Re-defining common mycorrhizal and fungal networks

Matthias C. Rillig 1,2*, Anika Lehmann 1,2, Luisa Lanfranco 3, Tancredi Caruso 4, David Johnson 5

1 Freie Universität Berlin, Institute of Biology, 14195 Berlin, Germany

2 Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany

3 Università di Torino, Dipartimento di Scienze della Vita e Biologia dei Sistemi, 10125, Torino, Italy

4 School of Biology and Environmental Science, University College Dublin, Ireland

5 The University of Manchester, Department of Earth and Environmental Sciences, Manchester, M13 9PT, United Kingdom

* Corresponding author: M. Rillig, rillig@zedat.fu-berlin.de, +49 30 838 53165. Freie Universität Berlin, Institut für Biologie, Altensteinstr. 6, D- 14195 Berlin, Germany

Abstract

The current use of the term 'common mycorrhizal network' (CMN) stipulates a direct link between plants formed by the mycelium of a mycorrhizal fungus. This means that a specific case (involving hyphal continuity) is used to define a much broader phenomenon of hyphae interlinking among plant roots. We here offer a more inclusive definition of the common mycorrhizal network as a network formed by a fungus among plant roots, irrespective of the type of connection or interaction, not limited to direct hyphal linkages. We propose the term 'common mycorrhizal networks with hyphal continuity' (CMN-HC) to capture the more specific case, which is important to study for some (notable carbon and nutrient exchange), but not all functions of a common mycorrhizal network. In addition, we introduce the term 'common fungal network (CFN)' to include networks of any type of connection formed by any type of fungus; this includes also non-mycorrhizal fungi, and indeed a combination of non-mycorrhizal and mycorrhizal networks.

We feel this new set of three hierarchical terms (CMN-HC, CMN and CFN) can usher in a period of research activity unburdened by some of the difficulties (logistics, experimental design challenges) of studying CMN-HC and thus can help attract additional researchers to this fascinating topic of mycorrhizal ecology.

Keys words: common mycorrhizal network, carbon exchange, hyphae, fungal networks, nutrient transport

Introduction

Virtually all fungi have hyphal growth forms that form mycelia, and thus, can be considered to form 'networks'. For mycorrhizal fungi, which form symbioses with plants, much attention has focused on their ability to interconnect two or more plants (of the same or different species) whereupon they are considered to have formed a 'common mycorrhizal network' (CMN). This definition means that a necessary condition for the existence of a CMN is the continuity of fungal mycelium from one plant to the other, a direct connection that does not involve a 'step' that passes through the soil rather than fungal cytoplasm. The definition has the advantage that it is very clear, as recently exemplified in an article critically surveying the literature in this field [1].

While this is a clear and generally accepted definition it has some significant shortcomings that make communication about this topic more challenging than it needs to be, and that potentially inhibits scientific progress by being too restrictive. For example, the definition is restricted to only mycorrhizal fungi, it ignores situations where mycelial networks can form close to other roots, or indeed fungi, without directly colonizing them, and it takes a binary view of any continuous networks that are formed (i.e. CMNs are considered only present or absent). Here we present a more inclusive view of fungal networks with the aim of stimulating research without being restricted to the narrow definition of CMNs.

CMNs and categories

As is often the case with definitions in biology, the degree of connectedness via mycorrhizal fungi is clearly viewed as two categories: CMN and non-CMN. However, as with any system of categories there is the danger of amplifying and exaggerating differences when cases are close to the border of these categories. What does this mean specifically for CMNs? Imagine a situation where a mycorrhizal fungal hypha originating from one plant root extends to the surface of another root: the mycelium of this fungus did not directly connect the two roots, so this is, by the currently accepted definition, not a CMN. As soon as a hypha enters the root, then a CMN is established. Imagine next a situation where 1,000 hyphae grow between two root systems, not one connecting the two with mycelial continuity, hyphae just emanating from one of the two host plants involved, intermingling with the roots, and growing along the root surface; this, again, does not fit with the current definition of a CMN. As soon as one of the 1000 hyphae grows into the other plant, however, a CMN is established. The question is: are these two situations really so different? The point of this exercise is to illustrate that hyphal linkages among plants occur along a gradient of connectivity, and crucially, where functional consequences may be non-linear in response to the degree of connectivity, and that these connections may also be dynamic through time. This is the case for many classical ecological networks such as plant-pollinator networks and food webs, which are known to rewire frequently in response to both natural temporal and spatial variability (e.g. seasonality) and perturbations [2,3]. Any ecological network can, therefore, be conceived as a structure fluctuating around an average configuration but taking, from time to time and place to place, multiple specific, local configurations, and there are now methods being developed to model the fluctuations of such dynamical networks [4].

We propose that defining CMNs based on a sharp boundary condition of direct hyphal connection between roots does not capture the reality of a gradient of fungal interactions with roots (Fig. 1). Allied to this issue is a need to better understand the factors controlling movement of resources through individual hyphae within a network [5]. In the previous hypothetical example, the single hypha generating a CMN could conceivably be a conduit for all resources channeled through the 1000 individual hyphae forming the overall fungal network, or it could transfer nothing. Our observations of ectomycorrhizal networks suggest there can be extreme selectivity and directionality in resource transfer through specific hyphae (Fig. 2). While there may be a range of mechanisms operating independently of the degree of connectivity that control such directionality, this observation makes it hard to predict the degree to which ‘hyphal connectivity’ (number of individual hyphae with access to a resource) relates to ‘functional connectivity’ (the number of hypha actively involved in accessing a resource). Identification of the molecular, biochemical and environmental controls of resource transfer through individual hyphae within networks may therefore improve the ability to predict the functional significance of the extent of hyphal cytoplasmic continuity.

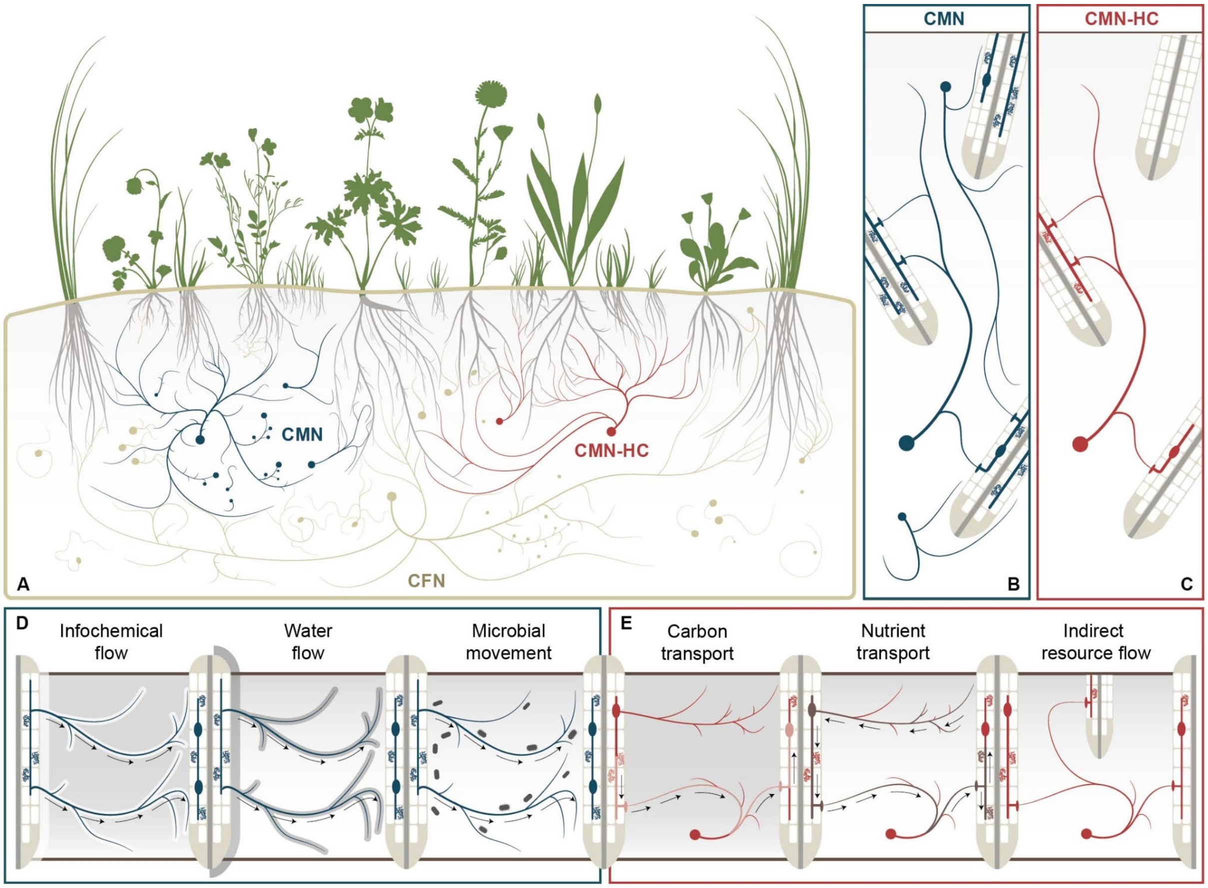

Fig. 1 The common mycorrhizal network (CMN) is conceptualized as any linkage formed by the mycelium of a mycorrhizal fungus among two (or more) host plants (A), irrespective of whether hyphal continuity is present or not (e.g. B, where hyphal continuity occurs and fungi also grow on the surface of other roots, and C, where only hyphal continuity occurs). Even in the absence of direct hyphal links with cytoplasmic continuity from plant to plant, several functions can be mediated by the CMN, including infochemical flow, as well as water flow and transport of microbes (D). When the specific case of hyphal continuity (HC) occurs, a phenomenon that does have functional consequences particularly in terms of nutrient and carbon transport, or in terms of subsidy of mycorrhizal colonization in one plant by another (E), then the CMN is further specified as a CMN-HC, a common mycorrhizal network with hyphal continuity. The common fungal network (CFN) encompasses connections of any kind between plants formed by any type of fungus (A), and thus is the most general case.

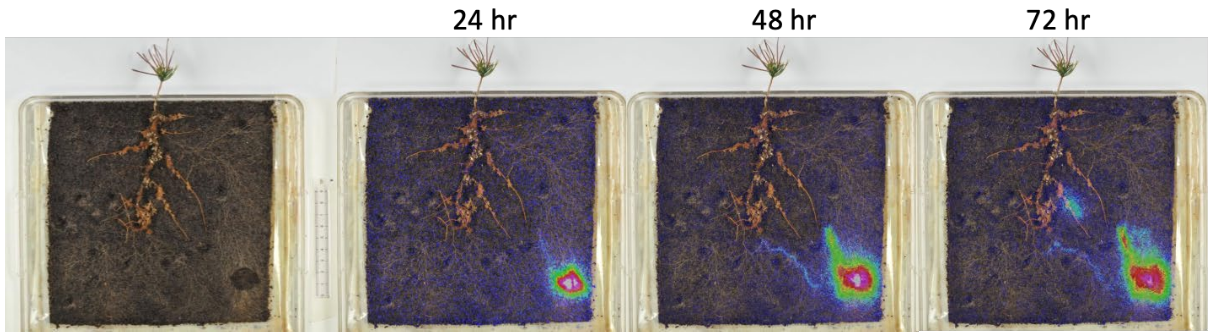

Fig. 2. Ectomycorrhizal fungal network formed by Paxillus involutus in association with Scots pine (Pinus sylvestris). The left hand image shows extensive growth of hundreds of individual ectomycorrhizal hyphae into a circular patch (bottom right) of peat into which a synthetic non-metabolizable amino acid tagged with 14C was added (14C-aminoisobutyric acid; 14C-AIB). The subsequent false-color images show the dynamics of 14C-AIB movement during a 72 hour period through the fungal network and accumulation in certain ectomycorrhizal root tips. The images highlight extreme directionality and selectivity in nutrient transport through hyphae, and illustrate how continuity of particular hyphae may or may not confer 'functional continuity' (unpublished data from David Johnson, Rosnida Tajuddin and Mark D. Fricker).

Functional differences between hyphal cytoplasmic continuity and non-continuity

Clearly, direct hyphal connection can permit the flow of material from one plant root to another via the mycelium in a way that is not possible without such a connection [6]. For example, carbon flow from one plant to the other has been critical for the evolution of mycoheterotrophic plants that have an achlorophyllous stage to their life cycle [7], while for green plants, this mechanism may at least subsidize the mycorrhizal fungal structures in the target plant, if nothing else [8]. A similar situation may occur for mineral nutrients, which are also translocated within the mycelium, where only in the presence of a direct hyphal connection plant to plant exchanges can occur. Even if nutrients could also reach a target plant when the mycelium eventually turns over, this would occur on a different time scale. Another important function of hyphal continuity is the ability of seedling recruits to become rapidly colonized and integrated into an established fungal network [9]. This situation enables new recruits to benefit from mycelia that have been 'paid for' with carbon from other plants, giving them a potential significant advantage over recruits that have to pay for their own exclusive hyphal network. However, the benefits gained from such a circumstance does not necessarily involve exchange of resources from one plant to another. Indeed, how resources are distributed by mycorrhizal plants and fungi under these circumstances remains unclear.

However, mycorrhizal fungal hyphae are involved in other functions that do not require the presence of hyphal continuity, and which operate independently of neighboring host plants. For example, the mycelium could 'unload' substances, like infochemicals [10,11] and energy-rich molecules [12], close to the root system of the target plant, and these can still have an effect without a direct mycelium connection [13]. Simply getting the chemicals closer to the target root, or indeed to the mycorrhizal fungal hyphae associated with other plants, works, because it gets them there faster than diffusion through soil, and with fewer opportunities for their decomposition. Another example is the transport of bacteria that hitch a ride on the hyphae of mycorrhizal fungi [14,15], which can have functional significance in terms of soil resource mobilization: there is no direct connection required for this to work either. And the same is probably true for water, which tends to flow mostly along the outside of the hyphae [16], so that there is not a necessity for a direct connection between roots.

Thus, we assert that mycelial continuity is certainly functionally relevant, as carbon and nutrient exchanges will likely not occur without it, but this feature does not account for all the functions carried out by the fungal mycelium interacting with root systems.

Experimental challenges brought about by the current CMN definition

The currently used, narrow CMN definition (our CMN-HC) requires the exclusion of alternative or complementary transport routes, such as soil-based pathways. The current definition therefore necessitates rather complex experimental designs with many conditions that need to be met, but which are hardly ever met in reality, especially in the field, as has recently been extensively discussed 1. We fear that the bar for field experimentation in particular may be so high that it turns off researchers from this critical line of inquiry, especially when they are not explicitly interested in carbon and nutrient exchange and the mechanisms underpinning these exchanges. Using the broader definition proposed here would open the door to broad experimentation on this important ecological topic without researchers succumbing to criticism about semantics, irrespective of whether or not a direct hyphal connection occurs or not; thus attracting researchers interested in mycorrhizal links. When a restriction to hyphal-only pathways is necessary, researchers can specify that they work on the CMN-HC.

A new and more inclusive definition of fungal networks

We propose to refer to any situation where mycorrhizal fungi - which inevitably form a network, because the fungus is almost always a network itself - interact with root systems of different plants as a CMN (Fig. 1). This definition includes all possible interactions, including the hyphal continuity, but also intermingling of the hyphae with the roots and mycorrhizal hyphae of a target plant. There is then a special case where there is hyphal continuity from one root to another, which we would propose to call CMN-HC (Fig. 1), so a special case of a common mycorrhizal network with hyphal continuity (HC). There is no a priori reason a special case should be used to define a more general feature: here this means that hyphal continuity is a special case, and the more general feature is fungal networks interacting with non-mycorrhizal and mycorrhizal root systems.

Research on fungal networks has almost exclusively focused on mycorrhizal fungi, which is perhaps not surprising given the importance of the symbiosis for evolutionary, ecological, and agricultural processes and systems. But fungal networks prevail across the entire Kingdom and so it seems illogical to have a definition that focuses on a small, albeit important, subset of the global population. To capture the overarching mode of growth of many fungi, we additionally introduce the term common fungal networks (CFN; Fig. 1) to acknowledge this even more general case. Moreover, acknowledgment of the importance and ubiquity of CFNs opens-up the potential for other guilds of fungi to form networks with the full range of interaction previously described (Fig. 1). Notably pathogenic fungi are known to co-colonise roots of different plants, which is a key mode by which the fungi spread infection [17,18]. The fact that there has been far less research on ‘common pathogenic fungal networks’ may be partly because of the lack of appropriate terminology capturing this fascinating and important feature of this group of fungi. Thus, an additional set of terms could be proposed, capturing a range of functionally important groups of fungi, such as pathogens.

We thus arrive at a hierarchy of three cases (Table 1): a common fungal network (CFN), formed by any fungus, and also including non-mycorrhizal fungi, at any degree of connection; a common mycorrhizal network (CMN), referring to the network formed by mycorrhizal fungi connecting among roots irrespective of hyphal cytoplasmic continuity; the common mycorrhizal network with direct hyphal connections among plants (CMN-HC). Equivalent terms could be proposed to capture other groups of fungi, such as pathogens.

Table 1. The hierarchy of new terms and re-definitions proposed here, tabulated by fungi involved and the degree of hyphal connection (also see Fig. 1). This terminology can be expanded to capture also other functional groupings of fungi, such as pathogens.

	Fungi involved	Degree of hyphal connection
Common fungal network (CFN): a mycelial network formed by any fungi, interlinking among plant roots or other hyphae	Any	Any
Common mycorrhizal network (CMN)	Mycorrhizal fungi	Any
Common mycorrhizal network with hyphal continuity (CMN-HC)	Mycorrhizal fungi	Direct hyphal links among plant roots, not involving a soil phase

Advantages of the new definition

We see a number of clear advantages to embracing this broader definition of CMN. One clear and obvious advantage is that researchers would be encouraged to work on fungal networks, at any level and degree of connection. Delineating the HC part is technically exceptionally challenging, especially in field or near-field conditions, and not every research question requires that level of mechanistic resolution (Fig. 1). Using this new definition, people could specify the particular case of direct hyphal connection when they really mean it, and we would speak of the common mycorrhizal network or common fungal network as the normal, more general case of a fungal mycelium interacting with different roots.

Adopting this definition would make it much more straightforward to communicate the role of mycorrhizal fungal networks to the public. Given the exceptional public interest in this topic, especially in the context of the 'wood-wide web' 1, this alone is a very good reason for embracing this broader definition.

Finally, CMN understood the way we propose here does better justice to the multiple functions beyond nutrient and carbon exchange carried out by mycelial connections. Additionally, we believe that including CFN better promotes the study of common networks produced by fungi other than mycorrhizal fungi, or indeed a combination of connections via mycorrhizal and non-mycorrhizal fungi. For example, the balance of effects between pathogenic and mycorrhizal fungi can have profound impacts on ecosystem functioning [19] and the new definition helps acknowledge the role of other network forming species.

Conclusions

We propose to use the term common mycorrhizal network in any situation where one or more mycorrhizal fungi interact with two or more root systems, irrespective of the degree of connectivity or implied function. The term CMN-HC is used to denote the special case of hyphal connectivity; this is indeed a special case both in terms of degree of connection, functioning, and experimental effort and sophistication, and should thus be treated as such. Our terminology can be expanded to include also other groups of fungi.

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Competing interests

None declared.

Author contributions

MCR initiated the work and wrote the first draft. AL designed the conceptual figure. All authors (MCR, AL, LL, TC and DJ) reviewed the literature and contributed to the writing of the manuscript.

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