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# Mycoheterotrophy in the wood-wide web

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The prevalence and potential functions of common mycorrhizal networks, or the 'wood-wide web', resulting from the simultaneous interaction of mycorrhizal fungi and roots of different neighbouring plants have been increasingly capturing the interest of science and society, sometimes leading to hyperbole and misinterpretation. Several recent reviews conclude that popular claims regarding the widespread nature of these networks in forests and their role in the transfer of resources and information between plants lack evidence. Here we argue that mycoheterotrophic plants associated with ectomycorrhizal or arbuscular mycorrhizal fungi require resource transfer through common mycorrhizal networks and thus are natural evidence for the occurrence and function of these networks, offering a largely overlooked window into this methodologically challenging underground phenomenon. The wide evolutionary and geographic distribution of mycoheterotrophs and their interactions with a broad phylogenetic range of mycorrhizal fungi indicate that common mycorrhizal networks are prevalent, particularly in forests, and result in net carbon transfer among diverse plants through shared mycorrhizal fungi. On the basis of the available scientific evidence, we propose a continuum of carbon transfer options within common mycorrhizal networks, and we discuss how knowledge on the biology of mycoheterotrophic plants can be instrumental for the study of mycorrhizal-mediated transfers between plants.

The roots or rootlike structures of most land plants are colonized by mycorrhizal fungi, which help plants to take up growth-limiting soil nutrients in exchange for photosynthetically fixed carbon[1]. These ancient interactions generally have low specificity and, consequently, 'common mycorrhizal networks' can be formed when a mycorrhizal fungus simultaneously colonizes the roots of different plant individuals[2–4] (Box 1). On the basis of indications that these networks can transfer resources between trees[5], common mycorrhizal networks in forests were labelled the 'wood-wide web', a concept that has since been expanded into a widespread fungal network that allows trees to exchange nutritional resources and even information[6–9]. Although the existence of common mycorrhizal networks is not in doubt, researchers have recently pointed out that scientific support is still lacking for many of these popular claims[10–14] and have identified a bias in citing positive effects of common mycorrhizal networks in the scientific literature[10]. The widespread occurrence and importance of common mycorrhizal networks have therefore remained controversial, particularly in the scientific community[10–14].

Yet, as mentioned in all recent evaluations of the occurrence and potential functions of common mycorrhizal networks[10,12–14], there is

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**Fig. 1 | The intricate root matrix of a forest ecosystem on the slopes of Mount Pirongia in New Zealand.** The brown roots are those of *Beilschmiedia tawa* (Lauraceae, magnoliids), the dominant tree species at this location. The white-yellowish roots are those of *Thismia hillii* (Thismiaceae, monocots), a perennial non-photosynthetic, mycoheterotrophic plant, which is linked to *B. tawa* by a common mycorrhizal network of *Rhizophagus* sp. (Glomeraceae) arbuscular mycorrhizal fungi[122]. A thin layer of leaf litter was removed before this picture was taken. Scale bar, 1 cm.

one phenomenon in which the establishment and function of common mycorrhizal networks is undisputed: mycoheterotrophy. Here, non-photosynthetic mycorrhizal plants represent diverse 'positive controls' for the potential ecological and evolutionary consequences of common mycorrhizal networks. The existence of mycoheterotrophic plant species, hundreds of which obtain carbon from surrounding green plants through shared ectomycorrhizal or arbuscular mycorrhizal fungi, is natural evidence for both the persistent formation of common mycorrhizal networks and their ability to act as an important carbon source for plants. However, because most mycoheterotrophic plants tend to be small understory herbs seen only during flowering and fruiting, they are usually ignored or considered as exceptions to the mutualistic carbon-for-nutrients exchange typical of the mycorrhizal symbiosis[15] and therefore have received little attention in the controversies surrounding common mycorrhizal networks. We argue that these fascinating plants, which had a key role in the discovery of mycorrhizas[16] and are at the centre of questions about mycorrhizal cheating[17], continue to play their part as the 'sphinxes of mycorrhizal research'[18]—natural examples of mycorrhiza-mediated carbon uptake in plants within common mycorrhizal networks. To underline their unique importance, we briefly summarize the current knowledge on mycoheterotrophic plants, discuss how their biology contributes to our understanding of the occurrence and functions of common mycorrhizal networks and highlight how they can have a key role in advancing our knowledge in this controversial field.

## Mycoheterotrophy

Mycoheterotrophy is a plant trophic mode defined by the ability to obtain carbon from root- and/or rhizoid-associated fungi[19,20]. The most obvious examples are the ~580 species of diverse, leafless, achlorophyllous plants, known as full mycoheterotrophs[21] (Fig. 1), including dicots, monocots, a gymnosperm and a bryophyte (Box 1). These evolved from photosynthetic mycorrhizal ancestors at least 40 times across land plants[20] (Fig. 2b), and their obligate mycoheterotrophic mode of life has mostly been deduced from the absence of photosynthesis[22], the absence of a direct (that is, haustorial) link to any host plant (hence, they are not holoparasites[23]) and dense fungal colonization in their roots or rhizoids[16,19] (Fig. 2a).

### BOX 1

## Key features

- Fully mycoheterotrophic plants (~580 species) do not photosynthesize and rely on carbon from mycorrhizal fungi for their entire development, largely underground. They belong to liverworts (Aneuraceae), gymnosperms (Podocarpaceae), monocots (Petrosaviaceae, Burmanniaceae, Thismiaceae, Triuridaceae, Iridaceae, Corsiaceae and Orchidaceae) and eudicots (Polygalaceae, Gentianaceae and Ericaceae). Many species appear to be locally rare, and some are considered indicators for undisturbed common mycorrhizal networks.
- Initially mycoheterotrophic plants (~28,000 species) are non-photosynthetic plants completely dependent on fungi for carbon in their early developmental stages. They belong to clubmosses (Lycopodiaceae), ferns (Ophioglossaceae, Psilotaceae and Gleicheniaceae), monocots (Orchidaceae) and eudicots (Ericaceae).
- Partially mycoheterotrophic plants combine autotrophy and mycoheterotrophy as adults. This has been experimentally tested for only a few plant species so far, but stable isotope signatures of carbon suggest that partial mycoheterotrophy occurs in a wide range of ferns, monocots and eudicots.
- The fungi targeted by mycoheterotrophic plants belong to a wide range of ectomycorrhizal fungi (Atheliales, Boletales, Agaricales, Russulales, Thelephorales, Hymenochaetales, Gomphales, Cantharellales, Sebacinales, Leotiomycetes, Dothideomycetes and Pezizomycetes), arbuscular mycorrhizal fungi (Glomerales and Diversisporales) and saprotrophic fungi (mostly Agaricales). Fully mycoheterotrophic plants often show higher specificity towards narrow ectomycorrhizal or arbuscular mycorrhizal fungal lineages than green plants.
- Mycoheterotrophy evolved over 40 times across arbuscular mycorrhizal, ectomycorrhizal and orchid mycorrhizal symbioses. In a mycoheterotrophic interaction, the flow of carbon is reversed relative to the net plant-to-fungus carbon flow that is characteristic of ectomycorrhizas and arbuscular mycorrhizas. Because mycoheterotrophs have often evolved from photosynthetic ectomycorrhizal or arbuscular mycorrhizal plants, they are considered as examples of mutualism breakdown.
- Symbiotic germination, in which dust-like seeds or plant spores with little or no reserves rely on fungal carbon for germination, is often considered a prerequisite for the evolution of initial and full mycoheterotrophy.
- Common mycorrhizal networks are formed when the same individual of mycorrhizal fungus physically links the roots of two or more individual plants, belonging to the same or different species. These networks have the potential to transfer molecules or signals among plants, and this has been the focus of many investigations.
- 'Wood-wide web' is a term coined by *Nature* in 1997. Although its initial use referred to resource transfer between specific trees and tree seedlings through a common mycorrhizal network, popular media has considerably broadened this concept to a fungal network through which most trees in a forest share resources and information.

The fungi of mycoheterotrophic plants have been repeatedly identified as fungi that form ectomycorrhizas or arbuscular mycorrhizas with green plants[24,25] or as free-living wood- or litter-decaying fungi[26]. Several DNA barcoding studies have found support for ectomycorrhizal

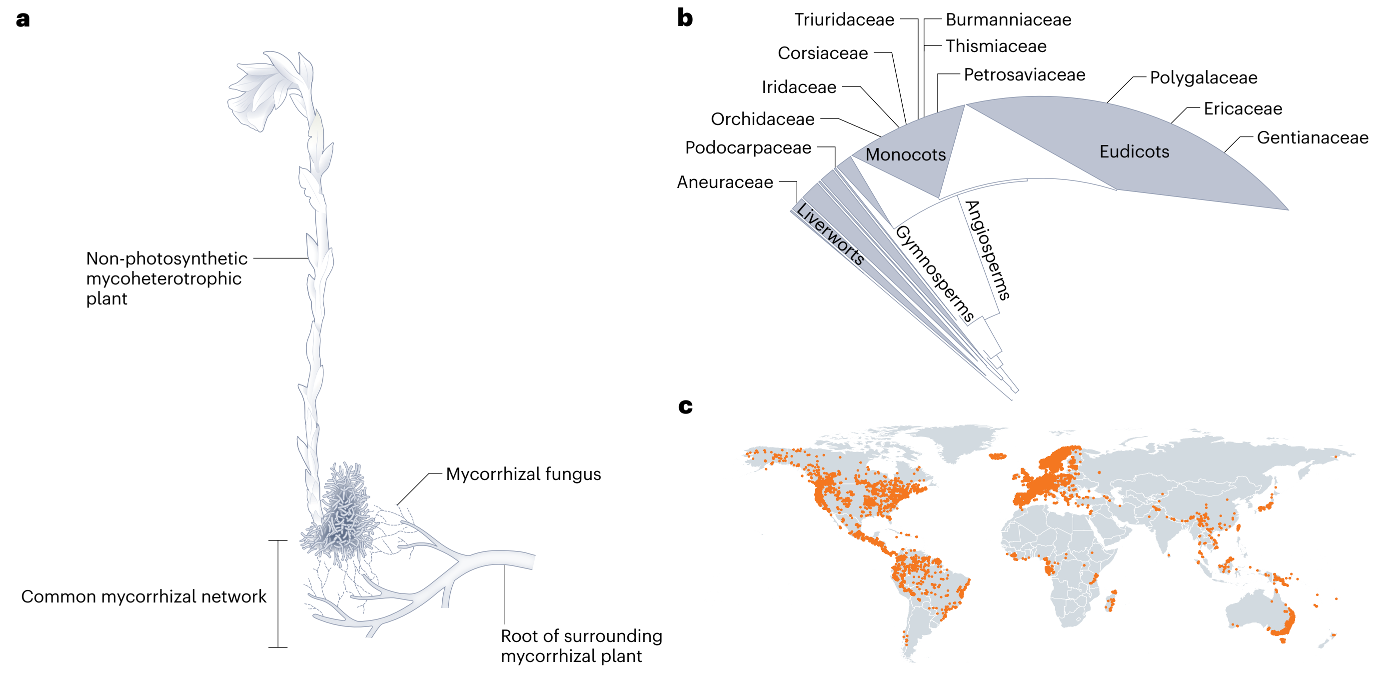

**Fig. 2 | Mycoheterotrophy in plants and its phylogenetic and geographic distribution. a**, Full mycoheterotrophy as evidence for interplant net carbon transfer through common mycorrhizal networks, with the example of the non-photosynthetic *Monotropa uniflora* (Ericaceae) linked to tree roots via ectomycorrhizal Russulaceae fungi. **b**, Occurrence of achlorophyllous mycoheterotrophic plants in families across the plant tree of life. **c**, Global distribution of observations of fully mycoheterotrophic angiosperms growing on arbuscular or ectomycorrhizal fungi based on available data from natural history collections (data from ref. 63).

or arbuscular mycorrhizal fungi simultaneously colonizing the roots of mycoheterotrophic plants and those of surrounding plants[25,27,28]. Ectomycorrhizal and arbuscular mycorrhizal fungi are obligate biotrophs with little or no capabilities for saprotrophy[29,30] or plant cell wall degradation[31]; therefore, mycoheterotrophy requires a carbon source such as a nearby photosynthetic host for the non-photosynthetic plant's fungi. These neighbouring plants provide all the carbon required by the mycorrhizal fungi[1,32], and via these fungi, carbon is provided to the mycoheterotrophic plant, thus creating a tripartite symbiosis. Natural abundances of stable carbon isotopes show that (fully) mycoheterotrophic plants have isotope signatures like those of their mycorrhizal fungi[33–35], which are enriched in heavy carbon and nitrogen isotopes compared with photosynthetic understory plants growing at the same location[36,37]. Tracer experiments using $^{13}$C or $^{14}$C and mycoheterotrophic plants growing on ectomycorrhizal fungi have provided additional evidence that fungi provide a pathway for the transfer of carbon from green plants to mycoheterotrophs[38–42].

Mycoheterotrophy is not limited to non-photosynthetic plants. Initial mycoheterotrophs obtain carbon during germination and their non-photosynthetic early developmental stages, and then they rely on photosynthesis later in development[19]. All ~28,000 species of orchids are considered initial mycoheterotrophs (some on ectomycorrhizal fungi but most on saprotrophic fungi, which do not form common mycorrhizal networks). Outside orchids, this mode of life is also known in Ericaceae and several genera of ferns and clubmosses, whose gametophytes are non-photosynthetic and colonized by ectomycorrhizal or arbuscular mycorrhizal fungi[20,43]. Importantly, initially mycoheterotrophic plants reveal that reliance on carbon from mycorrhizal fungi connected to photosynthetic plants is dynamic and can change over plant development[44].

In addition to initial mycoheterotrophs, some adult photosynthetic plants are known to obtain carbon from fungi, a mode of life known as 'partial mycoheterotrophy'[45] or 'mixotrophy'[46]. Carbon dioxide assimilation measurements indicate that the green orchid *Corallorhiza trifida* obtains 85% of its carbon from ectomycorrhizal fungi colonizing its roots[47]. In Orchidaceae and Ericaceae, natural abundances of stable isotopes intermediate between those of fully mycoheterotrophic species and autotrophic plant species provide further support for the existence of partial mycoheterotrophy[36,48,49]. In these partially mycoheterotrophic mature plants, the proportional gain of carbon from mycorrhizal fungi has been estimated to vary from near 0% to 84%[36]. Isotope studies indicate that carbon uptake in partial mycoheterotrophs can vary according to light levels, season, soil nutrients and developmental stage[50–54]. In some species, the ability to obtain considerable amounts of carbon from mycorrhizal fungi is supported by the natural occurrence of 'albino' plants and populations, which persist despite their non-functional photosynthesis[46,55–57]. Furthermore, analysis of natural abundances of stable isotopes suggests that partial mycoheterotrophy might be common in understory, photosynthetic, arbuscular mycorrhizal plants[58].

## The autotrophy–mycoheterotrophy continuum

Partially mycoheterotrophic plants are often closely related to fully mycoheterotrophic species and embedded in lineages where initial mycoheterotrophy is observed or suspected[21]. Evolutionary reconstructions support a stepwise evolution of mycoheterotrophy, from initial through partial to full mycoheterotrophy[59,60]. Overall, these observations support a model in which carbon uptake from mycorrhizal fungi is dynamic and can vary over ecological, evolutionary and plant developmental scales, leading to a continuum of carbon transfer options within common mycorrhizal networks, both ecological and evolutionary (Fig. 3). This continuum provides a functional framework to address questions regarding common mycorrhizal networks and their potential for interplant resource transfer. In particular, plants and fungi at the mycoheterotrophy end-point are expected to reveal common biological characteristics, which are instrumental for mycorrhizal-mediated

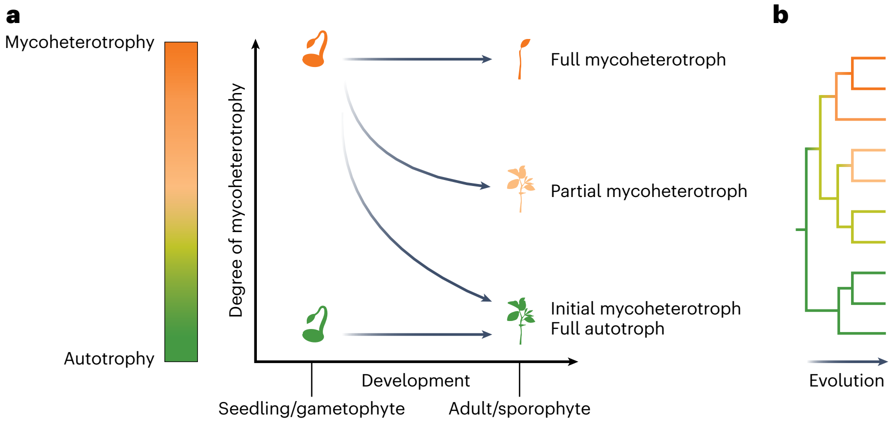

**Fig. 3 | The autotrophy–mycoheterotrophy continuum of mycorrhizal plants. a**, The continuum over plant development. **b**, The continuum over evolutionary timescales (based on ref. 21).

carbon transfer between green plants. Here we focus on carbon as the resource transferred, though others (for example, mineral nutrients) may be relevant to common mycorrhizal networks[61,62], as mycoheterotrophy is likely to primarily inform carbon transfer via common mycorrhizal networks.

## Common mycorrhizal networks are widespread

Karst et al.[10] questioned the claim that common mycorrhizal networks are widespread in forests. To evaluate this claim, they exclusively focused on evidence from trees and highlighted that, with current technology, it is difficult to confirm that continuous, non-transient mycelial connections exist between trees in the field. They concluded that support for the widespread occurrence of common mycorrhizal networks is limited, owing to the paucity of information on common mycorrhizal network structure, and especially dynamics, in the field.

However, because fully mycoheterotrophic plants growing on ectomycorrhizal or arbuscular mycorrhizal fungi provide natural evidence for the occurrence of common mycorrhizal networks, their distributions and those of their associated fungi offer additional information on the prevalence of common mycorrhizal networks. Locally, fully mycoheterotrophic plants are often rare (or difficult to observe), yet globally they have a wide distribution that is closely associated with the occurrence of forests[63] (Fig. 2c). Unlike typical mycorrhizal-generalist photosynthetic plants, individual species of fully mycoheterotrophic plants often show high specificity in their interactions with mycorrhizal fungi, including extreme specificity to a single ectomycorrhizal or arbuscular mycorrhizal lineage[64]. However, mycorrhizal specificity is not a requirement for mycoheterotrophy[65,66]. The fungi themselves belong to a phylogenetically wide range of arbuscular and ectomycorrhizal fungi—in fact, only a few major lineages of mycorrhizal fungi have not (yet) been found to be targeted by full mycoheterotrophs[67]. In the arbuscular mycorrhizal symbiosis, full mycoheterotrophs preferentially associate with Glomeraceae[68,69], which is the most abundant family of arbuscular mycorrhizal fungi in forests globally[70]. Several fully mycoheterotrophic Ericaceae species have also been found to associate with ectomycorrhizal fungi that are common in temperate forests[71]. Therefore, the global occurrence of fully mycoheterotrophic plants growing on mycorrhizal fungi and the wide range and distribution of fungi supporting these interactions strongly indicate that the potential for the formation of common mycorrhizal networks and carbon transfer is widespread.

Full mycoheterotrophs can take up several years to develop, from germination to fruiting[43,72], and mycoheterotrophic fern gametophytes live up to several years[73], showing that the physical link between mycorrhizal fungi—often a single fungus—and a neighbouring photosynthetic host plant is either maintained or continuously renewed over years. These observations further demonstrate the capacity of common mycorrhizal networks to persistently link the roots of different plant species under natural circumstances. Not surprisingly, mycoheterotrophs are considered indicators of undisturbed mycorrhizal networks such as old-growth forests[74–77].

## Common mycorrhizal networks facilitate carbon transfer between plants

The hypothesis that carbon is transferred between plants through common mycorrhizal networks is central to the current debate on the wood-wide web[10–14]. Although multiple pulse–chase experiments have shown that labelled carbon is transferred from a donor tree to a receiver tree or sapling[4,78–81], it remains under dispute whether carbon was transferred through a soil or mycorrhizal pathway[10,12]. However, to experimentally rule out the possibility that carbon is transferred through the soil rather than through a common mycorrhizal network, plant root systems would have to be separated by an air gap that physically separates the soil but still allows fungal hyphae to cross. As mycorrhizal fungi grow through soil and soil solution, it is challenging to maintain ecological relevance with this set-up. Also, because fungal hyphae are coated with aqueous films and fungal cell walls use apoplastic transport, this would not provide absolute proof for active carbon transport through a common mycorrhizal network.

Nevertheless, without carbon transfer via common mycorrhizal networks, mycoheterotrophic plants cannot exist. Because fully mycoheterotrophic plants provide evidence for carbon uptake from mycorrhizal fungi by plants (Fig. 2a), both the plants and their mycorrhizal fungi offer us clues into the mycorrhizal pathway. There is clear evidence that a wide range of photosynthetic plants also obtain carbon via this pathway, in both the arbuscular and ectomycorrhizal symbioses[36,59,82,83], and that the fungi involved also sustain mycoheterotrophic plants, which ultimately evolved from autotrophic ancestors[21,60]. Given the widespread existence of fully, initially and partially mycoheterotrophic plants, the question is not whether net carbon transfer between green plants occurs through common mycorrhizal networks, but rather how important this transfer is.

Mycoheterotrophic plants can also provide clues about the mechanisms by which plants get carbon from mycorrhizal fungi[14]. Although relatively few studies have focused on fungus-to-plant transport in mycoheterotrophic plants, they provide an important framework to explore mycorrhizal-mediated carbon uptake in green plants. It is often assumed that mycoheterotrophic plants obtain carbon from the ‘digestion’ of degenerating fungal hyphae or active lysis of hyphae, but given the quantity of fungal biomass in the roots of fully mycoheterotrophic plants, this mechanism has been considered insufficient to account for the full carbon demand of the plant[19]. Indeed, Kuga et al.[84] showed that carbon transfer from a *Ceratobasidium* fungus to the orchid *Spiranthes sinensis* occurs through both active transport and fungal degradation. Moreover, the fungal-induced growth of mycoheterotrophic protocorms (underground seedlings) of the orchid *Dactylorhiza purpurella* precedes lysis of fungal hyphae[85]. Also, the rapid transfer of $^{14}$C from fungus to the orchid *Goodyera repens*—plant-respired $^{14}CO_2$ was detected within seven hours[86]—indicates active carbon transfer from fungus to plant across intact membranes.

Carbon-labelling and genomic studies of mycoheterotrophic orchids have further revealed that trehalose is actively transported from fungus to plant and is probably the main carbon source supporting mycoheterotrophy for these species[32,87–89] (but see ref. 90). In vitro germination experiments with ectomycorrhizal Ericaceae, which are initially mycoheterotrophic, provide clear evidence that the developing plants can use trehalose as their only carbon source[43]. Trehalose is an important component of carbohydrate conversion and biosynthesis in algae, early-branching land plants and fungi, including ectomycorrhizal fungi and arbuscular mycorrhizal fungi, whereas sucrose has these roles in vascular plants[91–93]. The presence of a metabolic pathway in vascular plants for utilizing fungal trehalose as a carbon source may thus be an important component for mycorrhizal-mediated carbon uptake.

## Plants benefit from carbon transfer through common mycorrhizal networks

An outstanding challenge is to assess the effect of carbon transfer through common mycorrhizal networks on plants and plant communities[10,12,13]. The difficulty of quantifying carbon transfer through common mycorrhizal networks has been highlighted as a major reason for this challenge[11,12]. According to isotope mixing models, carbon gain in some partially mycoheterotrophic orchids and Ericaceae species is considerable and may constitute more than half of the total carbon budget of the plant[94]. Similar levels of carbon gain have been reported for candidate partial mycoheterotrophs associated with arbuscular mycorrhizal fungi[58]. The autotrophy and mycoheterotrophy end-points in these two-source mixing models are averages of whole-plant signatures. These averages usually show some variation[95], and the resulting estimates are therefore prone to large uncertainties[96]. Importantly, this technique only provides a unidirectional estimate of fungus-to-plant carbon fluxes. Although a photosynthetic plant may receive carbon from mycorrhizal fungi, it may still be a net carbon donor to these fungi[5].

In pulse–chase experiments on trees and tree saplings, only relatively small gains have been detected in aboveground plant tissue (<10% of the carbon acquired in plant tissue during the experiment[97–99] (but see ref. 100)), although factors such as low labelling intensity, the duration of the experiment and the heterogeneity of carbon partitioning may lead to considerable underestimates of net carbon gain[101]. A pulse–chase experiment on *Cephalanthera damasonium*, a partially mycoheterotrophic orchid, highlighted the importance of the latter process; even though the investigated plants perform photosynthesis, the resulting photosynthates are not used for the growth of perennial underground organs[54]. Similarly, Simard et al.[5] estimated that 13% to 45% of the total fungal carbon acquired in the roots was translocated to foliar tissue in tree saplings. Mycorrhizal-mediated carbon gain can therefore be considerably underestimated on the basis of measurements of aboveground tissue. Finally, dual-labelling experiments allow for the measurement of bidirectional carbon transfer between two plants connected by a common mycorrhizal network and thus the inference of net carbon transfer between plants when carbon transfer in one direction is larger than in the opposite direction. Only small levels (<10% of the total amount of carbon fixed by both plants) of net transfer have been reported using this technique[5,79], but always over short experiments (carbon 'pulse' periods of several hours followed by a 'chase' period of seven to nine days).

In the ectomycorrhizal symbiosis, it has been suggested that small amounts of carbon gain might be a by-product of nitrogen uptake[97]. But several studies indicate that nitrogen is transferred from the fungus to the plant in a non-organic form[102–105]. Similarly, in the arbuscular mycorrhizal symbiosis, both phosphorous and nitrogen are transferred from the fungus to the plant without carbon[106,107]. Carbon uptake is therefore unlikely to be solely a by-product of nutrient uptake. Yet, it is clear that carbon uptake by plants from mycorrhizal fungi may constitute only a minute fraction of the total plant biomass in forest ecosystems or even in individual plants[97]. Also, because no study has reported a positive effect on plant growth or performance due to carbon gain from common mycorrhizal networks, this phenomenon has been considered 'physiologically insignificant'[14]. Henriksson et al.[13] argued that if carbon uptake from mycorrhizal fungi influenced tree establishment and survival, seedling abundance and growth should be higher within the zone of active roots and associated mycorrhizal fungi of large trees than outside this zone—a concept known as the 'mother tree hypothesis'[13,14]. In line with this view, a slight carbon gain through mycorrhizal fungi is effective only if it outweighs interplant competition for light, nutrients and space, as well as growth-supressing negative plant–soil feedbacks. However, according to our knowledge of the dynamics of mycoheterotrophy in relation to environmental factors and plant development, even a minute amount of carbon during a particular developmental stage can be a determining factor in the success of plant establishment and development if it outweighs potential costs[108]. We therefore propose focusing on the question of whether small amounts of carbon gain can lead to niche expansion of species or a competitive advantage, rather than comparing overall plant performance under different environmental conditions. Similarly, on an ecosystem level, the absolute amount of plant carbon uptake from common mycorrhizal networks probably has an insignificant contribution to overall carbon cycling processes. Nevertheless, if widespread, mycoheterotrophy could be a determining factor in the composition of the forest understory vegetation, which not only includes the next generation of canopy trees but also can make up the majority of plant species in forest stands[109], is a substantial component of the carbon sink of forests[110] and is an overlooked reservoir of biodiversity[111]. The timing and the ecological drivers of carbon transfer, rather than its relative contribution to plant biomass, may therefore be of central importance to plant communities. Nevertheless, some researchers will continue to focus on the need for conclusive physiological evidence of relevant net plant-to-plant transfer via fungi, while others will continue to focus on demonstrating fitness effects for the plants receiving any such transfer from neighbouring plants via shared fungi. Mycoheterotrophic plants represent a natural reference point, so far untapped, for both of those research lines.

## Cheating the mycorrhizal symbiosis

The occurrence of carbon uptake by plants from mycorrhizal fungi has been further questioned from an evolutionary perspective: "Why should mycorrhizal fungi export carbon at all when the evolutionary stability of the symbiosis is based on fungal import of plant carbon in exchange for nutrients such as nitrogen?"[13]. This view ignores the fact that cheating is ubiquitous in mutualisms, as predicted by theory[112], and the mycorrhizal mutualism is no exception, as there are clear indications that both mycorrhizal plants and fungi behave as cheaters[18,59,71,113,114]. Experiments indicate that mycorrhizal nutrient exchange dynamics are better understood as community-wide interactions between multiple players rather than as strict exchanges between individual plants and their symbionts[115,116]. In addition, our knowledge from mycoheterotrophy stresses the importance of temporal dynamics of resource exchange in the mycorrhizal symbiosis, which can change in rate and direction over time. While plants can be mycoheterotrophic during early developmental stages, they may be autotrophic and thus mutualistic during later stages. This may stabilize the symbiosis through selection for net overall fitness benefits for both partners over their lifetimes[117]. Thus, the multiple independent evolutionary shifts towards mycoheterotrophy within mycorrhizal plant lineages as part of the autotrophy–mycoheterotrophy continuum provide unequivocal examples supporting the evolutionary stability of mycoheterotrophy without the need to invoke fungal altruism.

## Mycoheterotrophic plants as positive controls for carbon transfer in common mycorrhizal networks

By explicitly positioning the current debate on the occurrence and functions of common mycorrhizal networks in the context of the autotrophy–mycoheterotrophy continuum of the mycorrhizal symbiosis (Fig. 3), fully mycoheterotrophic plants emerge as positive controls for mycorrhizal-mediated transfer of carbon between plants. While at the autotrophic side of the continuum, small gains of carbon are difficult to measure and their effects hard to assess, plants positioned at the mycoheterotrophic side provide essential clues on the ecology and physiology of fungus-to-plant carbon transfer. These clues can help to uncover the true extent of resource transfer in common mycorrhizal networks and their importance in plant biology and biodiversity.

In particular, future studies on the genomics and metabolomics of mycoheterotrophic plants are needed to reveal the mechanisms, composition, quantity and chronology of metabolite transfers from fungus to plant; characterize the metabolic pathways involved in storage and allocation by the plant of the carbon and nutrients received from fungal partners; and determine any metabolite fluxes from plant to fungus and their roles in establishing, maintaining or repaying the fungal association[96]. Further investigation of common molecular, morphological, developmental and biochemical characteristics of mycoheterotrophic plants and their mycorrhizal fungi are necessary to reveal potential partially or initially mycoheterotrophic plant lineages beyond those that include fully mycoheterotrophic species[118–120], and to identify potential predispositions for fungus-to-plant carbon transfer through phylogenetic comparative analyses. Recent advances in the cultivation of fully and initially mycoheterotrophic plants provide important opportunities to study these aspects[43].

Continued molecular identification and genome sequencing of the mycorrhizal fungi associated with mycoheterotrophic plants and their interaction patterns in mycorrhizal networks are necessary to assess the fungal diversity involved in mycorrhizal-mediated resource transfer[28] and will eventually reveal the genetic and metabolic pathways of the fungal partner. Finally, key insight into the regulation of the mycorrhizal symbiosis will probably develop from uncovering the environmental conditions under which mycoheterotrophy occurs[121]. Labelling studies at forest sites where partially mycoheterotrophic plants occur will provide insights into these aspects. Subsequently, these genomic, metabolomic, morphological, biochemical, symbiotic and environmental data will allow for targeted detection of mycorrhizal-mediated carbon gain in plants, including trees and their saplings.

## Conclusions

Mycoheterotrophy provides natural evidence for the prevalence of common arbuscular and ectomycorrhizal networks and for their ability to mediate physiologically and evolutionarily relevant net carbon transfer among plants. The widespread occurrence of mycoheterotrophy, involving diverse plants and mycorrhizal fungi, suggests that persistent common mycorrhizal networks are common, particularly in forests, and can support net carbon transfer between green plants. How common the latter phenomenon is remains to be determined. The autotrophy–mycoheterotrophy continuum of mycorrhizal plants provides a functional framework to address this question. In particular, the biology of plants and fungi involved in the mycoheterotrophy end of the continuum offers essential tools to test for mycorrhizal-mediated resource transfer between plants. Mycoheterotrophy on mycorrhizal fungi and its widespread occurrence challenge the dogma of carbon-for-nutrients transfer in the mycorrhizal symbiosis as well as the assumption that all green plants are strict autotrophs. Hence, this phenomenon offers exciting opportunities for the investigation of common mycorrhizal networks and their function. In this sense, mycoheterotrophic plants may be exceptions that both prove and challenge rules.

## References

1. Smith, S. E. & Read, D. J. *Mycorrhizal Symbiosis* 3rd edn (Academic Press, 2008).
2. Newman, E. Mycorrhizal links between plants—their functioning and ecological significance. *Adv. Ecol. Res.* **18**, 243–270 (1988).
3. Gorzelak, M. A., Asay, A. K., Pickles, B. J. & Simard, S. W. Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. *AoB Plants* **7**, plv050 (2015).
4. van der Heijden, M. G. A., Martin, F. M., Selosse, M. A. & Sanders, I. R. Mycorrhizal ecology and evolution: the past, the present, and the future. *New Phytol.* **205**, 1406–1423 (2015).
5. Simard, S. W. et al. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* **388**, 579–582 (1997).
6. Wohlleben, P. *The Hidden Life of Trees: What They Feel, How They Communicate—Discoveries from a Secret World* (Greystone Books, 2016).
7. Grant, R. Do trees talk to each other? *Smithsonian* 48–57 (March 2018).
8. Sheldrake, M. *Entangled Life: How Fungi Make Our Worlds, Change Our Minds and Shape Our Futures* (Random House, 2020).
9. Simard, S. W. *Finding the Mother Tree: Discovering the Wisdom of the Forest* (Knopf Doubleday, 2021).
10. Karst, J., Jones, M. D. & Hoeksema, J. D. Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests. *Nat. Ecol. Evol.* **7**, 501–511 (2023).
11. 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).
12. Figueiredo, A. F., Boy, J. & Guggenberger, G. Common mycorrhizae network: a review of the theories and mechanisms behind underground interactions. *Front. Fungal Biol.* **30**, 735299 (2021).
13. Henriksson, N. et al. Re-examining the evidence for the mother tree hypothesis—resource sharing among trees via ectomycorrhizal networks. *New Phytol.* **239**, 19–28 (2023).
14. Robinson, D. G. et al. Mother trees, altruistic fungi, and the perils of plant personification. *Trends Plant Sci.* **29**, 20–31 (2024).
15. Bever, J. D. et al. Rooting theories of plant community ecology in microbial interactions. *Trends Ecol. Evol.* **25**, 468–478 (2010).
16. Kamienski, F. Les organes végétatifs du *Monotropa hypopitys* L. *Mem. Soc. Natl Sci. Nat. Math. Cherb.* **24**, 5–40 (1882).
17. Johnson, N. A., Graham, J. A. & Smith, F. A. Functioning of mycorrhizal associations along the mutualism–parasitism continuum. *New Phytol.* **135**, 575–585 (1997).
18. Bidartondo, M. I. The evolutionary ecology of myco-heterotrophy. *New Phytol.* **167**, 335–352 (2005).
19. Leake, J. R. The biology of myco-heterotrophic ('saprotrophytic') plants. *New Phytol.* **127**, 171–216 (1994).
20. Merckx, V. S. F. T. (ed.) *Mycoheterotrophy: The Biology of Plants Living on Fungi* (Springer, 2013).
21. Jacquemyn, H. & Merckx, V. S. F. T. Mycorrhizal symbioses and the evolution of trophic modes in plants. *J. Ecol.* **107**, 1567–1581 (2019).
22. Graham, S. W., Lam, V. K. & Merckx, V. S. F. T. Plastomes on the edge: the evolutionary breakdown of mycoheterotroph plastid genomes. *New Phytol.* **214**, 48–55 (2017).
23. Heide-Jørgensen, H. S. *Parasitic Flowering Plants* (Brill, 2008).
24. Taylor, D. L. & Bruns, T. D. Independent, specialized invasions of the ectomycorrhizal mutualism by two non-photosynthetic orchids. *Proc. Natl Acad. Sci. USA* **94**, 4510–4515 (1997).

25. Bidartondo, M. I. et al. Epiparasitic plants specialized on arbuscular mycorrhizal fungi. *Nature* **419**, 389–392 (2002).
26. Ogura-Tsujita, Y., Gebauer, G., Hashimoto, T., Umata, H. & Yukawa, T. Evidence for novel and specialised mycorrhizal parasitism: the orchid *Gastrodia confusa* gains carbon from saprotrophic *Mycena*. *Proc. R. Soc. B* **276**, 761–767 (2009).
27. Bidartondo, M. I., Kretzer, A. M., Pine, E. M. & Bruns, T. D. High root concentration and uneven ectomycorrhizal diversity near *Sarcodes sanguinea* (Ericaceae): a cheater that stimulates its victims? *Am. J. Bot.* **87**, 1783–1788 (2000).
28. Gomes, S. I. F., Fortuna, M. A., Bascompte, J. & Merckx, V. S. F. T. Mycoheterotrophic plants preferentially target arbuscular mycorrhizal fungi that are highly connected to autotrophic plants. *New Phytol.* **235**, 2034–2045 (2022).
29. Tisserant, E. et al. Genome of an arbuscular mycorrhizal fungus provides insight into the oldest plant symbiosis. *Proc. Natl Acad. Sci. USA* **110**, 20117–20122 (2013).
30. Lindahl, B. D. & Tunlid, A. Ectomycorrhizal fungi—potential organic matter decomposers, yet not saprotrophs. *New Phytol.* **205**, 1443–1447 (2015).
31. Kohler, A. et al. Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nat. Genet.* **47**, 410–415 (2015).
32. Jiang, Y. et al. Plants transfer lipids to sustain colonization by mutualistic mycorrhizal and parasitic fungi. *Science* **356**, 1172–1175 (2017).
33. Trudell, S. A., Rygiewicz, P. T. & Edmonds, R. L. Nitrogen and carbon stable isotope abundances support the mycoheterotrophic nature and host specificity of certain achlorophyllous plants. *New Phytol.* **160**, 391–401 (2003).
34. Zahn, F. E. et al. Novel insights into orchid mycorrhiza functioning from stable isotope signatures of fungal pelotons. *New Phytol.* **239**, 1449–1463 (2023).
35. Gomes, S. I. F. et al. Stable isotope natural abundances of fungal hyphae extracted from the roots of arbuscular mycorrhizal mycoheterotrophs and rhizoctonia-associated orchids. *New Phytol.* **239**, 1166–1172 (2023).
36. Hynson, N. A. et al. in *Mycoheterotrophy: The Biology of Plants Living on Fungi* (ed. Merckx, V. S. F. T.) 297–342 (Springer, 2013).
37. Gomes, S. I. F., Merckx, V. S. F. T., Kehl, J. & Gebauer, G. Mycoheterotrophic plants living on arbuscular mycorrhizal fungi are generally enriched in $^{13}$C, $^{15}$N, and $^{2}$H isotopes. *J. Ecol.* **108**, 1250–1261 (2020).
38. Björkman, E. *Monotropa hypopitys* L.—an epiparasite on tree roots. *Physiol. Plant.* **13**, 308–327 (1960).
39. McKendrick, S. L., Leake, J. R. & Read, D. J. Symbiotic germination and development of myco-heterotrophic plants in nature: transfer of carbon from ectomycorrhizal *Salix repens* and *Betula pendula* to the orchid *Corallorhiza trifida* through shared hyphal connections. *New Phytol.* **145**, 539–548 (2000).
40. McKendrick, S. L., Leake, J. R., Taylor, D. L. & Read, D. J. Symbiotic germination and development of myco-heterotrophic plants in nature: ontogeny of *Corallorhiza trifida* and characterisation of its mycorrhizal fungi. *New Phytol.* **145**, 523–537 (2000).
41. Bougoure, J. J., Brundrett, M. C. & Grierson, P. F. Carbon and nitrogen supply to the underground orchid, *Rhizanthella gardneri*. *New Phytol.* **186**, 947–956 (2010).
42. Bidartondo, M. I., Bruns, T. D., Weiß, M., Sérgio, S. & Read, D. J. Specialized cheating of the ectomycorrhizal symbiosis by an epiparasitic liverwort. *Proc. R. Soc. B* **270**, 835–842 (2003).
43. Figura, T., Tylová, E., Šoch, J., Selosse, M.-A. & Ponert, J. *In vitro* axenic germination and cultivation of mixotrophic Pyroloideae (Ericaceae) and their post-germination ontogenetic development. *Ann. Bot.* **123**, 625–639 (2019).
44. Schweiger, J. M. I., Bidartondo, M. I. & Gebauer, G. Stable isotope signatures of underground seedlings reveal the organic matter gained by adult orchids from mycorrhizal fungi. *Funct. Ecol.* **32**, 870–881 (2018).
45. Gebauer, G. & Meyer, M. $^{15}$N and $^{13}$C natural abundance of autotrophic and myco-heterotrophic orchids provides insight into nitrogen and carbon gain from fungal association. *New Phytol.* **160**, 209–223 (2003).
46. Julou, T. et al. Mixotrophy in orchids: insights from a comparative study of green individuals and nonphotosynthetic individuals of *Cephalanthera damasonium*. *New Phytol.* **166**, 639–653 (2005).
47. Cameron, D. D., Preiss, K., Gebauer, G. & Read, D. J. The chlorophyll-containing orchid *Corallorhiza trifida* derives little carbon through photosynthesis. *New Phytol.* **183**, 358–364 (2009).
48. Zimmer, K. et al. Wide geographical and ecological distribution of nitrogen and carbon gains from fungi in pyroloids and monotropoids (Ericaceae) and in orchids. *New Phytol.* **175**, 166–175 (2007).
49. Liebel, H. T. et al. C and N isotope signatures reveal constraints to nutritional modes in orchids of the Mediterranean and Macaronesia. *Am. J. Bot.* **97**, 903–912 (2010).
50. Preiss, K., Adam, I. K. & Gebauer, G. Irradiance governs exploitation of fungi: fine-tuning of carbon gain by two partially myco-heterotrophic orchids. *Proc. R. Soc. B* **277**, 1333–1336 (2010).
51. Hynson, N. A., Mambelli, S., Amend, A. S. & Dawson, T. E. Measuring carbon gains from fungal networks in understory plants from the tribe Pyroleae (Ericaceae): a field manipulation and stable isotope approach. *Oecologia* **169**, 307–317 (2012).
52. Matsuda, Y., Shimizu, S., Mori, M., Ito, S.-I. & Selosse, M.-A. Seasonal and environmental changes of mycorrhizal associations and heterotrophy levels in mixotrophic *Pyrola japonica* (Ericaceae) growing under different light environments. *Am. J. Bot.* **99**, 1177–1188 (2012).
53. Suetsugu, K., Ohta, T. & Tayasu, I. Partial mycoheterotrophy in the leafless orchid *Cymbidium macrorhizon*. *Am. J. Bot.* **105**, 1595–1600 (2018).
54. Lallemand, F. et al. Mixotrophic orchids do not use photosynthates for perennial underground organs. *New Phytol.* **221**, 12–17 (2019).
55. Roy, M. et al. Why do mixotrophic plants stay green? A comparison between green and achlorophyllous orchid individuals in situ. *Ecol. Monogr.* **83**, 95–117 (2009).
56. Stöckel, M., Meyer, C. & Gebauer, G. The degree of mycoheterotrophic carbon gain in green, variegated and vegetative albino individuals of *Cephalanthera damasonium* is related to leaf chlorophyll concentrations. *New Phytol.* **189**, 790–796 (2011).
57. Matsuda, Y. et al. Communities of mycorrhizal fungi in different trophic types of Asiatic *Pyrola japonica* sensu lato (Ericaceae). *J. Plant Res.* **133**, 841–853 (2020).
58. Giesemann, P., Rasmussen, H. N. & Gebauer, G. Partial mycoheterotrophy is common among chlorophyllous plants with *Paris*-type arbuscular mycorrhiza. *Ann. Bot.* **127**, 645–653 (2021).
59. Lallemand, F. et al. The elusive predisposition to mycoheterotrophy in Ericaceae. *New Phytol.* **212**, 314–319 (2016).
60. Wang, D., Jacquemyn, H., Gomes, S. I. F., Vos, R. A. & Merckx, V. S. F. T. Symbiont switching and trophic mode shifts in Orchidaceae. *New Phytol.* **231**, 791–800 (2021).
61. Zackrisson, O., Nilsson, M.-C., Dahlberg, A. & Jäderlund, A. Interference mechanisms in conifer–Ericaceae–feathermoss communities. *Oikos* **78**, 209–220 (1997).
62. Smith, J. M., Whiteside, M. D. & Jones, M. D. Rapid nitrogen loss from ectomycorrhizal pine germinants signaled by their fungal symbiont. *Mycorrhiza* **30**, 407–417 (2020).

63. Gomes, S. I. F., van Bodegom, P., Merckx, V. S. F. T. & Soudzilovskaia, N. Global distribution of mycoheterotrophic plants. *Glob. Ecol. Biogeogr.* **28**, 1133–1145 (2019).
64. Merckx, V., Bidartondo, M. I. & Hynson, N. A. Myco-heterotrophy: when fungi host plants. *Ann. Bot.* **104**, 1255–1261 (2009).
65. Hynson, N. A. & Bruns, T. D. Evidence of a myco-heterotroph in the plant family Ericaceae that lacks mycorrhizal specificity. *Proc. R. Soc. B* **276**, 4053–4059 (2009).
66. Roy, M. et al. Two mycoheterotrophic orchids from Thailand tropical dipterocarpacean forests associate with a broad diversity of ectomycorrhizal fungi. *BMC Biol.* **7**, 51 (2009).
67. Hynson, N. A. & Bruns, T. D. Fungal hosts for mycoheterotrophic plants: a nonexclusive, but highly selective club. *New Phytol.* **185**, 598–601 (2010).
68. Merckx, V. S. et al. Mycoheterotrophic interactions are not limited to a narrow phylogenetic range of arbuscular mycorrhizal fungi. *Mol. Ecol.* **21**, 1524–1532 (2012).
69. Perez-Lamarque, B., Selosse, M.-A., Öpik, M., Morlon, H. & Martos, F. Cheating in arbuscular mycorrhizal mutualism: a network and phylogenetic analysis of mycoheterotrophy. *New Phytol.* **226**, 1822–1835 (2020).
70. Větrovský, T. et al. GlobalAMFungi: a global database of arbuscular mycorrhizal fungal occurrences from high-throughput sequencing metabarcoding studies. *New Phytol.* **240**, 2151–2163 (2023).
71. Bidartondo, M. I. & Bruns, T. D. Extreme specificity in epiparasitic Monotropoideae (Ericaceae): widespread phylogenetic and geographical structure. *Mol. Ecol.* **10**, 2285–2295 (2001).
72. Leake, J. R., McKendrick, S. L., Bidartondo, M. I. & Read, D. J. Symbiotic germination and development of the myco-heterotroph *Monotropa hypopitys* in nature and its requirement for locally distributed *Tricholoma* spp. *New Phytol.* **163**, 405–423 (2004).
73. Winther, J. & Friedman, W. Arbuscular mycorrhizal symbionts in *Botrychium* (Ophioglossaceae). *Am. J. Bot.* **94**, 1248–1255 (2007).
74. Franklin, J. F. et al. *Ecological Characteristics of Old-Growth Douglas-Fir Forests* (United States Department of Agriculture, 1981).
75. Cheek, M. & Williams, S. in *African Plants: Biodiversity, Taxonomy and Uses* (eds Timberlake, J. & Kativu, S.) 39–49 (Royal Botanic Gardens Kew, 1999).
76. Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y. & Kranabetter, J. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fenn. (Hels)* **36**, 307–327 (2002).
77. Moola, F. & Vasseur, L. Recovery of late-seral vascular plants in a chronosequence of post-clearcut forest stands in coastal Nova Scotia, Canada. *Plant Ecol.* **172**, 183–197 (2004).
78. Philip, L., Simard, S. & Jones, M. Pathways for below-ground carbon transfer between paper birch and Douglas-fir seedlings. *Plant Ecol. Divers.* **3**, 221–233 (2010).
79. 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).
80. 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).
81. 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).
82. Suetsugu, K. et al. Isotopic evidence of arbuscular mycorrhizal cheating in a grassland gentian species. *Oecologia* **192**, 929–937 (2020).
83. Suetsugu, K. et al. Isotopic and molecular data support mixotrophy in *Ophioglossum* at the sporophytic stage. *New Phytol.* **228**, 415–419 (2020).
84. Kuga, Y., Sakamoto, N. & Yurimoto, H. Stable isotope cellular imaging reveals that both live and degenerating fungal pelotons transfer carbon and nitrogen to orchid protocorms. *New Phytol.* **202**, 594–605 (2014).
85. Hadley, G. & Williamson, B. Analysis of the post-infection growth stimulus in orchid mycorrhiza. *New Phytol.* **70**, 445–455 (1971).
86. Cameron, D. D., Johnson, I., Read, D. J. & Leake, J. R. Giving and receiving: measuring the carbon cost of mycorrhizas in the green orchid, *Goodyera repens*. *New Phytol.* **180**, 176–184 (2008).
87. Smith, S. E. Physiology and ecology of orchid mycorrhizal fungi with reference to seedling nutrition. *New Phytol.* **65**, 488–499 (1966).
88. Ponert, J., Šoch, J., Vosolsobě, S., Čiháková, K. & Lipavská, H. Integrative study supports the role of trehalose in carbon transfer from fungi to mycotrophic orchid. *Front. Plant Sci.* **12**, 793876 (2021).
89. Li, M. H. et al. Genomes of leafy and leafless *Platanthera* orchids illuminate the evolution of mycoheterotrophy. *Nat. Plants* **8**, 373–388 (2022).
90. Ho, L. H. et al. GeSUT4 mediates sucrose import at the symbiotic interface for carbon allocation of heterotrophic *Gastrodia elata* (Orchidaceae). *Plant Cell Environ.* **44**, 20–33 (2021).
91. Bécard, G., Doner, L. W., Rolin, D. B., Douds, D. D. & Pfeffer, P. E. Identification and quantification of trehalose in vesicular-arbuscular mycorrhizal fungi by in vivo $^{13}$C NMR and HPLC analyses. *New Phytol.* **118**, 547–552 (1991).
92. Martin, F., Boiffin, V. V. & Pfeffer, P. E. Carbohydrate and amino acid metabolism in the *Eucalyptus globulus*–*Pisolithus tinctorius* ectomycorrhiza during glucose utilization. *Plant Physiol.* **118**, 627–635 (1998).
93. Lunn, J. E., Delorge, I., Figueroa, C. M., Van Dijck, P. & Stitt, M. Trehalose metabolism in plants. *Plant J.* **79**, 544–567 (2014).
94. Selosse, M.-A. & Roy, M. Green plants eating fungi: facts and questions about mixotrophy. *Trends Plant Sci.* **14**, 64–70 (2009). 2009.
95. Farquhar, G. D., Ehleringer, J. R. & Hubick, K. T. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **40**, 503–537 (1989).
96. Leake, J. R. & Cameron, D. D. Physiological ecology of mycoheterotrophy. *New Phytol.* **185**, 601–605 (2010).
97. Simard, S. W. et al. Mycorrhizal networks: mechanisms, ecology and modelling. *Fungal Biol. Rev.* **26**, 39–60 (2012).
98. Klein, T., Siegwolf, R. T. W. & Körner, C. Belowground carbon trade among tall trees in a temperate forest. *Science* **352**, 342–344 (2016).
99. 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).
100. Avital, S., Rog, I., Livne-Luzon, S., Cahanovitc, R. & Klein, T. Asymmetric belowground carbon transfer in a diverse tree community. *Mol. Ecol.* **31**, 3481–3495 (2022).
101. Klein, T., Rog, I., Livne-Luzon, S., van der Heijden, M. G. A. & Körner, C. Belowground carbon transfer across mycorrhizal networks among trees: facts, not fantasy. *Open Res. Eur.* **3**, 168 (2023).
102. Selle, A. et al. The high-affinity poplar ammonium importer PttAMT1.2 and its role in ectomycorrhizal symbiosis. *New Phytol.* **168**, 697–706 (2005).
103. Couturier, J. et al. The expanded family of ammonium transporters in the perennial poplar plant. *New Phytol.* **174**, 137–150 (2007).

104. Nehls, U. & Plassard, C. Nitrogen and phosphate metabolism in ectomycorrhizas. *New Phytol.* **220**, 1047–1058 (2018).
105. Stuart, E. K. & Plett, K. L. Digging deeper: in search of the mechanisms of carbon and nitrogen exchange in ectomycorrhizal symbioses. *Front. Plant Sci.* **10**, 1658 (2020).
106. Govindarajulu, M. et al. Nitrogen transfer in the arbuscular mycorrhizal symbiosis. *Nature* **435**, 819–823 (2005).
107. Karandashov, V. & Bucher, M. Symbiotic phosphate transport in arbuscular mycorrhizas. *Trends Plant Sci.* **10**, 22–29 (2005).
108. Bidartondo, M. I., Burghardt, B., Gebauer, G., Bruns, T. D. & Read, D. J. Changing partners in the dark: isotopic and molecular evidence of ectomycorrhizal liaisons between forest orchids and trees. *Proc. R. Soc. B* **271**, 1799–1806 (2004).
109. Gilliam, F. S. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* **57**, 845–858 (2007).
110. Dirnböck, T. et al. Substantial understory contribution to the C sink of a European temperate mountain forest landscape. *Landsc. Ecol.* **35**, 483–499 (2020).
111. Landuyt, D. et al. The functional role of temperate forest understorey vegetation in a changing world. *Glob. Change Biol.* **25**, 3625–3641 (2019).
112. Bronstein, J. L., Alarcón, R. & Geber, M. The evolution of plant–insect mutualisms. *New Phytol.* **172**, 412–428 (2006).
113. Merckx, V. & Bidartondo, M. I. Breakdown and delayed cospeciation in the arbuscular mycorrhizal mutualism. *Proc. R. Soc. B* **275**, 1029–1035 (2008).
114. Walder, F. & van der Heijden, M. Regulation of resource exchange in the arbuscular mycorrhizal symbiosis. *Nat. Plants* **1**, 15159 (2015).
115. Henriksson, N. et al. The mycorrhizal tragedy of the commons. *Ecol. Lett.* **24**, 1215–1224 (2021).
116. Durant, E. et al. Herbivore-driven disruption of arbuscular mycorrhizal carbon-for-nutrient exchange is ameliorated by neighboring plants. *Curr. Biol.* **33**, 2566–2573 (2023).
117. Field, K. J. et al. From mycoheterotrophy to mutualism: mycorrhizal specificity and functioning in *Ophioglossum vulgatum* sporophytes. *New Phytol.* **205**, 1492–1502 (2015).
118. Eriksson, O. & Kainulainen, K. The evolutionary ecology of dust seeds. *Perspect. Plant Ecol. Evol. Syst.* **13**, 73–87 (2011).
119. Giesemann, P., Rasmussen, H. N., Liebel, H. T. & Gebauer, G. Discreet heterotrophs: green plants that receive fungal carbon through *Paris*-type arbuscular mycorrhiza. *New Phytol.* **226**, 960–966 (2020).
120. Perotto, S. & Balestrini, R. At the core of the endomycorrhizal symbioses: intracellular fungal structures in orchid and arbuscular mycorrhiza. *New Phytol.* https://doi.org/10.1111/nph.19338 (2023).
121. Sheldrake, M. et al. A phosphorus threshold for mycoheterotrophic plants in tropical forests. *Proc. R. Soc. B* **284**, 20162093 (2017).
122. Gomes, S. I., Aguirre-Gutiérrez, J., Bidartondo, M. I. & Merckx, V. S. Arbuscular mycorrhizal interactions of mycoheterotrophic *Thismia* are more specialized than in autotrophic plants. *New Phytol.* **213**, 1418–1427 (2017).

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## Author contributions

The focus of this Perspective was conceived by all the authors. V.S.F.T.M. led the writing, with contributions from S.I.F.G., D.W., C.V., H.J., F.E.Z., G.G. and M.I.B.

## Competing interests

The authors declare no competing interests.

## Additional information

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