Title: Systematic mapping of experimental approaches to studying common mycorrhizal networks

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Abstract

Mycorrhizal fungi can interlink and connect plants in a common mycorrhizal network (CMN). Studying CMNs is challenging due to pathways of material transfer but also plant and mycorrhizal effects that have to be tested and controlled in order to be able to evaluate the presence and magnitude of a specific CMN effect. These controls let to a clear but strict definition of CMN which requires experiments to fulfill specific criteria: at least two plants are connected by the CMN, all plants are mycorrhized, the roots of the connected plants are separated, there is a CMN treatment tested, and the hyphal continuity is tested.

Here, we evaluate the evidence base of the CMN research specifically for arbuscular mycorrhiza via a systematic mapping approach. We found that not all studies were testing true CMNs but rather common fungal networks (CFN), including filamentous fungi other than the targeted mycorrhizal fungi. The number of articles conducting experiments on CMNs drops strongly with increasingly stringent fulfillment of the CMN definition. Additionally, there is a focus on lab studies and specific fungal strains; however, researchers have used diverse plant species setups. Also plant, fungal and resource transfer responses are preferentially measured, while microbial community metrics and ecosystem functions and processes are neglected.

We see a need to strengthen the CMN evidence base and thus we call for a renewed research effort on CMN, focusing on a whole range of levels of mechanistic resolution (from CFN to CMN with and without hyphal continuity). Additionally, neglected experimental situations (e.g. field studies in general) and microbial community or ecosystem-level responses should be included in future research.

1 Introduction

The mycelium of filamentous fungi consists of hyphae with which the fungi explore the soil and interact with the environment, including its resources, with competitors or plant hosts (Moore *et al.*, 2020). Among filamentous fungi, the group of mycorrhizal fungi is prominent for their ability to connect host plants of the same but also different species via their hyphae (Newman 1988), due to low host specificity (Sanders, 2003; Leake *et al.*, 2004). By this, a nutrient-based symbiosis is established centered around resource transfer between these mycorrhizal fungi and the majority of land plants in both natural and agricultural systems (Parniske, 2008; Brundrett, 2009; Brundrett & Tedersoo, 2018). In exchange for photosynthetically-derived C (Jiang *et al.*, 2017; Luginbuehl *et al.*, 2017), the fungi transport mineral nutrients to the plant hosts (e.g. P and N; Smith & Smith, 2011). The simultaneous colonization of multiple host plants by one fungal genet results in the formation of a mycorrhizal mycelium interlinking plant roots - a common mycorrhizal network (CMN; Molina & Trappe, 1982). Multiple genets of the same or different fungal species and more than two plants of the same or different species can be involved in a CMN; as long as one genet connects the roots of a minimum of two different plants, the classical definition of a CMN is fulfilled (Horton, 2015; Karst *et al.*, 2023). Such a CMN enables the transfer of resources (e.g. C, N, P and water) (Weremijewicz *et al.*, 2016), infochemicals (Barto *et al.*, 2011), and even microbes (de Novais *et al.*, 2020) among neighboring plants with effects on seedling establishment and plant competition (Merrild *et al.*, 2013; Weremijewicz *et al.*, 2018).

Research on CMNs is challenging due to the many different effects and pathways of material transfer that have to be tested and controlled in order to be able to evaluate the presence and magnitude of a specific CMN effect. There are three major pathways (root, hyphal and soil-water pathways) and effects (mycorrhiza, root and CMN effect) of interest in CMN studies.

The root pathway allows resource transfer via roots from a donor plant to receiver plants by exudates and rhizodeposits (Simard *et al.*, 1997; Figueiredo *et al.*, 2021). The same is true for the hyphal pathway. Hyphae of any species and guild can transfer resources over various distances (e.g. Deacon, 1996; Fricker *et al.*, 2017; Schütz *et al.*, 2022) from the donor plant rhizosphere bringing material into close proximity of a receiver plant with or without a continuous hyphal connection among roots. Also, resources can flow passively from a donor root into close proximity of the receiver plant rhizosphere by the soil-water pathway. To avoid confounding effects introduced by the existence of these pathways, researchers have to consider mycorrhiza, root and CMN effects in their experimental designs (Karst *et al.*, 2023).

The mycorrhiza effect is the result of any physiological, morphological and functional changes in the mycorrhized plant due to the process and maintenance of the root colonization (Bennett & Groten, 2022). Testing the mycorrhiza effect is important for evaluation of the magnitude and sign of the mycorrhiza-mediated effects on the plant hosts; this requires an additional treatment testing inoculated and non-inoculated plants. Non-colonized plants are not a control for a CMN treatment as all plants have to be mycorrhized in CMN studies.

The root effect includes root-root interactions, such as facilitation or competition (Schenk, 2006), when roots are allowed to intermingle; the latter is the real world condition. In CMN studies, root systems of interlinked plants have to be experimentally spatially separated. This is an artificial condition necessary to disentangle the root and the hyphal pathway.

The CMN effect manifests in plants interlinked by the same mycorrhizal network providing the mycorrhiza effect while excluding any root effect. The CMN effect is tested via treatments affecting the connectivity of the interlinking mycorrhizal network (Bonneau *et al.*, 2019). These treatments can involve hyphal severing (e.g. rotated cores) and/or affect the soil volume explored by the mycorrhiza (e.g. mesh pots with different mesh apertures). The CMN effect has to be disentangled from mycorrhiza and root effects and the root, hyphal but also the soil-water pathways, in order to obtain unequivocal evidence for direct CMN effects unconfounded by other direct or indirect resource transfer pathways (Warren *et al.*, 2008).

In their strictest form, CMN studies cover a combination of treatments and interventions, some of which represent natural conditions (all plants mycorrhized) and some are highly artificial (roots of interlinked plants are separated to suppress root-root interactions and the root pathway) affecting additional system components, like other soil microbes (e.g. bacteria movement across "hyphal highways"). Matching all the different conditions and controls requires elaborate experimental designs. Over the years of research, different setups to study CMNs experimentally have developed from straightforward network formation between fungi and plants growing in the same test unit (e.g. Vankessel *et al.*, 1985; Walter *et al.*, 1996) to combinations of rotated (Johnson *et al.*, 2001) or static compartments with or without different mesh apertures (e.g. Bethlenfalvay *et al.*, 1991; Watkins *et al.*, 1996) and/or integrated air gaps within the growth systems (Meding & Zasoski, 2008) allowing for ever further manipulation and control of direct and indirect pathways and mycorrhiza, root and CMN effects (Bonneau *et al.*, 2019).

In addition to these complex experimental test systems, the fungi themselves present another level of complexity in our understanding of CMN effects. In the actual meaning of the term CMN, the focus is exclusively on the mycorrhizal fungi; thus, species of arbuscular, arbutoid or ectomycorrhizal fungi are the interlinking genet connecting the roots of at least two plants (Newman, 1988; Karst *et al.*, 2023). However, there is a substantial body of literature (e.g. field studies) investigating hyphal networks formed by mycorrhizal fungi in the presence of other types of fungi. These other fungi could also have the potential of forming hyphal networks interlinking with roots of different plants and even with the mycorrhizal networks (e.g. Neil, 1986; Rekah *et al.*, 2001). What at first sounds like hair-splitting implies completely different ecological meanings and inferences. While the complex configuration involving many different types of fungi represents a real world scenario (i.e. in soil, mycorrhizal networks are under the influence of other fungal species interacting or even interlinking with the mycorrhizal mycelium and host plant roots modulating any potential CMN-mediated effect), the mycorrhiza-exclusive configuration is highly artificial but necessary to test the mechanisms underpinning the resource transfer between mycorrhizal fungi and their plant hosts (i.e. dedicated efforts or in vitro studies have to be conducted to eliminate interference of non-mycorrhizal fungi). To resolve this conceptual issue, we follow here the terminology suggested by Rillig et al. (2023) which is based on a hierarchy of exclusiveness. First, the common fungal networks (CFN) describe genets of any filamentous fungi (including mycorrhizal fungi) interlinking the roots of a minimum of two plants. Second, the common mycorrhizal network (CMN) is formed by mycorrhizal fungal genets interlinking roots of at least two host plants, thus excluding any other filamentous fungi capable of forming a CFN.

Here, we systematically map the evidence base of experimental CMN research with an explicit focus on AM fungi. These endomycorrhizal fungi are members of the Glomeromycotina (Spatafora *et al.*, 2016) and form a symbiosis with approximately 70% of all vascular plants ((Brundrett & Tedersoo, 2018); compared to approximately 2% for ectomycorrhizal fungi) with an almost global distribution ((Soudzilovskaia *et al.*, 2020); with exceptions of e.g. boreal forest regions). They are ecological and economically important fungi (Smith & Read, 2008). It is known that the CMN effect varies with AM fungal and plant species (Milkereit *et al.*, 2018; Awaydul *et al.*, 2019) while the magnitude and the consequences for plant community composition are still unclear (Milkereit *et al.*, 2018; Figueiredo *et al.*, 2021; Karst *et al.*, 2023). We will analyze the evidence base to test for i) what fungal networks were tested in CMN studies (true CMNs or CFNs), ii) which setting was used (controlled lab studies or field conditions), iii) what methods were applied to test for CMN effects, iv) to what degree do experimental setups fulfill the CMN definition, v) what AM fungal species were tested (single species or mixtures of known composition or natural communities), vi) what plant species were tested (single species or mixtures with low or high species density) and vii) what was measured in CMN studies (plant, fungal, community parameters, or ecosystem processes and functions). We expect a limited suite of studies to fulfill the strict CMN rules giving rise to a restricted evidence base.

2 Methods

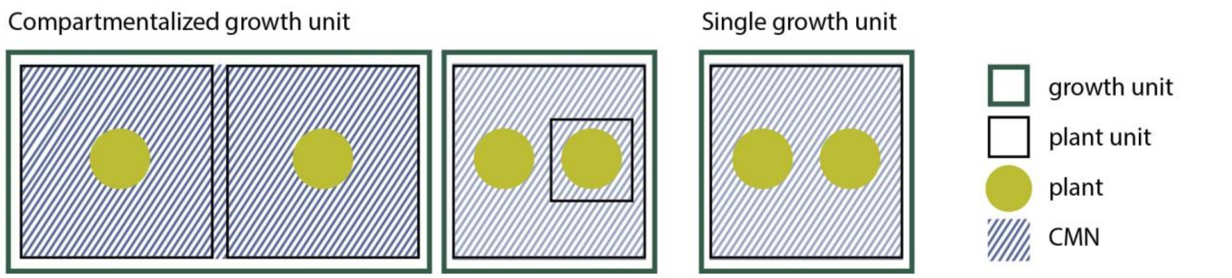
2.1 Search string development

As a first step, we searched the literature with a preliminary topic search in Web of Science Core Collection with default settings on January 2023 and retrieved 385 articles: TS = (("common" OR "shared") AND ("mycel*" OR "*mycorrhiz*") AND "network*").
Second, we modified the search string from Karst et al. (2023) to build an additional search string: TS = (("common mycorrhiza*" or "mycorrhiza*" or "common ectomycorrhiza*" or "common arbuscular"or "common mycel*" or "common fung*" or "common hyph*") Near/5 ("network*" OR "connection*" OR "interconnection*")).
In June 2023 we ran both search strings (no 1. and 2) to collect articles and to update the preliminary search. We exported bibliometric data of these articles (author, title, year, publication journal, year and doi), and combined them with the preliminary search outcomes. After eliminating duplicates, we screened the 589 articles for matching our inclusion/exclusion criteria. First, studies needed to target the concept of CMNs by mentioning directly the term CMN or describe the phenomenon of plants interlinked by mycorrhizal fungi in title, abstract and/or introduction. Second, studies had to present at least one experiment with AM fungi or both AM fungi and ectomycorrhiza (e.g. in case of plant species forming both types of mycorrhiza) interlinking a minimum of two plants irrespective of the growth system or setting. The resulting 123 articles were used to build our database for the analyses (Figure S1). We followed the Roses guideline for systematic maps (Haddaway *et al.*, 2017).
To evaluate the proportion of CMN studies in the broad field of mycorrhiza research, we conducted an additional search in the Web of Science Core Collection with default settings in June 2023. We used the search string TS = (“mycorrhiza*”) to acquire article output per year on the general topic, irrespective of the type of mycorrhiza. Additionally, we refined the article collection via the Web of Science category “ecology” to get article outputs with specific assignment to the subject area of ecology. In combination with the outcomes of our search 1 and 2 representing the research output for common mycorrhizal studies, we were able to

estimate the contribution of CMN research to the general field of mycorrhiza and specifically in the field of ecology.

2.2 Terminology

We included different test systems in our database, which we categorize broadly into single and compartmentalized growth units. Compartmentalized growth units consist of multiple plant units which become interlinked by the mycorrhizal network (Figure 1). In contrast, single growth units (e.g. in a pot or field plot) contain all components of a CMN and are characterized by a lack of separators, barriers or any inserted compartments. Thus, single growth units consist of just one plant unit. A plant unit holds the test plant(s). It can be a compartment, pot or field plot. Plant units can hold one or multiple species and/or plant individuals. They can be rectangular or circular, with or without (mesh) barriers, static or rotatable and by this allow for interlinking of plants by a CMN within or across different plant units.



Compartmentalized growth unit	Single growth unit
Plants grow in compartments or pots which can be combined to form complex growth unit setups.	Plants grow together in pots or field plots
The plant units become interlinked by the mycorrhizal network. (When multiple plants per plant unit are present, then these also get interlinked within a plant unit.)	The plants within the growth unit become interlinked. The growth unit is the plant unit.
Apply different types of barriers or seperators (e.g. with or without mesh).	No application of seperators or barriers with in the growth unit.
A plant unit contains at least one plant and is connected with at least another plant unit.	A plant unit contains at least two plants.

Figure 1 Illustration of different growth units included in this database. Compartmentalized growth units contain at least two plant units interlinked by a CMN while single growth units include all the plants and the CMN which are not further linked to any additional compartments. The growth units are the experimental units to which the experimental treatments are applied. Experimental treatments can involve plant species, AM fungal species, barrier or separator types.

2.3 Screening and coding

We included data on study setting (lab or field experiment). Further, we gathered information on how the fungi interlinking the plants were controlled for (e.g. Was there an inoculum added to a sterile growth substrate? Was an inoculum added to a living background soil? Was there no inoculum but a whole soil community the origin of the interlinking fungi?). Following this, we assigned the experiments to either the CMN (common mycorrhizal networks) or CFN (common fungal networks) group. The CMN group includes only experiments in the absence of soil fungi other than the target AM fungi; this is achieved by sterilizing the growth substrate and adding an AM fungal inoculum. The CFN group includes experiments in which also other fungi were present in the test substrate (Rillig *et al.*, 2023).

We collected information on the test system to evaluate each experiment if, how and to what degree it fulfills the CMN criteria. First, more than one plant had to be connected. This criterion is fulfilled for all studies passing the initial screening. Second, all plants have to be mycorrhized. This criterion had two outcomes: all plants mycorrhized (e.g. separating two compartments with a mesh [1µm < mesh aperture < 51µm]) or application of a mycorrhiza effect treatment. Third, the roots of the interlinked plants have to be separated. This criterion had three possible outcomes: plant roots were not separated (e.g. plants grew together in one pot or plot), application of a root effect treatment (e.g. accomplished by using meshes with aperture bigger or smaller than 50µm, or solid barriers or no barriers at all) or plant roots were separated. Fourth, evaluation of the CMN effect. This criterion had two outcomes: no CMN was tested or a CMN treatment was applied (e.g. different mesh apertures or mechanically severing hyphal connections between growth units). Fifth, testing hyphal continuity between interlinked plants. This criterion had two outcomes: yes or no. In order to test for hyphal continuity, any resource transfer (e.g. nutrients, water) through hyphal, root or mass flow and solute diffusion (Haystead *et al.*, 1988) have to be excluded, which can be accomplished by e.g. air gaps and water-proofed but hyphae-penetrable membranes. It does not prove a continuous hyphal connection from one plant root system to another across separated growth units (Figueiredo *et al.*, 2021) but it comes closest.

We captured data on the AM fungal and plant species used in the experiments. For AM fungi, we compiled information on the species origin (e.g. Was a single species or species mixture of known composition used? Was a soil community used?) and the species name (http://www.amf-phylogeny.com/, 2023). For the test plants, we noted the species and number of individuals used per plant unit and growth unit (Figure 1).

Additionally, we gathered data on the measured response variables. We grouped the data in five categories: plant parameters (e.g. biomass, nutrient concentrations), fungal parameters (e.g. root colonization), resource transfer (e.g. transfer of water, C, N, P), microbial community (i.e. community composition metrics for soil fungi and/or bacteria) and ecosystem functions and processes (e.g. soil enzymes, respiration, soil aggregation, soil pH, CEC).

2.4 Analysis

Each article provided one study (data row) to the data table. We analyzed the overall diversity of CMN experiments and investigated in detail, if and how studies fulfilled the CMN criteria, which fungi and plants they used and what response variables were measured. The visual analysis and all produced figures were done in R (version 4.2.2) with the packages ggplot2 and ggpubr (R Core Team, 2022; Wickham, 2023).

3 Results

3.1 Designs

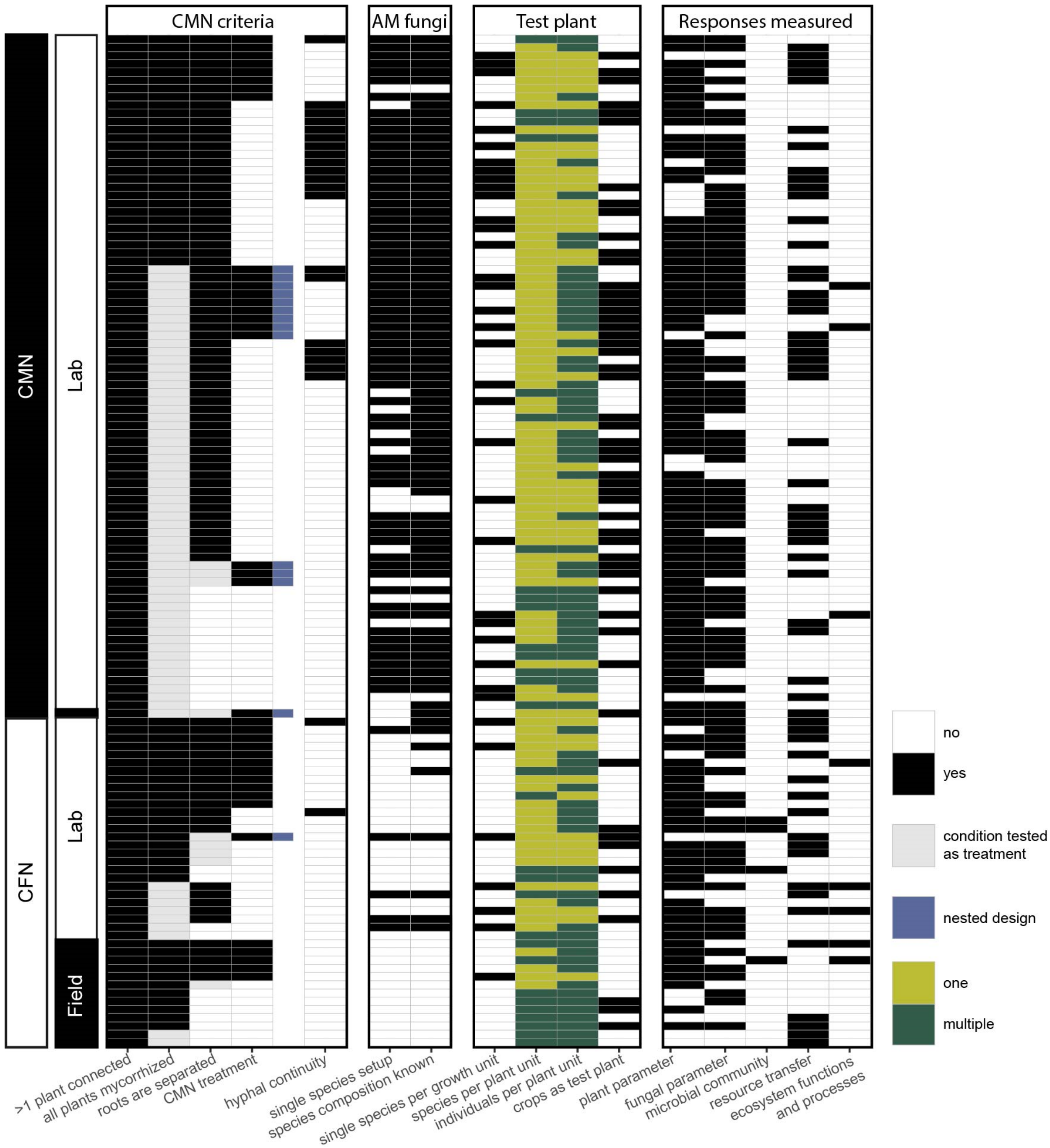


Figure 2 Overview of study designs, AM fungi and plant hosts tested and response variables measured in the data base. Studies were performed in the field or under controlled lab conditions (also including in vitro studies), testing either controlled AM fungal networks in sterilized substrates excluding non-mycorrhizal fungi (CMN) or AM fungal networks including non-mycorrhizal fungi (CFN). The five major CMN criteria are presented (at least two plants are connected by a mycorrhizal network, all plants are mycorrhized, all plant roots were separated, a CMN effect was tested and hyphal continuity was tested). Experiments with nested designs were indicated by color (e.g. a mycorrhizal network treatment nested

within an AM fungal treatment means that the subgroup of AM fungal treatment fulfills the criteria of connected plants to be mycorrhized). AM fungal parameters comprise single or multi species setups, with indication if species composition (AM fungal species names) was known (yes or no). Plant parameters include single or multi species setups (one or multiple species per growth unit) with indication how many species and individuals were grown in a plant unit and if tested plants were crops or not. Response variables comprise plant and fungal parameters, resource transfer (e.g. C, N, P, water), community composition and ecosystem functions and processes (e.g. soil respiration, soil aggregation, soil enzyme activity). The heatmap indicates presence (filled tiles), absence (white tiles) or application of a treatment (gray tiles; i.e. condition is tested when being absent and present) of specific data. For explanation of colors see figure legend.

Of the overall 123 analyzed studies, 109 studies were conducted under controlled environmental conditions in the greenhouse or climate chambers (Figure 2); of these, 13 studies were done using *in vitro* systems (e.g. petri dishes filled with agar medium). Overall, the majority of studies (83 of 123) worked with mycorrhizal networks excluding any other fungi. These studies were all lab studies with one exception: Ingraffia *et al.* (2021) used mesocosms placed outside to test for arbuscular mycorrhiza, root and CMN effects under field conditions. Studies testing CFNs by not controlling for the exclusion of non-mycorrhizal fungi, were done in 14 cases in the field and 28 cases in the lab.

Considering the CMN criteria, we found that across all settings 64 cases applied a (AM) fungal treatment while in 59 cases all test plants were colonized by (AM) fungi in the growth substrate (Figure 2). The roots of interlinked plants were kept separated in 88 cases, while in 26 cases roots intermingled. In 9 studies a root effect treatment was applied. A CMN treatment was only realized in 38 of 123 studies. In 14 studies, either the root, the mycorrhiza or both effects were tested additionally as treatments beside the CMN effect treatment (these cases are highlighted in Figure 2 as “nested designs"). Irrespective of any CMN criteria, in 22 studies across all settings, air gaps and water-proofed membranes were used to suppress the passive mass flow through the soil-water interface.

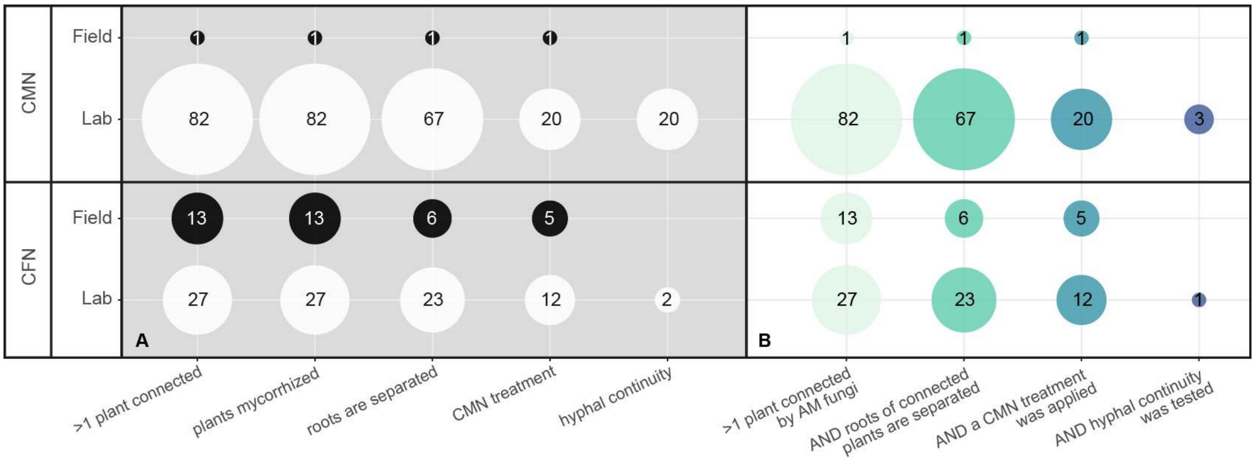


Figure 3 Balloon graph showing cases of occurrence of (A) CMN criteria (more than one plant is connected by the CMN, all plants are mycorrhized, the roots of the connected plants are separated, there is a CMN treatment tested, hyphal continuity is tested) for the two types of CMNs (controlled AM fungal networks in sterilized substrates excluding non-mycorrhizal fungi (CMN) or AM fungal networks including non-mycorrhizal fungi (CFN)) separated for field and lab studies. In (B) cases of occurrence for studies fulfilling the 1 to 4 CMN criteria are shown. For each CMN criterion, cases of “yes” and “treatment” were counted. The balloons represent frequency of occurrence for each category represented by their size; exact study numbers are given as balloon overlays.

By further investigating the CMN criteria, we found that despite the setting or the CMN type established, some criteria are more often fulfilled than others (Figure 3). When considering each criterion in isolation, the root separation, the application of a CMN treatment or test for hyphal continuity are the limiting factors (Figure 3A). When examining how many studies can fulfill an increasing number of CMN criteria, the numbers of articles drop drastically. For lab studies with controlled AM fungal networks, only 20 of 82 articles present experiments with at least two mycorrhized plants interlinked while their root systems are separated, plus a CMN treatment was applied to test for the CMN effect. Only 3 of these 82 articles test for hyphal continuity (Figure 3B). For studies testing CFNs, a similar pattern can be found.

3.2 AM fungi

Overall, 72 of the 123 studies used single AM fungal species, while 53 cases tested species assemblages or natural communities in their experiments (Figure 2). Experiments focusing on AM fungi excluding other non-mycorrhizal fungi, applied in 67 cases single species and in 16 cases species assemblages. In studies including other non-mycorrhizal fungi, 5 articles presented data on single species and 35 on assemblages and natural communities.

Single AM fungal species were only tested in lab studies. Assemblages and natural communities were used in 14 field and 37 lab studies, respectively.

Of the 123 studies, 84 reported the names of the AM fungal species used; these studies were all on single species and species assemblages conducted in the lab with the exception of the study by Ingraffia *et al.* (2021) which was done under field conditions. For studies excluding other non-mycorrhizal fungi, 76 studies reported information on the applied species and 7 did not. For studies including other non-mycorrhizal fungi, 8 cases presented data on species names and 32 did not.

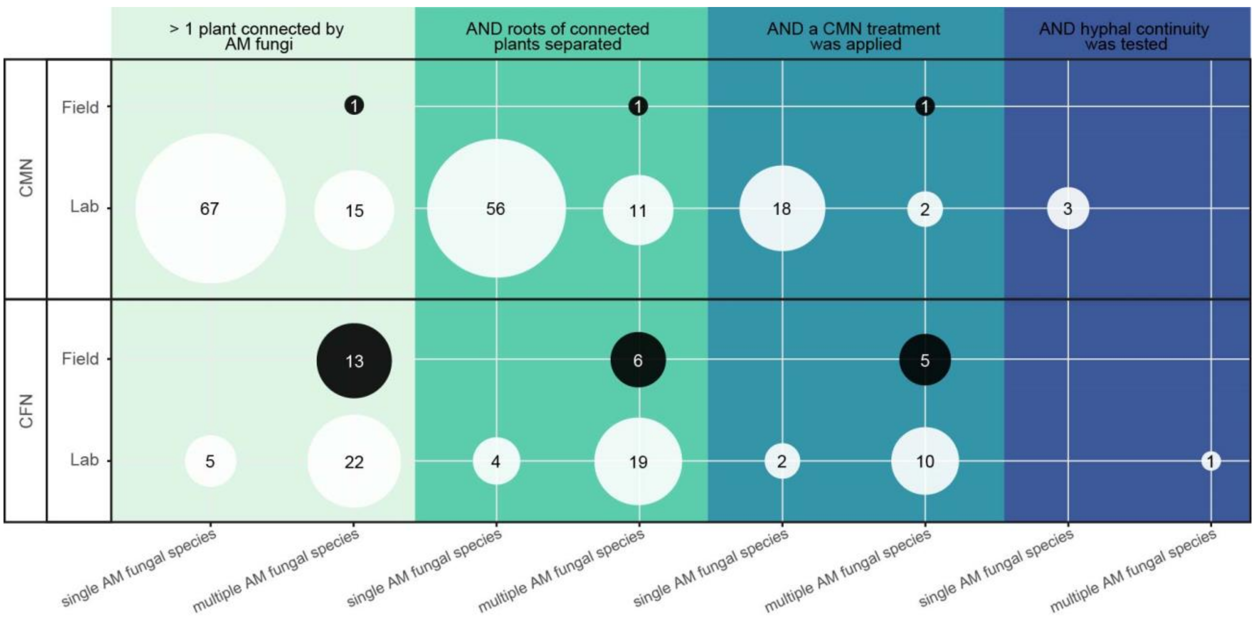


Figure 4 Balloon graph depicting cases of occurrence of single (single species/strains) or multiple AM fungal species (AM fungal assemblages, and natural communities) setups for studies fulfilling the different CMN criteria (more than one plant is connected by the CMN, all plants are mycorrhized, the roots of the connected plants are separated, there is a CMN treatment tested, hyphal continuity is tested) for the two types of CMNs (controlled AM fungal networks in sterilized substrates excluding non-mycorrhizal fungi (CMN) or AM fungal networks including non-mycorrhizal fungi (CFN)) separated for field and lab studies. For each CMN criterion, cases of "yes" and "treatment" were counted. The balloons represent frequency of occurrence for each category represented by their size; exact study numbers are given as balloon overlays.

When evaluating the AM fungal species tested in the context of the CMN criteria, we found that with an increasing number of fulfilled criteria the majority of studies worked on singles species (Figure 4). This holds true for the test of the CMN and hyphal continuity. For field setting, no data on single species experiments are available.

In the articles included in our database, 23 different AM fungal species were used (Figure S2). They derived from the orders Archaeosporales, Diversisporales, Entrophosporales, Glomerales and Paraglomerales. The dominant AM fungal species in the database are from the order Glomerales: *Funneliformis mosseae*, *Rhizophagus intraradices* and *Rhizophagus irregularis*. However, studies testing the criteria of CMN and hyphal continuity used 14 and 7 different species/strains, respectively.

3.3. Test plants

The test plants covered a broad variety of species of trees, shrubs, herbs and grasses (see species list in SUPPS), with an agricultural context in 53 studies. The experiments varied in plant species diversity per growth unit (Figure 2). 37 of 123 studies conducted their experiments on one plant species, while in 86 cases multiple plant species were tested. This pattern was consistent when grouping studies into CMN (30 single, 53 multi-species cases) or CFN (7 single, 33 multi-species cases) but also lab (36 single, 73 multi-species cases) and field studies (1 single, 13 multi-species cases). The majority of studies used one plant species per plant unit (93 single, 30 multi-species cases). We found similar proportions for CMN (68 single, 15 multi-species cases) and CFN (25 single, 15 multi-species cases) studies and lab (88 single, 21 multi-species cases) and field (5 single, 9 multi-species cases) experiments.

The number of individual plants, irrespective of the species, varied across the studies. In general, there are cases with a single or multiple individuals per plant unit, representing low and high density. High density plant setups were justified with the main rationale to boost CMN establishment by providing more potential hosts. 48 of 123 studies tested one individual plant in a plant unit. Again, similar patterns were found for CMN (35 single, 48 multi-individuals cases) and CFN (13 single, 27 multi-individuals cases) studies and lab (46 single, 63 multi-individuals cases) and field (2 single, 12 multi-individuals cases) experiments.

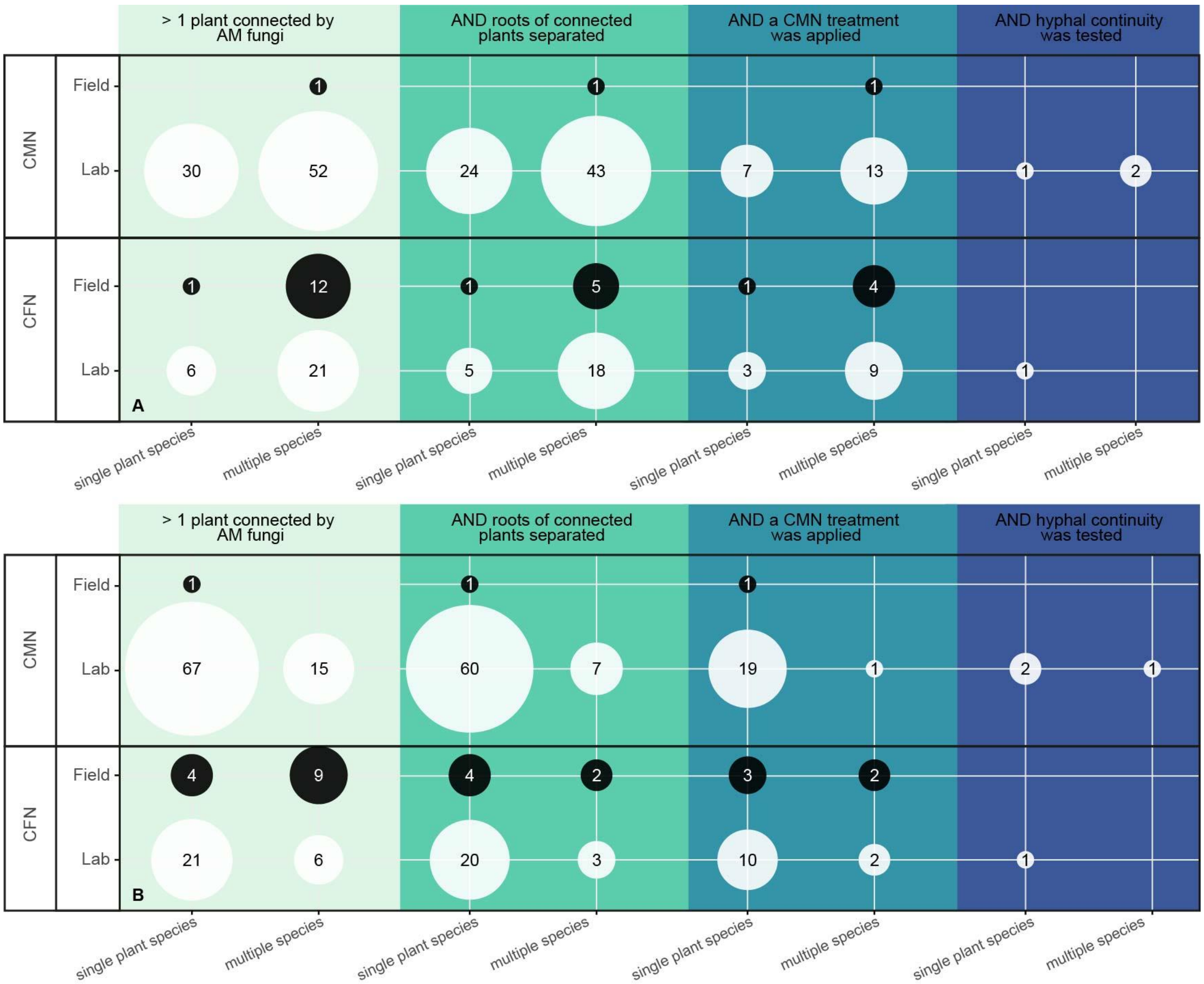


Figure 5 Balloon graph depicting cases of occurrence of single or multiple plant species setup for studies fulfilling the different CMN criteria (more than one plant is connected by the CMN, all plants are mycorrhized, the roots of the connected plants are separated, there is a CMN treatment tested, hyphal continuity is tested) for the two types of CMNs (controlled AM fungal networks in sterilized substrates excluding non-mycorrhizal fungi (CMN) or AM fungal networks including non-mycorrhizal fungi (CFN)) separated for field and lab studies. In (A) the plant species diversity per growth unit and in (B) per plant unit is depicted. The balloons represent frequency of occurrence for each category represented by their size; exact study numbers are given as balloon overlays.

Across the different CMN criteria, a comparable number of cases for single and multiple plant species tested in the growth and plant units can be found for the test of CMN and hyphal continuity (Figure 5). For studies fulfilling the first 3 criteria, we found that multiple species per growth unit but single species per plant unit are the preferred setup type.

3.4. Response variables

CMN studies investigated a wide range of response variables with the majority of studies focusing on plant (103 of 123 articles) and fungal (87 of 123 articles) parameters and also resource transfer (56 of 123 articles). Reports on CMN effects on microbial community composition (4 of 123 articles) or ecosystem functions and processes (8 of 123 cases) were scarce (Figure 2).

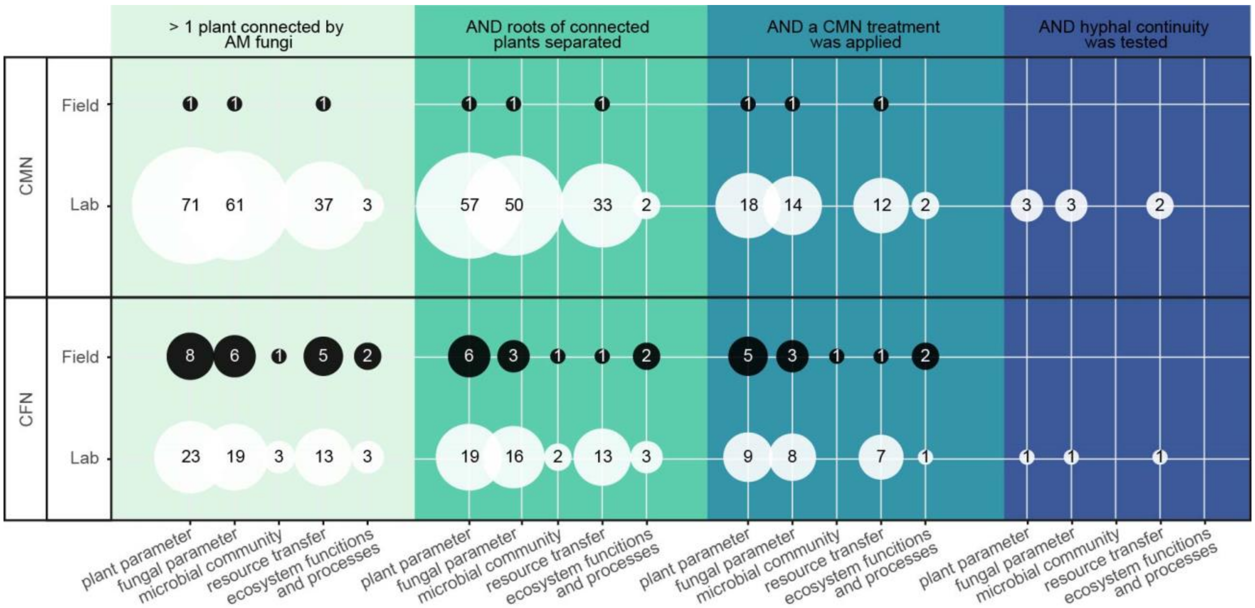


Figure 6 Balloon graph showing cases of occurrence of response variable categories (plant and fungal parameters, resource transfer, microbial community and ecosystem functions and processes) for studies fulfilling the different CMN criteria. Data is presented separately for lab and field studies and the two types of CMNs (controlled AM networks in sterilized substrates [CMN] vs. diverse fungal species networks including AM fungal species [CFN]). The balloons represent frequency of occurrence for each category represented by their size; exact study numbers are given as balloon overlays. One study can contribute to multiple response variable categories.

With regard to the CMN criteria, studies using the basic design of a minimum of two plants interconnected by mycorrhizal fungi present data from all five response variable categories (Figure 6). Only studies controlling for a pure AM fungal network do not test for microbial community composition due to the substrate sterilization steps. With increasing numbers of CMN criteria, articles reporting on microbial community effects or ecosystem functions and processes strongly decline.

3.5 Trends over time

In the years 1945 till 2023, 32722 articles were available in the general field of mycorrhizal research, and 4465 articles in the specific field of mycorrhiza in the Web of Science subject category “ecology”. When focusing only on common mycorrhizal network studies by using our search strings (see methods), we found 589 articles. Thus, CMN research represents 1.8% or 13.2% of the whole mycorrhiza or ecology-specific related research publications, respectively (Figure 7).

In general, the publication number for the overall topic of CMN (including actual CFN systems) is increasing (Figure 7). When considering the different CMN criteria, we found that the testing of CMN as a treatment with consideration of the hyphal continuity additionally to the basic criteria (more than one plant is connected by the CMN, while all plants are mycorrhized and their roots are separated) occurred after 2010.

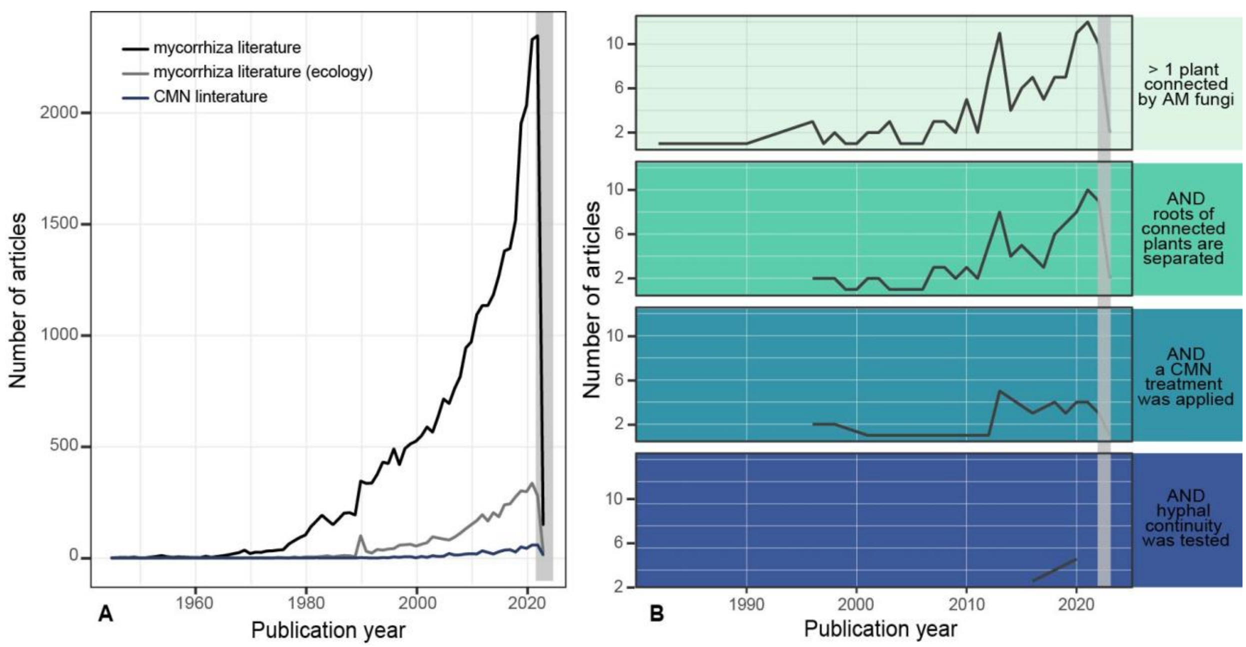


Figure 7 (A) Number of articles published for the general topic “mycorrhiza” (black line), for the Web of Science subject category “ecology” (gray line) and the specific topic “common mycorrhizal networks” (blue line). Data derived from Web of Science Core collection from January 2023. The mycorrhiza search output includes studies on all types of mycorrhiza, while the CMN search output comprises only ecto- and arbuscular mycorrhiza. (B) Number of cases for the different CMN criteria (at least two plants are connected by the CMN, all plants are mycorrhized, the roots of the connected plants are separated, there is a CMN treatment tested, hyphal continuity is tested) across publication years covered with our database.

The gray area covers the year 2022 to 2023. At the time of the search these years were not yet complete.

4 Discussion

Our analyses revealed a broad spectrum of test systems united under the umbrella of "common mycorrhizal networks". We identified research gaps and preferred experimental setups affecting the CMN evidence base. Based on these findings, we formulate recommendations for future research efforts in the field of CMN.

The biggest challenge in CMN research is the strict CMN definition and its interpretation in experiments. All articles passing the first screening step in our systematic mapping looked at the concept "common mycorrhizal network"; i.e. a mycorrhizal hyphal network interacting with at least two plants. The screening of the potential matching articles and parametrization of their experimental components (e.g. growth system, fungi, plants) showed a wide spectrum of growth systems and plant-fungal configurations: growth units which contained the network-forming fungi and one plant (which is not a CMN by definition, thus these articles were excluded from the final database), growth units comprising a minimum of two plants (the growth unit is the plant unit, see Figure 1), and a variety (in terms of numbers, shapes, size and barrier systems) of compartmented systems with and without air gaps between the individual plant units. Additionally, the articles could be grouped into studies testing CMNs formed exclusively by mycorrhizal fungi and those actually testing a CFN (i.e. beside mycorrhizal fungi other filamentous fungi potentially capable of forming common fungal networks were present (see Rillig *et al.*, 2023)). All these different experimental systems can be found when reading the CMN literature (Figure 2), although the CMN definition describes a very clear configuration: the roots of a minimum of two plants (of the same or different species) are connected (linked and colonized) by at least one mycorrhizal fungal genet (or multiple genets each linking and colonizing at least two plants) and the connection has to be continuous in terms of cytoplasmic flow across the network (Horton, 2015; Karst *et al.*, 2023).
This definition indeed postulates a strict and definite set of criteria that have to be fulfilled in order for an experiment to give unequivocal evidence on CMN effects (e.g. C, N or P transfer from one plant unit to another via the connecting mycorrhizal hyphae).

Meeting all these criteria comes with enormous challenges in mechanistically dissecting the role of CMNs, as recently summarized with a focus on ectomycorrhiza (Karst *et al.*, 2023), but which applies similarly for AM. There is a clear progression of mechanistic resolution from CFN to

CMN (the way we define it here) and to CMN with hyphal cytoplasmic continuity, with each step necessitating increasingly difficult methods and experimental setups (e.g. plants and connecting fungi in one plant unit vs. compartmentalized growth units with air gaps; testing of whole microbial soil community vs. defined AM fungal strains or assemblages). We clearly show here that a decreasing number of papers meet the most stringent challenges to show a CMN with hyphal cytoplasmic continuity (Figure 3). In fact, the number of papers precipitously drops such that only a handful of papers fulfill the strictest criterion with strong impacts on the extent and information content of the CMN evidence base.

For a strong evidence base on the functioning and ecological impact of CMNs, we need to dissect the mechanisms to the level of showing that hyphal continuity is responsible for any observed effects, which is a necessity for certain questions (e.g. questions centering around the bidirectional nutrient transfer within the CMN), but not for others (e.g. passive transport of water or microbes along hyphal surfaces to close proximity of receiver plant roots).
From our database, we found that studies on pathogenic infection induced signaling (Alaux *et al.*, 2020) and nutrient competition (for shaded vs non-shaded plants by Weremijewicz *et al.* (2016); and between invasive and native plants by Xia *et al.* (2020) and Shen *et al*. (2020)) were capable of fulfilling all CMN criteria (Figure 3). These studies were all done in the lab with one study testing a CFN and the other three a CMN and measuring plant and fungal parameters and resource transfer variables (Figure 6). The limited number of articles passing all CMN criteria highlights that more studies with such mechanistic resolution are needed to achieve critical levels of experimental evidence to come to generalizable conclusions for direct CMN functions (i.e. CMN-mediated effects with evident cytoplasmic hyphal continuity, e.g. for the testing of C, N and/or P transfer within a CMN (see Rillig *et al.*, 2023)).

4.1. Recommendations for improvement of the CMN evidence base

Of the 123 articles included in our database, only four met all CMN criteria. But this does not mean that the remaining studies are incorrect or of low value. On the contrary, there are particular research questions that do not require proof of hyphal continuity, for example. Such indirect CMN-mediated effects occur without a continuous cytoplasmic hyphal link between plant roots but still have measurable, physiological effects on the interlinked plants. For example, the transport of bacteria (de Novais *et al.*, 2020) or infochemicals (Barto *et al.*, 2011) across the hyphal networks is a phenomenon that manifests even without cytoplasmic continuity between connected plant roots as long as hyphae of the network are in close proximity to the receiver root system. The intent to meet all CMN criteria irrespective if this is even necessary for testing the targeted hypothesis and disentangling all effects under question could overload an experimental design with severe side effects. Setting up experiments capturing CMNs with hyphal continuity can be laborious, logistically and financially demanding. This could have the following consequences: (1) The decision to keep the sample size low, which affects the statistical power of the study; low statistical power is a well-known issue in the ecological field of research (Deressa *et al.*, 2023; Kimmel *et al.*, 2023). As a consequence, low statistical power aggravates the detection of small effects causing potentially informative and valuable studies to never be published due to lack of significant effects (file-drawer problem). Also, low-power studies are vulnerable to type M and S errors. Thus, low power studies can severely affect the CMN evidence base. (2) Avoidance of experimental designs with additional treatments, like stressors for the test plants and/or fungi, modulating CMN-mediated effects. These studies do exist but their numbers are low (e.g. Wilson *et al.*, 2006; Workman & Cruzan, 2016; Burke *et al.*, 2018; He *et al.*, 2022) limiting the CMN evidence base and our capability to draw general conclusions for potential CMN-mediated benefits against plant- or fungi-targeted stressors.

To strengthen the CMN evidence base with new research insights and robust data, we offer the following two recommendations:(1) Consider carefully which CMN criteria have to be fulfilled in order to answer the research question under study; for example, is a direct or an indirect effect in focus and thus is testing for hyphal continuity necessary. For some questions it is important to show hyphal continuity in a CMN, whereas for others it may be fine to work with CFN: this just needs to be stated clearly upfront. (2) Report all necessary details on the test system, including information on the growth and plant unit, test plants and fungal species and the experimental design. Along the same lines, we recommend illustrations of the test system and designs to improve communication of complex growth and/or pant unit designs (see for example: Weremijewicz *et al.*, 2016; Milkereit *et al.*, 2018; Shen *et al.*, 2020).

4.2. In-depth evaluation of the CMN evidence base

Beside the strong constraint presented by only a few studies fulfilling the most stringent CMN criteria, we detected further imbalances in our database. First, there is a clear difference in the number of field vs. laboratory studies. This is not unexpected because of the given challenges for experimental setups. There are no field studies that fulfilled all 5 CMN criteria. It is noteworthy that these studies may exist for common ectomycorrhizal networks (see Karst *et al.*, 2023), but here we focus on arbuscular mycorrhizas. Additionally, only one field study did test a

CMN in the actual sense (Ingraffia *et al.*, 2021). In the other studies the networks are formed by CFNs; this is unavoidable when conducting field experiments as no field site can be adequately sterilized to reduce other filamentous fungi potentially capable of forming CFNs while successfully reinoculating the soil and plants with a defined AM fungal species or assemblage. Thus, the CMN evidence base is dominated by studies conducted under controlled environmental conditions while field studies are underrepresented.

Second, the study focus shifted over the years (Figure 7). We found that CMNs (criterion 1 to 4 fulfilled) have been conducted since the 1990s. Testing the hyphal continuity criterion, on the other hand, is a new aspect appearing only after 2010. Beside the experimental challenges, this time lag explains the low number of articles contributing to our knowledge about hyphal continuity effects. The time lag is a consequence of the increasing mechanistically knowledge about the functioning of CMNs gained over time and the resultant necessity to control for additional underlying, confounding effects (Warren *et al.*, 2008).

Third, we find that single AMF species are preferably used in CMN studies, while in CFN studies, whole communities and more rarely addition of defined AM fungal assemblages or single species to a full microbial background were applied. Although a broad variety of strains was used across the database, the majority of studies worked with *Funneliformis mosseae*, *Rhizophagus intraradices* and *Rhizophagus irregularis*; thus the evidence base for CMN builds strongly on strains of the family *Glomeraceae*. The frequent use of these strains is unsurprising as these are, in general, popular strains in AM fungal research (Koricheva *et al.*, 2009; Leifheit *et al.*, 2014; Augé *et al.*, 2015). Only few studies in our dataset compared the influence of single and multiple AM fungal species on plants connected via a CMN (Püschel *et al.*, 2007; Derelle *et al.*, 2015). The abundance and diversity of the interlinking genets is an understudied aspect of CMN research. Studies testing CMNs (up to 4 fulfilled criteria) with different AM fungal species are scarce (Peng *et al.*, 2013; Awaydul *et al.*, 2019; Qiao *et al.*, 2020). Thus, there is a clear knowledge gap centering around the abundance and diversity of CMN edges (mycorrhizal fungal genets).

Fourth, we find that in CMN studies multiple plant species per growth unit are primarily tested but within a plant unit monocultures are preferred. Multiple plant individuals per plant unit are the preferred set-up across the database. With regards to the test plants, the CMN evidence is broadly supported. There is no focus on specific plant species or families, and setups with multiple plant species per growth unit are more common than monocultures. This is potentially caused by the research interest in studies investigation plant invasion (Shen *et al.*, 2020; Xia *et al.*, 2020), performance of seedlings connected to con- or heterospecific nurse plants (e.g.

Burke *et al.*, 2018) or nutritional competition (e.g. Milkereit *et al.*, 2018) under the influence of CMNs. Studies investigating the effect of the abundance and diversity of the connected plant species (CMN nodes) are more uncommon (e.g. Heinemeyer *et al.*, 2012; Li *et al.*, 2023). This knowledge gap aligns with the limited research on the abundance and diversity of the CMN edges (AM fungal genets). Thus, exploring the complexity of a CMN in terms of its nodes and edges clearly represents an open research opportunity.

Fifth, our systematic mapping revealed that plant, fungal and resource transfer measurements are the dominant response variables in CMN research articles, while studies targeting community (e.g. Mickan *et al.*, 2021; Fernández *et al.*, 2022) and ecosystem function and process responses (e.g. Muneer *et al.*, 2020; Li *et al.*, 2023) are scarce. The evidence base is well supported for the plant and fungal performance but the impact of CMNs on microbial communities and ecosystem functions and properties (e.g. decomposition or soil aggregation) and vice versa is understudied. Thus, researching the role of CMN in driving soil functions and processes is a promising focus of future work.

5 Conclusions

Our systematic mapping of the CMN literature highlighted that in general, the publication numbers focusing on the research field of CMNs and those contributing to our database are relatively low compared to the research field of “mycorrhiza”. Just 1.8% of the mycorrhizal literature (irrespective of the mycorrhiza type) addressed the concept of CMN, making it a ‘niche topic’ in mycorrhizal research (Figure 7). There is a large public interest in common mycorrhizal networks (Karst *et al.*, 2023), and given this fascination of the public with this topic it is surprising that the total number of papers is a relatively small percentage of papers on mycorrhizas. The conclusion from this is that given this interest and the potential significance of this topic, there needs to be a greater research effort dedicated to unraveling the functioning of CMN. Our systematic mapping exercise reveals an overall relatively small number of studies on CMNs formed by AM fungi, with the number of studies meeting the criteria of the highest degree of mechanistic resolution dropping off sharply. This leaves us with a comparatively thin evidence base from which to draw strong conclusions about the effects and interactions of CMN - which is surprising given the general perception of a central importance of CMN for the ecology of AM. We thus call for a renewed research effort on CMN, focusing on a whole range of levels of mechanistic resolution (from CFN to CMN with and without hyphal continuity), and to also include neglected experimental situations, such as field studies in general, as well as soil microbial community or ecosystem-level responses.

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Competing interests

None declared.

Author contributions

AL conducted the systematic mapping, analyses and wrote the first draft. MCR and AL contributed to the writing of the manuscript.

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Supplementary Material

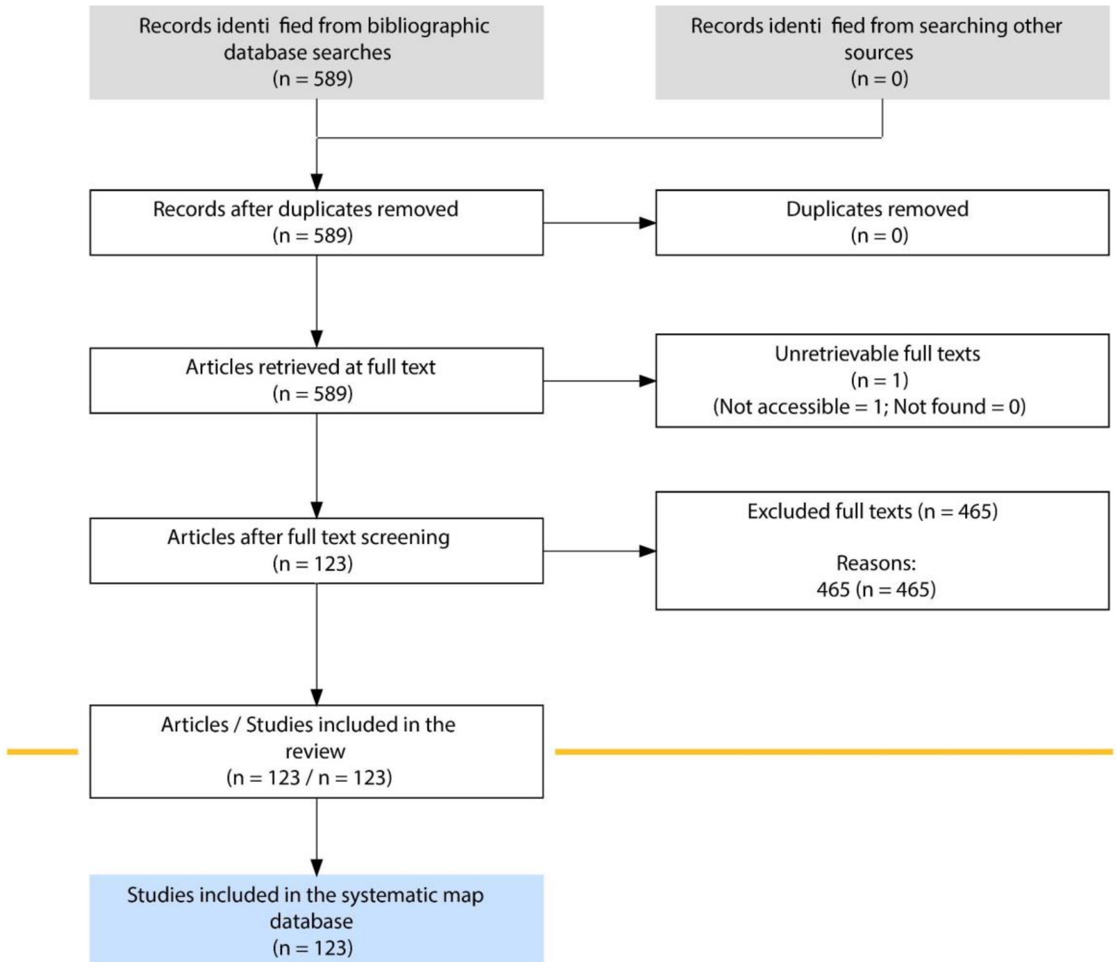

Figure S1. Roses flow diagram (https://estech.shinyapps.io/roses_flowchart/). The two major filtering exclusion criteria were the concept of CMN and the reporting of an experiment. Of the 589 articles, 139 were opinion, review, documentary paper or observational studies.

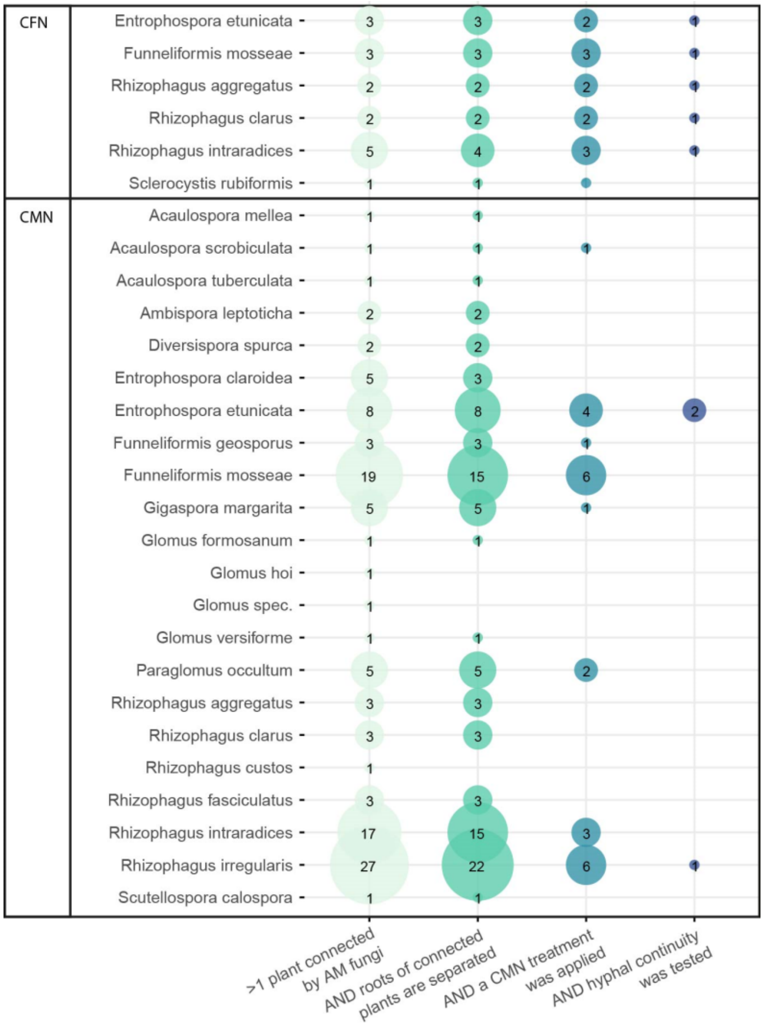

Figure S2 Balloon graph on cases of occurrence of AM fungal species used in CMN experiments for studies fulfilling the different CMN criteria (more than 1 plant is connected by the CMN, all plants are mycorrhized, the roots of the connected plants are separated, there is a CMN treatment tested, hyphal continuity is tested) for the two types of CMNs (controlled AM fungal networks in sterilized substrates excluding non-mycorrhizal fungi (CMN) or AM fungal networks including non-mycorrhizal fungi (CFN)) separated for field and lab studies. Species names were sorted by family and alphabet.
One study can contribute multiple AM fungal species counts to the analyses. The balloons represent frequency of occurrence for each category represented by their size; exact study numbers are given as balloon overlays.

Table S1 Plant species used as hosts in CMN experiments in studies included in our database

Species name	Species name	Species name
Achillea millefolium	Ceratopetalum apetalum	Festuca idahoensis
Allium ampeloprasum	Cicer arietinum	Festuca ovina
Allium cepa	Cichorium intybus	Festuca pratensis
Ambrosia artemisiifolia	Cinnamomum camphora	Flaveria bidentis
Andropogon gerardii	Cirsium oleraceum	Gaillardia aristata
Antennaria dioica	Cirsium purpuratum	Geranium molle
Anthoxanthum odoratum	Citrullus lanatus	Gliricidia sepium
Arisaema triphyllum	Citrus aurantium	Glycine max
Artemisia annua	Citrus jambhiri	Guarea guidonia
Artemisia ludoviciana	Citrus natsudaidai	Guazuma ulmifolia
Bastardiopsis densiflora	Citrus trifoliata	Helianthus annuus
Aster ericoides	Cleistogene squarrosa	Hevea brasiliensis
Atriplex sagittata	Clematis stans	Hieracium caespitosum
Banksia menziesii	Coix lachryrma-jobi	Hierarcium pilosella
Betula pendula	Crepis capillaris	Holcus lanatus
Bidens pilosa	Crotalaria retusa	Hordeum vulgare
Brachypodium sylvaticum	Cucumis sativus	Inga edulis
Bromus hordeaceus	Cynodon dactylon	Inula conyzae
Bromus erectus	Daucus carota	Jatropha curcas
Bromus hordeaceus	Dichantium aristatum	Keckiella antirrhinoides
Bromus madritensis	Echinops sphaerocephalus	Koeleria cristata
Bromus vulgaris	Eclipta prostrata	Kummerowa striata
Broussonetia papyrifera	Eleusine coracana	Lactuca sativa
Cajanus cajan	Elymus canadensis	Leymus chinensis
Calamagrostis epigejos	Elymus nutans	Linum usitatissimum
Campanula rotundifolia	Elymus sibiricus	Lolium multiflorum
Capsicum annuum	Eriogonum fasciculatum	Lolium perenne
Carica papaya	Eucalyptus marginata	Lycopersicon esculentum
Ceiba pentandra	Eucalyptus tetrodonta	Madia gracilis
Celosia cristata	Eupatorium adenophorum	Maianthemum racemosum
Centaurea maculosa	Festuca rubra	Marrubium vulgare

Medicago truncatula	Quercus agrifolia	Trichilia casaretti
Melaleuca preissiana	Raphanus sativus	Trifolium microcephalum
Melaleuca preissianaSchauer	Retama sphaerocarpa	Trifolium pratense
Nassella pulchra	Salvia mellifera	Trifolium repens
Nicotiana attenuata	Sanicula bipinnata	Trifolium subterraneum
Oryza sativa	Setaria italica	Tripleurospermum inodorum
Panicum bisulcatum	Setaria viridis	Triticum aestivum
Panicum clandestinum	Sibbaldia procumbens	Triticum durum
Panicum maximum	Silene vulgaris	Triticum turgidum
Paspalum notatum	Solanum lycopersicum	Urochloa brizantha
Pennisetum glaucum	Solanum tuberosum	Urochloa decumbens
Phleum pratenseand	Solidago canadensis	Vachellia seyal
Pinguicula grandiflora	Solidago virgaurea	Verticordia nitens
Pisum sativum	Sorghastrum nutans	Vicia faba
Plantago lanceolata	Sorghum × drummondii	Vigna unguiculata
Plantago media	Sorghum bicolor	Vulpia myuros
Poa pratensis	Sporobolus robustus	Zea mays
Populus trichocarpa	Tagetes tenuifolia	
Pseudoroegneria spicata	Theobroma cacao	