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PERSPECTIVE

Mycorrhizal Networks

Clarifying the definition of common mycorrhizal networks

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Abstract

1. Common mycorrhizal networks (CMNs) are an enigmatic feature of soil and mycorrhizal ecology. The current use of the term 'common mycorrhizal network' stipulates a direct, continuous physical link between plants formed by the mycelium of mycorrhizal fungal genets. This means that a specific case (involving hyphal continuity) is used to define a much broader phenomenon of hyphae interlinking among roots of different plants.
2. We here embrace a more inclusive definition of the CMN as a network formed by mycorrhizal fungal genets among roots of different plants, irrespective of the type of connection or interaction, and not limited to direct hyphal linkages. Implicitly, this broader version of the term has been used by many researchers already.
3. We propose using the term 'common mycorrhizal networks with hyphal continuity' (CMN-HC) to capture the more specific case of a continuous link via hyphae between the roots of different plants, which is important to study for some (notable carbon and nutrient exchange), but not all functions of a CMN (e.g. transfer of infochemicals or microbes).
4. In addition, and becoming more general than CMN, we introduce the term 'common fungal network' (CFN) to include networks of any type of connection formed between different plants by any type of fungus; this includes also non-mycorrhizal fungi, and indeed a combination of non-mycorrhizal and mycorrhizal networks.
5. We assert that this new conceptual framework incorporating three hierarchical terms (CMN-HC, CMN and CFN), ranging from the most specific to the very broad, can usher in a period of new research activity on fungal networks.

KEYWORDS
carbon exchange, common mycorrhizal network, fungal networks, hyphae, nutrient transport, plant

1 | INTRODUCTION

Soil fungi, and in particular mycorrhizal fungi, have important effects on plants, plant communities and ecosystems (Powell & Rillig, 2018), and part of these effects are attributed to the formation and functioning of mycelial networks. Virtually all filamentous fungi develop hyphae that form mycelia, which function as a network foraging for resources and transporting materials. For mycorrhizal fungi, which establish symbioses with plants, much attention has focused on their ability to connect two or more plants (of the same or different species) whereupon they are considered to have formed a 'common mycorrhizal network' (CMN).

The original definition of a CMN focused on the fungi held in common by multiple plant individuals, even belonging to different species—hence forming a network (Horton, 2015). Over time and with increasing knowledge, the emphasis of the definition shifted towards the interlinking of the plants by the fungi. Physical connectedness with hyphal cytoplasmic continuity became critical to the definition of CMN and the quest for unequivocal evidence of the mechanism of resource transfer among interlinked plants through the hyphal-root network, excluding any transfer processes through the soil-water phase (Karst et al., 2023). This new definition has the advantage that it is very clear, as recently exemplified in an article critically surveying the literature in this field (Karst et al., 2023).

Despite its clarity and general acceptance, the definition 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 does not include situations where mycorrhizal fungal networks can form close to other roots, or indeed fungi, without directly colonizing them. The strict definition also takes a binary view of any continuous networks that are formed (i.e. CMNs are considered only present or absent). In addition, the definition excludes other filamentous non-mycorrhizal fungi potentially capable of forming common networks with plant roots. Here we present a more inclusive view of fungal networks with the aim of (1) clarifying the term CMN, (2) investigating the importance of hyphal connectedness and (3) introducing the concept of other non-mycorrhizal fungal networks held in common by interlinked plants.

2 | CMN RELATED TERMINOLOGY AS CURRENTLY USED

In the CMN literature, the usage of some specific terms—sometimes synonymously—can be a source of confusion. Thus, we first discuss the three most common terms used in describing the concept of CMNs: (1) The extraradical mycelium can be formed by one or multiple fungal genets emerging from one root and growing into the soil matrix (e.g. for scavenging). Such a configuration wis not itself a CMN but can be the starting point of a developing CMN with hyphae growing towards roots of other plants interacting and/or connecting with them. (2) The common mycelial network is a problematic term causing confusion because it uses the same abbreviation as CMN despite meaning something different. The original definition by Horton (2015) reads: 'The connected mycelium of an individual fungus colonizing roots of multiple plants of the same or different species is a common mycelial network'. Thus, it describes the mycelium as a continuous genet connecting and colonizing roots of at least two plants. Thus, a common mycelial network is the smallest unit of a CMN. (3) The CMN was defined by Horton (2015) as: 'Multiple individuals of multiple fungus species colonizing multiple plant species make up a common mycorrhizal network'. Thus, a CMN is formed by multiple mycorrhizal fungal genets, each connecting and colonizing roots of two or more plants of the same or different species. The number of genets or interlinked plants or the number of different mycorrhizal or plant species (abundance or diversity of edges and nodes in the network) is not an additional criterion. For these definitions, the emphasis lies on the continuity—the connectedness—of the interlinking hyphal network, which the connected plants have in common.

The 'connection' of roots by the fungal mycelium not only is the core of CMN research but also causes the largest conceptual problems. The time point when a CMN is established, following the definition, is when the genet interlinks and colonizes roots of two plants. The connection is necessary for direct CMN effects (e.g. resource transfer), but CMNs also have indirect effects that become effective when root and hyphae come into close proximity (e.g. microbial and infochemical transfer). In the following, we offer more detail on the point of direct and indirect CMN-mediated effects and the importance of hyphal continuity and hence network connectedness, which leads us to then propose an updated concept and terminology.

3 | FUNCTIONAL DIFFERENCES BETWEEN HYPHAL CYTOPLASMIC CONTINUITY AND NON-CONTINUITY—DIRECT AND INDIRECT CMN-MEDIATED EFFECTS

CMNs can be complex structures enabling a range of functions and causing various direct and indirect effects. We define direct effects as any effect due to the continuous hyphal connection, whereas indirect effects can occur without continuous hyphal connection. Both effect types have experimentally measurable, physiological impacts on the interlinked plants.

The most prominent direct CMN effect is related to the flow of carbon and mineral nutrients (e.g. N, P) from one plant (donor) root to another (receiver) via the mycelium (Figure 1) that necessitates a continuous cytoplasmic flow through the mycelium between the linked root systems (e.g. Selosse et al., 2006). The 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 (Leake, 1994), while for green plants, this mechanism may at least subsidize the mycorrhizal fungal structures in the target plant, if nothing else (Robinson & Fitter, 1999). A similar situation may occur for mineral nutrients, which are also translocated within the mycelium, where only in the presence of a direct

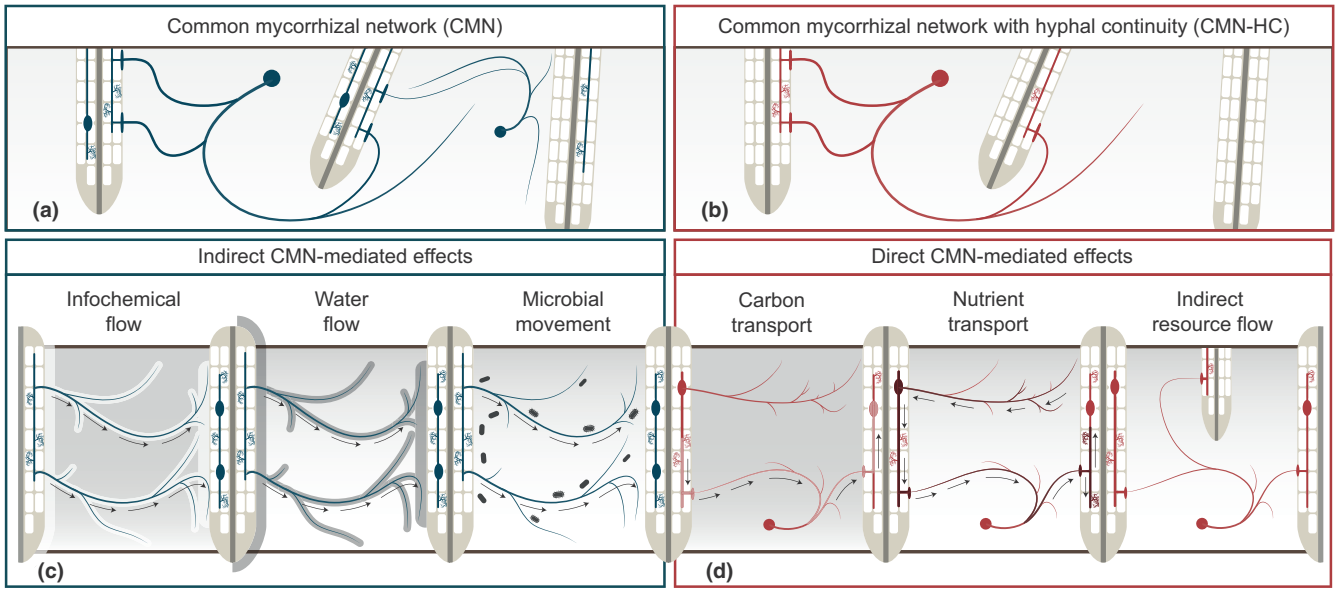

FIGURE 1 The common mycorrhizal network (CMN) is conceptualized as any linkage formed by the mycelium of a mycorrhizal fungus among two (or more) host plants (a), irrespective of whether hyphal continuity is present or not (e.g. a, where hyphal continuity occurs and fungi also grow on the surface of other roots and b, where only hyphal continuity occurs). Even in the absence of direct hyphal links with cytoplasmic continuity from plant to plant, several indirect effects can be mediated by the CMN, including infochemical flow, as well as water flow and transport of microbes (c). When the specific case of hyphal continuity (HC) occurs, a phenomenon that does have functional consequences particularly in terms of nutrient and carbon transport (direct CMN-mediated effects), or in terms of subsidy of mycorrhizal colonization in one plant by another (d), then the CMN is further specified as a CMN-HC, a CMN with hyphal continuity.

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 (perhaps weeks or longer).

Another important direct CMN effect depending on hyphal continuity is the ability of seedling recruits to become rapidly colonized and integrated into an established fungal network (Van Der Heijden & Horton, 2009). 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 (Figure 1). However, the benefits gained from such a circumstance do 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.

Mycorrhizal fungal hyphae are involved in other functions that do not require the presence of hyphal continuity, and which operate independently of neighbouring host plants, resulting in indirect CMN-mediated effects. For example, the mycelium could 'unload' substances, including infochemicals (Johnson & Gilbert, 2015; Pons et al., 2020) and energy-rich molecules (Luthfiana et al., 2021), close to the root system of the target plant, and these can still have an effect without a direct mycelium connection (Barto et al., 2012). Simply getting the chemicals closer to the target root, or the mycorrhizal fungal hyphae associated with the target plants, is effective because they arrive there faster than by 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 (Jiang et al., 2021; Mafla-Endara et al., 2021), which can have functional significance in terms of soil resource mobilization: there is no direct hyphal connection required for this to work either. And the same is probably true for water, which tends to flow mostly outside the hyphae (Kakouridis et al., 2022) so that there is not a necessity for a direct hyphal 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 (or fungal mycelia of several fungi) interacting with root systems. However, the original and currently used definitions focus on the connectedness of CMN.

4 | CMN CONNECTEDNESS AND THE PROBLEM WITH CATEGORIES

As is often the case with definitions in biology, the degree of connectedness via mycorrhizal fungi is viewed as categories: in this case there are 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 1000 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? With the current definition, the answer would be yes. But how many hyphal connections are actually needed to trigger a physiological response or a measurable effect caused by direct CMN effects? The answer is thus far unknown. In the previous hypothetical example, the single hypha generating a CMN could conceivably be a conduit for all resources channelled through the 1000 individual hyphae forming the overall fungal network, or it could transfer nothing. In fact, we do not have a good way to predict the degree to which 'hyphal connectivity' (the number of individual hyphae with access to a resource) relates to 'functional connectivity' (the number of hyphae 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.

The point of this exercise is to illustrate that hyphal linkages among plants occur along a gradient of connectivity, and that these connections may also be dynamic through time and functionally different. Any ecological network (e.g. plant–pollinator networks, food webs and also CMNs) can rewire frequently in response to both natural temporal and spatial variability (e.g. seasonality) and perturbations (CaraDonna et al., 2017; Evans et al., 2013); thus they can 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 (Caruso et al., 2022). Thus, 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 (Figure 1).

5 | A NEW AND MORE INCLUSIVE CONCEPTUALIZATION OF FUNGAL NETWORKS USING A HIERARCHY OF TERMS

The currently used, narrow CMN definition requires the exclusion of alternative or complementary transport routes, such as soil-based pathways. The current definition therefore necessitates rather complex and highly challenging experimental designs with many conditions that need to be met (Lehmann & Rillig, 2024): (1) at least two plants are connected, (2) all plants need to be colonized to account for mycorrhiza-mediated physiological, morphological and functional effects on the connected plants, (3) the root systems of the connected plants have to be separated to exclude root-mediated effects confounding any CMN effect, (4) a CMN treatment has to be applied to exclude hyphal-mediated effects confounding any CMN effect and (5) a test for hyphal continuity (e.g. an air gap between growth compartments) to exclude the soil–water pathway. All these CMN criteria are hardly ever met in reality, especially in the field, as has recently been extensively discussed for the case of ectomycorrhiza (Karst et al., 2023). Also, for arbuscular mycorrhizal fungi, the most stringent criteria for CMN have been met only in a handful of experimental studies (Lehmann & Rillig, 2024). 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. This would critically endanger the evidence base of the CMN research field.

To overcome this dilemma, we propose to refer to any situation where at least one mycorrhizal fungal genet interacts (connecting and colonizing or growing in close proximity) with the roots of a minimum of two plants of the same or different species as a CMN (Figure 1). This definition includes direct and indirect CMN-mediated effects and thus includes the case of hyphal continuity, but is not invalidated by a lack of hyphal continuity. Starting from this general CMN definition, we further propose to explicitly call the mycorrhizal network with hyphal continuity 'CMN-HC (common mycorrhizal network with hyphal continuity)'. The CMN-HC is essential to test for all direct CMN-mediated effects (Figure 1). The CMN-HC is thus a special case of a CMN. We see no necessity to introduce an additional term where the HC condition is not met, as this would simply reflect the absence of certain experimental controls.

Furthermore, 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 fungal Kingdom and so it seems unnecessarily limiting to restrict the concept of fungal interactions with roots of different plants to a small, albeit important, subset of the global fungal population. To capture the overarching mode of growth of many fungi, we introduce the term common fungal networks (CFNs; Figure 1) to acknowledge this even more general case. Thus, a CFN describes the general phenomenon of at least one filamentous fungal genet (irrespective of its phylogenetic or guild membership) linking up a minimum of two plants (of the same or different species) (Table 1).

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. Notably pathogenic fungi are known to co-colonize roots of different plants, which is a key mode by which the fungi spread infection (Neil, 1986; Rekah et al., 2001). The fact that there has been far less research on 'common pathogenic fungal networks' may be partly because of the lack of an appropriate conceptual framework capturing this fascinating and important feature of this group of fungi. Thus, an additional set of concepts and 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 CMN, referring here to the network formed by mycorrhizal fungal genets interlinking roots of different plants irrespective of hyphal cytoplasmic continuity; and the CMN with direct hyphal connections among plants (CMN-HC). Equivalent terms could be proposed to capture other groups of fungi, such as pathogens.

6 | ADVANTAGES OF THE NEW DEFINITION

We see a number of clear advantages to embracing this differentiation between the broader definition of CMN and the special case CMN-HC. One clear and obvious advantage is that researchers would be encouraged to work on mycorrhizal networks, at any level and degree of connection. Delineating the hyphal continuity aspect in CMNs is technically exceptionally challenging, especially in field or near-field conditions, and not every research question requires that level of mechanistic resolution (see direct and indirect CMN-mediated effects, Figure 1).

Using the new proposed definition and differentiation improves clarification of the plant-fungal-network under study and helps clarify any inferences that can be drawn from experimental data. Experimental designs not testing hyphal continuity are also targeting CMNs but come with limitations with regard to data interpretability: they do not allow testing of direct CMN-mediated effects. In fact, this reflects the current reality, as the vast majority of papers on arbuscular mycorrhizal fungi do not meet the stringent CMN-HC experimental criteria, and many studies are actually studies of CFNs, as they fail to exclude hyphae other than mycorrhizal hyphae (Lehmann & Rillig, 2024).

In general, communication about the role of mycorrhizal fungal networks with the public would improve. Given the exceptional public interest in this topic, especially in the context of the 'wood-wide web' (Karst et al., 2023), this alone is a very good reason for embracing this broader definition.

TABLE 1 The hierarchy of new terms and re-definitions proposed here, tabulated by fungi involved and the degree of hyphal connection (also see Figure 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)—this is a new use of the term introduced here	Mycorrhizal fungi	Any
Common mycorrhizal network with hyphal continuity (CMN-HC)	Mycorrhizal fungi	Direct hyphal links among plant roots, not involving a soil phase

TABLE 2 Examples of research questions aligning with the three different hierarchical levels of concepts for fungal networks introduced here: common mycorrhizal network with hyphal continuity (CMN-HC), common mycorrhizal network (CMN) and common fungal network (CFN).

Fungal network type	Examples of research questions
CMN-HC	• Degree of connectedness: how many direct, continuous hyphal connections between interlinked plants of a CMN are necessary to induce measurable direct effects on either plant performance (e.g. nutrient transfer, plant growth) or soil properties (e.g. soil aggregation, soil organic matter processing)? Is there a threshold-type response in terms of the number of hyphal connections? • Network complexity: are direct effects of CMN-HC a function of the diversity of fungal phylotypes participating in the connection?
CMN	• Degree of proximity: when are hyphae close enough to a root to have an indirect CMN-mediated effect on the target plant, without connecting via root colonization? Is there a distance threshold? Is there a threshold in terms of the number of hyphae growing in proximity to a root? • Global change/environmental stressor effects: can a CMN without direct hyphal connectivity contribute to stress tolerance and mediate effects of global environmental change?
CFN	• Evidence of existence: do other filamentous fungi (beside mycorrhizal fungi) form networks held in common by multiple plants? • Functioning: how do these networks function, what CFN-mediated effects are possible? Are such effects comparable to those of CMN? • Interactions with other networks: how are CFN effects mediated by the concurrent existence of a CMN and vice versa?

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 filamentous 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 (Semchenko et al., 2018) and the new definition helps acknowledge the role of other network forming species.

Finally, clearly structuring research questions so that they align with the different levels of the hierarchy of the terms proposed here (Table 2) is likely to facilitate progress in our understanding of fungal linkages among plants.

7 | CONCLUSIONS

We propose to use the term CMN 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 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 also include other groups of fungi.

While we see this new framework as clearly advantageous, there is no normative necessity to embrace it; we see this paper rather as a starting point of a discussion. Changing established terms is never popular, and thus we recommend that authors of future papers clearly state the definition they have embraced to avoid confusion.

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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CONFLICT OF INTEREST STATEMENT

None declared.

DATA AVAILABILITY STATEMENT

No data are used in this manuscript.

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