with a grey shade proportional to the number of times that the corresponding plant and fungus interact in the field). In the right panel, we see the same network, once the rows and columns have been ordered to maximize the packing of non-zero elements (i.e. non-white cells) along the matrix diagonal (see Table 1 for details).

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