nature ecology & evolution

Perspective

https://doi.org/10.1038/s41559-023-01986-1

Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests

Received: 18 August 2022

Accepted: 6 January 2023

Published online: 13 February 2023

Check for updates

Justine Karst [1] ✉, Melanie D. Jones [2] & Jason D. Hoeksema [3]

A common mycorrhizal network (CMN) is formed when mycorrhizal fungal hyphae connect the roots of multiple plants of the same or different species belowground. Recently, CMNs have captured the interest of broad audiences, especially with respect to forest function and management. We are concerned, however, that recent claims in the popular media about CMNs in forests are disconnected from evidence, and that bias towards citing positive effects of CMNs has developed in the scientific literature. We first evaluated the evidence supporting three common claims. The claims that CMNs are widespread in forests and that resources are transferred through CMNs to increase seedling performance are insufficiently supported because results from field studies vary too widely, have alternative explanations or are too limited to support generalizations. The claim that mature trees preferentially send resources and defence signals to offspring through CMNs has no peer-reviewed, published evidence. We next examined how the results from CMN research are cited and found that unsupported claims have doubled in the past 25 years; a bias towards citing positive effects may obscure our understanding of the structure and function of CMNs in forests. We conclude that knowledge on CMNs is presently too sparse and unsettled to inform forest management.

Mycorrhizal fungi are important mutualists of many plant species. The functional relevance of common mycorrhizal networks (CMNs), however, has been debated for decades. Beyond the scientific interest in this topic, the idea that trees benefit from being connected belowground by mycorrhizal fungal hyphae has taken hold in popular media. Recently, CMNs—usually with the popularized moniker the wood-wide web—have appeared in high-profile books[1–3], newspapers[4,5], magazines[6,7], documentaries[8,9], films[10], TED talks[11], podcasts[12–14] and even television series[15,16]. Some of these media sources portray that trees, especially old and large ones, directly provide resources to other trees via these networks, and arguments are now being made to change forest management and policy based on this information[1,17–20]. Although popular and widespread, is there strong scientific evidence supporting these claims?

In this Perspective, we articulate the various ways that CMNs have been studied in forests and how they differ from other definitions of mycorrhizal networks (Box 1). Upon reviewing various sources of popular media (Supplementary Note 1), we identified three common claims: (1) CMNs are widespread in forests; (2) resources are transferred through CMNs, resulting in increased tree seedling performance; and (3) mature trees preferentially send resources and defence signals to offspring through CMNs. We systematically evaluated the published evidence to support these claims primarily from CMN studies in forests because field experiments are most relevant to making inferences on forest function, and because the role that adult trees play in forests can only be examined in the field. Seedling establishment in forests is a critical phase of plant fitness and forest dynamics, and thus an

[1]Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada. [2]Department of Biology, University of British Columbia, Kelowna, British Columbia, Canada. [3]Department of Biology, University of Mississippi, Oxford, MS, USA. ✉e-mail: karst@ualberta.ca

https://doi.org/10.1038/s41559-023-01986-1

BOX 1

Definitions of mycorrhizal networks

The word networks is commonly used in multiple ways by the research community with regard to mycorrhizal interactions. We recognize three specific usages of the term: (1) common mycorrhizal (or mycelial) networks; (2) bipartite mycorrhizal interaction networks; and (3) mycorrhizal networks.

Common mycorrhizal (or mycelial) networks. Common mycorrhizal (or mycelial) networks (CMNs) are physical, continuous linkages among the roots of at least two different individual plants, by the same genetic individual of mycorrhizal fungus. Such networks have the potential to mediate plant–plant interactions and plant performance via the transfer of molecules among plants and thus have been the main source of hypotheses and focus of experimental investigations testing those hypotheses since the origins of this field[22,49]. These phenomena (in particular their occurrence among trees) are the main focus of common claims in the popular media about mycorrhizal networks in forests—claims that we have found to be largely disconnected from evidence. As such, studies of CMNs in forests under this definition are the focus of our review, as we are responding to such claims.

Although arbuscular mycorrhizas and ectomycorrhizas differ in their structure and function[35,112], CMNs among trees in forests are potentially formed by either type. Field experiments have mostly focused on potential CMNs formed by ectomycorrhizal fungi, but relevant field experiments have also manipulated potential arbuscular mycorrhizal networks[60,67,68], and we have included these studies in our review. Moreover, arbuscular mycorrhizal and other types of fungi (for example, endophytic and pathogenic) may be present in the ectomycorrhizal-focused experiments and could potentially form common mycelial networks (a more general network definition that is sometimes used and also abbreviated as CMN).

Bipartite mycorrhizal interaction networks. Bipartite mycorrhizal interaction networks are defined based on lists of species of plants and fungi that do and do not interact with each other within a particular community. For example, Toju et al.[113] used next-generation sequencing of plant and fungal DNA from root samples in a temperate forest in Japan to define an interaction network among 37 plant species and 387 fungal operational taxonomic units. Under this definition, the nodes of the network are plant and fungal species and the linkages among nodes are instances of interaction between particular plant and fungal species, agnostic of whether plants are ever physically connected through the mycelium of fungi. As such, we do not evaluate such studies here.

Mycorrhizal network. Mycorrhizal networks are defined simply as the presence of web-like mycelial growth of mycorrhizal fungi attached to a single plant root system. It is well established that such associations with mycorrhizal fungi can be beneficial to the performance of plants, including forest trees[114]. We do not dispute the importance of mycorrhizas to plants. As such, we did not include studies in which CMN effects were explored by comparing the performance of seedlings near larger plants that were either mycorrhizal or not (for example, ref. [115]) because in these studies the effects of CMNs cannot be separated from fungal-mediated effects (that is, the effect of simply having been colonized by mycorrhizal or other fungi emanating from the larger tree).

important phase of growth to also study. We next examined how results from CMN research are interpreted and communicated by scientists, showing that many of the claims from earlier literature are incorrectly cited in subsequent literature. Finally, we end by offering suggestions on directions and approaches for the study of CMNs going forward.

Evaluating three popular claims about CMNs

CMNs are widespread in forests (claim 1)

Mycoheterotrophs—plants that acquire carbon from mycorrhizal fungi colonizing the roots of other plants—provide strong evidence that CMNs exist and transfer resources between plants in forests[21]. However, popular claims about CMNs in forests are centred on trees and tree seedlings; thus, this is where we focus our attention. As the roots of trees and seedlings intermingle closely, and many mycorrhizal fungi are host generalists, fungal links should be common[22]. Ectomycorrhizal fungal genets (that is, mycelia that originated from a single spore) can span metres[23–25]—a distance that is probably greater than that between intermingling roots. However, with current technology, it is difficult to confirm that continuous, non-transient mycelial connections exist between trees in the field[21,22,26,27]. To visually observe CMNs in situ necessarily fragments and destroys the network. In the absence of direct observations (but see ref. [28]), a number of methods have been used to infer CMN structure in forests. The strongest evidence for CMN structure—network size and partner connectivity—comes from genotyping fungal and plant DNA from mycorrhizal roots, then mapping fungal genets and their tree symbionts in forests[29–33]. Although genet mapping indicates only discrete fungal and plant locations, when conducted at fine scales, maps can provide strong evidence for a spatially continuous mycelium linking the roots of different trees in close proximity[31,32]. Despite its promise, genotyping trees and fungi is an intensive, arduous task, and as a consequence only five studies have been performed across two forest types[29–33]. That is, only two tree species of an estimated 73,300 worldwide[34] and only three ectomycorrhizal fungi have been mapped in relation to CMNs. Furthermore, the permanence of fungal connections is unknown. Hyphae and mycorrhizal roots turn over quickly[35] and are grazed[36,37]—processes that break connections. Even if an advancing genet connects roots, a disconnected mycorrhizal network emerges if, at the trailing edge, hyphal connections senesce or are fragmented, leaving behind isolated mycorrhizal roots. This resulting topology is not a CMN, yet is consistent with the results of CMN mapping, and has vastly different functional consequences.

In lieu of genotype mapping, other lines of evidence are often used to infer the presence and structure of CMNs, notably identifying ectomycorrhizas formed by the same fungal species on different trees[38–44]. In some cases, mycorrhizal root tips from different tree species are sampled in close proximity, making claims about the potential for CMNs plausible. However, the presence of shared species does not mean a genet is shared. Some species of ectomycorrhizal fungi form small, transient genets[45,46]; therefore, even though they are colonized by the same species, each tree could be colonized by a different genet of that fungus, meaning that a CMN did not exist. Furthermore, we stress that not all evidence is equal. By similarly weighing different lines of evidence as support for the presence of CMNs, we undermine strong evidence and simultaneously inflate weak evidence. This issue is concerning because it may exaggerate the frequency at which CMNs occur in forests. For example, CMNs have even been assumed to be

BOX 2

Results from laboratory studies on CMN structure and function

CMNs can be observed and manipulated under laboratory conditions. Non-mycorrhizal seedlings planted close to mycorrhizal seedlings in sterile substrates[90–92,116] will be colonized by hyphae that grow from the mycorrhizal seedling. If grown in a thin layer of substrate between transparent plates, autoradiography can be used to observe CMNs and the movement of radioactive elements between seedlings. Direct observations of ^{14}C moving >20 cm from one seedling to the roots of another[90–92] are still the best evidence for the movement of resources within a CMN formed by woody plant species. Similar approaches can be used for phosphorus[117], but are not practical for other resources (for example, N (extremely short half-life) and H_2O (beta particles with low energy)).

Resource transfer among tree seedlings can also be measured with stable isotopes, yet some confounding effects can obscure interpretation of these studies. Solid barriers prevent CMNs, but they also prevent the flow of soil solution[118]—a possible pathway for sizeable transfer of resources[85,119]. Resources moving in soil solution can be accounted for using <1-µm mesh or severing hyphae; when similar amounts of resources are transferred in the presence of a CMN compared with these controls[85,116,120], CMNs need not be invoked. For instance, in the single peer-reviewed greenhouse study testing kin effects, ^{13}C was transferred through the soil solution, not a CMN[85]. A similar result occurred in a non-peer-reviewed greenhouse study[101]. Moreover, simple hyphal extension may explain what has been interpreted as CMN-mediated interplant resource transfer. For instance, hyphae growing from a compartment with dry soil into one containing hydraulically lifted water could explain greater D_2O in receiver seedlings without invoking transport through a CMN[121]. Likewise, experiments that find greater resource transfer between two mycorrhizal seedlings than between two non-mycorrhizal seedlings[122,123] do not provide strong evidence of a role for CMNs.

The single peer-reviewed study that has addressed the phenomenon of signalling among forest tree species in response to insect damage was a greenhouse pot study[100]. Although Song et al.[100] found that access to potential CMNs increased carbon transfer to and upregulated defence enzymes by receiver seedlings after damage to donor seedlings, these effects disappeared when root interactions were allowed (the natural situation under which CMNs form). In another experiment that included both a control for movement of solutes through soil and a treatment where the roots of seedlings intermingled, the results were not consistent with CMNs stimulating seedling survival or growth[124]. Instead, survival was improved when the roots of two seedlings were in close contact, whereas survival tended to decrease when CMNs could have formed through hyphal contact only, or in soil solution control treatments[124]. Furthermore, seedling growth did not differ among the hyphal and root treatments[124]. Although we focus here on woody species, there is good evidence for CMN-mediated transport of defence signals in a well-controlled investigation on bean plants[125]. Regardless of whether root interactions were allowed, aphids were repelled relative to soil solution or severing controls.

In conclusion, autoradiography has definitively demonstrated movement of carbon from one tree seedling to the mycorrhizal roots of another via a CMN, but most other laboratory studies on resource transfer lack the full suite of controls required to interpret the results, and sometimes overlook ecologically relevant treatments, namely neighbouring roots. Moreover, pot studies necessarily use seedlings, not adult trees. Just as we would not assume that a drug effective in human cell lines is also effective in human bodies, we should not apply knowledge from pot studies without testing that the effects also occur in forests. Mature trees are not large seedlings, and forests may have emergent properties.

present wherever plants of the same mycorrhizal type occur together in a forest[47,48].

In summary, we find that support for this claim is limited, owing to the paucity of information on CMN structure, and especially dynamics, in the field. Adjacent roots are often colonized by the same species of mycorrhizal fungi, suggesting that fungal links should be common. However, too few forests have been mapped, and of those, only two studies demonstrate actual continuity of fungal links among trees[31,32]. Whether these links persist long enough to be functional is unknown.

Resources are transferred through CMNs and increase seedling performance (claim 2)

Although CMNs have been studied since the 1960s[49], the study by Simard et al.[50] was groundbreaking because it was the first replicated, controlled field study testing resource transfer. The results from this study have been interpreted as evidence that CMNs equalize resources within a plant community—a view that was a major departure from competitive frameworks[51]. Implicit in this view, and captured in this popular claim, is that fungi forming CMNs are physical extensions of roots (that is, passive conduits in which the direction of resource flow is determined by plants). This view conflicts with fungal behaviours involving purpose and intent[52] and overlooks that mycorrhizal fungi do not always benefit their plant partners. For example, ectomycorrhizal fungi can aggravate nitrogen limitation of their tree partners in boreal forests[53–55]. Despite the profound ecological and evolutionary consequences, the debate on CMN function remains unresolved because field experiments have not conclusively demonstrated CMN-mediated interplant resource transfer or that any such transfer affects plant performance[26,56]. From our review of field studies in forests (see Box 2 for conclusions from laboratory and greenhouse studies), we conclude that, for every study interpreting CMNs as mediating interplant resource transfer or benefitting seedling performance, the results can be explained without invoking CMNs (Fig. 1). This does not mean that CMN effects do not occur, but that we must be aware that they have not been shown definitively to occur in the field.

Our conclusion is based on evaluating 26 field studies (including our own)[50,57–81] (see Supplementary Note 2 for search details) that examined the influence of CMNs on resource transfer between plants[50,58–64,77–80] or seedling performance (growth, survival or physiology)[57,59,65–76,81]. Most studies were in western North America, although tropical forests and other temperate forests were also included (Supplementary Fig. 1). Seventy-seven per cent were in ectomycorrhizal forests, of which 35% were focused on Douglas fir (*Pseudotsuga menziesii*). Experiments in which putative CMNs were manipulated lasted approximately 2 years or less, except one, where the experiment ran for 5 years[66].

Methods to evaluate CMN function rely on natural or created physical barriers (Fig. 2). By comparing belowground resource transfer between plants of different mycorrhizal types (for example, ectomycorrhizal and arbuscular mycorrhizal) with transfer between plants of the same mycorrhizal type, researchers take advantage of a natural barrier

https://doi.org/10.1038/s41559-023-01986-1

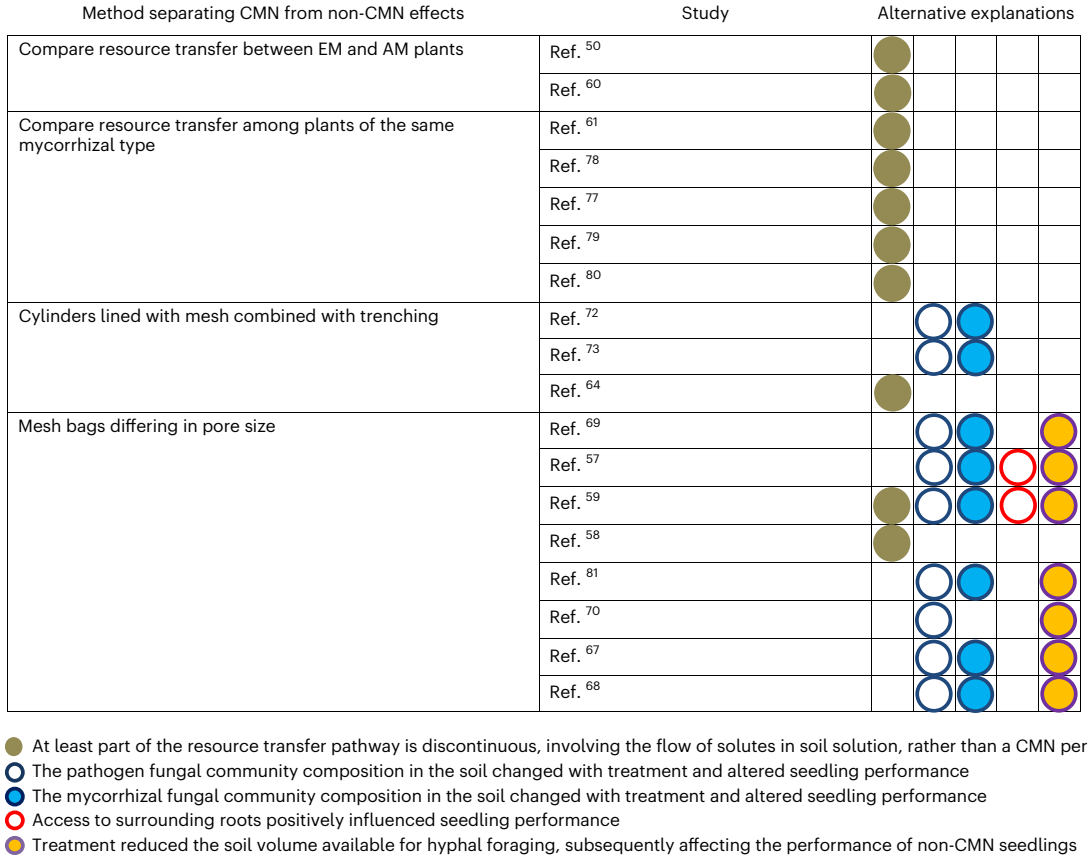

Fig. 1 | Alternative explanations for the results of peer-reviewed, published field studies claiming positive effects of CMNs on interplant resource transfer or seedling performance for at least one set of environmental conditions. In some studies, the alternative explanations had already been identified by the authors, but they are often overlooked by researchers citing the original studies. Studies that reported only negative or no significant CMN effects are not listed. See Fig. 2 for the methods used to evaluate CMNs in forests. AM, arbuscular mycorrhizal; EM, ectomycorrhizal.

to CMN-mediated transfer[50,60,62] (Fig. 2a) because CMNs cannot form between trees of different mycorrhizal types. Any belowground transfer of resources between trees of differing mycorrhizal types would necessarily involve passage through the soil outside of the hyphae. Natural barrier experiments can only be used to investigate resource transfer, not seedling performance. The other common approach is to use physical barriers that decrease the contact or extension of hyphae and/or roots between focal plants (Fig. 2b–d). In forests, access by seedlings to roots and/or potential CMNs of neighbouring trees has been manipulated by using mesh bags differing in pore size[57–59,63–71,74,76,81] (Fig. 2b) or mesh cylinders of a constant pore size with trenching around them[72,73,75] (Fig. 2c). The fate of labelled resources and/or the performance of seedlings is then compared among mesh treatments.

While relying on natural barriers has the advantage of allowing intermingling of roots as would occur in forests, it has notable shortcomings[82]. First, there is no certainty that mycelial connections are continuous between plants of the same mycorrhizal types—the feature that defines a CMN. Most importantly, in the natural barrier approach, the estimate of relative transfer through the soil pathway is confounded by functional and structural differences between types of mycorrhizal fungi[82]. In particular, ectomycorrhizal fungi can form denser, more extensive mycelia than arbuscular mycorrhizal fungi, which may increase the absorption of resources from the soil solution[83,84], resulting in higher transfer of substances exuded from the roots of one plant to an ectomycorrhizal neighbour plant compared with an arbuscular mycorrhizal neighbour plant, even in the absence of a CMN. As a result, the magnitude of transfer between ectomycorrhizal plants through the soil pathway may be underestimated when transfer from an ectomycorrhizal to an arbuscular mycorrhizal plant is used as a control. However, Lerat et al.[60] found the opposite pattern, where more carbon was transferred from a labelled arbuscular mycorrhizal plant to another arbuscular mycorrhizal plant than to an ectomycorrhizal neighbour plant. Nonetheless, in that study differences in the timing of leaf expansion, and thus transpiration between the plant species, were not accounted for and could have explained the higher carbon transfer to the arbuscular plants. Although there may be confounding effects introduced into an experiment using plants of different mycorrhizal types, these types of controls are still necessary. Some studies[61,77–80] assessed belowground resource transfer only among trees of the same mycorrhizal types and thus transfer through the soil pathway could not be estimated (that is, there was no control). Excluding estimates of transfer through the soil pathway is problematic because it can be sizeable[82,85].

Physical barriers comprising meshes of different pore sizes allow for more controlled examination of CMN function by allowing for the movement of exudates or water through the soil solution while preventing the formation of CMNs (<1-µm mesh) or allowing hyphal but not root contact (20–250-µm mesh) between plants. Similar to studies relying on natural barriers, however, there are shortcoming with experiments using physical barriers to manipulate putative CMNs. First, when seedlings are grown within mesh bags designed to prevent the formation of CMNs with nearby plants (mesh < 1 µm), the performance of the seedlings may be compromised by restricting the volume of soil explored by the seedlings' own mycorrhizal hyphae[56,72]. Similar to roots, hyphae may become pot bound under this treatment, and this restriction on foraging may decrease seedling performance. When these no-CMN treatments are compared with treatments that

https://doi.org/10.1038/s41559-023-01986-1

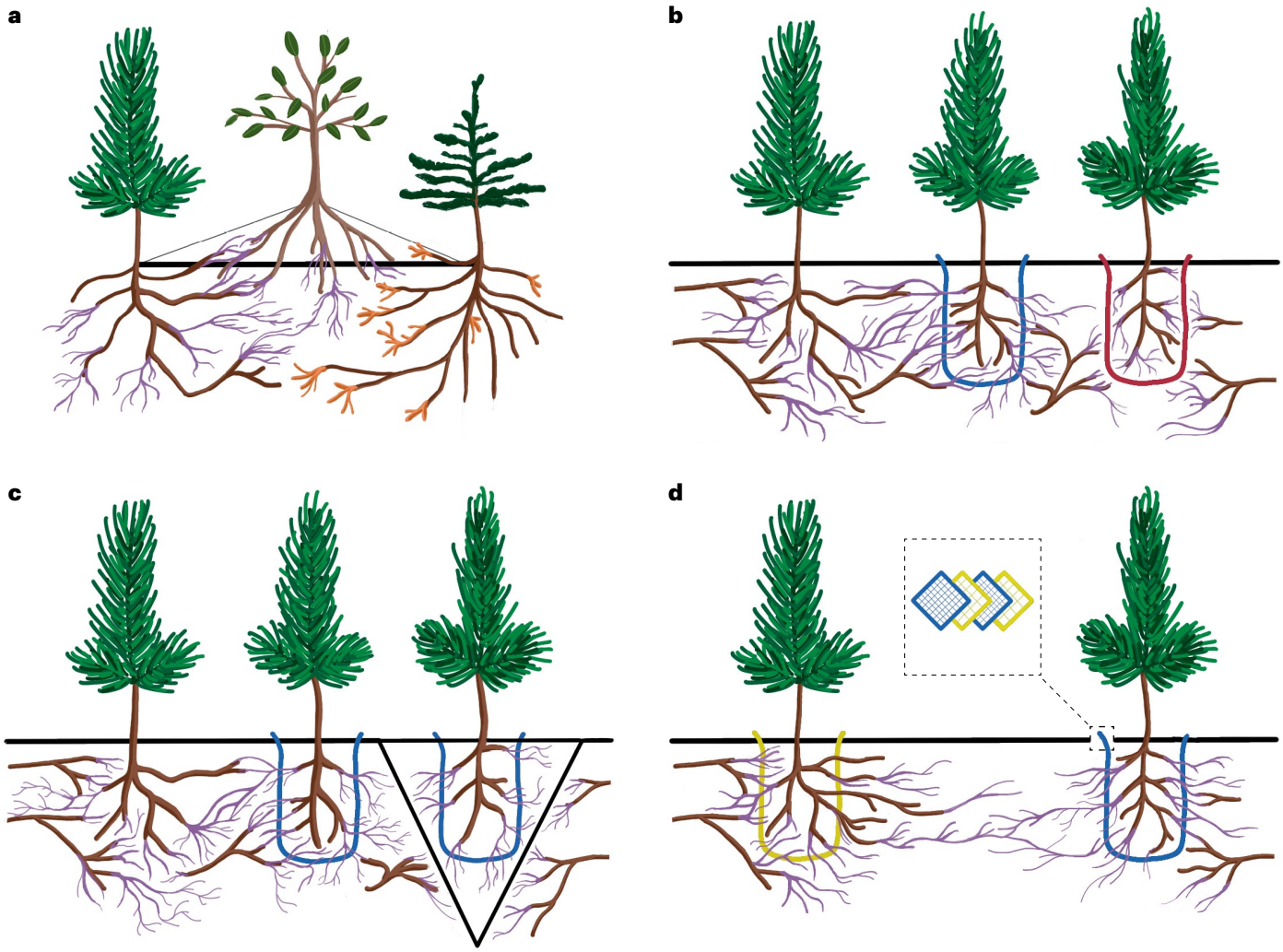

Fig. 2 | Methods used to evaluate CMNs in forests. a, Resource transfer is compared between plants of the same and different mycorrhizal types. The purple hyphae are ectomycorrhizal and the orange hyphae are arbuscular mycorrhizal. The roots of seedlings or trees intermingle and bulk flow of water is unrestricted. **b**, Seedlings are grown in containers made of single mesh layers, which form physical barriers either to roots but not hyphae (blue line; 20–250-µm pore size) or to roots and hyphae (red line; <1-µm pore size). **c**, Seedlings are grown in containers lined with a single layer of mesh (blue line) that is a barrier to roots but not hyphae. To extend the volume available for seedling hyphae to forage but exclude root contact, some seedlings are grown in identical containers and the soil around them is trenched (black V). **d**, Seedlings are grown in containers made of mesh with multiple layers (inset) designed to allow hyphae but exclude roots and create an air gap that eliminates bulk flow of water through a soil pathway. Resource transfer is compared between these seedlings (on the right) and those in contact with soil pathways, fungal hyphae and roots (seedling on the left, which is contained in coarse mesh: >2-mm pore size; yellow line).

allow potential contact with CMNs, but that also allow unlimited soil volume to be explored by mycorrhizal fungi of the focal seedling, CMN effects may be inflated. This potential confounding effect of mesh pore size on seedling performance is demonstrated in the results of studies such as McGuire[69], Bingham and Simard[81] and Teste et al.[59]. In all of these studies, a decrease in the survival of seedlings in fine-mesh bags was interpreted as a consequence of having no access to CMNs, but it could also be explained by the reduced soil volume available to foraging hyphae associated with the seedling.

To circumvent the confounding effects of mesh pore size, trenching around mesh cylinders of a single pore size (20–44 µm) that allows the transit of hyphae but not roots has been used to prevent access to a CMN while maintaining a large soil volume for egressing hyphae[72,73,75] (Fig. 2c). However, in any experiment using mesh barriers or trenching, the fungal community composition, including pathogens, may differ as a response to the treatment, potentially confounding the effects on seedling performance[56]. No field study has characterized potential treatment effects on both mycorrhizal and pathogenic fungi. However, in the four field experiments that have evaluated mesh effects on mycorrhizal fungal communities, changes in ectomycorrhizal colonization[76], ectomycorrhizal fungal diversity[86] and community composition[87] have been reported. In one case where there were no mesh effects on ectomycorrhizal fungal community composition[70], pathogens may have influenced seedling survival. Specifically, Pec et al.[70] concluded that CMNs switch from being a benefit to a detriment to seedlings growing in stands with high tree mortality caused by insect attack. However, earlier research in those stands had indicated that soil pathogens increased with the extent of tree mortality[88]. Thus, an alternative explanation is that in stands with high tree mortality, seedlings grown in mesh bags that prevent hyphal ingress were protected from surrounding pathogens, and as a result had higher survival than seedlings with supposed access to a CMN. These confounding effects on pathogenic and mycorrhizal fungal communities must be considered in interpreting results; fungal- versus CMN-mediated effects must be distinguished.

Almost universally, treatments with mesh openings of between 20 and 250 µm are referred to as CMN treatments, with the assumption that CMNs formed because there was little barrier to hyphal

https://doi.org/10.1038/s41559-023-01986-1

BOX 3

Future experiments testing the structure and function of CMNs in forests

There remains much potential for field experiments to inform our understanding of the structure and function of CMNs in forests, as many of the potential confounding factors and alternative explanations that we identified can be minimized.

We recommend several potential research directions:

- Map the genotypes of trees and mycorrhizal fungi in a wide range of forests worldwide; include fine-scale temporal and spatial[31,32] surveys to demonstrate continuous fungal connections associated with more than one tree and understand the permanence of these connections.
- Test the relevance of CMN topology on tree growth[126] and the resilience of fungal networks[33].
- Design experiments that rank CMN effects on interplant resource transfer and seedling performance against a range of ecological factors[65,67,68].
- Focus on ecologically relevant resources when evaluating CMN-mediated resource transfer between plants, such as water and nitrogen[56].
- Use dye tracers to test for plant-to-plant water flow through root and CMN pathways[64].

In experiments using natural barriers to CMN connections:

- Collect additional data to attempt to quantify the relative strength of the soil versus CMN pathways; for example, the relative densities of arbuscular mycorrhizal and ectomycorrhizal hyphae in soils.
- Take care to evaluate resource uptake between plants of different mycorrhizal types under similar physiological conditions (for example, similar leaf phenology) to avoid confounding effects on the transpiration stream.

In experiments using physical barriers to CMN connections:

- Examine the effects on the composition of the whole fungal community (including pathogens) to generate hypotheses on the roles of different fungal taxa or guilds.
- Include air-gap treatments to separate the pathway of bulk water flow through soil from CMNs[64].
- Minimize container effects on both seedling roots and associated mycorrhizal hyphae by using larger containers, or control for these effects experimentally[72,73].
- Include a treatment where roots of the experimental plants can grow together, as they would under natural conditions, so that root versus CMN effects can be estimated, with the recognition that root effects may be of primary importance in some cases.
- Include efforts to genotype fungi putatively connecting root systems to provide better evidence that CMNs have formed[58], or include treatments that would make confirmation of CMN formation easier. For example, if seedlings were planted into sterile soil inside mesh bags with a pore size of 20–250 µm, mycorrhiza formation would occur only if hyphae entered from outside, thereby indicating the formation of a CMN[90]. In two other treatments, inoculation or not of the sterile soil in mesh bags with a pore size of <1 µm with inoculum-containing soil would allow mycorrhiza-mediated effects to be separated from CMN-mediated effects.
- Combine natural with physical barriers to investigate CMNs. For example, use plant species of a different mycorrhizal type[71,72] or inoculated with host-specific mycorrhizal fungi[117] into experiments using physical barriers. This approach would help to quantify soil pathways in resource transfer and account for container effects and shifts in microbial community composition with mesh treatments.
- Use novel approaches to visualizing the movement of elements through CMNs[127].

Incorporate the myco-perspective into field experiments:

- Investigate tree-mediated resource transfer between fungi.
- Investigate CMN effects on fungal performance.
- Investigate how CMN structure and function may be determined by fungal behaviour in response to variation in the relative nutrient status or traits of alternative tree hosts.
- Investigate how nutrients absorbed by hyphae from the soil are distributed among plants within the CMN[116,117].

growth and root systems of the same mycorrhizal type were in close contact. Nonetheless, in the 18 field studies using such mesh barriers, this assumption was almost never tested. This limitation must be acknowledged when interpreting the results. Only two of these studies showed that a CMN probably existed between pairs of experimental trees or seedlings. Teste et al.[58] used microsatellites of *Rhizopogon vinicolor* to determine that one of four pairs of experimental seedlings was colonized by the same fungal genet and, therefore, was probably connected by a CMN. The transfer of dye from a recently cut tree stump to an experimental seedling observed by Warren et al.[64] could have happened only via an intact CMN or root graft (Fig. 2d). To our knowledge, this single observation by Warren et al.[64] is the strongest evidence that CMNs can transfer a resource between plants in the field, but its influence on seedling performance is unknown. In the vast majority of studies where the presence of CMNs was not confirmed, any responses of seedlings to treatments allowing hyphal access to neighbouring roots can only be ascribed to potential CMN formation, and may instead have been a response to one of the confounding factors described in this section.

An important treatment to include in a CMN study is one where both neighbouring roots and hyphae are allowed to intermingle because this represents the normal condition under which trees interact in a forest, and interacting roots may alter or offset CMN effects. Positive responses to potential CMN (mesh = 20–250 µm) treatments relative to no-CMN (pore size < 1 µm) treatments cannot, on their own, be interpreted to mean that seedlings will receive resources or perform better as a result of CMNs in a forest. In nature, CMNs are not isolated from root–root interactions. When included in field studies, the effects of root interactions on seedlings can be substantial and may reinforce or counteract any effects of CMNs[57,59,66,70,72–74,76]. Across the 13 studies that included a no-mesh treatment[57,59,65,66,69–76,81] and the 28 experiments these studies encompass, only five experiments (18%) showed significant positive CMN effects that were not completely offset by negative root effects[69,74,81]. Some authors argue that a positive seedling response in a no-mesh treatment could be due to the formation of a CMN alone[57,63], but roots and CMNs are typically both present when there is no mesh barrier. In fact, a review of strictly trenching studies—field experimental comparisons of only root/CMN and no-root/no-CMN

https://doi.org/10.1038/s41559-023-01986-1

treatments, with no attempt to isolate CMN from root effects—supports the conclusion that the net result of belowground interactions among forest trees is typically negative[89]. Future experiments are needed (Box 3) that convincingly tease apart the effects of root–root interactions, CMN connections and soil pathways among trees, with the aim of understanding their relative importance and context dependency.

Owing to all of these potentially confounding effects, none of the experimental approaches thus far used in field experiments in forests can definitively demonstrate that either: (1) resources flowed from one root system to another through a CMN (a conclusion similar to that reached by ref. [26]); or (2) the potential to form a CMN resulted in differences in plant growth or survival. Results from laboratory and greenhouse studies do not fare much better than field experiments. Aside from the few studies using autoradiography[90–92], most other laboratory studies on resource transfer lack the full suite of controls required to interpret the results, and sometimes overlook ecologically relevant treatments, namely neighbouring roots (Box 2). Instead, results from field studies highlight that seedling responses to putative CMNs are highly context dependent. Putting aside the many confounding effects, and assuming that CMNs formed in all treatments where mycorrhizal hyphae of one tree could reach the roots of another tree of the same mycorrhiza type, we found that potential access to CMNs resulted in positive, neutral and negative effects on seedling performance. The responses depended on tree species[67,68,70,72,74], soils[74], the distance between trees and seedlings[57,81], the extent of overstory tree mortality[70], the duration of interaction[66] and the neighbourhood[67,68]. Not only was a range of responses observed, it was also not possible to generalize the results, nor to predict the responses, even for one forest type.

In summary, resources can be transferred belowground between trees but CMNs do not necessarily mediate the flow. Confounding effects of common approaches used in experiments preclude definitive conclusions on CMN function. Even if we ignore the possible confounding effects, the results from field studies are still not consistent with the claim that CMNs promote seedling performance (survival or growth) adjacent to adult trees. There is approximately equal evidence that connecting to a putative CMN improves or inhibits seedling performance, and neutral effects are the most common.

Mature trees communicate preferentially with offspring through CMNs (claim 3)

That trees preferentially send resources or signals warning of insect damage to offspring through CMNs has gained recent traction in the popular media and scientific literature[1,2,93–99]. Yet, we found no evidence from peer-reviewed, published studies in forests to support this claim. The single peer-reviewed, published study that has addressed the phenomenon of signalling among tree species through CMNs in response to insect damage was a pot study in a greenhouse[100] (Box 2); however, any signalling was cancelled when root interactions were allowed between neighbouring seedlings—the natural situation where CMNs would form. In the single peer-reviewed, published greenhouse study testing kin effects, carbon was transferred through the soil solution, not a CMN[85] (Box 2). The claim seemingly relies on results from graduate theses, but the results from these studies either do not support[101] or actually run counter to the claim[102]. There appears to be only one study evaluating carbon transfer from relatively old, living trees (125–275 years old) to conspecific seedlings, but it does not control for the soil pathway[103]. In the single peer-reviewed, published field study where trees were attacked by insects[70], putative CMN effects on seedlings were evaluated years after the attack, so the study could not have assessed any signals adult trees may have emitted.

In summary, there is no current evidence from peer-reviewed, published field studies to support this claim. Whether signalling or kin recognition occurs through a CMN among trees in a forest remains to be demonstrated.

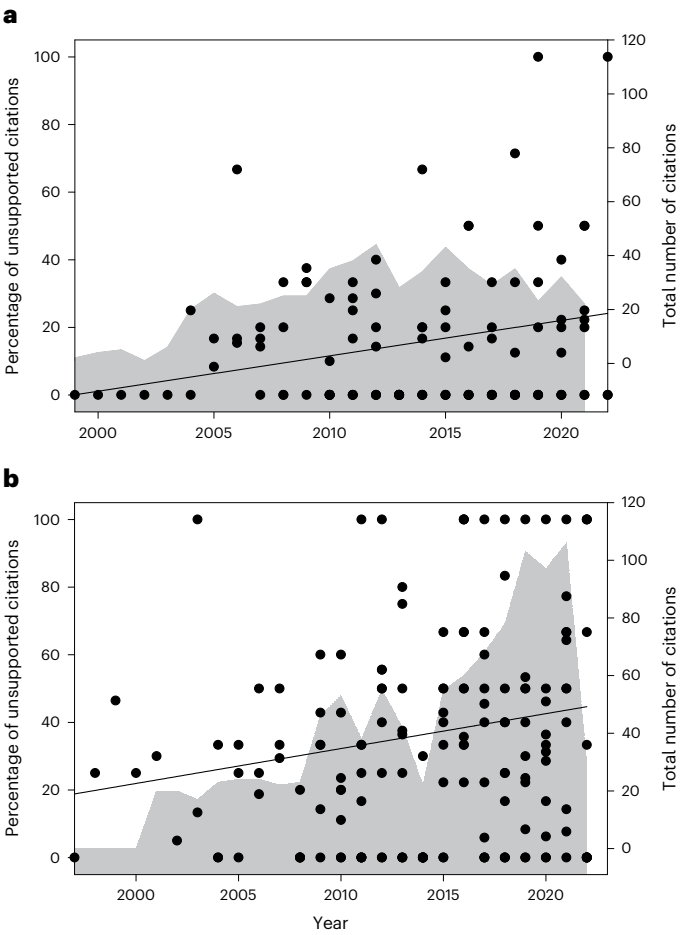

Fig. 3 | Percentage of unsupported citations through time of influential studies on CMNs. a,**b**, Percentage of unsupported citations through time of influential studies on CMN structure (**a**; for example, topology or architecture) and function (**b**; effects on interplant resource transfer and/or seedling performance). For each influential study, the number of unsupported citations was divided by the total number of citations for a given year and multiplied by 100 to convert it to a standardized count (black circles). A negative binomial regression was used to predict the count of unsupported citations over time, indexing time to the year in which a citation first occurred (that is, the year when a citation first occurred among the group was set to 1 and each year following was numbered consecutively). The back-transformed negative binomial regression was $y = 0.75 + 1.047x$ ($P = 0.012$) for **a** and $y = 18.8 + 1.032x$ ($P = 0.025$) for **b**. The grey shading represents the total number of citations per year.

CMN citations in the literature are biased towards positive effects of CMNs

We identified 18 influential field studies, defined as those having at least 50 citations on the Web of Science (Supplementary Note 2) and evaluated citations of these studies. We assigned a citation as supported if the evidence was strong for the statement or unsupported if the evidence was weak or absent, or if alternative interpretations, such as those described above, were consistent with the evidence. Indeed, some of the unsupported citations came from earlier publications of our own.

We evaluated 593 papers citing seven influential studies on CMN structure and 1,083 papers citing 11 influential studies on CMN function (Supplementary Note 2). For both sets of studies, the rate of unsupported citations increased with time, rising to ~25% of all citations about CMN structure and almost 50% of citations about CMN function (Fig. 3). For each year of the publication record for studies on CMN structure, 1.047 times more unsupported citations were

present ($P = 0.012$; 95% confidence interval = 1.010–1.086). For each year of the publication record for studies on CMN function, 1.032 times more unsupported citations were present ($P = 0.025$; 95% confidence interval = 1.004–1.060).

There is bias in the citations making unsupported statements (Supplementary Note 3). The unsupported statements tend to overstate results and disregard confounding effects in a way that promotes positive effects of CMNs in forests. Specifically, overinterpretation was the most common reason for unsupported citations of influential studies on CMN structure, and for a single study[38] they made up to 88% of unsupported citations (Supplementary Table 1). For instance, Diédhiou et al.[104], Grelet et al.[105], Kennedy et al.[39] and Horton et al.[38] provided evidence for the potential for CMNs to form, yet the most frequent type of unsupported statement was to cite these studies as evidence for the presence of CMNs in forests. Likewise, Beiler et al.[29] described the topology of a putative CMN, yet the most common unsupported statement was to cite this study as evidence for interplant resource transfer in CMNs.

Overlooking confounding effects in experiments made up the most common unsupported statements citing influential studies on CMN function. For a single study[69], they made up to 84% of unsupported citations (Supplementary Table 2). For instance, carbon moving through soil pathways (not intact CMNs) is consistent with the results of Simard et al.[50], Lerat et al.[60], Teste et al.[58,59] and Klein et al.[61], yet this pathway is often disregarded in lieu of a singular focus on CMNs. In line with this fixation on positive responses to CMNs, the confounding effects of manipulating CMNs by using mesh of varying pore sizes on fungal species composition, hyphal foraging and root interactions are effectively ignored in the literature. The other common unsupported statement among studies of CMN function was citing a study for evidence of CMN-mediated interplant resource transfer when it was not evaluated (Supplementary Table 2). In some studies, alternative explanations had already been identified by the authors, but they were often overlooked by researchers citing the original studies. These types of unsupported statements are an issue because we scientists, probably without intent, have become vectors for unsubstantiated claims and thus may be shaping the public narrative with an increasingly inaccurate characterization of CMNs.

Conclusions and moving forward

We conclude that popular claims of singular positive effects of CMNs in forests are disconnected from evidence. We also show bias in citing positive effects within the research community. The functional role of CMNs in plant communities and ecosystems has been controversial for decades, and we are not the first to highlight unknowns, confounding effects and gaps in knowledge[21,22,26,27,82,106–109]. What is new is the wave of popular science that has overlooked uncertainty about CMN structure and function to espouse a singular narrative—that trees benefit from being connected by CMNs. As mycorrhiza researchers who have investigated the function of CMNs, we are thrilled that the public has become as excited as we are about the many roles that fungi play in forests. Nonetheless, it is important for the public and scientific community to understand the nature and extent of the evidence for the roles played by CMNs in forests. The inaccurate framing of CMNs in forests in the popular media, and bias in citing original studies, necessitates improvements in communication and citation practices (Supplementary Note 4). In line with previous calls[110], we believe that the anthropomorphism currently present in some science communication on CMN function in forests[1,2] should be reconsidered. We also agree with previous statements[111] that more evidence is needed before forests are managed to protect CMNs per se.

While many excellent studies, for their time, have been conducted on the role of CMNs in forests, we suggest that the most concerning issue is the rigour with which the results of these studies have been transmitted and interpreted. Moving forward, we offer some approaches to future CMN field studies that will address alternative explanations and ease interpretations of results (Box 3). We lack strong evidence that CMNs are widespread and persist long enough to be functional in forests; hence, more CMN maps that include fine-scale temporal and spatial surveys are needed from diverse forests worldwide. We can design experiments that rank CMN effects on interplant resource transfer and seedling performance against a range of ecological factors. For example, studies such as refs. [65,75,81] went beyond testing for a CMN effect on seedling survival to ranking CMN effects among ecological factors such as seedling genetics, stand type and regional climates; this approach is crucial for understanding how ecological interactions function in forests. For experiments using natural or physical barriers, we need to carefully acknowledge, or better yet, eliminate confounding effects (Fig. 2 and Box 3). Finally, by incorporating the myco-perspective into field experiments, we can ask what role fungi play in forest CMNs. All of our suggested approaches involve existing methods; thus, we do not believe they are beyond reach.

Let us devise new experiments, demand better evidence, think critically about alternative explanations for results and become more selective with the claims we disseminate. If not, we risk turning the wood-wide web into a fantasy beneath our feet.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The datasets analysed in the current study are available from the University of Alberta Dataverse at https://doi.org/10.5683/SP3/88MZYX.

References

1. Wohlleben, P. *The Hidden Life of Trees: What They Feel, How They Communicate—Discoveries From a Secret World* Vol. 1 (Greystone Books, 2016).
2. Simard, S. W. *Finding the Mother Tree: Discovering the Wisdom of the Forest* (Knopf Doubleday Publishing Group, 2022).
3. Powers, R. *The Overstory* (W. W. Norton & Company, 2018).
4. Jabr, F. The social life of forests. *New York Times Magazine* https://www.nytimes.com/interactive/2020/ 12/02/magazine/tree-communication-mycorrhiza.html (2020).
5. Kaplan, S. With forests in peril, she's on a mission to save 'mother trees'. *Washington Post* (27 December 2022).
6. Chung, D. & Williams, R. T. Talking trees. *Natl Geogr.* **233**, 6 (2018).
7. Grant, R. Do trees talk to each other? *Smithsonian Magazine* https://www.smithsonianmag.com/science-nature/the-whispering-trees-180968084/ (2018).
8. Schwartzberg, L. *Fantastic Fungi. Moving Art* (2019).
9. Druyan, A. *Cosmos: Possible Worlds: the Search for Intelligent Life on Earth* (2020).
10. Mills, M. *C'mon C'mon* (2020).
11. Simard, S. W. How trees talk to each other. *YouTube* https://www.youtube.com/watch?v=Un2yBgIAxYs (2016).
12. Abumrad J & Krulwich, R. From tree to shining tree. *Radiolab* https://radiolab.org/episodes/from-tree-to-shining-tree (2016).
13. Geddes, L. Unearthing the secret social lives of trees. *The Guardian Science Weekly* https://www.theguardian.com/science/audio/2021/ apr/29/unearthing-the-secret-social-lives-of-trees-podcast (2021).
14. Davies, D. Trees talk to each other. 'Mother Tree' ecologist hears lessons for people, too. *National Public Radio* https://www.npr.org/sections/health-shots/2021/05/04/993430007/trees-talk-to-each-other-mother-tree-ecologist-hears-lessons-for-people-too (2021).
15. Braff, Z. Midnight train to Royston. *Ted Lasso* (2021).
16. Murphy, R. Welcome, friends. *The Watcher* (2022).

17. Milović, M., Kebert, M. & Orlović, S. How mycorrhizas can help forests to cope with ongoing climate change? *Pregledni Članci Rev.* **5**, 279–286 (2021).
18. Simard, S. W. & Austin, M. E. in *Climate Change and Variabilty* (eds Simard, S. W. & Austin, M. E.) 275–302 (IntechOpen Europe, 2010).
19. Domínguez-Núñez, J. A. in *Structure and Functions of the Pedosphere* (eds Giri, B. et al.) 365–391 (Springer, 2022).
20. Authier, L., Violle, C. & Richard, F. Ectomycorrhizal networks in the anthropocene: from natural ecosystems to urban planning. *Front. Plant Sci.* **13**, 900231 (2022).
21. Selosse, M.-A., Richard, F., He, X. & Simard, S. W. Mycorrhizal networks: des liaisons dangereuses? *Trends Ecol. Evol.* **21**, 621–628 (2006).
22. Newman, E. Mycorrhizal links between plants—their functioning and ecological significance. *Adv. Ecol. Res.* **18**, 243–270 (1988).
23. Bonello, P., Bruns, T. D. & Gardes, M. Genetic structure of a natural population of the ectomycorrhizal fungus *Suillus pungens*. *New Phytol.* **138**, 533–542 (1998).
24. Dahlberg, A. & Stenlid, J. Size, distribution and biomass of genets in populations of *Suillus bovinus* (L.: Fr.) Roussel revealed by somatic incompatibility. *New Phytol.* **128**, 225–234 (1994).
25. Kretzer, A. M., Dunham, S., Molina, R. & Spatafora, J. W. Microsatellite markers reveal the below ground distribution of genets in two species of *Rhizopogon* forming tuberculate ectomycorrhizas on Douglas fir. *New Phytol.* **161**, 313–320 (2004).
26. Figueiredo, A. F., Boy, J. & Guggenberger, G. Common mycorrhizae network: a review of the theories and mechanisms behind underground interactions. *Front. Fungal Biol.* **2**, https://doi.org/10.3389/ffunb.2021.735299 (2021).
27. Leake, J. et al. Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Can. J. Bot.* **82**, 1016–1045 (2004).
28. Trappe, J. M. & Fogel, R. in *The Belowground Ecosystem: a Synthesis of Plant-Associated Processes* (ed. Marshall J. K.) 205–214 (Colorado State Univ., 1977).
29. Beiler, K. J., Durall, D. M., Simard, S. W., Maxwell, S. A. & Kretzer, A. M. Architecture of the wood-wide web: *Rhizopogon* spp. genets link multiple Douglas-fir cohorts. *New Phytol.* **185**, 543–553 (2010).
30. Beiler, K. J., Simard, S. W. & Durall, D. M. Topology of tree–mycorrhizal fungus interaction networks in xeric and mesic Douglas-fir forests. *J. Ecol.* **103**, 616–628 (2015).
31. Beiler, K. J., Simard, S. W., LeMay, V. & Durall, D. M. Vertical partitioning between sister species of *Rhizopogon* fungi on mesic and xeric sites in an interior Douglas-fir forest. *Mol. Ecol.* **21**, 6163–6174 (2012).
32. Lian, C., Narimatsu, M., Nara, K. & Hogetsu, T. *Tricholoma matsutake* in a natural *Pinus densiflora* forest: correspondence between above- and below-ground genets, association with multiple host trees and alteration of existing ectomycorrhizal communities. *New Phytol.* **171**, 825–836 (2006).
33. Van Dorp, C. H., Simard, S. W. & Durall, D. M. Resilience of *Rhizopogon*–Douglas-fir mycorrhizal networks 25 years after selective logging. *Mycorrhiza* **30**, 467–474 (2020).
34. Cazzolla Gatti, R. et al. The number of tree species on Earth. *Proc. Natl Acad. Sci. USA* **119**, e2115329119 (2022).
35. Tedersoo, L. & Bahram, M. Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biol. Rev.* **94**, 1857–1880 (2019).
36. Setälä, H. Growth of birch and pine seedlings in relation to grazing by soil fauna on ectomycorrhizal fungi. *Ecology* **76**, 1844–1851 (1995).
37. Kanters, C., Anderson, I. C. & Johnson, D. Chewing up the wood-wide web: selective grazing on ectomycorrhizal fungi by collembola. *Forests* **6**, 2560–2570 (2015).
38. Horton, T. R., Bruns, T. D. & Parker, V. T. Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseudotsuga menziesii* establishment. *Can. J. Bot.* **77**, 93–102 (1999).
39. Kennedy, P. G., Izzo, A. D. & Bruns, T. D. There is high potential for the formation of common mycorrhizal networks between understorey and canopy trees in a mixed evergreen forest. *J. Ecol.* **91**, 1071–1080 (2003).
40. Kennedy, P. G., Smith, D. P., Horton, T. R. & Molina, R. J. *Arbutus menziesii* (Ericaceae) facilitates regeneration dynamics in mixed evergreen forests by promoting mycorrhizal fungal diversity and host connectivity. *Am. J. Bot.* **99**, 1691–1701 (2012).
41. Horton, T. R., Molina, R. & Hood, K. Douglas-fir ectomycorrhizae in 40- and 400-year-old stands: mycobiont availability to late successional western hemlock. *Mycorrhiza* **15**, 393–403 (2005).
42. Buscardo, E. et al. Is the potential for the formation of common mycorrhizal networks influenced by fire frequency? *Soil Biol. Biochem.* **46**, 136–144 (2012).
43. Hewitt, R. E., Chapin, F. S. III, Hollingsworth, T. N. & Taylor, D. L. The potential for mycobiont sharing between shrubs and seedlings to facilitate tree establishment after wildfire at Alaska arctic treeline. *Mol. Ecol.* **26**, 3826–3838 (2017).
44. Jia, S., Nakano, T., Hattori, M. & Nara, K. Root-associated fungal communities in three *Pyroleae* species and their mycobiont sharing with surrounding trees in subalpine coniferous forests on Mount Fuji, Japan. *Mycorrhiza* **27**, 733–745 (2017).
45. Hortal, S. et al. Beech roots are simultaneously colonized by multiple genets of the ectomycorrhizal fungus *Laccaria amethystina* clustered in two genetic groups. *Mol. Ecol.* **21**, 2116–2129 (2012).
46. Wadud, M. A., Nara, K., Lian, C., Ishida, T. A. & Hogetsu, T. Genet dynamics and ecological functions of the pioneer ectomycorrhizal fungi *Laccaria amethystina* and *Laccaria laccata* in a volcanic desert on Mount Fuji. *Mycorrhiza* **24**, 551–563 (2014).
47. Germain, S. J. & Lutz, J. A. Shared friends counterbalance shared enemies in old forests. *Ecology* **102**, e03495 (2021).
48. Simard, S. W. et al. Partial retention of legacy trees protect mycorrhizal inoculum potential, biodiversity, and soil resources while promoting natural regeneration of interior Douglas-fir. *Front. For. Glob. Change* **3**, https://doi.org/10.3389/ffgc.2020.620436 (2021).
49. Björkman, E. Monotropa hypopitys L.—an epiparasite on tree roots. *Physiol. Plant.* **13**, 308–327 (1960).
50. Simard, S. W. et al. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* **388**, 579–582 (1997).
51. Read, D. The ties that bind. *Nature* **388**, 517–518 (1997).
52. Aleklett, K. & Boddy, L. Fungal behaviour: a new frontier in behavioural ecology. *Trends Ecol. Evol.* **36**, 787–796 (2021).
53. Franklin, O., Näsholm, T., Högberg, P. & Högberg, M. N. Forests trapped in nitrogen limitation—an ecological market perspective on ectomycorrhizal symbiosis. *New Phytol.* **203**, 657–666 (2014).
54. Hasselquist, N. J. et al. Greater carbon allocation to mycorrhizal fungi reduces tree nitrogen uptake in a boreal forest. *Ecology* **97**, 1012–1022 (2016).
55. Näsholm, T. et al. Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? *New Phytol.* **198**, 214–221 (2013).
56. Hoeksema, J. D. in *Mycorrhizal Networks* (ed. Horton, T. R.) 255–277 (Springer Netherlands, 2015).
57. Teste, F. P. & Simard, S. W. Mycorrhizal networks and distance from mature trees alter patterns of competition and facilitation in dry Douglas-fir forests. *Oecologia* **158**, 193–203 (2008).
58. Teste, F. P., Simard, S. W., Durall, D. M., Guy, R. D. & Berch, S. M. Net carbon transfer between *Pseudotsuga menziesii* var. *glauca* seedlings in the field is influenced by soil disturbance. *J. Ecol.* **98**, 429–439 (2010).

59. Teste, F. P. et al. Access to mycorrhizal networks and roots of trees: importance for seedling survival and resource transfer. *Ecology* **90**, 2808–2822 (2009).
60. Lerat, S. et al. ^{14}C transfer between the spring ephemeral *Erythronium americanum* and sugar maple saplings via arbuscular mycorrhizal fungi in natural stands. *Oecologia* **132**, 181–187 (2002).
61. Klein, T., Siegwolf, R. T. W. & Korner, C. Belowground carbon trade among tall trees in a temperate forest. *Science* **352**, 342–344 (2016).
62. He, X., Bledsoe, C. S., Zasoski, R. J., Southworth, D. & Horwath, W. R. Rapid nitrogen transfer from ectomycorrhizal pines to adjacent ectomycorrhizal and arbuscular mycorrhizal plants in a California oak woodland. *New Phytol.* **170**, 143–151 (2006).
63. Schoonmaker, A. L., Teste, F. P., Simard, S. W. & Guy, R. D. Tree proximity, soil pathways and common mycorrhizal networks: their influence on the utilization of redistributed water by understory seedlings. *Oecologia* **154**, 455–466 (2007).
64. Warren, J. M., Brooks, J. R., Meinzer, F. C. & Eberhart, J. L. Hydraulic redistribution of water from *Pinus ponderosa* trees to seedlings: evidence for an ectomycorrhizal pathway. *New Phytol.* **178**, 382–394 (2008).
65. Bingham, M. A. & Simard, S. W. Seedling genetics and life history outweigh mycorrhizal network potential to improve conifer regeneration under drought. *For. Ecol. Manag.* **287**, 132–139 (2013).
66. Kranabetter, J. M. Understory conifer seedling response to a gradient of root and ectomycorrhizal fungal contact. *Can. J. Bot.* **83**, 638–646 (2005).
67. Liang, M. et al. Soil fungal networks maintain local dominance of ectomycorrhizal trees. *Nat. Commun.* **11**, 2636 (2020).
68. Liang, M. et al. Soil fungal networks moderate density-dependent survival and growth of seedlings. *New Phytol.* **230**, 2061–2071 (2021).
69. McGuire, K. L. Common ectomycorrhizal networks may maintain monodominance in a tropical rain forest. *Ecology* **88**, 567–574 (2007).
70. Pec, G. J., Simard, S. W., Cahill, J. F. & Karst, J. The effects of ectomycorrhizal fungal networks on seedling establishment are contingent on species and severity of overstorey mortality. *Mycorrhiza* **30**, 173–183 (2020).
71. Corrales, A., Mangan, S. A., Turner, B. L. & Dalling, J. W. An ectomycorrhizal nitrogen economy facilitates monodominance in a neotropical forest. *Ecol. Lett.* **19**, 383–392 (2016).
72. Booth, M. G. Mycorrhizal networks mediate overstorey–understorey competition in a temperate forest. *Ecol. Lett.* **7**, 538–546 (2004).
73. Booth, M. G. & Hoeksema, J. D. Mycorrhizal networks counteract competitive effects of canopy trees on seedling survival. *Ecology* **91**, 2294–2302 (2010).
74. Brearley, F. Q. et al. Testing the importance of a common ectomycorrhizal network for dipterocarp seedling growth and survival in tropical forests of Borneo. *Plant Ecol. Divers.* **9**, 563–576 (2016).
75. Dehlin, H. et al. Tree seedling performance and below-ground properties in stands of invasive and native tree species. *N. Z. J. Ecol.* **32**, 67–79 (2008).
76. Newbery, D. M. & Neba, G. A. Micronutrients may influence the efficacy of ectomycorrhizas to support tree seedlings in a lowland African rain forest. *Ecosphere* **10**, e02686 (2019).
77. Oliveira, I. R. et al. Nutrient deficiency enhances the rate of short-term belowground transfer of nitrogen from *Acacia mangium* to *Eucalyptus* trees in mixed-species plantations. *For. Ecol. Manag.* **491**, 119192 (2021).
78. Paula, R. R. et al. Evidence of short-term belowground transfer of nitrogen from *Acacia mangium* to *Eucalyptus grandis* trees in a tropical planted forest. *Soil Biol. Biochem.* **91**, 99–108 (2015).
79. Nygren, P. & Leblanc, H. A. Dinitrogen fixation by legume shade trees and direct transfer of fixed N to associated cacao in a tropical agroforestry system. *Tree Physiol.* **35**, 134–147 (2015).
80. Liu, Y., Chen, H. & Mou, P. Spatial patterns nitrogen transfer models of ectomycorrhizal networks in a Mongolian scotch pine plantation. *J. For. Res.* **29**, 339–346 (2018).
81. Bingham, M. A. & Simard, S. Ectomycorrhizal networks of *Pseudotsuga menziesii* var. *glauca* trees facilitate establishment of conspecific seedlings under drought. *Ecosystems* **15**, 188–199 (2012).
82. Robinson, D. & Fitter, A. The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. *J. Exp. Bot.* **50**, 9–13 (1999).
83. Chen, W., Koide, R. T. & Eissenstat, D. M. Root morphology and mycorrhizal type strongly influence root production in nutrient hot spots of mixed forests. *J. Ecol.* **106**, 148–156 (2018).
84. Jones, M. D., Durall, D. M. & Tinker, P. B. A comparison of arbuscular and ectomycorrhizal *Eucalyptus coccifera*: growth response, phosphorus uptake efficiency and external hyphal production. *New Phytol.* **140**, 125–134 (1998).
85. Pickles, B. J. et al. Transfer of ^{13}C between paired Douglas-fir seedlings reveals plant kinship effects and uptake of exudates by ectomycorrhizas. *New Phytol.* **214**, 400–411 (2017).
86. Teste, F. P., Simard, S. W. & Durall, D. M. Role of mycorrhizal networks and tree proximity in ectomycorrhizal colonization of planted seedlings. *Fungal Ecol.* **2**, 21–30 (2009).
87. Bingham, M. A. & Simard, S. W. Mycorrhizal networks affect ectomycorrhizal fungal community similarity between conspecific trees and seedlings. *Mycorrhiza* **22**, 317–326 (2012).
88. Pec, G. J. et al. Change in soil fungal community structure driven by a decline in ectomycorrhizal fungi following a mountain pine beetle (*Dendroctonus ponderosae*) outbreak. *New Phytol.* **213**, 864–873 (2017).
89. Coomes, D. A. & Grubb, P. J. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Monogr.* **70**, 171–207 (2000).
90. Finlay, R. D. & Read, D. J. The structure and function of the vegetative mycelium of ectomycorrhizal plants. *New Phytol.* **103**, 143–156 (1986).
91. Brownlee, C., Duddridge, J. A., Malibari, A. & Read, D. J. The structure and function of mycelial systems of ectomycorrhizal roots with special reference to their role in forming inter-plant connections and providing pathways for assimilate and water transport. *Plant Soil* **71**, 433–443 (1983).
92. Wu, B., Nara, K. & Hogetsu, T. Can ^{14}C-labeled photosynthetic products move between *Pinus densiflora* seedlings linked by ectomycorrhizal mycelia? *New Phytol.* **149**, 137–146 (2001).
93. Anten, N. P. R. & Chen, B. J. W. Detect thy family: mechanisms, ecology and agricultural aspects of kin recognition in plants. *Plant Cell Environ.* **44**, 1059–1071 (2021).
94. Dominguez, P. G. & Niittylä, T. Mobile forms of carbon in trees: metabolism and transport. *Tree Physiol.* **42**, 458–487 (2021).
95. Yu, R.-P., Lambers, H., Callaway, R. M., Wright, A. J. & Li, L. Belowground facilitation and trait matching: two or three to tango. *Trends Plant Sci.* **26**, 1227–1235 (2021).
96. Simard, S. W. in *The Word for World is Still Forest* (eds Springer, A. & Turpin, E.) 66–72 (K Verlag and Haus der Kulturen der Welt, 2017).
97. Simard, S. W. in *Memory and Learning in Plants* (eds Baluska, F. et al.) 191–213 (Springer, 2018).
98. Boyno, G. & Demir, S. Plant–mycorrhiza communication and mycorrhizae in inter-plant communication. *Symbiosis* **86**, 155–168 (2022).
99. Rasheed, M. U., Brosset, A. & Blande, J. D. Tree communication: the effects of "wired" and "wireless" channels on interactions with herbivores. *Curr. For. Rep.* **9**, 33–47 (2023).

100. Song, Y. Y., Simard, S. W., Carroll, A., Mohn, W. W. & Zeng, R. S. Defoliation of interior Douglas-fir elicits carbon transfer and stress signalling to ponderosa pine neighbors through ectomycorrhizal networks. *Sci. Rep.* **5**, 8495 (2015).
101. Gorzelak, M. A. *Kin-Selected Signal Transfer Through Mycorrhizal Networks in Douglas-Fir*. PhD thesis, Univ. British Columbia (2017).
102. Asay, A. K. *Mycorrhizal Facilitation of Kin Recognition in Interior Douglas-Fir (*Pseudotsuga menziesii *var.* glauca*)*. MSc thesis, Univ. British Columbia (2013).
103. Orrego, G. *Western Hemlock Regeneration on Coarse Woody Debris is Facilitated by Linkage into a Mycorrhizal Network in an Old-Growth Forest*. MSc thesis, Univ. British Columbia (2018).
104. Diédhiou, A. G. et al. Multi-host ectomycorrhizal fungi are predominant in a Guinean tropical rainforest and shared between canopy trees and seedlings. *Environ. Microbiol.* **12**, 2219–2232 (2010).
105. Grelet, G.-A. et al. New insights into the mycorrhizal *Rhizoscyphus ericae* aggregate: spatial structure and co-colonization of ectomycorrhizal and ericoid roots. *New Phytol.* **188**, 210–222 (2010).
106. Van der Heijden, M. G. A. & Horton, T. R. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *J. Ecol.* **97**, 1139–1150 (2009).
107. Babikova, Z., Johnson, D., Bruce, T., Pickett, J. & Gilbert, L. Underground allies: how and why do mycelial networks help plants defend themselves? *BioEssays* **36**, 21–26 (2014).
108. Alaux, P.-L., Zhang, Y., Gilbert, L. & Johnson, D. Can common mycorrhizal fungal networks be managed to enhance ecosystem functionality? *Plants People Planet* **3**, 433–444 (2021).
109. Simard, S. W. et al. Mycorrhizal networks: mechanisms, ecology and modelling. *Fungal Biol. Rev.* **26**, 39–60 (2012).
110. Flinn, K. The idea that trees talk to cooperate is misleading. *Scientific American* https://www.scientificamerican.com/article/the- idea-that-trees-talk-to-cooperate-is-misleading/ (2021).
111. Högberg, P. & Högberg, M. N. Does successful forest regeneration require the nursing of seedlings by nurse trees through mycorrhizal interconnections. *For. Ecol. Manag.* **516**, 120252 (2022).
112. Teste, F. P., Jones, M. D. & Dickie, I. A. Dual-mycorrhizal plants: their ecology and relevance. *New Phytol.* **225**, 1835–1851 (2020).
113. Toju, H., Guimarães, P. R., Olesen, J. M. & Thompson, J. N. Assembly of complex plant–fungus networks. *Nat. Commun.* **5**, 5273 (2014).
114. Smith, S. E. & Read, D. J. *Mycorrhizal Symbiosis* 3rd edn (Elsevier, 2008).
115. Nara, K. Ectomycorrhizal networks and seedling establishment during early primary succession. *New Phytol.* **169**, 169–178 (2006).
116. Arnebrant, K., Ek, H., Finlay, R. D. & Söderström, B. Nitrogen translocation between *Alnus glutinosa* (L.) Gaertn. seedlings inoculated with *Frankia* sp. and *Pinus contorta* Doug, ex Loud seedlings connected by a common ectomycorrhizal mycelium. *New Phytol.* **124**, 231–242 (1993).
117. Finlay, R. D. Functional aspects of phosphorus uptake and carbon translocation in incompatible ectomycorrhizal associations between *Pinus sylvestris* and *Suillus grevillei* and *Boletinus cauipes*. *New Phytol.* **112**, 185–192 (1989).
118. Cahanovitc, R., Livne-Luzon, S., Angel, R. & Klein, T. Ectomycorrhizal fungi mediate belowground carbon transfer between pines and oaks. *ISME J.* **16**, 1420–1429 (2022).
119. Teste, F. P., Veneklass, E. J., Dixon, K. W. & Lambers, H. Is nitrogen transfer among plants enhanced by contrasting nutrient-acquisition strategies? *Plant Cell Environ.* **38**, 50–60 (2015).
120. Simard, S. W. et al. Reciprocal transfer of carbon isotopes between ectomycorrhizal *Betula papyrifera* and *Pseudotsuga menziesii*. *New Phytol.* **137**, 529–542 (1997).
121. Egerton-Warburton, L. M., Querejeta, J. I. & Allen, M. F. Common mycorrhizal networks provide a potential pathway for the transfer of hydraulically lifted water between plants. *J. Exp. Bot.* **58**, 1473–1483 (2007).
122. He, X., Critchley, C., Ng, H. & Bledsoe, C. Nodulated N_2-fixing *Casuarina cunninghamiana* is the sink for net N transfer from non-N_2-fixing *Eucalyptus maculata* via an ectomycorrhizal fungus *Pisolithus* sp. using $^{15}NH_4^+$ or $^{15}NO_3^-$ supplied as ammonium nitrate. *New Phytol.* **167**, 897–912 (2005).
123. He, X., Critchley, C., Ng, H. & Bledsoe, C. Reciprocal N ($^{15}NH_4^+$ or $^{15}NO_3^-$) transfer between nonN_2-fixing *Eucalyptus maculata* and N_2-fixing *Casuarina cunninghamiana* linked by the ectomycorrhizal fungus *Pisolithus* sp. *New Phytol.* **163**, 629–640 (2004).
124. Bingham, M. A. & Simard, S. W. Do mycorrhizal network benefits to survival and growth of interior Douglas-fir seedlings increase with soil moisture stress? *Ecol. Evol.* **1**, 306–316 (2011).
125. Babikova, Z. et al. Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecol. Lett.* **16**, 835–843 (2013).
126. Birch, J. D., Simard, S. W., Beiler, K. J. & Karst, J. Beyond seedlings: ectomycorrhizal fungal networks and growth of mature *Pseudotsuga menziesii*. *J. Ecol.* **109**, 806–818 (2021).
127. Färkkilä, S. M. A. et al. Fluorescent nanoparticles as tools in ecology and physiology. *Biol. Rev.* **96**, 2392–2424 (2021).

Acknowledgements

We thank I. Mounts, S. Draud and D. Durall for participating in early discussions. I. Mounts provided the Web of Science search term and aided in screening studies for inclusion. R. Jackson formatted and cross-checked the unsupported citations for accuracy and made Supplementary Fig. 1. C. Karst designed Fig. 2.

Author contributions

The focus of this Perspective was conceived by all of the authors and the writing was shared. J.K. led the evaluation of citations, with feedback from M.D.J. and J.D.H.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-023-01986-1.

Correspondence should be addressed to Justine Karst.

Peer review information *Nature Ecology & Evolution* thanks Peter Kennedy, Toby Kiers and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

nature portfolio

Corresponding author(s): Justine Karst

Last updated by author(s): YYYY-MM-DD

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed
☐	☒ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒ The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒ A description of all covariates tested
☐	☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒ For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No software was used
Data analysis	IBM Corp. Released 2021. IBM SPSS Statistics for Windows, Version 28.0. Armonk, NY: IBM Corp

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The datasets analysed are available at University of Alberta Dataverse https://doi.org/10.5683/SP3/88MZYX

Human research participants

Policy information about studies involving human research participants and Sex and Gender in Research.

Reporting on sex and gender	*Use the terms sex (biological attribute) and gender (shaped by social and cultural circumstances) carefully in order to avoid confusing both terms. Indicate if findings apply to only one sex or gender; describe whether sex and gender were considered in study design whether sex and/or gender was determined based on self-reporting or assigned and methods used. Provide in the source data disaggregated sex and gender data where this information has been collected, and consent has been obtained for sharing of individual-level data; provide overall numbers in this Reporting Summary. Please state if this information has not been collected. Report sex- and gender-based analyses where performed, justify reasons for lack of sex- and gender-based analysis.*
Population characteristics	*Describe the covariate-relevant population characteristics of the human research participants (e.g. age, genotypic information, past and current diagnosis and treatment categories). If you filled out the behavioural & social sciences study design questions and have nothing to add here, write "See above."*
Recruitment	*Describe how participants were recruited. Outline any potential self-selection bias or other biases that may be present and how these are likely to impact results.*
Ethics oversight	*Identify the organization(s) that approved the study protocol.*

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We are concerned that recent claims in the popular media about common mycorrhizal networks (CMNs) in forests are disconnected from evidence, and that bias toward citing positive effects of CMNs has developed in the scientific literature. We evaluated evidence to support claims made in the popular media primarily from CMN studies in forests. Given the importance of research in shaping messages in the popular media, we also examined how results from CMN research are interpreted and communicated by scientists. To do this, we examined the accuracy of statements citing influential field studies on CMN structure and function.
Research sample	To identify papers on common mycorrhizal network (CMN) function (interplant resource transfer or seedling performance) and structure (topology, architecture), we searched Web of Science – Core Collection on May 4, 2022 using the search string below. The search string was provided by Ian Mounts, University of Mississippi. The following search string was put into Title, Abstract, and Author Keywords joined by 'OR' ("common mycor* network*") OR ("common mycor* connection*") OR ("common mycor* interconnection*") OR ("mycor* network*") OR ("mycor* connection*") OR ("mycor* interconnection*") OR ("common mycor*") OR ("common ectomycor* network*") OR ("common ectomycor* connection*") OR ("common ectomycor* interconnection*") OR ("ectomycor* network*") OR ("ectomycor* connection*") OR ("ectomycor* interconnection*") OR ("common ectomycor*") OR ("common mycel* network*") OR ("common mycel* connection*") OR ("common mycel* interconnection*") OR ("mycel* network*") OR ("mycel* connection*") OR ("mycel* interconnection*") OR ("common mycel*") OR ("common fung* network*") OR ("common fung* connection*") OR ("common fung* interconnection*") OR ("fung* network*") OR ("fungal connection*") OR ("fungal interconnection*") OR ("common hyph* network*") OR ("common hyph* connection*") OR ("common hyph* interconnection*") OR ("hyph* network*") OR ("hyph* connection*") OR ("hyph* interconnection*") OR ("common hyph*") We further refined 'Topic' with 'Forest' joining it with the above search with 'AND'. We selected articles in English, excluded reviews, and set the time period from 1997–2022. We screened the resulting papers relevant to CMN function and structure, and from this list, we identified 'influential' field studies, defined as those having at least 50 citations, and evaluated citations of those studies.
Sampling strategy	We evaluated 593 papers citing seven influential studies on CMN structure and 1083 papers citing eleven influential studies on CMN function. The influential studies are listed in the Supplementary Information
Data collection	We evaluated citations on whether statements were supported by evidence presented in the referenced paper. In some cases, we disagreed with some main conclusions from influential studies (see Supplementary Tables 1 & 2). Citations of such studies were not always considered supported, if they simply repeated the conclusions of authors in the referenced study; rather, in some cases we deemed such citations unsupported if the evidence in the referenced study was weak or absent, or if alternative interpretations were consistent with the evidence. Citations outside common mycorrhizal network research were included in our evaluation. For each

	paper, one person identified statements citing the respective influential study, and scored them as supported or unsupported. Next, two other people confirmed the scoring of unsupported citations. Any disagreements were flagged, discussed, and resolved.
Timing and spatial scale	Timing: 1997–2022, spatial scale: worldwide
Data exclusions	Book chapters, non-retrievable sources, commentaries, studies in arts, and papers in languages other than English were not reviewed
Reproducibility	Two other people confirmed the scoring of unsupported citations. Any disagreements were flagged, discussed, and resolved.
Randomization	This does not apply to our analyses--there were no groupings.
Blinding	Not applicable

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging