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REVIEW

Mycorrhizal Networks

The functionality of arbuscular mycorrhizal networks across scales of experimental complexity and ecological relevance

E. Magkourilou[1] | **C. A. Bell**[2] | **T. J. Daniell**[3] | **K. J. Field**[1]

[1]Plants, Photosynthesis and Soil, School of Biosciences, University of Sheffield, Sheffield, UK

[2]School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK

[3]Molecular Microbiology: Biochemistry to Disease, School of Biosciences, University of Sheffield, Sheffield, UK

Correspondence
E. Magkourilou
Email: emagkourilou1@sheffield.ac.uk

K. J. Field
Email: k.j.field@sheffield.ac.uk

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Abstract

1. One of the most prevalent symbioses on Earth is that formed between the majority of land plants and arbuscular mycorrhizal (AM) fungi. Through these intimate associations, AM fungi transfer soil nutrients to their plant hosts in exchange for photosynthetically fixed carbon resources.
2. It has been hypothesised that this nutritional mutualism is evolutionarily stable because both partners are in control of the exchange of resources and can discriminate between partners according to whichever offers the highest returns.
3. However, in nature, plant–AM symbioses are exposed to a wealth of additional biotic and abiotic interactions which can affect the regulation of carbon-for-nutrient exchange between symbionts. Moreover, the extraradical hyphae of AM fungi make up underground networks that may be interactive or physically connected, known as common mycorrhizal networks (CMNs). These can link neighbouring plants, potentially further influencing resource distribution across the network. How these layers of complexity interact to influence resource regulation and allocation between plants and AM fungi is not often considered by experimental designs.
4. Here, we review resource allocation in AM symbioses, scaling up from evidence from reductionist experimental systems using axenic root organ cultures to complex systems incorporating multiple neighbouring plants dealing with other, co-occurring symbionts.
5. As experimental designs increase in scale and ecologically relevant complexity, the carbon-for-nutrient exchange between plants and their AM symbionts is increasingly subject to disruption associated with the wider ecological context, such as the intricacies of the plant-fungal interactions in a CMN or the presence of co-occurring organisms.

KEYWORDS
biological markets, common mycorrhizal networks, mycorrhizal symbiosis, plant symbionts, plant-symbiont resource regulation

1 | ARBUSCULAR MYCORRHIZAL SYMBIOSES: AN OVERVIEW

One of the oldest (Redecker et al., 2000) and most widespread (Brundrett & Tedersoo, 2018) symbiotic associations on Earth is that which occurs between the roots (or rhizoids) of nearly all plants and mycorrhizal fungi. The most common type is formed between arbuscular mycorrhizal (AM) fungi of the *Glomeromycotina* subphylum (Spatafora et al., 2017) and 72% of vascular plant species (Brundrett & Tedersoo, 2018). AM fungi are obligate biotrophs, relying on their plant hosts for their entire carbon (C) nutrition (Bago & Bécard, 2002; Figure 1). In exchange, through their extraradical mycelium, AM fungi forage for and supply their hosts with critical soil nutrients such as phosphorus (P) and nitrogen (N; Smith & Read, 2010; Figure 1).

Increased access and assimilation of soil nutrients are considered the primary benefits of associating with AM fungi for plants, especially in nutrient-poor soils where P and N are the main growth limiting factors (Mosse & Phillips, 1971; Smith & Read, 2010). Plant responses to AM colonisation range from positive to negative, varying substantially within (Ellouze et al., 2015; Sawers et al., 2017; Watts-Williams, 2022) and between species and often depending on the combination of plant-fungal species involved (Hoeksema et al., 2010; Klironomos, 2003). However, the extent and mechanisms, as well as the external influences, that govern the exchange of resources and the outcomes of the symbiosis remain unresolved in the vast majority of instances. Evidence suggests that nutritional outcomes and plant growth responses driven by the relationship are very context-dependent (Bennett & Groten, 2022), with biotic factors such as cultivar (Elliott et al., 2021; Ellouze et al., 2015; Sawers et al., 2017; Thirkell et al., 2016; Watts-Williams, 2022), species or functional group of both plant host and AM fungi (Klironomos, 2003), as well as abiotic factors such as CO_2 concentration (Field et al., 2012; Thirkell et al., 2020) influencing the mycorrhizal receptivity of host plants and the functioning of the symbiosis (Caris et al., 1998; Thirkell et al., 2021; Treseder, 2004).

In addition to positive growth responses, plant benefits derived from associating with AM fungi may also include enhanced responses to abiotic constraints such as drought (Ruiz-Lozano et al., 2016; Symanczik et al., 2018) and protection against biotic pressures, including pests and diseases (Berdeni et al., 2018; Cameron et al., 2013; Jung et al., 2012; Koricheva et al., 2009; Sikes et al., 2009). Although it is theoretically and technically challenging to decouple the nutritional from the non-nutritional benefits provided to plants by AM fungi (Delavaux et al., 2017), it does appear that host mycorrhiza-induced resistance and tolerance against pathogens are not necessarily related to AM-mediated nutrient provision (De Kesel et al., 2021; Fritz et al., 2006; Jung et al., 2012; Liu et al., 2007; Schouteden et al., 2015; Vos et al., 2012). In any case, the overall costs and benefits of AM symbioses appear very context-dependent (Bennett & Groten, 2022), despite studies often measuring only a single trait (e.g. plant growth promotion) and rarely considering the implications on AM fungi themselves.

AM fungal hyphae grow outwards from colonised roots into the surrounding soil, forming a mycelial web known as a 'mycorrhizal network' (MN). In some cases, hyphae meet and fuse via anastomosis (de Novais et al., 2017). The MN of 1 AM genotype or the anastomosis of separate mycelia can reach and colonise neighbouring plants of the same or different species, forming what is then described as a 'common mycorrhizal network' (CMN; Giovannetti et al., 2004; Mikkelsen et al., 2008). Studies on the capacity of such networks to facilitate the transfer of C between plants first appeared in the 1980s (e.g. Francis & Read, 1984). The implications that such interplant C transfer could have on plant diversity were also addressed using laboratory microcosms (Grime et al., 1987) with debate soon arising as to the mechanisms involved (Grime et al., 1988). Further debate

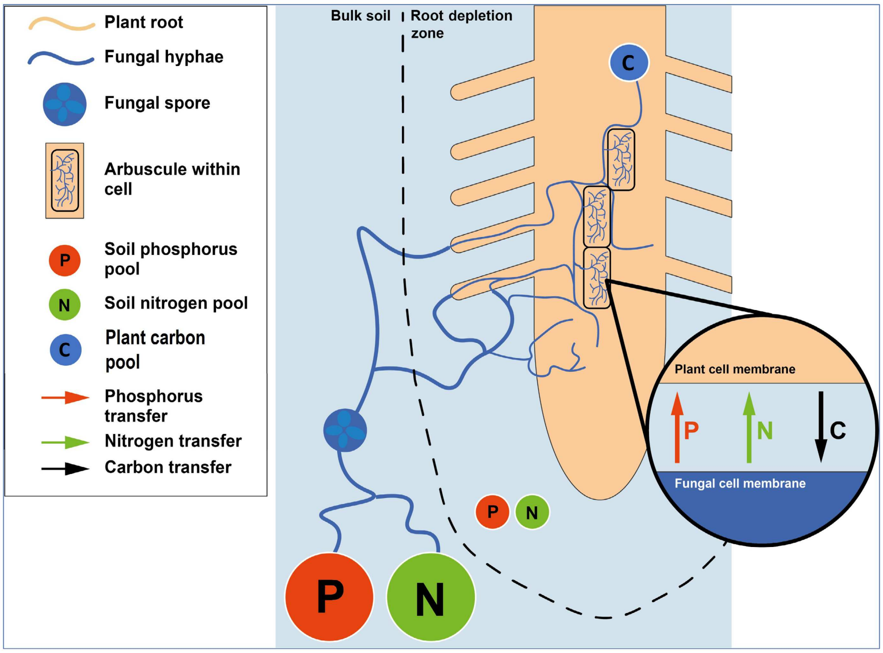

FIGURE 1 Schematic representation of arbuscular mycorrhizal hyphae extending from the root depletion zone to the inside of the plant host roots where C-for-nutrient exchange occurs between the two partners (adapted from Watts et al., 2023).

about the ecological relevance of CMNs, especially in terms of the impact on plant hosts (Fitter et al., 1998), began almost as soon as the idea of ectomycorrhizal (ECM) CMNs facilitating net C transfer between forest trees started to gain traction (Robinson & Fitter, 1999; Simard et al., 1997). Recently, this debate has resurfaced (Henriksson et al., 2023; Karst et al., 2023; Robinson et al., 2023), raising important questions about the suitability of experimental designs employed to study ECM CMNs in forests and highlighting how findings from relevant studies have been extrapolated or miscited to support claims that are not unequivocally supported by the underlying data.

Despite the ongoing debate, it is clear that CMNs exist across mycorrhizal types, including AMs, and that they play a potentially important role in plant community composition and ecosystem function (Tedersoo et al., 2020). In ECM systems, C movement from host trees to a MN (potentially a CMN) and then further to neighbouring trees of similar and distinct phylogenies has been detected (Cahanovitc et al., 2022). Similarly, in microcosms including both ECM and AM trees, C transfer between individuals has also been detected; however, in this case, the proportion of transfer occurring via a CMN versus alternative means such as by diffusion through the soil could not be determined (Avital et al., 2022). In AM systems, experimental evidence supports a role for CMNs in modulating resource allocation below-ground (Mikkelsen et al., 2008) and allowing for the transmission of signals (e.g. for defence) between neighbouring plants (Alaux et al., 2020; Babikova et al., 2013; Barto et al., 2012; Song et al., 2010, 2014).

2 | REGULATION OF RESOURCE ALLOCATION IN AM SYMBIOSES

The evolution and dynamics behind the bidirectional resource exchange between AM fungi and their host plants are often described using a 'biological markets' framework (e.g. Noë & Kiers, 2018). One interpretation of this model suggests that nutrients supplied by AM fungi and plants are 'commodities' to be traded, and both 'partners' perceive the cost and benefits of the symbiosis, discriminating among alternative partners according to who offers the best 'exchange rate' (Werner et al., 2014). Theoretical models have proposed this is underpinned by a tightly coupled C-for-P exchange (Fitter, 2006); however, the exact principles of biological market theory and how it applies in the context of plants and AM fungi remain a topic of debate (Kiers et al., 2016; van der Heijden & Walder, 2016; Walder & van der Heijden, 2015). For example, access to alternative partners is a prerequisite for partner discrimination, and in the case of AM fungi, MNs and CMNs allow this to occur. However, although MNs are an integral part of AM fungal community structure and function, it is unclear how the presence of a CMN influences resource regulation and, specifically, whether they provide a route by which sanctions and preferential resource allocation in plant-mycorrhizal symbioses can be undermined (Kiers & Denison, 2008). It is possible that the effectiveness of host-imposed punishment could be altered, as fungi denied resources by one host plant may receive resources from another plant connected to the same CMN (Kiers & Denison, 2008).

The majority of research conducted to assess mycorrhizal resource exchange deploys experimental designs based either on monoxenic culture of AM fungi with a plant, usually a root organ culture on sucrose-rich media, or on pots filled with either a sterilised or natural soil, as well as with non-soil mixes such as sand and perlite. All approaches have yielded important and interesting findings; however, each is not without constraints. As such, the appropriate caveats must be applied when interpreting data and generalisations on the regulation of resource allocation in AM symbioses should be made with caution. The renewed debate around the functionality of CMNs is raising the bar on how research on CMNs is conducted and reported, which is timely considering the number of critical research questions that remain unresolved.

This review aims to assess the extent to which AM symbioses, and CMNs in particular, operate via C-for-nutrient exchanges. More specifically, we explore under which scenarios plant and AM fungal partners appear to be able to control the C-for-nutrient exchange for their own benefit (e.g. as per a 'reciprocal rewards' type of regulation suggested by Kiers et al., 2011) or equally, what are the conditions that can disrupt such an exchange. To do so, we categorise evidence gathered across a gradient of ecological complexity and relevance; from simple monoxenic experimental systems involving single plant–AM interactions to more complex (and ecologically relevant) soil-based systems sometimes involving multiple plant hosts, AM fungi and other co-occurring symbionts. This allows us to reflect on the strengths and weaknesses of each experimental approach; but also, as we critically evaluate findings from different approaches, we are able to provide alternative or additional mechanisms for the allocation of resources. Although there is some evidence for a coupled C-for-nutrient exchange in simple AM–plant symbioses, new patterns emerge as the scale of observation expands from simplified axenic systems to soil systems incorporating communities of plants coexisting with other non-mycorrhizal symbionts. By revealing the caveats and context dependencies of past findings, and by linking them to more recent studies, we aim to inform the continued debate on the regulation of resources across AM–plant symbioses (Noë, 2021; Prescott et al., 2020, 2021) and to help strengthen future experiments.

3 | EXPERIMENTAL APPROACHES FOR INVESTIGATING RESOURCE ALLOCATION IN AM SYMBIOSES

3.1 | Compartmentalised monoxenic microcosms

Using compartmentalised Petri dishes containing root organ cultures and AM fungi, it has been shown that the AM fungal uptake and supply of P (Bücking & Shachar-Hill, 2005) and N (Fellbaum et al., 2012) to roots is triggered by increased C supply via a plant host, in line with a 'reciprocal rewards' mode of regulation. Further evidence from monoxenic microcosms supports this, suggesting that roots preferentially allocate more C to AM compartments that offer a more generous supply of fungal-acquired nutrients (Kiers et al., 2011). While a 'reciprocal rewards'-based mechanism could explain the evolutionary stabilisation of the AM–plant symbioses (Kiers & van der Heijden, 2006), it is important to note that in some cases (e.g. Kiers et al., 2011) the C movement from root to fungus and the P movement from fungus to root have been tested on separate plate systems, and thus, a direct link between the two flows within each system cannot be drawn.

By tagging rock phosphate apatite with fluorescent quantum-dot nanoparticles and tracking its movement, it has also been shown that AM fungi can transfer P from 'rich' to 'poor' patches of the same MN (van 't Padje, Bonfante, et al., 2021; van 't Padje, Werner, et al., 2021; Whiteside et al., 2019) or across a CMN linking two separate root compartments (van 't Padje et al., 2020). Consequently, in the latter case, roots growing in these 'poorer' P patches were found to acquire more P transferred from the other 'richer' side of the CMN, although this effect was not instantaneous (van 't Padje et al., 2020). This evidence suggests that, at least in vitro, when patches of a CMN have restricted access to nutrients, the entire MN might be supported (in terms of C) by a single host, while the least contributing host might benefit directly through nutrient acquisition from the CMN without giving much in return. However, when P concentration is high or when it does not vary greatly between different parts of a MN, transport of P might be compromised as, rather than distributing P across the network where it can be taken up by roots, the fungus might increase the allocation of P to its storage structures (van 't Padje, Bonfante, et al., 2021; van 't Padje, Werner, et al., 2021; Whiteside et al., 2019). That said, this hypothesis contrasts with findings from a visual assessment of fungal structures where high P availability increased the formation of branched absorbing structures at the expense of storage structures (Olsson et al., 2014).

Under conditions of limited C availability, AM fungi accumulate more P in their spores and hyphae (Hammer et al., 2011) likely because C provision to hyphae, and especially to spores, becomes reduced (Olsson et al., 2014). Potentially, this is a strategy that the fungus has evolved to supply nutrients with a better exchange rate if either root demand for nutrients or plant C supply increase at a later stage (van 't Padje, Bonfante, et al., 2021; van 't Padje, Werner, et al., 2021; Whiteside et al., 2019). Although the exact mechanisms behind such a strategy remain unresolved, a level of detection of the changing conditions by the MN would appear necessary, as would the capacity of this signal to then be transferred to arbuscules where the fungus would be able to control the rate of nutrient exchange through changes in nutrient transporters for C-based sugars (Doidy et al., 2012) and/or lipids (Jiang et al., 2017; Keymer et al., 2017) as well as fungal-acquired N (Koegel et al., 2013, 2017) and P (Walder et al., 2015; Xie et al., 2013). It is likely that plant C does not represent a significant cost to the plant as it is typically fixed surplus to requirements and that other, more parsimonious explanations such as source-sink dynamics regulate, or at least influence, resource allocation among plants and AM fungi (Corrêa et al., 2023; Prescott et al., 2020, 2021; van der Heijden & Walder, 2016).

An additional pattern of increased AM fungal allocation of P to roots with a higher C root status has been shown using a four-compartment Petri dish system where 'donor' roots were connected via a CMN to two 'receiver' roots of varying C status (Lekberg et al., 2010). It was also suggested that C was transported from one root section to the other via AM fungi, with the strength being stronger in the direction from C-rich to C-limited roots (Lekberg et al., 2010). However, in either case, the transferred C remained in the fungal tissue of both the C-rich and the C-limited roots (Lekberg et al., 2010). This distinction is important as it adds to the evidence contradicting the significance of plant-to-plant C transfer (e.g. Pfeffer et al., 2004; Voets et al., 2008) and suggests that any fungal-mediated C movement is likely primarily of benefit to the fungus.

From experiments involving compartmentalised monoxenic microcosms, it appears overall that both AM and plant partners are able to control the bidirectional C-for-nutrient exchange characteristic of AM symbioses, although the level of control seems to be impacted by abiotic conditions. The exact mechanisms underpinning this remain unresolved and could be equally attributed (at least partly) to other drivers such as sink-source dynamics. The monoxenic approach to investigating dynamics and regulation of mycorrhizal function, whether as one-on-one or CMN-wide interactions between plants and fungi, has a number of strengths and weaknesses. Monoxenic systems are simpler and more easily manipulated or controlled than those that include soil and other microbes. As such, causation can be attributed with more confidence and more mechanistic insights revealed. On the other hand, their artificial nature (notably the absence of soil and the lack of photosynthetic plant materials through use of root organ culture), lack of ecological complexity as well as the potentially altered AM fungal evolution stemming from the continuous in vitro propagation (Kokkoris & Hart, 2019) limit our ability to draw conclusions on what really governs resource allocation in natural AM ecosystems.

3.2 | Soil-based microcosms with a single plant host

Despite the mechanistic insights that monoxenic systems can potentially provide, an important consideration with any such reductionist approach is that the results might not be representative of what occurs in more natural, complex settings. Reciprocal allocation of resources between symbionts in monoxenic experiments involving root organ culture might not be representative of effects observed where whole plants in soil-based experiments are used as, among other things, the lack of a photosynthetic plant shoot is likely to influence nutrient demand and thus sink strength dynamics between host plant and AM fungi (Smith & Smith, 2011). Another consideration relates directly to the challenge of transferring experimental techniques and conclusions from tightly controlled and highly simplified plate systems to more complex soil-based systems. For example, AM fungal-mediated increases in the uptake of quantum-dot apatite were not detected in either root or shoot in a soil-based experiment (van 't Padje, Bonfante, et al., 2021; van 't Padje, Werner, et al., 2021), although they were detected in similar monoxenic experiments (e.g. van 't Padje, Bonfante, et al., 2021; van 't Padje, et al., 2021; Whiteside et al., 2019).

Experiments conducted in soil-based experiments have also shown how the functional significance of mycorrhizal symbioses, and even the partner selection process, can be strongly influenced by environmental conditions, which typically (and necessarily) remain constant in axenic systems. For example, the preferential allocation of plant-fixed C to the more beneficial fungal partner has been shown to decrease with increasing soil P availability (Ji & Bever, 2016). This is likely because under high P availability (e.g. fertilisation) the C allocation to AM fungi by host plants sometimes decreases considerably as the mycorrhizal-derived benefits are also reduced (Olsson et al., 2010). Similarly, in high or low P soils, plants might favour the direct over the mycorrhizal P uptake pathway, while under intermediate, suboptimal conditions the mycorrhizal pathway may become preferred (Zhang et al., 2021). This suggests that the dynamics of resource regulation of a single plant species might change as its 'fungal collaboration gradient' (Bergmann et al., 2020) changes from a 'do-it-yourself' resource uptake to a 'mycorrhizal outsourcing' of resource uptake according to external conditions.

Ultimately, although environmental conditions (e.g. elevated atmospheric CO_2 concentrations) do not always influence the levels of mycorrhizal colonisation or the total amount of plant C that AM fungi receive (e.g. Thirkell et al., 2021), changes in environmental conditions can still influence how plants associate with AM fungi species and vice versa (Forczek et al., 2022). For example, the level of CO_2 in the atmosphere has been found to influence plant-to-AM fungi C dynamics, with shifts in the AM taxa that received most of the plant C at ambient or elevated CO_2 levels correlating with niche and life history strategies (Drigo et al., 2010). This could have knock-on effects on plant–AM symbioses and the distribution of resources if the fungal species that receive most of the plant C became dominant over time. In a different case, the preferential allocation of plant C to the more beneficial AM fungi and a reciprocal differential P uptake decreased with shading (Zheng et al., 2015). A similar pattern was observed in a separate experiment, where even though *Medicago trunculata* preferentially allocated C to *Funneliformis mosseae* over *Claroideoglomus claroideum* under simulated drought conditions, this was not the case under a shading treatment (Forczek et al., 2022). The lack of a shading-induced preferential allocation of resources could be explained by the reduction in the availability of above-ground resources caused by the shading treatment which, as previously described, can lead plants to reduce their overall C allocation to AM fungi (Olsson et al., 2010). But even if it does not translate to a detectable change in how a plant allocates C to AM fungi, shading can still lead to a rapid shift in the mycorrhizal community composition (Forczek et al., 2022). Ultimately, all of these examples point to the importance of considering the longer-term implications relating to the regulation of C-for-nutrient exchange, such as the potential longer-term benefits of maintaining simultaneous root colonisation by different AM fungi ('evolutionary bet-hedging'; Veresoglou et al., 2022), even in the absence of consistent synergistic effects of inoculations with multiple AM species (e.g. Jansa et al., 2008; Martina et al., 2013). Although relevant data are scarce, incorporating some longer-term cost–benefit calculations into biological markets or trade balance models would greatly benefit their prediction capacity on how the C-for-nutrient exchange is regulated under different scenarios.

Using a split-root experimental system, where each fungal partner is inoculated separately in different parts of the root similar setup, Bever et al. (2009) demonstrated increased plant C delivery to the more beneficial (i.e. growth-promoting) of 2 AM fungal symbionts tested. A similar pattern was later confirmed where the preferential allocation of C from a plant to 2 AM fungi separated by a split-root system was matched by a differential P uptake by the 2 AM fungi (Zheng et al., 2015). It is important to note that split-root designs might introduce positive bias as it has been evidenced that spatial separation of fungal partners might be required for partner discrimination, and thus, the preferential allocation of C by plants to the more mutualistic AM fungi (Ji & Bever, 2016). That said, in other cases, reducing spatial structure by mixing soil has increased the abundance of the more 'cooperative' AM fungal symbionts (Verbruggen et al., 2012), suggesting that plants preferentially associate with more mutualistic species, even under mixed species conditions. It might well be that in split-root systems, plants favour different parts of their root system rather than specifically different AM fungi.

Despite the caveats and context dependencies, there is evidence from soil-based experiments that plant hosts preferentially allocate more C to AM fungal partners that offer a more generous supply of nutrients in return (Bever et al., 2009; Kiers et al., 2011; Lendenmann et al., 2011; Zheng et al., 2015). However, another important aspect which limits our understanding of resource regulation and allocation in AM–plant symbioses is the oversight of the potential impact of other co-occurring organisms that might compete for plant and/or fungal resources. This is particularly important considering that, for example, AM colonisation can increase the attractiveness and consumption of plants by above-ground insect herbivores (Koricheva et al., 2009). In turn, the presence of above-ground insect herbivores alters the mycorrhizal fungal community composition and can lead to reduced (Gehring & Whitham, 2002) or increased (Frew et al., 2023) mycorrhizal colonisation (Figure 2a). In other cases, above-ground herbivory does not affect the degree to which plants are colonised by AM fungi (Charters et al., 2020; Zhao et al., 2024), although this appears affected by atmospheric CO_2 concentrations (Charters et al., 2020; Figure 2a).

Above-ground herbivory can also reduce root C concentrations and increase foliar P of mycorrhizal plants (Frew et al., 2023; Figure 2a). Frew et al. (2024) hypothesised that when above-ground herbivores or pathogens infect a mycorrhizal plant host, the AM fungal communities in the roots might be shaped by the capacity of the AM species to either (i) tolerate the herbivore/pathogen-induced constraints on plant C or (ii) enhance plant defences against the same herbivores/pathogens. Additionally, as well as the amount of C, the shift in the type of C provided to AM fungi in response to phytophagous pest interactions is likely to also be an important factor

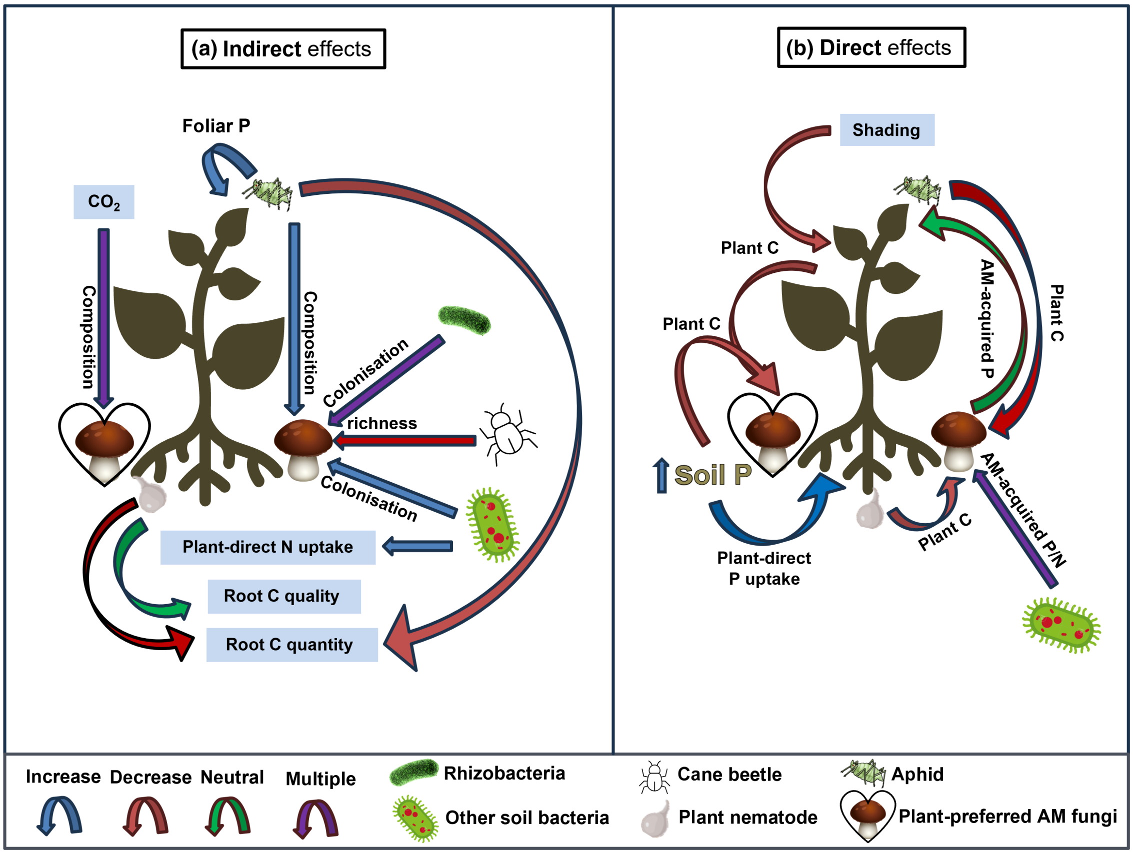

FIGURE 2 Illustrative summary of how above and below-ground complexity might have (a) indirect and (b) more direct effects on the C-for-nutrient exchange in plant-arbuscular mycorrhizal (AM) symbioses. The information is drawn from the referenced studies in the above section (i.e. Bell et al., 2022, 2024; Charters et al., 2020; Frew, 2022; Jiang et al., 2021; Larimer et al., 2014; Rozmoš et al., 2021; Svenningsen et al., 2018; Zhang et al., 2016, 2024). The direction and colour of the arrows illustrate the direction of influence as per the legend.

in determining the community composition (Bell et al., 2024). For example, some plant pests might induce plant limitation of certain C compounds to AM fungi more than others, thereby indirectly selecting AM species that may themselves have a preferential C usage or an ability to cope with less of a certain resource (i.e., fatty acids or hexose sugars).

Below-ground, root-herbivory by cane beetle larvae (*Dermolepida alborhirum*) changes the community structure of AM fungi and reduces AM fungal species richness in roots (Frew, 2022; Figure 2a). Plant P concentration also becomes reduced (Frew, 2022), although it remains unclear whether this is due to a reduction in fungal-acquired P or an impact on the plant's own capacity to acquire P directly. Certain bacterial genera, such as *Halangium*, *Pseudomonas*, *Devosia* and *Sulfurifustis* also commonly associate with AM fungi and stimulate AM fungi colonisation (Zhang et al., 2024; Figure 2a). Plant inoculation with the bacterial genus *Devosia* was specifically found to lead to enhanced direct N uptake by the plant (Zhang et al., 2024; Figure 2a) which could mean that these plants become less reliant on AM fungi for their N nutrition. AM fungi and rhizobacteria also often act synergistically on plant growth, although rhizobia inoculation can lead to neutral (Pérez-De-Luque et al., 2017) or even negative effects on AM colonisation (Larimer et al., 2014; Figure 2a). Regardless of whether they might be synergistic or not, interactions between AM fungi and other organisms are typically not captured by most studies focusing on C-for-nutrient exchange in plant-mycorrhizal symbioses. However, this is important because any indirect impact on AM fungi (e.g. degree of colonisation) or the plant (e.g. uptake of N via non-mycorrhizal means) might influence the extent that each can control the C-for-nutrient exchange.

The presence of multiple, simultaneous and diverse symbionts on the plants can also have other, more direct impacts on the C-for-nutrient exchange between AM fungi and their plant hosts. For example, certain soil bacteria appear to suppress (Svenningsen et al., 2018) or enhance (Jiang et al., 2021; Zhang et al., 2016) the P-delivery capacity of AM fungi (Figure 2b). It has been demonstrated in vitro that the AM fungus's capacity to obtain N from an organic source can increase upon the presence of the soil bacterium *Paenibacillus* sp. and the protist *Polysphondylium pallidum*, but other chitinolytic bacteria such as *Janthinobacterium* sp. did not have an effect (Rozmoš et al., 2021; Figure 2b). Also, the allocation of plant C-to-AM fungi decreases dramatically following plant exposure to aphids (Charters et al., 2020) or plant-parasitic nematodes (Bell et al., 2022), although in both cases the supply of fungal-acquired nutrients to the plants was largely maintained (Figure 2b). A split-root experiment found that roots colonised by AM fungi and/or potato cyst nematodes (PCN) accumulate more plant C than asymbiotic roots (per gram of root), possibly because roots with symbionts represent a greater sink for plant C than those without (Bell et al., 2024). Furthermore, roots colonised by AM fungi receive more C than roots of the same host that are infected with PCN in a spatially separated compartment within a split-root experiment, which, again, could simply suggest that AM fungi represent a larger C sink than PCN (Bell et al., 2024). An alternative, not mutually exclusive hypothesis, is that plants may preferentially allocate C-to-AM-hosting roots rather than those hosting PCN to selectively enhance mutualist interactions and limit the effects of parasitic infection (Bell et al., 2024). It could also be true, however, that plants simply have a greater degree of control over the plant–AM fungi flow rather than the plant–parasite flow, or that the supply of resources towards AM fungi is simply an indirect consequence of the plant trying to shuttle resources away from PCN (Bell et al., 2024). In any case, more research is needed to understand the multiple ways that other symbionts can influence the C-for-nutrient exchange directly or indirectly so that this information can then be built into appropriate biological markets, or other, models.

Contrary to expectations based on a 'reciprocal rewards' mode of regulation, it appears that above- or below-ground herbivory drives asymmetry in the C-for-nutrient exchange between plants and AM symbionts. Another consideration for the theoretical framework of the interactions between AM fungi and other co-occurring symbionts is that individual organisms such as aphids or PCN function as distinct entities with the aim of acquiring resources to produce a second generation. In contrast, due to their coenocytic hyphae and spores, heterokaryotic nuclear organisation, and ability to fuse to form vast networks (Kokkoris et al., 2020), AM fungi cannot be easily classified as distinct, singular entities. This in turn might have implications on the evolution of dynamics of inter- and intra-species competition between mycorrhizal fungi and result in the acquisition of C for the benefit of the entire MN rather than a single part of it consisting of a single genet. Moreover, the lifetime and cycle of co-occurring symbionts are likely to influence the C-for-nutrient exchange between hosts and their mycorrhizal symbionts. For example, aphids are seasonal, and one generation of PCN feeding lasts around 6 weeks, whereas, despite the patchy and ephemeral nature of the fungal colonisation and fungal intracellular structures (Friese & Allen, 1991), AM associations may last the entirety of a plant's lifetime. This could mean that in nature AM fungi might have evolved to endure relatively short periods of a pathogen/parasite-constrained C flow before supply returns to pre-stress levels. As such, given the impacts of plant and fungal phenologies as well as the impacts of any additional biotic and abiotic interactions, considerations and extrapolations of AM functionality to an ecosystem or even global scale should be undertaken with careful thought.

Overall, while some evidence of the ability of plant and AM fungal partners to each control the C-for-nutrient exchange also stems from soil-based experiments, this is increasingly influenced or disrupted by various factors such as environmental conditions, the presence of additional/multiple symbionts, and the specific experimental design used (e.g. split root). More research is needed on the varied ways that biotic and abiotic factors influence the C-for-nutrient exchange, and the longer implications of such factors need to be understood and incorporated into relevant models. As with monoxenic approaches, soil-based experimental systems have strengths and weaknesses. Soil-based experiments add some necessary ecological complexity, and their findings are likely to be more realistic than those stemming from monoxenic plate-based systems. However, increased ecologically complexity (e.g. a more diverse soil microbial community) can lead to additional, interactive indirect or direct consequences to both plant and fungal partners which in turn make it more challenging to predict or explain the mechanism behind resource allocation between symbionts. One such limitation is the difficulty of accounting for AM fungal C respiration, especially in a complex soil system with a diverse microbial community. Additionally, when soil-based systems involve only one plant, it is important to consider that plant–plant interactions are lacking and specific hypotheses such as the ability of AM fungi to associate with more beneficial plant hosts within a CMN cannot be tested.

3.3 | Common mycorrhizal networks and multi-species interactions in soil-based experiments

Although MNs and CMNs are an integral part of AM fungal functioning, it is unclear how the presence of a CMN influences resource regulation and to what extent it can facilitate resource transfer between plants. Early evidence from soil-based systems suggests that resources such as C (e.g. Graves et al., 1997) and P (e.g. Mikkelsen et al., 2008) are transferred across a MN. However, it is not always clear whether this transfer tends to be bidirectional between plants (Lerat et al., 2002) or unidirectional (Pfeffer et al., 2004) based on the unique characteristics of a 'donor' and a 'receiver' plant (Selosse et al., 2006). The physiological significance of interplant C transfer between host plants is also unclear, with a more mycocentric view of the transfer being required (Fitter et al., 1998).

In line with the 'reciprocal rewards' hypothesis for regulation of symbiotic C-for-nutrient exchange, experiments using two CMN-connected plants, one shaded and one non-shaded, suggest that AM fungi retain their 'bargaining power' and provide the plant assumed to supply more C to the CMN (i.e. the non-shaded plant) with more nutrients (Faghihinia & Jansa, 2022; Fellbaum et al., 2014; Weremijewicz et al., 2016). However, it is important to consider these results in the context of the experimental design since shading does not always lead to a reduction in plant C flow (Faghihinia & Jansa, 2022; Olsson et al., 2010) and in other cases (e.g. Fellbaum et al., 2014) the strength of the plant C-source is assumed rather than experimentally quantified. Other potentially confounding impacts implicit in treatments such as shading include those on plant growth or metabolism (altering sink strength of the host plant for nutrients), or even the variability of plant species responses to shading (e.g. Semchenko et al., 2010), which could substantially influence the results.

C-for-nutrient exchange across a CMN depends on the AM fungal and plant species forming a network. In one experiment consisting of flax (*Linum usitatissimum*) and sorghum (*Sorghum* *bicolor*) linked to the same CMN, sorghum contributed more C-to-AM network despite receiving fewer nutrient returns (Walder et al., 2012). Interestingly, this type of asymmetry was only observed when the CMN comprised a single AM fungal species (*Rhizophagus irregularis*; formerly *Glomus intraradices*); when the CMN consisted of another AM fungal species, *Funneliformis mosseae* (formerly *Glomus mosseae*), both plants received similar amounts of nutrients from the CMN, although plant C inputs remained uneven (Walder et al., 2012). The functioning of a CMN in terms of the allocation of nutrients to plants could not be explained by the expression of genes that regulate orthophosphate (Pi) transporters (Walder et al., 2015), suggesting that another regulatory mechanism must be at play. The consequences of varied plant benefits derived from CMNs can be important in understanding wider plant community structure and function. Invasive plant species, for instance, may receive a greater nutritional benefit from incorporation into CMNs than native plant species, but again the exact patterns of AM fungal-mediated nutrient transfers to different plant hosts depend on the fungal species comprising the CMN (Awaydul et al., 2019).

Plant community diversity can have impacts on the C inputs into a CMN, with more diverse plant communities associated with greater movement of C into CMNs than those comprising fewer species (Řezáčová et al., 2018). Similarly, more diverse plant communities are associated with greater benefits in terms of fungal-derived N although the direction and strength of the transfer appear to be species-specific (Ingraffia et al., 2021). Such species specificity was also reflected in terms of mycorrhizal-growth responses by plant hosts, which could be attributable to the higher amounts of N transferred by the AM fungi (Ingraffia et al., 2021). In a different example, no differences in C investment to the CMN were found between a C_3 and a C_4 plant at either low or elevated temperatures (Řezáčová et al., 2018). In fact, C_3 plants were found to supply the CMN with similar amounts of C at both temperatures, despite their growth being negatively affected, AM root abundance being suppressed and also the C_3 hosts receiving less fungal-acquired N compared with the C_4 hosts at the elevated temperature (Řezáčová et al., 2018).

Despite increasing attention and experiments involving CMNs, relatively little is known about the distance over which nutrients and C can be conveyed by extraradical mycorrhizal fungal hyphae (Werner et al., 2014) and how this might be influenced by the varied abiotic and biotic factors. For instance, N can be transported between plants across a distance of 12 cm (the maximum distance tested), presumably via mycorrhizal hyphal connections, however, this again appears to be species-specific with no significant transfer being detected when the CMN was comprised by the AM fungal species *Rhizophagus irregularis* (Schütz et al., 2022). CMN-mediated N transfer between plants also appears to be influenced by the levels of N availability in the soil as well as the source-sink strength dynamics of the plant hosts (e.g. C_3 vs C_4 physiology; Muneer et al., 2023). Overall, the diversity in CMN functionality is likely due to a combination of biotic and abiotic factors such as variation in sink-source strengths of plant hosts and fungal symbionts (Walder & van der Heijden, 2015), potentially partly driven by differences in plant physiologies (Muneer et al., 2023; Řezáčová et al., 2018), and indeed the capacity of individuals within the network to control the C-for-nutrient exchange (Werner & Kiers, 2015).

When considering the significance of CMNs in wider ecosystems, it is important to note that any impact of CMN function on inter-specific plant and/or fungal competition could indirectly generate further feedbacks on mycorrhizal resource exchange across the network (Bücking et al., 2016; Figure 3). By influencing belowground resource transfer and competition, CMNs can enhance plant growth (Muneer et al., 2023), sometimes promoting and perpetuating size inequality and resource sink strengths among neighbouring plants (Merrild et al., 2013; Weremijewicz et al., 2016; Weremijewicz & Janos, 2013; Figure 3). Plant-fungal interactions, the importance of symbiont compatibility, and the high variability in plant growth responses (e.g. Castelli & Casper, 2003; Klironomos, 2003) allow CMNs to play a role in fungal-mediated soil feedbacks, where one plant species promotes or discourages AM fungal species so that it enhances its performance relative to other, co-occurring plant species (Selosse et al., 2006; Figure 3).

The role of CMNs is not limited to enhancing plant nutrient uptake; their role in mediating plant–plant interactions appears to be important, particularly where plants linked to a CMN are also influenced by other co-occurring organisms. CMNs can function as a highway for plant–plant communication phytohormones, disease resistance and induced defence signals (Alaux et al., 2020; Babikova et al., 2013; Barto et al., 2012; Song et al., 2010, 2014; Figure 3). Co-occurring organisms that compete for plant C resources can lead to asymmetry in C-for-nutrient exchange between the plant and AM fungi (Bell et al., 2022; Charters et al., 2020). In these scenarios, the pest-infested plant reduces the movement of C via the export of hexose sugars from root to AM fungi but maintains the flow of fatty acids, presumably thereby providing enough C-to-AM fungal partners to maintain the symbiosis (Bell et al., 2024). Such regulatory mechanisms are likely further modulated across multiple hosts that are linked by a CMN (Bell et al., 2021; Figure 4).

For example, in the presence of an assumed CMN, parasitism of *Trifolium pratense* by the stem holoparasite *Cuscuta australis* reduced the acquisition of AM fungal-mediated N of the smaller parasitised plant relative to its non-parasitised neighbour (Yuan et al., 2021). In this case, the non-parasitised plant also grew larger, which in turn supports the hypothesis that CMNs preferentially transport nutrients to larger plants or that differential nutrient supply from a CMN to plants amplifies plant size inequality (Awaydul et al., 2019; Merrild et al., 2013; Weremijewicz et al., 2016). Additionally, it is plausible in this case that the CMN provided more N to the non-parasitised plant as that plant was providing more C in return. Durant et al. (2023) found that plants with aphids reduced the amount of C supplied to MN(s) (potentially a CMN) while uninfested neighbouring plants likely maintained C flow into the MN(s), helping to support the wider MN(s). In this case, the AM fungi maintained P transfer to both infested and non-infested plants (Durant et al., 2023) suggesting that the net C inputs into a MN are more important than one-on-one

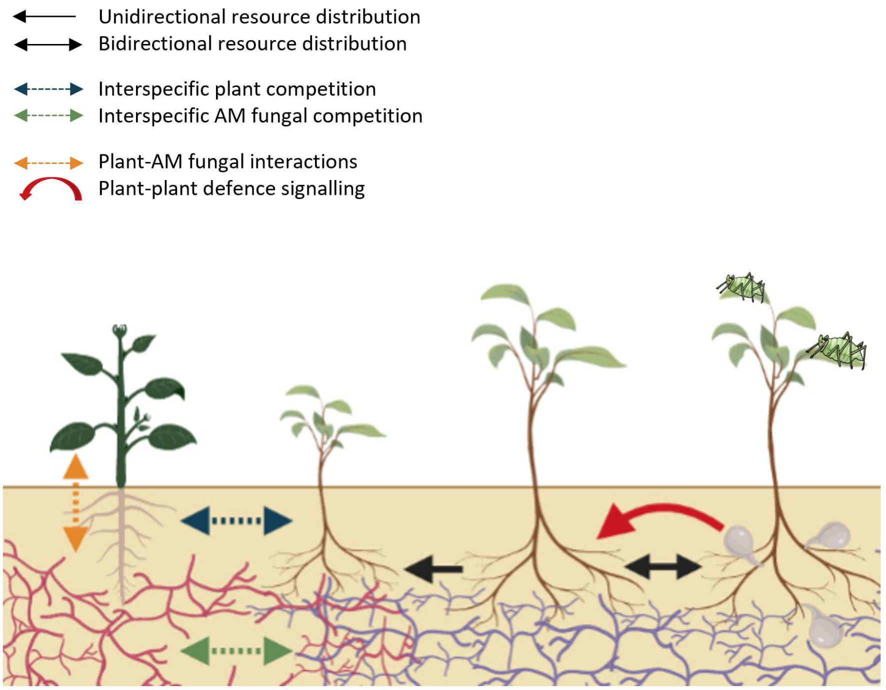

FIGURE 3 Summary of the various possible ecological implications of common mycorrhizal networks (CMNs). The black arrows show the movement of resources (e.g. carbon and phosphorus) across the network. This can be bidirectional between plants or unidirectional from a 'donor' plant to a 'receiver' plant. Blue and green arrows illustrate how CMNs can influence interspecific plant and fungal competition respectively. This below-ground resource competition can promote size inequality among neighbouring plants. The orange arrow illustrates plant-fungal interactions. Symbiont compatibility and the high variability in plant growth responses mean that CMNs can play a role in fungal-mediated soil feedbacks and plant-fungal community structure. The red arrow from a plant attacked above-ground by aphids and below-ground by plant-parasitic nematodes to a healthy plant refers to the ability of CMNs to facilitate plant–plant communication by transfer of phytohormones and defence signals.

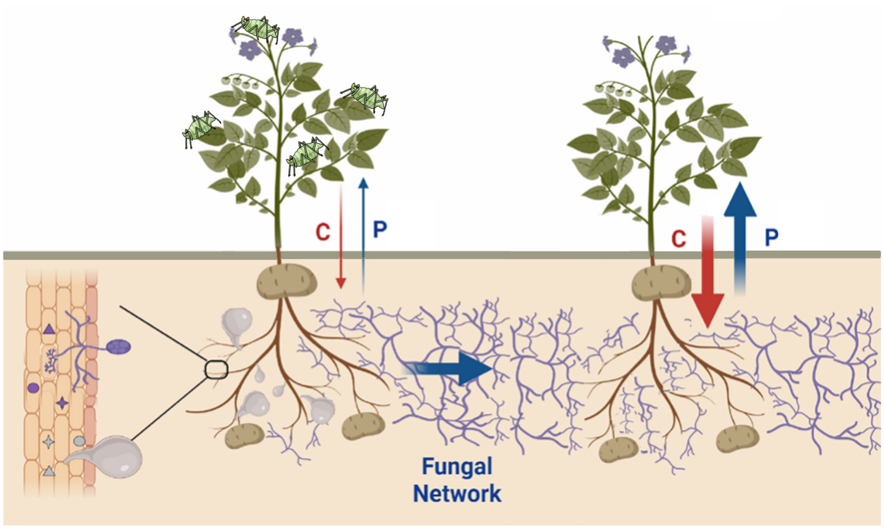

FIGURE 4 Potential scenario for the allocation of resources between a CMN and its plant hosts in the presence of competing above- and below-ground herbivores. The strain imposed on plant C supply by herbivores leads to a reduced allocation of C to the CMN by the plants. In turn, the CMN reduces the allocation of P to the infected plant host and directs resources away towards a non-infected plant host that is offering more C in return. Red arrows—plant-to-symbionts C flow; Blue arrows—AM fungi to host P flow; width of arrows—flow strength (adapted from Bell et al., 2021).

interactions in maintaining MN functionality. This also supports the idea that the presence of a CMN potentially undermines the capacity of the plant hosts to control AM fungi by denying them resources (Kiers & Denison, 2008). As in previous studies that created C sinks across a CMN, either by shading (Fellbaum et al., 2012) or by chemically altering nutrient gradients in vitro (Lekberg et al., 2010; van 't Padje, Bonfante, et al., 2021; van 't Padje, Werner, et al., 2021; Whiteside et al., 2019), these results demonstrate how CMNs are responsive and resilient and potentially have an important role to play in ameliorating the impacts of plant stresses.

Overall, experiments involving multiple symbionts have shown that CMNs can play a role in facilitating resource transfer between plants and influencing plant–plant interactions within an ecosystem. However, CMNs can also play other roles such as in plant–plant communication through the transfer of phytohormones and defence signals. Moreover, their overall functioning is highly

BOX 1 Open questions and considerations for future research

- Is conceptualising the resource exchange in AM symbioses as a 'market' or as requiring 'further regulation' helpful; could biological markets models be expanded to include longer-term cost–benefit implications as well as other parameters such as 'C-for-defence'?
  - It has been suggested that given that most plants fix C in surplus to their requirement (i.e. 'Surplus C Hypothesis'), plant C provision to microbial symbionts such as AM fungi could be viewed as 'one organism's waste being another organism's resource' rather than as a 'cost' (Prescott et al., 2020). A rebuttal to this suggested that even if fixed C is in surplus and thus could be considered as 'waste', it could still be traded as long as the host plants have some control over the timing and/or the recipients of the C (Noë, 2021). The response that followed clarified that just because 'trading strategies' would benefit organisms does not mean that these necessarily exist (Prescott et al., 2021). Additionally, source-sink dynamics have been proposed as an alternative, more parsimonious framework to conceptualise the symbioses (Corrêa et al., 2023; van der Heijden & Walder, 2016).
- Can we increase the resolution to determine the specific compounds that constitute plant C and AM-acquired soil nutrients, and how does any variation in these influence the C-for-nutrient exchange?
- How can the direct impact of any co-occurring symbiont on the C-for-nutrient exchange in the plant–AM symbioses (e.g. reduced plant C availability) be disentangled from any indirect impacts (e.g. reduced AM fungal colonisation)?
  - Balancing ecological realism and mechanistic resolution is difficult, requiring a diverse set of experimental designs ranging from axenic plates to field studies to address this key question.
- How should the quantities and composition of any symbionts (mutualistic, parasitic or pathogenic) applied to a host be determined and how should 'controls' be conceptualised?
  - Despite their ubiquity in nature, most studies consider non-mycorrhizal plants as 'controls' (Kuyper et al., 2023). Similarly, the addition of another symbiont to a mycorrhizal plant is considered a 'treatment', although, in nature, plants typically interact with multiple organisms simultaneously. Additionally, the use of high densities of parasites/pathogens can be useful for proof-of-concept, but this may not reflect the ever-changing parasite/pathogen load commonly seen in nature.
- How does microbial composition (e.g. choice of AM species and interactions between AM fungi and bacteria) influence C-for-nutrient exchange between different partners?
  - Although the mechanisms cannot be easily disentangled experimentally due to the complexity of the soil microbial community, it is important that experimental designs carefully consider the origin, type and treatment (e.g. sterilisation and use of microbial washes) of the growth medium and have sufficient experimental controls to disentangle the driving cause of any observed effects.
- How can the presence of CMNs be reliably established experimentally, especially in soil-based systems? How much experimental effort should be invested in this?

- Perhaps proving absolute hyphal continuity of CMNs in experiments is too restrictive and should not be the focus, as even indirect mycelium connection could have important implications (e.g. bacterial interactions and hyphal exudation; Rillig et al., 2024).

context-dependent, influenced by both biotic and abiotic factors (e.g., the number or identity of plant and fungal species involved). All of these factors appear to then feed into (and often compromise) the ability of plants, and especially that of AM fungi, to control the C-for-nutrient exchange for their own benefit. While soil-based experimental systems that incorporate multiple plants and other non-mycorrhizal symbionts are more ecologically relevant than the other experimental systems reviewed here, this increased complexity likely compromises our ability to draw clear causal links. It is also more challenging to get a detailed mechanistic understanding of the relationships occurring in the system.

4 | CONCLUSIONS

Here, we have reviewed resource allocation within systems of AM symbioses of different complexity, from those using single root organ cultures to those incorporating plants dealing with multiple, co-occurring organisms and the presence of CMNs in soil-based systems. We find that although there is some evidence for a preferential allocation of resources to more beneficial partners and for a tight link between plant-mediated and AM fungal-mediated resource flows, there is also growing evidence that the dynamics behind the partner selection process and the characteristic bidirectional nutrient exchange are context-dependent. Factors such as resource abundance, soil microbial composition, the presence of other symbionts, and the compatibility of plant and AM species are all likely to play an important role in the strength and direction of resource allocation in AM symbioses.

Overall, it appears that the extent of a tightly coupled C-for-nutrient exchange in AM symbioses (in particular one that resembles a 'reciprocal rewards' type of regulation) might decrease with increasing experimental system complexity. More specifically, at the CMN scale, nutrient exchange is not always balanced, and one plant host might maintain the CMN while neighbouring plant hosts benefit from the fungal-mediated nutrient allocation without providing much in return. Strict regulation of C-for-nutrient exchange by both plant host and their AM symbionts might be less evident under increased ecological complexity as other drivers such as source-sink dynamics (Walder & van der Heijden, 2015) and a C-for-defence exchange (Frew et al., 2024) become increasingly important.

To improve the capacity of biological market or trade balance models to describe the C-for-nutrient exchange, 'service' provision (such as defence enhancement) should be incorporated alongside 'goods' provision (such as C or P acquisition). More research using varied biological systems across multiple scales is also needed to fully comprehend the role of CMNs in modulating the C-for-nutrient exchange and to test hypotheses quantitatively (e.g. using meta-analyses) while ensuring the inclusion of mechanisms or outcomes commonly overlooked by one plant × one fungus experiments. Apart from increasing our fundamental understanding of how AM fungi might utilise CMNs, how they interact with other co-occurring organisms, and how this then influences the C-for-nutrient exchange, it is also vital that experimental designs include CMNs so we can better address the plethora of unresolved questions (Box 1), including pertinent topics such as the role of CMNs in enhancing ecosystem functionality, and specifically their role in sustainable farming practices (Alaux et al., 2021; Wipf et al., 2019).

AUTHOR CONTRIBUTIONS

Emily Magkourilou and Katie J. Field conceived the idea and the scope of the review. Emily Magkourilou led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for the publication.

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CONFLICT OF INTEREST STATEMENT

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DATA AVAILABILITY STATEMENT

No data were generated or used for this manuscript.

ORCID

E. Magkourilou https://orcid.org/0000-0003-0195-5653
C. A. Bell https://orcid.org/0000-0002-7437-2793
K. J. Field https://orcid.org/0000-0002-5196-2360

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