# CONFLUENCE

## The Common Mycelial Network (CMN) of Forests

Caroline Hildebrand

### Introduction

Permeating the organic layer of the forest floor is a thick, interwoven matrix composed of fine white threads of fungal hyphae collectively known as mycelium. The majority of fungal biomass dwells underground in the form of mycelium, twisting and twining through an ocean of soil. Though most people associate the word fungi with mushrooms, the sight of a mushroom marks the mere tip of the mycelial iceberg that dwells below the terrestrial surface, intermingling with plant roots, soil fauna and microbiota. It may come as a surprise that the largest organism in the world is a fungus whose mycelium spans hundreds of square miles in eastern Oregon (Stamets 2005). Despite their enormous size, even such large fungi remain invisible to the average viewer until they produce an aboveground fruiting body, often in the form of a mushroom. As such, it can be easy to overlook the essential role fungi play in the healthy functioning of every ecosystem that plants inhabit. One such role is that of the Common Mycelial Network, or Common Mycorrhizal Network (CMN). In a CMN, the root systems of plants and trees interconnect belowground via a mycelial net of symbiotic fungal partners, extending as wide as the mycelium can grow. The CMN unites multiple plant species and mycorrhizal fungi in an internet of individuals, enabling transfer of isotopic carbon, nitrogen, phosphorous, water and chemical messages between plants and fungi across species, space, and time (Simard and Durall 2004).

*Mycorrhizal fungi*

Types of fungi can be understood according to their functional roles in an ecosystem. A fungus may function in one or more of the following ways: as decomposing saprotrophs, as aggressive pathogens, as immuno-enhancing endophytes, or as plant-partnering mycorrhizae. This paper will focus on mycorrhizal symbiosis, a relationship in which mycorrhizal fungi and plants depend on one another for the exchange nutrients, signals, and water belowground. Mycorrhizal symbiosis is the most widespread and ancient form of mutualism on Earth. It is thought that mycorrhizal fungi facilitated the terrestrialization of plants over 500 million years ago (Field 2018) by giving early plants access to essential nutrients in early-stage, undeveloped soils on a largely volcanic planet Earth. Over 83 percent of plants today form mycorrhizal associations with fungi, linking with mycorrhizal fungal mycelium as an extension of their root networks. In exchange for the fungus' unique ability to unlock and transport soil nutrients, minerals and water for plant uptake, the plant gives carbon to the fungus in the form of carbohydrates (Giovanetti 2001).

*AM and EcM Symbiosis*

The two most abundant types of mycorrhizal associations on Earth are ectomycorrhizas (EcM) and arbuscular mycorrhizas (AM). Mycorrhizal

associations are classified by the structure of the fungal hyphae and how they connect to the host plant root cells (Brundrett 2004). EcM associations can be distinguished from AM associations by the presence of the Hartig net and fungal mantle. As the fungal mantle sheaths the plant root with EcM fungal hyphae, the Hartig net penetrates the spaces between the root cells with hyphal branches, thus building a direct pathway for nutrient exchange between plant and fungus (Teste, Simard, Durall, Guy, Jones, and Schoonmaker 2009). AM fungi are indistinguishable by macroscopic features, but microscopically they penetrate the cell walls of the plant root with root-like hyphal structures called arbuscules. In AM fungi, arbuscular tips are the site of nutrient exchange between plant and fungus (Brundrett and Tendersoo 2018).

The taxonomic group that encompasses EcM

fungi harbors the greatest phylogenic diversity of mycorrhizae. EcM fungi fall into two of the largest fungal phyla: the mushroom-forming Basidiomycota (>50 lineages) and the Ascomycota (>40 lineages) (Vincenot and Selosse 2017). On the other hand, AM fungi as a group is species-poor and fall completely within the single phyla Glomeromycota (Bonfante and Genre 2010). Despite the diversity of EcM fungi, as a mycorrhiza they are generally more narrowly specialized than AM fungi, as defined by the number of host plant families with which they form associations. In terms of species numbers, EcM fungi colonize a mere three percent of plant species, while over 80% of plant species form mutualisms with AM fungi.

It should be noted that although AM fungi colonize the greatest number of different plant species, EcM fungi are essential to the flourishing of the largest plant biota by size: trees. Shrubs and herbaceous plants are generally associated with AM fungi, while most trees and woody plants form mutualisms with EcM fungi. In a mixed forest ecosystem, overstory plants are generally colonized by EcM and the understory is dominated by AM, although there do exist overlaps in temperate and tropical regions (Gorzelak, Asay, Pickles and Simard 2015, Brundrett 2009). Universally, EcM fungi are almost entirely dominant as forests mature into late-successional stages (Kadowaki, Yamamoto, Sato et al. 2018).

Many trees that associate with EcM fungi are obligate mycotrophs, which means they cannot survive without the relationship with a mycorrhizal fungus. This notion is particularly true with coniferous trees: 100 percent of the members in the Pinaceae family are entirely dependent on their EcM symbionts. AM fungi, on the other hand,
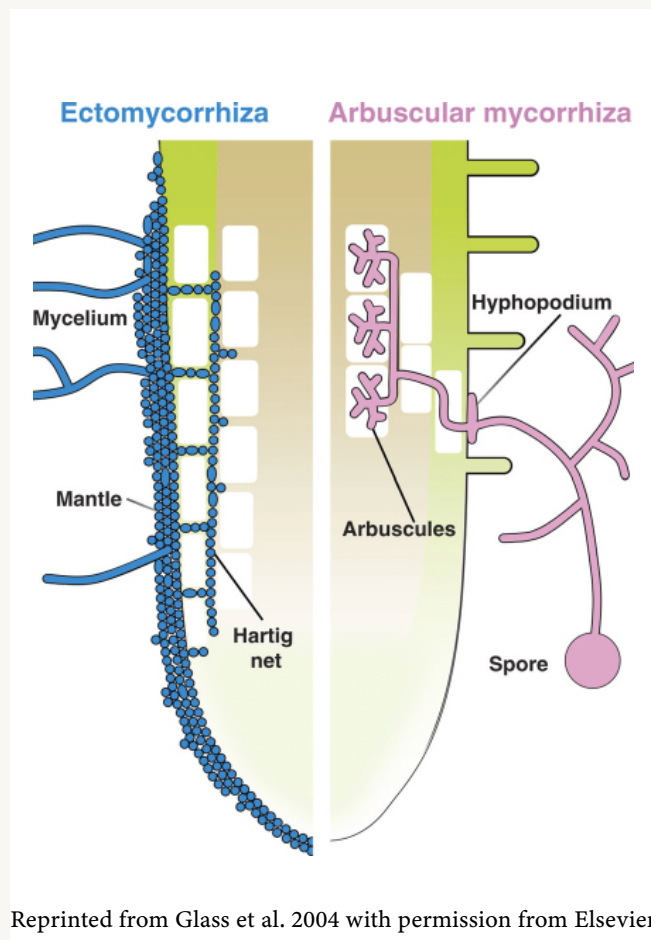
**Figure 1.** Depiction of root colonization structures of EcM (blue) and AM (pink) fungi at the plant root tip

form obligate mutualisms with their host plants, and while the host plant can generally survive without its mycorrhizal fungal partners, the fungus cannot (Tendersoo 2017, Brundrett 2009).

*The Common Mycorrhizal Network*

Both AM and EcM associations are generally mutualistic relationships in which both fungus and plant benefit. In exchange for carbon in the form of sugars produced by the plant in photosynthesis, the fungal mycelium accesses and transports minerals and water for plant uptake. The internal anatomy of both EcM and AM extraradical mycelia that live on the root tips of plants act as a conduit for indirect exchange between plants across the forest, as long as they are connected to the CMN (Simard and Durall 2004, Song and Simard 2015). This internal transport through the fungi provides an advantageously direct pathway for resource allocation, protecting valuable nutrients from interference in the soil ecosystem during transport. A CMN will harness and then protect nutrients, water and minerals from microorganisms, soil fauna, cation

adsorption by soil particles, or physical disruption of the soil horizon itself (Philip and Simard 2010). EcM fungi share an ancestry with saprotrophs and can readily decompose organic matter and transfer it directly to the CMN, a trait not shared by AM fungi (Lakau, Zhu and Ordonez 2015).

The CMN exists in many forms, ranging from simple relationships between two plants and one fungus to more complex connections with multiple species of both plants and fungi (Simard 2004). The simplest example of a CMN is that of a mycorrhizal fungus and a mycoheterotroph, such as Monotropa. Monotropa, an achlorophyllous plant that does not photosynthesize, acquires all of its organic carbon from surrounding autotrophic trees by plugging into the network through an EcM myorrhiza (McKendrick 2000). As species of fungi and plants are added to the matrix, CMNs will increase in complexity, varying along spectrums of spatial range and host receptivity. EcM fungi are the largest of the two mycorrhizal fungus types. A single EcM can span up to 90 square meters whereas AM fungi radii span up to about 20 cm as single
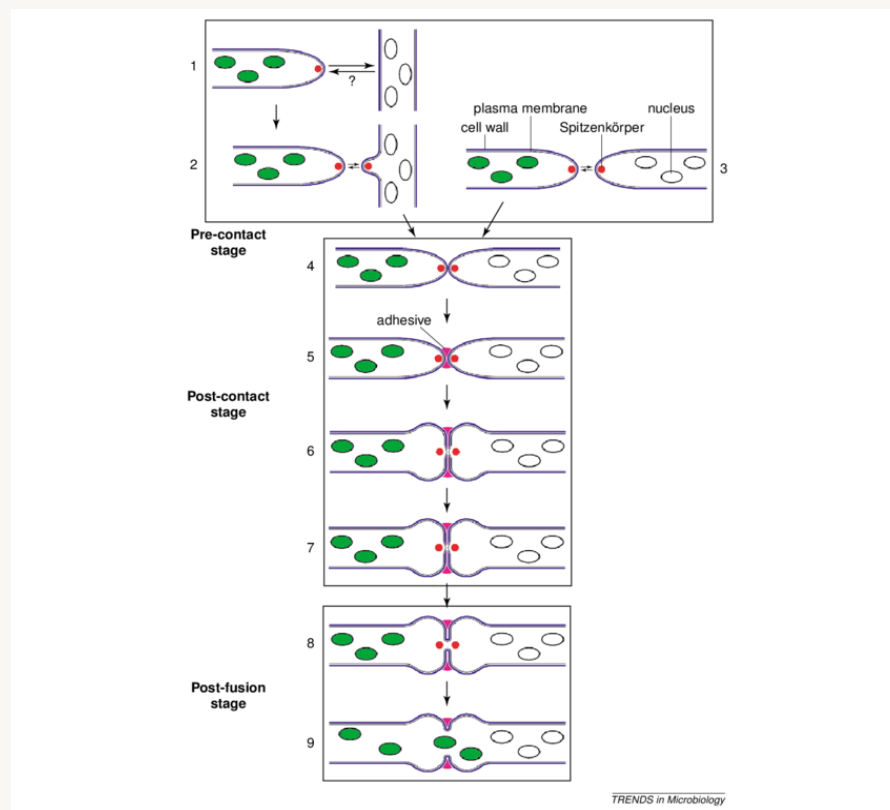


**Figure 2.** Stages of hyphal fusion between EcM fungi

genets (Wipf, Krajinski, van Tuinen, Recorbet, and Courty 2019). However, AM fungi connect with a greater diversity of plant species than EcM fungi. AM fungi are broad host generalists with the tendency to build diffuse symbioses among many plant species while EcMs tend to be host specialists, colonizing multiple plants of a single host species (Lang, Seven and Polle 2011). Still, it should be noted that EcM mycelial networks are not limited to a single species of plant. It is common for disparate EcM individuals that are associated with only one plant species to connect with groups of other EcM fungi associated with other plant species. In these instances, hyphae from individual EcM fungi will fuse together and extend the web of resource transport and signal transfer, expanding the network throughout an entire forest stand (Wipf et al. 2019).

The CMN is a relationship formed out of necessity. Under ideal conditions, such as those of a greenhouse or under intense fertilization, plants that can live without a fungal associate will usually not form a symbiosis with mycorrhizal fungi. But when these isolated plants are exposed to the stresses of the unfacilitated environment, they do not perform as well as those with a CMN and will either plug into a CMN or whither (Simard and Vyse 2006, Teste et al. 2009). A study by Bingham and Simard (2011) showed mycorrhizal connection and interaction increasing along a drought stress gradient as long as plants were already partially connected to a CMN. This suggests that CMNs may be essential to forest re-establishment when faced with the stressors of climate change (Bingham and Simard 2011).

**Sharing the Burden: bidirectional resource transfer across forest communities**

The wider the CMN, the greater reach of signal fluxes and resource sharing across a forest community. Attaching to a CMN hooks individual plants up to a community of support that gives them a necessary competitive advantage when facing environmental stressors and unpredictable nutritional fluctuations. Fluxes of essential nutrients such as phosphorus (Eason et al. 1991, Gorzelak et al. 2015), carbon

(Simard et al. 1997a, Gorzelak et al. 2015), nitrogen (Teste et al. 2009, Gorzelak et al. 2015), and water (Egerton-Warburton et al. 2007, Gorzelak et al. 2015) are balanced by the community as a whole. A CMN unites multiple plant and fungal species in a regulated system, with direction, magnitude and rate of transfer moderated through the mycorrhiza based on need and function of participating organisms. The CMN transfers nutrients in support of the entire community, varying in direction depending on source-sink ratios and needs of plants and fungi in the network (Simard and Durall 2004).

*Source-sink ratios*

Nutritional compounds exchanged between plants via the CMN are transported in the form of free amino acids. This movement can occur via diffusion and active transport, but most commonly they move along what is called a source-sink gradient (Heaton, Obara, Grau, Jones, Nakagaki, Boddy, and Fricker 2012, Simard 2009). A source-sink gradient forms in the presence of differing quantitative needs among plants and fungi connected by a CMN and controls the direction and quantity of carbon and nutrient transfer. Compounds move along the source-sink gradient by advective mass flow, transferring into the CMN via the Hartig net (Heaton et al. 2012, Simard 2009) and toward the organism with the greatest relative nutrient demands. The receiver, or sink, is generally in a position of nutrient deficiency or exhibiting a defense response. A receiver plant may be stressed for a number of reasons. It may be younger, smaller, located in a shaded patch, or experiencing drought stress, herbivory, or high transpiration demand. A fungus can be a receiver as well, especially during growth and cell expansion at mycelium fronts. Relative status of an individual as a receiver will essentially pull on the source-sink gradient and collect requested compounds from a donor plant, or source, which is generally illuminated, nutrient-enriched, water replete, defoliated, and/or greater in age and size (Heaton et al 2012).

Receiver and donor plants need not be the same

species, nor are these roles concrete. Philip et al (2010) studied the transfer of isotopic carbon between paper birch and shaded Douglas fir trees. They found that carbon flowed along the source-sink gradient produced by carbon assimilation differences and different organic nutrient demands, being photosynthesized by sunlit paper birch and toward shaded Douglas fir trees beneath the closed canopy (Simard et al. 1997). Another study by Lerat et al (2002) found that when the source-sink gradient changed along with the seasons, nutrient transfer direction changed as well. Carbon flowed from the foliated trout lily to the sugar maple in the spring, but in the fall when the maple fully extended its canopy it transferred its carbon to the trout-lily corms (Lerat et al. 2002). There is likely a benefit to collaborations between diverse plants with staggered phenological patterns and differing abilities for resource uptake.

*Posterity preservation: Resource transfer to seedlings and young trees*

The source-sink gradient generally allocates resources from mature trees to some of the most vulnerable members of the community. Seedlings that connect to an CMN in the wild have a greater chance of survival in their first years of growth, yielding greater heights and number of leaves than those isolated from community (Simard 2011). Nurse trees, or well-established trees with a mature canopy, have been found directly transferring carbon to shaded young trees until they can access the light themselves higher in the canopy (McGuire 2007). Seedlings that establish near nurse trees plugged into a CMN, regardless of species, have shown greater rates of survival and growth especially in stressed or harsh conditions such as deep shade (Simard 1997), drought (Horton 1999), or high elevation climate and soil (Perry 1989) compared to isolated seedlings. Mycorrhizal density declines with greater distance from established trees and so seedlings will thrive more under even the densest shaded canopy of a nurse tree compared to those planted farther away in adequate sunlight. The proximity of seedlings to nurse trees heightens access to a greater diversity of mycorrhizal fungi species, resulting in a

Reprinted from Read and Perez-Moreno 2003 with permission from John Wiley and Sons
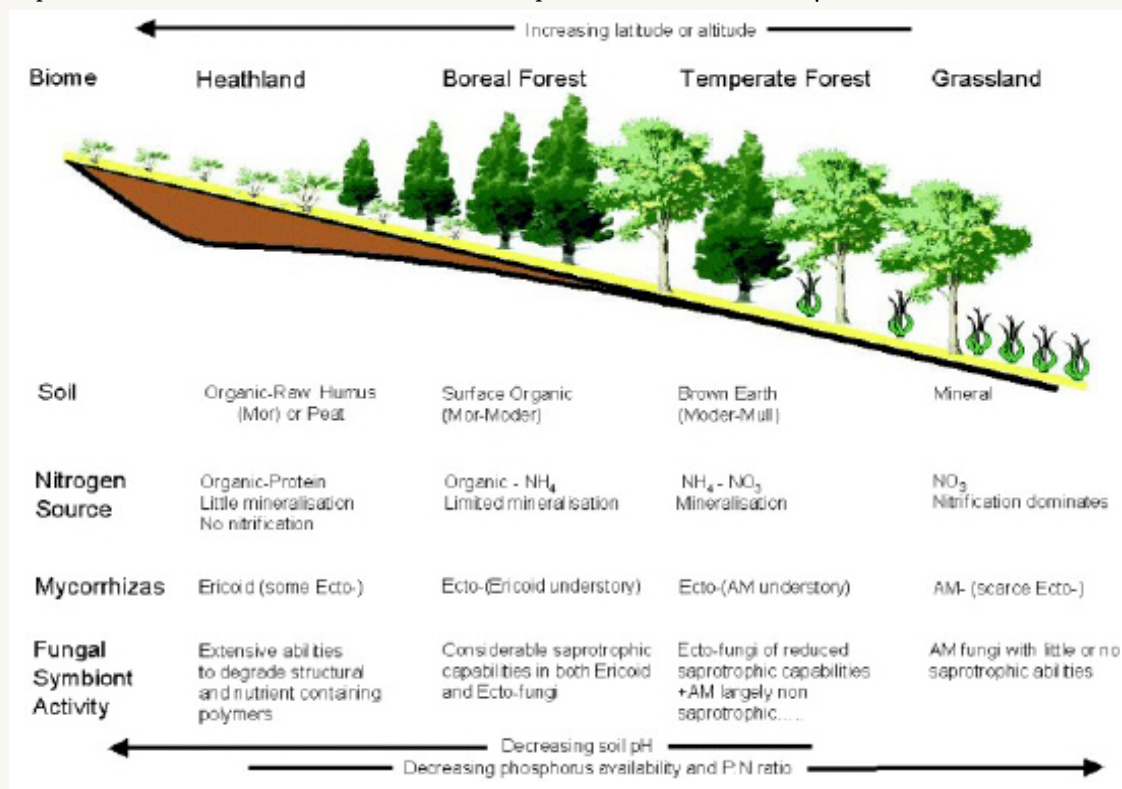


**Figure 3.** Forest succession and mycorrhizal partners

bigger pool of nutrients and an increased chance of survival in early years of life (Simard 1997).

*Favoritism and forest succession*

The pattern of allocating resources to the next generation of seedlings is different between AM and EcM fungi. While forests dominated by EcM fungi maintain a neutral to positive (i.e. self-reinforcing) feedback loop in response to new seedling establishment of EcM-accepting trees, AM fungi maintain a neutral or negative feedback loop with seedlings of the same AM tendency. As a result, AM forests will perpetuate mixed communities of species and eventually cede to EcM-dominated, more homogenous communities (Kadowaki et al. 2018). This can be visualized by the general pattern of forest succession from herbaceous shrubland to late-successional coniferous forest communities, as illustrated by the figure three.

It is important to remember that although tree species are more homogenous in these late-successional EcM forests, belowground the diversity of fungi is astoundingly complex compared to that of AM ecosystems of greater plant diversity, and an EcM fungal community will eventually outcompete the AM community because if its preferential treatment of insider plants (Kadowaki et al. 2018). The breadth of the EcM CMN's fungal diversity may provide a denser offering of nitrogen and phosphorous to its community members, and especially seedlings shaded under the dense canopy. This will save young EcM trees the nearly impossible energy-intensive toil of growing on their own accord in the first few years before finding a break in the canopy, while AM seedlings have to fight their way to the light (Koide and Dickie 2002).

The tendency for AM fungi to encourage a mixed forest ecosystem, while EcM fungi support like-hosted trees, holds implications in terms of forest resilience after disturbance such as fire or disease. Several established "edge" trees, or trees along the perimeter of a disturbance maintaining EcM mycorrhizal network strongholds, have shown to

be key to the re-establishment of coniferous forests on disturbed land. After a fire, seedlings of mixed EcM-AM tendency will flourish beneath an EcM-connected tree of a different species compared to the same species associated beneath an AM-associated tree, or those planted in unnetworked soils in the sunlight (Simard et al. 2009). EcM trees connected to a CMN in a late-successional forest can provide a link through time in which young trees may inherit the millenia-old nutritional network of their community elders. As such, the preservation of such trees can help perpetuate EcM relationships even after disturbance (Simard et al. 2009). EcM fungi thus increase ecological resilience for late-successional forest regimes in a way that AM edge plants do not (Simard and Vyse 2006, Simard 2004).

*Exceptions*

The direction and degree of resource transfer through the CMN is mostly regulated by source-sink gradients, but factors like the amount of mycorrhization (van der Heijden 2002) and levels of macronutrients in the soil (Simard and Durall 2004) hold significant influence as well. As mentioned earlier, mycorrhization can be disrupted by the addition of nitrogen into the soil via fertilization. Many EcM and AM fungi decline under elevated nitrogen conditions and seedlings being supplemented by bioavailable phosphorous and nitrogen are less likely to form mycorrhizal associations, likely due to the lack of necessity (Ekblad et al. 2016, Simard 2011). There are some interesting exceptions to the altruistic nature of resource transfer along the source-sink gradient as well. Contrary to expectation, the largest, oldest trees are not necessarily common donors to nutrient-depleted trees or seedlings. It is speculated that the amount of resources necessary for structural upkeep of massive trees is large enough to overwhelm and overpower the sink pull from the seedling. However, it should be noted that the expanse of these trees' root systems is likely beneficial to the continuity of the CMN (Simard and Durall 2004).

Another exception to nutrient-sharing within a CMN is competition amongst AM plants in the same network. In some cases, AM-associated plants will manipulate their own source-sink gradient to deprive weeds of nutrients (Simard, Asay, Beiler, Bingham, Deslippe, He, and Teste 2015). Fierce competition like this has not yet been found amongst EcM-associated trees, who are still more likely to support species that are also EcM-prone (Kadowaki et al. 2018).

**Chemical Warfare and Plant Communication: Messages, warnings and weapons sent via the CMN**

Individual plants in any ecosystem are bombarded by competition from other plants, insects, herbivores, diseases, parasites, and changes to environmental conditions. The CMN not only connects plants with communal nutritional resources but allies them against competition by other organisms through the conveyance of communicative signals, warnings, and fungicides and herbicides across a CMN (Wipf et al. 2019).

*Chemical Warfare*

The more established the CMN, the stronger, more united front the community has against competition. As the CMN expands its membership, so does the bioactive zone of protective allelochemicals produced by plants and mycorrhizal associates. These aggressive allelochemicals produce detrimental physiological responses in other organisms that compete with individuals in the CMN, uniting members in a front of synchronized chemical warfare (Barto et al., 2012). In one tablespoon of soil, there are an estimated $5 * 10^4$ species of microorganisms fighting for resources and space (Raynaud 2014). Soil fungi comprise the front lines of this microbial battle, their one-cell thick filamentous hyphae leaving them naked and exposed to the surrounding competition. But soil fungi are well-adapted to the fierce competition of the soil microbiome, and as such have incredible abilities to pointedly excrete defensive chemicals toward their competitors

(Stamets 2005). Mycorrhizal fungi are welcome defenders of their host plants. Both EcM and AM fungi will act on competitive challengers to its allied plants through allelopathy, a mechanism which inhibits the germination or growth of competition through allelochemicals (Barto et al., 2012).

Aboveground, the battle rages on, and plants connected to a CMN are at an advantage. Plants attacked by necrotrophic fungi or herbivorous caterpillars will warn other plants via the CMN system by sending out defensive signals (phytohormones) such as jasmonate, zeatin riboside and methyl silicate. These will induce preemptive defense responses, such as antagonistic enzyme activity or defensive gene expression, in plants on the other side of a forest stand (Song et al., 2010). One plant being defoliated by a caterpillar attack will emit defensive signals through the CMN, and "eavesdropping" plants in the network will then respond by producing volatile organic chemicals before they are attacked in turn (Babikova et al., 2013). Chemicals signals such as these are sent across CMNs within 24 to 50 hours which, relative to the general movement of nutrients and gene expression in tree-time, is incredibly rapid (Babikova et al., 2013).

*Communication*

Plant behavior responses to molecular signaling from the CMN are not limited to chemical defenses alone. Plants will respond in all kinds of ways to different phytohormones exchanged in the network by adjusting the timing and nature of actions like germination, growth, survival or death, foliar nutrition, and changed rate of photosynthesis (Barto et al., 2012, Wipf 2019). Meticulous coordination of behaviors such as rapid (breakaway) growth, defoliation of leaves in the autumn, or seed germination timing can all be beneficial to a community if done for the benefit of the greater good.

## Conclusion

The interrelational and expansive nature of CMNs has upended established notions of cutthroat biological competition between individual organisms existing in a struggle for survival of the fittest. CMNs challenge the notion of organisms competing as disparate individuals and instead reveal an interconnected web where cross-species, cross-kingdom exchange and collaboration outcompete individualism and isolation. In a CMN, each organism serves a vital role for the survival of the greater whole on a scale incomprehensible to current systems of thinking about individuality and interconnectedness. If an individual organism cannot be severed from the web, then where lies the separation between one organism and the next?

With land-use change at the forefront of causality during planet-wide ecological collapse (Brondizio et al. 2019), the phenomenon of CMNs changes the scale at which biological science, forestry, agriculture and conservation land management must be conducted. With CMNs in mind, ecosystem restoration, disturbance mitigation and ecological conservation need to be revised and approached with a more cross-disciplinary model, a mycelial network of collaborators that can interweave these new knowledge strands into planning and adaptation strategies. Effective conservation management can only take place by considering the irreplicable, interconnected, self-regulating nature of the Earth's ecosystems, such as those of CMNs, that formed over millions of years and first facilitated the marching of early organisms onto land. EcM fungal partners are predicted to facilitate the expansion of pioneer species into upper-limit landscapes and limit the contraction of lower-limit ranges as climates warm (Lankau et al. 2015). As ecotones shift and species march upslope and northward, it is essential to consider the underlying common networks that must perpetuate in order for that movement to succeed (Tendersoo 2017). Monitoring, encouraging, and protecting EcM and AM fungal biological and functional diversity creates a positive feedback loop that supports ecosystem recovery and overall resilience (Tendersoo 2017), and thus must be a key goal in good conservation science henceforth.

**Caroline Hildebrand** is an alumnae from the Master of Science in Environmental Sciences program. She graduated in May 2020.

# References

Amaranthus, M. P., & Perry, D. A. (1989). Rapid root tip and mycorrhiza formation and increased survival of Douglas-fir seedlings after soil transfer. New Forests, 3(3), 259-264.

Babikova, Z., Gilbert, L., Bruce, T. J., Birkett, M., Caulfield, J. C., Woodcock, C., ... & Johnson, D. (2013). Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. Ecology letters, 16(7), 835-843.

Barto, E. K., Weidenhamer, J. D., Cipollini, D., & Rillig, M. C. (2012). Fungal superhighways: do common mycorrhizal networks enhance below ground communication?. Trends in plant science, 17(11), 633-637.

Bingham, M. A., & Simard, S. W. (2011). Do mycorrhizal network benefits to survival and growth of interior Douglas-fir seedlings increase with soil moisture stress?. Ecology and evolution, 1(3), 306–316. doi:10.1002/ece3.24

Bonfante, P., & Genre, A. (2010). Mechanisms underlying beneficial plant–fungus interactions in mycorrhizal symbiosis. Nature communications, 1(1), 1-11, 48.

Brondizio, E. S., Settele, J., Díaz, S., & Ngo, H. T. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn.

Brundrett, M.C. and Tedersoo, L. (2018), Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol, 220: 1108-1115. doi:10.1111/nph.14976

Brundrett, M.C. Plant Soil (2009) 320: 37. https://doi.org/10.1007/s11104-008-9877-9

Brundrett, Mark. (2017). Global Diversity and Importance of Mycorrhizal and Nonmycorrhizal Plants. 10.1007/978-3-319-56363-3_21.

Eason WR, Newman EI, Chuba PN. 1991. Specificity of interplant cycling of phosphorus: the role of mycorrhizas. Plant and Soil 137:267–274. 10.1007/BF00011205

Egerton-Warburton LM, Querejeta JI, Allen MF. 2007. Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. Journal of Experimental Botany 58:1473–1483. 10.1093/jxb/erm009

Ekblad, A., Mikusinska, A., Ågren, G. I., Menichetti, L., Wallander, H., Vilgalys, R., ... & Eriksson, U. (2016). Production and turnover of ectomycorrhizal extramatrical mycelial biomass and necromass under elevated CO2 and nitrogen fertilization. New Phytologist, 211(3), 874-885.

Field, K.J. and Pressel, S. (2018), Unity in diversity: structural and functional insights into the ancient partnerships between plants and fungi. New Phytol, 220: 996-1011. doi:10.1111/nph.15158

Giovannetti, M., Fortuna, P., Citernesi, A.S., Morini, S. and Nuti, .M.P. (2001), The occurrence of anastomosis formation and nuclear exchange in intact arbuscular mycorrhizal networks. New Phytologist, 151: 717-724. doi:10.1046/j.0028-646x.2001.00216.x

Glass, N. L., Rasmussen, C., Roca, M. G., & Read, N. D. (2004). Hyphal homing, fusion and mycelial interconnectedness. Trends in microbiology, 12(3), 135-141.

Gorzelak, M. A., Asay, A. K., Pickles, B. J., & Simard, S. W. (2015). Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. AoB PLANTS, 7, plv050. doi:10.1093/aobpla/plv050

Heaton, L., Obara, B., Grau, V., Jones, N.,

Nakagaki, T., Boddy, L., & Fricker, M. D. (2012). Analysis of fungal networks. Fungal Biology Reviews, 26(1), 12-29.

Horton, T. R., Bruns, T. D., & Parker, V. T. (1999). Ectomycorrhizal fungi associated with Arctostaphylos contribute to Pseudotsuga menziesii establishment. Canadian Journal of Botany, 77(1), 93-102.

Kadowaki, K., Yamamoto, S., Sato, H. et al. Mycorrhizal fungi mediate the direction and strength of plant–soil feedbacks differently between arbuscular mycorrhizal and ectomycorrhizal communities. Commun Biol 1, 196 (2018) doi:10.1038/s42003-018-0201-9

Koide, R. T., & Dickie, I. A. (2002). Effects of mycorrhizal fungi on plant populations. In Diversity and Integration in Mycorrhizas (pp. 307-317). Springer, Dordrecht.

Lang C, Seven J, Polle A. 2011. Host preferences and differential contributions of deciduous tree species shape mycorrhizal species richness in a mixed Central European forest. Mycorrhiza 21:297–308. 10.1007/s00572-010-0338-y

Lankau, R. A., Zhu, K., & Ordonez, A. (2015). Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change. Ecology, 96(6), 1451-1458.

Lerat, S., Gauci, R., Catford, J. G., Vierheilig, H., Piché, Y., & Lapointe, L. (2002). 14 C transfer between the spring ephemeral Erythronium americanum and sugar maple saplings via arbuscular mycorrhizal fungi in natural stands. Oecologia, 132(2), 181-187.

McGuire, K. L. (2007). Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. Ecology, 88(3), 567-574.

Pandey, D., Kehri, H. K., Zoomi, I., Akhtar,

O., & Singh, A. K. (2019). Mycorrhizal fungi: Biodiversity, ecological significance, and industrial applications. In Recent Advancement in White Biotechnology Through Fungi (pp. 181-199). Springer, Cham.

Philip, L., Simard, S., & Jones, M. (2010). Pathways for below-ground carbon transfer between paper birch and Douglas-fir seedlings. Plant Ecology & Diversity, 3(3), 221-233.

Raynaud, X., & Nunan, N. (2014). Spatial ecology of bacteria at the microscale in soil. PLoS One, 9(1), e87217.

Read, D.J. and Perez-Moreno, J. (2003), Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance?. New Phytologist, 157: 475-492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Simard SW, Durall DM, Jones MD. 1997a. Carbon allocation and carbon transfer between Betula papyrifera and Pseudotsuga menziesii seedlings using a 13C pulse-labeling method. Plant and Soil 191:41–55. 10.1023/A:1004205727882

Simard, S. W., & Durall, D. M. (2004). Mycorrhizal networks: a review of their extent, function, and importance. Canadian Journal of Botany, 82(8), 1140-1165.

Simard, S., & Vyse, A. (2006). Trade-offs between competition and facilitation: a case study of vegetation management in the interior cedar–hemlock forests of southern British Columbia. Canadian Journal of Forest Research, 36(10), 2486-2496.

Simard, S., Asay, A., Beiler, K., Bingham, M., Deslippe, J., He, X., ... & Teste, F. (2015). Resource transfer between plants through ectomycorrhizal fungal networks. In Mycorrhizal networks (pp. 133-176). Springer, Dordrecht.

Smith SE, Read DJ (1997) Mycorrhizal Symbiosis.

(Academic Press, London)

Song, Y. Y., Simard, S. W., Carroll, A., Mohn, W. W., & Zeng, R. S. (2015). Defoliation of interior Douglas-fir elicits carbon transfer and stress signalling to ponderosa pine neighbors through ectomycorrhizal networks. Scientific reports, 5, 8495.

Song, Y. Y., Zeng, R. S., Xu, J. F., Li, J., Shen, X., & Yihdego, W. G. (2010). Interplant communication of tomato plants through underground common mycorrhizal networks. PloS one, 5(10), e13324.

Stamets, P. (2005). Mycelium running: how mushrooms can help save the world. Random House Digital, Inc..

Tedersoo, L. (Ed.). (2017). Biogeography of mycorrhizal symbiosis (Vol. 230). Tartu, Estonia: Springer.

Teste FP, Simard SW, Durall DM, Guy RD, Jones MD, Schoonmaker AL. 2009. Access to mycorrhizal networks and roots of trees: importance for seedling survival and resource transfer. Ecology 90:2808–2822. 10.1890/08-1884.1

Teste, F.P., Simard, S.W., Durall, D.M., Guy, R.D., Jones, M.D. and Schoonmaker, A.L. (2009), Access to mycorrhizal networks and roots of trees: importance for seedling survival and resource transfer. Ecology, 90: 2808-2822. doi:10.1890/08-1884.1

Van der Heijden, M. G., & Sanders, I. R. (2002). Mycorrhizal ecology: synthesis and perspectives. In Mycorrhizal ecology (pp. 441-456). Springer, Berlin, Heidelberg.

Vincenot L., Selosse MA. (2017) Population Biology and Ecology of Ectomycorrhizal Fungi. In: Tedersoo L. (eds) Biogeography of Mycorrhizal Symbiosis. Ecological Studies (Analysis and Synthesis), vol 230. Springer, Cham

Wipf, D., Krajinski, F., van Tuinen, D., Recorbet, G., & Courty, P. E. (2019). Trading on the arbuscular mycorrhiza market: from arbuscules to common mycorrhizal networks. New Phytologist.