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Application of network theory to potential mycorrhizal networks

Abstract The concept of a common mycorrhizal network implies that the arrangement of plants and mycorrhizal fungi in a community shares properties with other networks. A network is a system of nodes connected by links. Here we apply network theory to mycorrhizas to determine whether the architecture of a potential common mycorrhizal network is random or scale-free. We analyzed mycorrhizal data from an oak woodland from two perspectives: the phytocentric view using trees as nodes and fungi as links and the mycocentric view using fungi as nodes and trees as links. From the phytocentric perspective, the distribution of potential mycorrhizal links, as measured by the number of ectomycorrhizal morphotypes on trees of *Quercus garryana*, was random with a short tail, implying that all the individuals of this species are more or less equal in linking to fungi in a potential network. From the mycocentric perspective, however, the distribution of plant links to fungi was scale-free, suggesting that certain fungus species may act as hubs with frequent connections to the network. Parallels exist between social networks and mycorrhizas that suggest future lines of study on mycorrhizal networks.

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Introduction

A mycorrhizal network, also called a "common mycorrhizal network," can be defined as a belowground system of interconnected hyphae and roots. The complex mycorrhizal network that might exist in nature is not directly visible because of the fragility of fine roots and hyphal connections.

Intra- or interspecific mycorrhizal links can form between plant roots (Newman 1988; Newman et al. 1994). In the laboratory, a fragment of the network consisting of hyphae of a single fungus joining roots of two plants of the same or different species has been observed through transparent plates (Heap and Newman 1980a; Read et al. 1985; Read 1992) and by autoradiography (Francis and Read 1984; Read et al. 1985; Read 1992; Wu et al. 2001). Indirect evidence for a mycorrhizal network linking plants of the same or different species comes from transfer studies showing that C, N, and P move among mycorrhizal plants (see recent reviews by Read 1997; Simard et al. 2002; He et al. 2003) and from biodiversity studies showing that ectomycorrhizal fungus species are "common" or shared and therefore may link plants (e.g., Kennedy et al. 2003; Valentine et al. 2004).

Reductionist approaches have demonstrated transfer of nutrients among plants and fungi (Kramer and Wilbur 1949; Harley and McCready 1952; Melin and Nilsson 1953; Reid and Woods 1969; Cox and Tinker 1976; Heap and Newman 1980b; Chiariello et al. 1982; Ritz and Newman 1985; Johansen and Jensen 1996; Simard et al. 1997, 2002; Bidartondo et al. 2003; He et al. 2003, 2004). Studies at other scales have examined mycorrhizal networks from the perspectives of evolutionary ecology (Wilkinson 1998; Hart et al. 2003) and community structure (Read et al. 1985; Johnson et al. 1992, 2004; Read 1992, 1998; van der Heijden et al. 1998; Eom et al. 2000). Our purpose is to describe the architecture of a potential network to test the application of network theory to mycorrhizal networks.

The concept of a mycorrhizal network implies that the arrangement of plants and mycorrhizal fungi in a com-

munity shares properties with other networks—systems of nodes connected by links. Nodes are generally structures, objects, or stable intersections. Links may be tangible physical structures, electromagnetic waves, or social interactions. Although the term "network" is applied to arrangements of mycorrhizas and their hosts, studies of mycorrhizal networks have not exploited network analysis theory to describe the system. The architecture of a network includes measurements such as the number of links per node (called degree or connectivity), the degree distribution or probability that a node has a certain number of links, the directionality of links, and the path length or number of links needed to travel between two nodes (Barabási and Oltvai 2004).

An examination of other networks, including food webs, neural networks (both brain and computer architecture), cell metabolic networks, gene regulatory networks, protein networks, epidemiological networks, transportation networks, telecommunications networks, and social networks, might clarify questions and hypotheses about mycorrhizal networks. These provide models for the description of the architecture of a potential mycorrhizal network.

Examples of networks

We live in a world of networks. Evidence for a small world of human connections was discovered by Milgram (1967), developed into a play, *Six Degrees of Separation* (Guare 1990), and later made into a movie. Two recent books provide highly readable accounts of social networks, *Linked* by Barabási (2002) and *Six Degrees* by Watts (2003), and provide examples of metaphors or models from which to understand mycorrhizal networks. Such models focus on the framework of interactions rather than on the items exchanged. We describe three that have parallels with mycorrhizal networks.

Transportation networks Highways and airline routes exemplify transportation networks. In a road network, highways are links and cities are nodes. The number of highway routes entering a city is randomly dispersed around a mean. In an air travel network, airports are nodes, and the routes between airports are links. In contrast to highways, some airport nodes are hubs that connect many routes. Other nodes are airports in small towns linked by few routes.

A description of transportation routes shows possible connections, but does not tell how many planes per day actually fly a route or how many people are on the plane or what the people do when they get to their destination or how much money they spend. Network architecture describes potential interactions, but not the specifics of transfer.

Social networks Social network analysis is a perspective from which to describe interactions and relationships among players. In a social network, people are the nodes. Links between people include acquaintanceship and transfer of resources (Galaskiewicz and Wasserman 1994; Wasserman and Faust 1994). Social scientists use network analysis to explain influence. Networks create a structural cohesion that affects how an individual in the network reacts to change (Marsden and Friedkin 1994).

Affiliation networks: corporate boards of directors Corporations may be networked by buying and selling, and the people who sit on corporate boards of directors may be linked by social networks. In addition, some people may be on the board of directors of more than one corporation. This pattern, an affiliation or bipartite network, has two types of nodes (corporations and directors) with links between them (membership on the board of directors) (Watts 2003). Groups are affiliated by virtue of common membership.

Random and scale-free networks

Among several types of network architecture are random networks and scale-free networks, distinguished by the relative numbers of links per node (Barabási 2002; Bray 2003; Jasny and Ray 2003; Watts 2003).

Random networks In random networks, all nodes have the same probability of being attached to a link. Based on numbers of links and nodes, there is an average number of links per node. Nodes are approximately equal in importance and in connectedness. The mean number of links per node is significant because most nodes have that number of links, approximating a Poisson distribution (Barabási 2002; Watts 2003). Virtually no nodes have a number of links that deviate widely from the mean number of links per node, e.g., very few or very many per node. Addition of a new link will occur with equal probability for any node. Random networks occur with anything involving Brownian motion, e.g., liquids and gases, or with chance occurrences.

Scale-free networks In scale-free networks, some nodes are more linked than others (Barabási and Albert 1999; Barabási and Bonabeau 2003). A few nodes (called hubs) have a great number of links, whereas most nodes have few links, but those connect to hubs. Although there is an average number of links per node, that number is not significant because few nodes have the mean number of links per node. These networks are called "scale-free" because a log–log plot of these data yields a straight line with a negative slope—a power-law relationship (Barabási 2002).

A new node could extend a link to a hub, or a new link could extend out from a hub and "entrap" a new node.

Most social and technological networks as well as biological networks are scale-free (Barabási and Oltvai 2004). For example, the distribution of airline routes is

scale-free (Barabási 2002). Links among websites on the Internet are also scale-free (Barabási 2002).

Application to mycorrhizal networks

A network may be examined from several points of view. In mycorrhizal networks, nodes might be either plants or fungi. There is no a priori determination that trees or fungi are nodes or links. Both may be connected by multiple attachments to the other. The two perspectives are complementary views.

We first consider mycorrhizal networks from the plant-centered or phytocentric view. This seems obvious, especially to those of us above ground, and is based on evidence for nutrient transfer between plants linked by fungi (Francis and Read 1984; Finlay and Read 1986). Then, we consider mycorrhizal networks from the fungus-centered or mycocentric view (Fitter et al. 1998, 2000). This is an unfamiliar perspective based on a belowground view in which large masses of fungal hyphae belonging to a single organism are linked to other fungal organisms through plants. Finally, we consider mycorrhizal networks from the point of view of an affiliation network where both plants and fungi function as nodes that are linked at mycorrhizas.

Phytocentric network Trees are defined as nodes and mycorrhizal fungi as links. Each sampled tree, an individual that grew from one seed, is treated as a node. Each mycorrhizal morphotype is treated as a potential link, a possible route to another tree. Different species of fungi, identified as morphotypes, may create links with diverse properties. The concept of a phytocentric network is relatively easy to grasp because trees can be interpreted readily as individuals and fungi as links.

Mycocentric network Fungi are defined as nodes and trees as links. Individual fungi would be treated as nodes. We can consider an individual fungus to be the mass of mycelium that is derived from one dikaryon and that remains internally connected. It could include the fruiting body, but not as a node. Each mycorrhizal fungus species or morphotype is treated as a node and each tree as a potential link between fungi. The concept of a mycocentric network is less familiar but may be treated as the complement to the phytocentric network.

Affiliation network A mycorrhizal network might be a bipartite network with two sets of nodes—plants and fungi—that interconnect at mycorrhizal roots. In a parallel to corporate boards of directors, trees may be nodes that interact in ways not related to mycorrhizas, e.g., through herbivores or gas exchange. Likewise, fungi may be nodes that interact belowground in competition for nutrients and water. When a fungus links to more than one tree or a tree to more than one fungus, the two sets of nodes become potentially networked.

Are mycorrhizal networks random or scale-free?

In an oak savanna and woodland habitat, we sampled mycorrhizal diversity associated with individual trees (Valentine 2002; Valentine et al. 2002, 2004). We have a list of fungus species (characterized by morphotype) associated with each of 20 trees and a list of individual (numbered) mature trees of *Quercus garryana* associated with each of 40 fungus morphotypes. Although the trees are in a single site and each tree shares at least one morphotype with another tree, we do not have direct evidence that they share resources. Therefore, this is a demonstration of the application of network theory to a *potential* mycorrhizal network.

To determine whether this potential mycorrhizal network is random or scale-free, we plot the number of links on the x-axis and the number of nodes having that number of links on the y-axis (Barabási 2002; Barabási and Bonabeau 2003; Bray 2003; Watts 2003).

Architecture of the phytocentric network Is the distribution of links (morphotypes or fungus species) per node (tree) random or scale-free? We ask how many morphotypes each tree has—with the idea that morphotypes represent diverse links or possible routes to and from the tree. The number of trees having that number of morphotypes represents the number of nodes having that number of links (Fig. 1).

Most trees have the mean number of morphotypes (mean=3.9, Fig. 1). There is no peak of trees with one or two morphotypes, nor is there a long tail of trees with many morphotypes. There is a short tail of a few trees with more morphotypes. This distribution pattern tells us that all trees in an oak woodland are approximately equal in linkage to the network. No tree is more important than any other tree in terms of maintaining the connectivity of the network.

A random network forms by isolated links between two nodes; gradually, pairs link up (Barabási 2002). A new
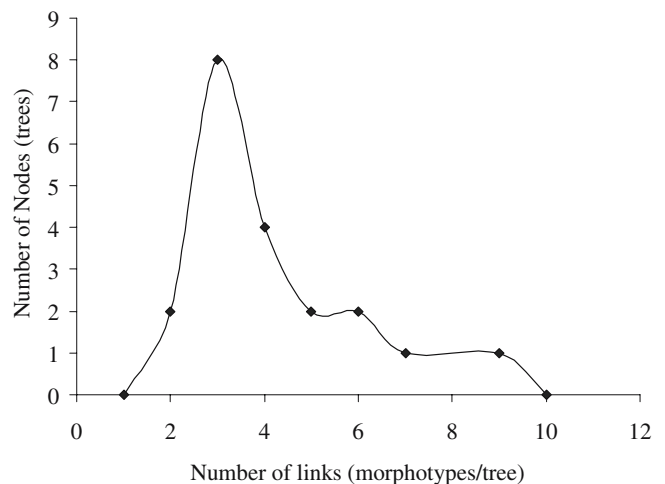
Fig. 1 Distribution of morphotypes per tree from the phytocentric perspective where individual trees are nodes and fungus morphotypes are links

morphotype would connect two trees at random. From the phytocentric point of view, fungal spores might arrive at random, so that fits well with the Poisson distribution of morphotypes on trees.
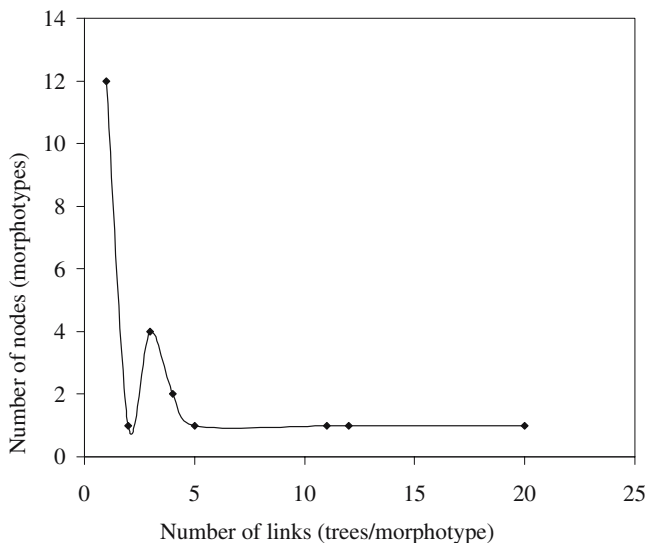
A random network does not support hubs (Barabási 2002). The data show that oaks do not have hubs. Larger or older trees are not necessarily hubs, although this would bear closer examination. No correlations were found between number of morphotypes per soil core and tree diameter or canopy diameter—a stand-in for age (Valentine 2002).

Architecture of the mycocentric network Is the distribution of links (trees) per node (fungus) random or scale-free? Here, we ask the complementary question—to how many trees is each fungus attached—with the idea that trees represent links or possible routes between fungi. The number of trees per fungus morphotype represents the number of links. The number of morphotypes associated with that number of trees represents the number of nodes having that number of links (Fig. 2).

Most morphotypes occur on only one tree each (Fig. 2). In addition, there is a long tail of few morphotypes that occur on many trees. Although a mean number of trees per morphotype can be calculated, there is no peak of morphotypes around the mean and no Poisson distribution. A log–log plot of such data gives a straight line—hence a power-law distribution (Fig. 3). This data is scale-free.

The scale-free distribution of trees on fungi tells us that not all mycorrhizal fungi are equivalent. A new tree more likely would be connected to a common morphotype. Some fungi are more important than others in maintaining the connectivity of the network. *Cenococcum geophilum*, arguably the most common ectomycorrhizal fungus on earth, might be a hub. *Tuber* species might also be hubs in this oak woodland.

In a scale-free network with some nodes (fungi), much more linked than others, new links to seedlings or saplings
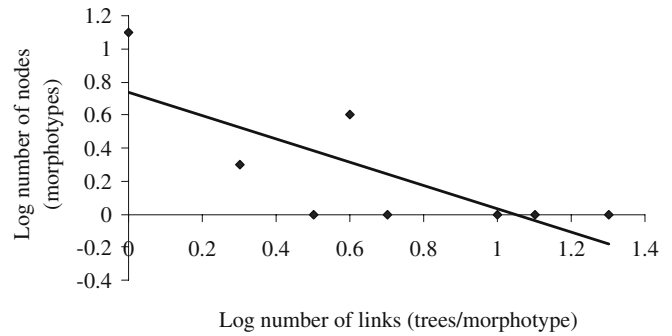
Fig. 3 Log–log plot of distribution of trees per morphotype (Fig. 2) from the mycocentric perspective

tend to form with the most-linked nodes (fungi). From the fungus (mycocentric) point of view, ectomycorrhizal fungi with links to the greatest number of trees would have the most opportunities to access carbon, and it is not surprising that these resource-rich nodes have the most linkages (Watts 2003).

One link per node (one tree per fungus) will maintain the connection—the attachment to the larger network. If a fungus is associated with one tree and that tree associates with other fungi, then the fungus with one connection is attached to the network. Metaphor: one flight a day from a small airport to a larger one will maintain access for the people of that area. We should not expect many trees between fungi.

Affiliation network architecture Affiliation networks may be either random or scale-free. Consider trees and fungi as two classes of nodes linked at mycorrhizas. The distribution histogram observed for an affiliation network of people on corporate boards resembles Fig. 1, with a peak around the mean plus a tail of the few people who are on multiple corporate boards (Watts 2003). This means that most people on corporate boards are on only a few boards, but a few people are on many boards. Interlocking groups play a critical role in determining economic landscapes.

In parallel to the corporate board situation, fungi that are linked to more trees of either the same or multiple species might have more "corporate power," i.e., greater control over resources. A person on two boards is a conduit for information. That is potentially true for fungi on two trees. A mycorrhizal network may relay signals in the form of plant hormones.

Relevance of mycorrhizal network architecture to community ecology

Knowing whether the network architecture of trees and tree species is random or scale-free tells whether trees are equivalent and essentially interchangeable or whether one individual or one species is more important than others. Similarly, knowing whether the fungi are linked in a random or scale-free manner provides information about the importance of diverse species. Network potential is a

Fig. 2 Distribution of trees per morphotype from the mycocentric perspective where fungus morphotypes or species are nodes and trees are links

measure of the importance of a fungus for the connectivity of the network.

Role of hubs A hub, i.e., a node with a high proportion of links, may be important in restoration or regeneration. For example, in timber sales in conifer forests, instead of complete clear-cutting, loggers may leave a few trees. If we could determine that all trees were equivalent or that certain individuals were hubs, the choice of which trees to leave to provide mycorrhizal inoculum could be made in an informed manner (Amaranthus and Perry 1994).

Role of connectivity In both random and scale-free networks, the number of links per node measures connectivity. Networks with high connectivity might provide more ecosystem resiliency. If fungi vary in their ability to take up water in drought stress conditions, then drought-susceptible fungi linked to trees with links to drought-resistant fungi might benefit from the network. Similarly, if fungi vary in their ability to access mineral nutrients, then linkage to a network might improve nutrient availability to all fungi in infertile soil conditions.

Food chains in aquatic ecosystems exhibit a network architecture that includes compartments or subgroups of taxa with many strong interactions. Disturbances such as loss or replacement of species had less impact on species within compartments than on the total community (Krause et al. 2003).

A theoretical analysis of networks that involve transport processes influenced by gradients showed that scale-free networks are less prone to congestion or jamming than random networks (Toroczkai and Bassler 2004). This suggests that the scale-free network of fungi might be better able to maintain transfer routes among its component organisms.

Future questions

What kinds of data do we need to describe the architecture of mycorrhizal networks? Several types of data would let us determine whether the observations on oaks can be generalized: mycorrhizas in plant communities with two or more ectomycorrhizal plants of the same species, mycorrhizas with other tree genera such as pine or Douglas fir, and communities with arbuscular mycorrhizas. To verify plants as nodes, we need to know which fungi form mycorrhizas with which individual plants. Molecular methods, e.g., amplified fragment length polymorphisms (AFLPs), can distinguish among roots of individuals of the same or different species. Similarly, molecular methods may determine whether a fungus species that is mycorrhizal with diverse plants is a single genotype and, therefore, a potential link.

Other measurements of mycorrhizas also could be examined, e.g., abundance of each morphotype or number of hyphae linked to a tree. Likewise, one could compare the number of fine roots of a tree as a node.

What is transferred or communicated among nodes? Physiological studies of mycorrhizal networks demonstrate transfer of materials (C, N, and P) and water through the network (Simard et al. 2002; He et al. 2003; Querejeta et al. 2003). In addition, an established network could transfer other signals with information about nutrient locations or climatic conditions. We might identify strong and weak links or links that transfer different signaling molecules.

How are new nodes or links added to the network? Networks are dynamic, for example, airlines may add routes or a person makes new social contacts. In mycorrhizal networks, both nodes and links are tangible. A tree may connect to a fungus or vice versa in a preliminary step that is followed by a connection to another node or link.

In random networks, a node connects to a link that initially does not reach another node. Then, connections are established. In an oak woodland, saplings that grew from seeds germinated outside the root–hypha zone of mature trees have ectomycorrhizas of hypogeous fungi (D. Southworth, unpublished data). Initially, these node links would be separate from the network, but as the woodland filled in, they could link to other saplings or trees as root–hypha zones overlap.

In scale-free networks, new links extend from hubs to unconnected nodes or from unconnected nodes to hubs. Seedling roots might attract hyphae from a mature tree or vice versa.

Supply and demand might influence the number of links in a mycorrhizal network. If a tree has carbon to offer, hyphae from other trees might link to it, or if a fungus is particularly proficient in taking up nitrogen, tree roots might link to it.

Conclusions

Network theory is a useful tool in the quantification of potential mycorrhizal networks. Here, it shows that the distribution of fungus links to trees in a woodland is random, whereas the distribution of tree links to fungi is scale-free. Parallels exist between social networks and mycorrhizal networks that suggest future lines of study on complex interactions among plant roots and mycorrhizal fungi and among plants.

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