Mycorrhizal networks: *des liaisons dangereuses*?

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Mycorrhizal associations, by which most land plants receive mineral nutrition, are diffuse and often non-specific. A common mycorrhizal network is formed when fungal mycelia colonize and link together the roots of two or more plants, sometimes of different species. Here, we discuss recent work showing how, under realistic ecological conditions, such networks can affect the physiology and ecology of plants by facilitating interplant nutrient exchange, acting as inoculum reservoirs for seedlings and altering plant competitive abilities. Although mechanisms for their evolutionary emergence remain unclear, investigating mycorrhizal networks profoundly modifies our understanding of plant communities.

Mycorrhizae as symbioses linking plants together

Most plant ecophysiology is shaped by symbioses in which the roots of ∼90% of terrestrial plant species associate with soil fungi to form mycorrhizae (see Glossary) [1]. Fungal hyphae extend far beyond the roots, exploiting soil mineral nutrients and water that are shared with the plant (Figure 1a). Although this symbiosis is often considered mutualistic because mycorrhizal fungi receive carbon from the plant, the net effect on plant fitness ranges from mutualistic to parasitic [2], depending on the ecological conditions and plant–fungus combinations.

Mycorrhizal associations are usually diffuse and non-specific [1,3]. One or more mycorrhizal fungi can colonize two or more plants, forming mycelial links in a common mycorrhizal network (CMN). CMNs originate not only from fungal genets colonizing neighboring roots during their growth, but also from hyphal fusions uniting previously separated mycelia (Figure 2). Such fusions, although often restricted to self or genetically close hyphae, can maintain CMN integrity. As early as 1960 [4,5], interplant hyphal links were occasionally mentioned [1] as being involved in the nutrition of some non-photosynthetic plants (Box 1), but their general ecological relevance had not been extensively investigated. After two decades of research in microcosms and, more recently, in natural ecosystems, CMNs are now considered to be major components of terrestrial ecosystems. Although CMNs have been reviewed elsewhere [6,7], we discuss here the accumulating evidence for CMNs and

their important, but debated, effects on plant communities, as well as reasons for their evolutionary emergence.

The two major common mycorrhizal networks

Conventional classifications of mycorrhizae are based on the ultrastructure of the root–fungus contact. In

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Glossary

Arbuscular endomycorrhizal (AM) network: a common mycorrhizal network linked by fungi forming arbuscular endomycorrhizae, named after arbuscular hyphal ramifications formed in root cells. Involve fungi belonging to the taxon Glomeromycetes.

Autotroph: a plant that obtains its carbon nutrition from its photosynthesis only.

Common mycorrhizal network (CMN): an underground network of mycorrhizal fungi linking roots of plants of the same or different species.

Ectomycorrhizal (ECM) mycorrhizal network: a common mycorrhizal network linked by ectomycorrhizal fungi, which build a hyphal sheath over the host root and usually do not penetrate the cell wall. They sometimes exhibit different mycorrhizal morphologies, depending on the host (e.g. some ECM fungi form intracellular penetrations in some orchid roots). Involve fungi belonging to the Basidiomycetes and Ascomycetes, and their hosts are often woody, long-lived plants [61].

Endomycorrhizae: a morphological type of mycorrhiza where fungal hyphae penetrate the cell wall of root cells. Basidiomycetes and Ascomycetes form intracellular hyphal coils in root cells in plants of the Orchidaceae and Ericaceae, respectively [1]. Glomeromycetes form arbuscular ramifications and AM mycorrhizae in root cells of most (>80%) plant species [1].

Genet: individual organism defined as a genotype (synonym: clone); can be fragmented into several ramets by vegetative growth or re-assembled by hyphal fusion.

Hemiparasite: in this instance, a photosynthetic plant that exploits the xylem sap of their hosts mainly for mineral nutrition.

Hyphal fusion: the fungal mycelium grows through three processes: hyphal terminal growth, hyphal lateral branching and secondary reconnection of separated hyphae (Figure 2, main text). In the latter process, hyphal fusion occurs when a hyphal tip contacts another, compatible (genetically identical or closely related) hypha. After dissolution of the cell wall, cytoplasmic continuity and exchanges are established [72].

Mixotrophy: a trophic strategy in plants combining photosynthesis and partial heterotrophy as carbon sources [e.g. by using partial mycoheterotrophy (Figure 1c, main text; Box 1)].

Mycoheterotrophy: a trophic strategy in non-photosynthetic plants that are devoid of chlorophyll. The carbon is provided by photosynthetic neighboring plants through a CMN (Figure 1b, main text; Box 1).

Mycorrhiza: a symbiotic association between a soil fungus and a plant root. It is often a mutualism (Figure 1a, main text), in which plant photosynthates are exchanged for mineral resources acquired by the fungus from the soil.

Parasite: in this instance, a non-photosynthetic plant that exploits carbon from other plants.
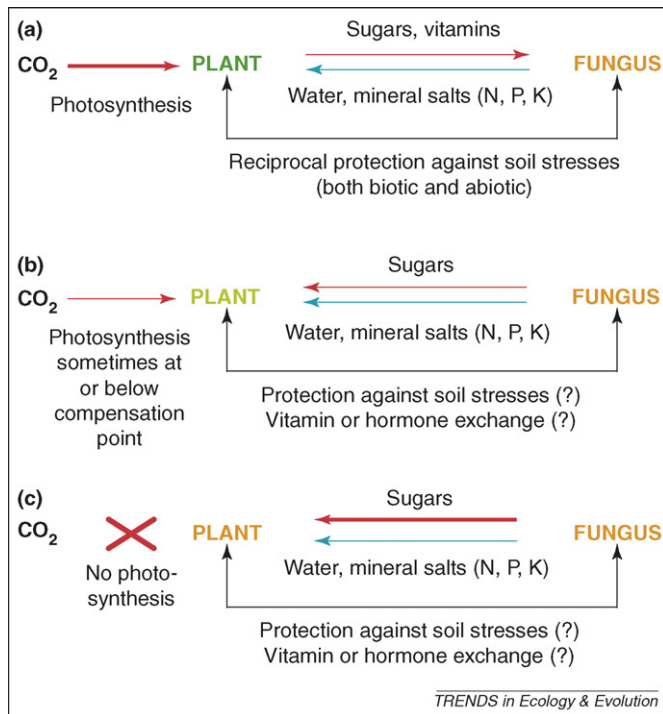
Soil feedback: an interaction between soil microflora and host plants that affects plant survival and growth as a result of changes in fungal population sizes and/or fungal community composition; can be positive or negative for plant survival, growth or fitness.

Ramet: individual organism defined as a morphological entity (topological continuity, e.g. all connected hyphae in a fungal mycelium).

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Figure 1. Diversity of resource transfers between plants and their mycorrhizal fungal partners. **(a)** reciprocal exchange for a common green plant; **(b)** nutrient flux for a mixotrophic plant exploiting fungal carbon as part of its carbon resources; and **(c)** nutrient flux for a mycoheterotrophic plant exploiting the fungus as its exclusive carbon source. In all cases, the fungus exploits water and mineral nutrients from the soil and receives carbon from other green plants with which it has formed mycorrhizae. '?' indicates possible effects that remain unknown. Abbreviations: K, potassium; N, nitrogen; P, phosphorus.

ectomycorrhizae, fungi remain between root cells, whereas they penetrate the cell walls in endomycorrhizae. However, a given fungal species can form different mycorrhizal ultrastructural types depending on its host [1,8,9]. The taxonomic identity of mycorrhizal fungi is thus more relevant than is the analysis of mycorrhizal morphology for the identification of a CMN. Indeed, most evidence for CMNs comes from identification, mainly by molecular fingerprinting, of the same fungal species on
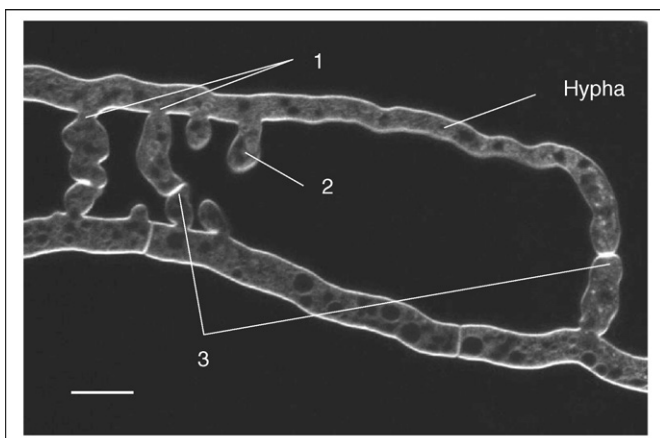
Figure 2. Confocal image (laser-scanning microscopy) of two neighboring hyphae of a mycelium of the ascomycete fungus *Neurospora crassa*, stained with the fluorescent marker FM4-64. These hyphae highlight the three processes that shape mycelial growth: (1) hyphal ramification; (2) apical growth of the hyphae; and (3) fusion of hyphae that reconnects separated parts of the mycelium. Scale bar = 10 mm. Reproduced with permission from [72].

two or more plants from the same stand. *In vitro* inoculations can test whether a fungus associates with two or more plant species, but artificial conditions or a lack of competitors might enable associations to form that would never do so *in situ*. Although preferred, direct evidence from the field, from observations of connecting hyphae, which are cryptic and fragile, or from nutrient transfers between connected plants (Boxes 1 and 2), is less easily obtained [6,7]. However, at least two types of CMNs have been identified by combining these different approaches.

Arbuscular endomycorrhizae
The asexual and obligate mycorrhizal Glomeromycetes form arbuscular endomycorrhizae (AM), named after their hyphae, which build arbuscular ramifications within root cells. Non-specificity has long been thought to be the rule [10], given that there are ∼200 recognized species of Glomeromycetes, whereas 60% of plant species form AM [1]. Although recent molecular analysis of fungal diversity has revealed plant preferences for some Glomeromycetes under field conditions [11–13], many fungal symbionts are shared between co-existing plant species. Our understanding of the level of symbiotic specificity remains limited because 'species' delineation is difficult in Glomeromycetes that are asexual and exhibit low morphological diversity [14]. Although the size of AM ramets is unknown, hyphae are likely to link neighboring plant roots, and hyphal fusions can maintain ramet continuity: in a model system, fusion occurred in 50% of contacts between genetically identical hyphae spreading from different hosts [15]. Although more data on Glomeromycetes morphology and population biology are required for assessing the extent of fungal sharing, some broad-spectrum species are likely to form AM networks [1,7].

Ectomycorrhizae
Many trees and shrubs from temperate and Mediterranean regions form ectomycorrhizae (ECMs) with Basidiomycete and Ascomycete fungi. ECM genets can extend over several meters [1,6] and thus include the roots of multiple hosts, probably forming ECM networks. The fine-scale assignment of a single ECM fungal genet to different co-occurring plants is still preliminary [16,17], and ramet delineation also awaits further study. Whereas some plants or fungal species exhibit specificity, most ECM fungi are generalist [3]. Earlier reports suggested that multi-host fungi dominate forest ecosystems (>90% of the ECM fungal community [9,18]); however, later studies, revealing more rare ECM fungi, showed only 12–48% to be multi-host fungal species [19–21]. Thus, ECMs can be non-specific and link plants of different species [16].

Sequences or RFLP patterns of the rDNA intergenic spacer (ITS) are frequently used to identify fungi on ECM roots; there are, however, some limitations. Although ITS exhibits low polymorphism among fungal 'species' recognized by classic taxonomy (i.e. based on morphology of fungal sporophores) [22], ITS sequences could be identical in closely related, host-specific cryptic (sub-) species. Despite increasing reports of cryptic species in ECM fungi

Box 1. Evolution of mycoheterotrophy

Mycoheterotrophic plants share three derived features [5,27,28]: (i) they neither photosynthesize nor have chlorophyll, but use fungal carbon instead (Figure 1c, main text); (ii) they specifically associate with a narrow fungal clade; and (iii) their fungi are mycorrhizal with other green plants that are the ultimate source of carbon for the mycoheterotroph [4,16,29]. Although the functional significance of their mycorrhizal specificity is still poorly understood, mycoheterotrophs are outstanding examples of nutrient exchange occurring through CMNs and have arisen repeatedly throughout plant evolution [5,27]. But how have they evolved?

Recently, green orchids from temperate forests phylogenetically related to mycoheterotrophic species were shown to exploit carbon from a CMN linking them to surrounding ECM trees ('mixotrophy'; Figure 1b, main text). This makes them valuable models for carbon flow through CMNs to photosynthetic receivers (Table I), [8,25,35–37]. In orchids, mixotrophy using a CMN could have arisen before, and probably facilitated the evolution of, mycoheterotrophy. Mixotrophy was probably first selected to compensate for low light levels in forests where these mixotrophic orchids typically live [25,36]. Mixotrophic orchids also show rare non-photosynthetic variants lacking chlorophyll [8,25] (Table I), which offer unique opportunities for understanding the evolutionary transition from mixotrophy to mycoheterotrophy. The low physiological and demographic success of these variants suggests that the survival of full mycoheterotrophs requires several complex changes beyond the loss of photosynthesis [25,63]. This could protect mycorrhizal networks against the too frequent appearance of pure carbon sinks.

However, the effects of mixotrophs on the fitness of linked plants and fungi should be quantified before evolutionary constraints can be discussed: mixotrophs and mycoheterotrophs are often considered parasites [27,29] without direct evidence. Some mycoheterotrophs might even stimulate the growth of their fungal partner [16,28] and thus compensate for carbon loss.

This example parallels the evolution of parasitism in Scrophulariaceae [64], a plant family encompassing fully non-chlorophyllous parasitic species. These parasites have arisen repeatedly from green hemiparasitic ancestors [64], exploiting the xylem sap of other plants for their mineral nutrition. Many hemiparasites are mixotrophic [65]. Mixotrophy therefore probably facilitated the repeated evolution of heterotrophy in both Scrophulariaceae and orchids, and associations that initially (in evolutionary time) provided mineral nutrition later became carbon sources. There is evolution to heterotrophy in these plants by 'biting the hand that feeds me'.

Table I. Evidence for mixotrophy supported by ECM networks in photosynthetic orchids from temperate forests

Species	Biomass carbon of fungal origin[a]	Photosynthesis rate in ambient light conditions[b]	Link to a CMN[c]	Refs
Cephalanthera damasonium	85%	Unknown	Unknown	[35]
	49% (and 100%[d])	Similar to respiration rate	ECM network	[25]
	33%	Unknown	ECM network	[36]
Cephalanthera longifolia	33% (and 100%[d])	Unknown	ECM network	[63]
Cephalanthera rubra	26%	Unknown	ECM network	[36]
	7%	Unknown	Unknown	[35]
Epipactis atrorubens	15%	Unknown	ECM network	[36]
Epipactis helleborine	14%	Unknown	ECM network	[36]
Epipactis distans	36%	Unknown	ECM network	[36]
Limodorum abortivum	unknown	Lower than respiration rate	ECM network	[37]
Listera ovata	27%	Unknown	Unknown	[35]

[a]The percentage of carbon recovered from fungi in orchid biomass was calculated from the $^{12}C:^{13}C$ ratio of orchids, as compared to the $^{12}C:^{13}C$ ratio of surrounding mycoheterotrophic and autotrophic plants (see [35] for methods).
[b]CO_2 exchanges under controlled light levels enabled the comparison of photosynthetic rate with respiration rate.
[c]Link to a CMN was assessed by identification of mycorrhizal fungi using molecular methods (sequencing of ribosomal DNA spacers, ITS).
[d]Non-photosynthetic, fully mycoheterotrophic variants without chlorophyll were found among green, photosynthetic mixotrophic individuals in two *Cephalanthera* populations.

[23], there are so far no data on their possible host specialization. Although probable, the existence of generalist ECM fungi and ECM networks linking several plant species still requires rigorous demonstration using population genetic tools.

Other common mycorrhizal networks

Other CMNs might exist. The ascomycetes forming endomycorrhizae in the Ericaceae plant family [1] might form a unique CMN; however, they could also integrate into ECM networks, because some fungi form both Ericaceae endomycorrhizae and ECM [24]. Many fungi live in healthy plant roots as endophytes [25]. Those that also grow in soils and reach large genet sizes, such as the poorly known 'dark septate endophytes' [1], could also form (or contribute to) interplant networks. Lastly, some plants have both ECM and AM, such as species in the genera *Acacia*, *Casuarina*, *Eucalyptus*, *Populus* and *Quercus* [26]. AM fungi often initially colonize plants and are joined or replaced by ECMs (perhaps reflecting the mechanism of evolutionary transition from the more ancient AM to the more recent ECM [1]). Dually colonized plants might enable interactions between AM and ECM networks. The physiological and ecological consequences of this have yet to be investigated.

Common mycorrhizal networks mediate nutrient transfers between plants

One important consequence of CMNs is nutrient transfer between plants [1,6]. We focus here on carbon transfer, recently demonstrated under natural conditions (see Box 2 for examples of other nutrient transfers). Mycorrhizae receive 20–40% of total host-plant photosynthates, with most transferred to soil mycelium [1], creating the potential for interplant carbon flow in CMNs. In addition, some non-photosynthetic plant species have evolved repeatedly to receive carbon through a CMN [4,5,27] ('mycoheterotrophic' plants; Figure 1c, Box 1). Recent molecular work has shown that such species are associated with ECM [4,16,28] or AM [29] networks. Labeling experiments have demonstrated carbon transfer from neighboring photosynthetic plants to mycoheterotrophs through an

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Box 2. Nitrogen and phosphorus transfers by CMN

Although they are often translocated from fungi to plants (Figure 1a, main text), mineral resources such as nitrogen can be transferred between plants via CMNs. N_2-fixing and non-fixing species (e.g. *Casuarina cunninghamiana* and *Eucalyptus maculata* [66]) provide a good source–sink relationship for investigating inter-plant nitrogen transfer, with the nitrogen gradient serving as the driving force.

Nitrogen

Nitrogen transfer through ECM and AM networks occurs mainly from N_2-fixing to non-fixing plants. It is generally stronger in AM (10–40%*) than in ECM networks (1–40%) and is greater when $^{15}NH_4^+$ (1~40%) rather than $^{15}NO_3^-$ (1~25%) is the external labeling nitrogen source [26]. However, two-way nitrogen transfers with net flow to N_2-fixing plants have been documented via AM networks from *Hordeum vulgare* to *Pisum sativum* (0.3% [67]) or via ECM networks from *Eucalyptus* to *Casuarina* (up to 40% [26,66]). Such a net nitrogen flux to N_2-fixing plants might reflect their high nitrogen demand: indeed, N_2 fixation could have evolved to help fuel a nitrogen-rich lifestyle [68]. Some N_2-fixing plants might not fully exploit fully their capacity to fix atmospheric N_2 but instead use soil nitrogen [68] and thus become relatively nitrogen demanding (i.e. possible receivers). Plants adapted to nitrogen-poor environments, such as nutrient-impoverished forests and woodlands, might accumulate provisional nitrogen and become nitrogen-rich relative to their needs (i.e. possible donors). In coexistence with nitrogen donors, nitrogen transfer to N_2-fixing plants might satisfy their higher nitrogen requirements.

Phosphorus

One-way phosphorus transfers have been reported more frequently [38] and there is one report of reciprocal phosphorus transfer (0.1%*) between *Hordeum vulgare* and *Pisum sativum* via AM networks [67]. Owing to its low mobility in soil and low requirement by plants, phosphorus transfer (0.1–2.0%) between plants is smaller than is nitrogen transfer [67]. Although transferred phosphorus has been found to move into receiver shoots [67], the magnitude and rate of phosphorus transfer have been too small to affect the phosphorus nutrition of the receiver and to be ecologically relevant, except perhaps under phosphorus-deficient conditions. By contrast, a greater amount of phosphorus is transferred from dying, decomposing roots of donor plants to living receivers [67].

ECM network [27]. Are the carbon budgets of green plants also affected by such carbon flows?

Carbon transfer occurs between green plants through ECM [30] and AM [31,32] networks in the field. Transfer is greater to plants linked in a CMN than those that are not [30,31], suggesting that carbon flux through soil pathways (e.g. exudate transfer or refixation of respiratory CO_2) does not account for all of the transfer. Carbon transfer is bidirectional in some studies [30,31], with a net flux toward one plant, significantly contributing to its total carbon uptake (up to 10% [30]). The magnitude and direction of carbon transfer appears to depend on fungus–plant combinations and on the plant environment (e.g. shading receivers increases carbon flow [30]). In AM networks, there is controversy as to whether the received carbon remains in fungal hyphae [33,34] or migrates to plant cells and aerial shoots [31] to contribute significantly to the metabolism of the receiving plant [33]. There is evidence of transfer to aerial plant parts for carbon obtained from

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* Percentage of transfer of element X is calculated using a labeled source X* as follows: $X_{transfer}\% = X^*content_{receiver}/(X^*content_{receiver} + X^*content_{donor}) \times 100$, where $X^*content_{plant} = atom \%X^* excess_{plant} \times total\ X_{plant}/atom\ \% excess_{labeled\ X}$.

ECM [6,30] and AM [6,31] networks in some experiments, but the importance for the total plant carbon budget has yet to be quantified. Moreover, some experiments failed to detect any carbon flux via AM networks [34].

Recent studies have shown that some green forest orchids linked to an ECM network have a $^{13}C:^{12}C$ ratio that is intermediate between autotrophic and mycoheterotrophic plants [25,35,36]. $^{13}C:^{12}C$ values depend on the carbon source and indicate that up to 85% of the carbon of these orchids is of fungal origin (Table I in Box 1). These orchid species, phylogenetically close to true mycoheterotrophic orchids, have limited photosynthetic efficiency for environmental [25] or physiological [37] reasons (Box 1). They combine mycoheterotrophic and photosynthetic carbon sources in a strategy called 'mixotrophy' [25]. However, whether mixotrophy occurs in green plants unrelated to mycoheterotrophic species remains unknown. Indeed, mycoheterotrophy and orchid mixotrophy are associated with mycorrhizal features that are absent in other plants, such as high mycorrhizal specificity and lysis of fungal hyphae in infected root cells [1,8,25,27]. It is not known whether these features are prerequisites for carbon uptake from a CMN. Moreover, ECM fungi can extract organic carbon from soil [1], whose contribution to the carbon budget of mycoheterotrophs and mixotrophs remains unquantified. Given this early state of knowledge, it is unsurprising that the overall importance of CMNs in carbon cycles of terrestrial ecosystems is currently unknown.

Mineral nutrients can also be transferred through CMNs (Box 2) and transfers can be affected by other soil organisms: for example, earthworm grazing increases phosphorus transfer to a receiver plant [38], whereas collembolan disturbance reduces carbon transfer through fungal networks [39]. These interactions open a Pandora's Box of soil complexity and could explain some of the contradictions reported between nutrient transfer studies. Consideration of soil biodiversity in its entirety is required to understand the mechanisms and significance of CMN-mediated nutrient transfers in terrestrial ecosystems.

Common mycorrhizal networks mediate interactions between plants

CMNs can mediate interactions between plants other than nutrient transfer. In a CMN, two plants can provide carbon unequally to a shared fungus, and/or acquire nutrients unequally from a fungus that they both support, entailing a net benefit for one species to the detriment of the other. Relocation of transferred carbon from fungi to plant tissues is not as important as was once argued [7]: the carbon obtained by fungi from CMNs can also benefit the host plant by increasing fungal vigor at the expense of other plants. Fungal-mediated soil feedbacks exist in AM networks of temperate ecosystems [13,40–42], where one plant species 'cultivates' AM fungi that increase (positive feedback [13]) or decrease (negative feedback [40–42]) its performance compared with co-occurring species. Such feedbacks are likely to shape plant community structure at the local scale: by altering the competitive abilities of dominant species, negative feedbacks might result in

greater community diversity [6,43,44]; conversely, positive feedbacks can contribute to species replacement and lowered community diversity by favoring one plant species in a CMN. Positive feedbacks might be involved in ecological succession: for example, in chaparral–forest transitions, shrubs (*Arbutus* and *Arctostaphylos* spp.) associated with ECM fungi favor ECM colonization of neighboring tree seedlings [20,45]. Similarly, invasive weedy plants might benefit from CMNs [32]. However, the direct demonstration of a CMN role in soil feedbacks, facilitation of ecological succession or weed invasion awaits experimental manipulation of fungal presence and diversity.

CMNs can also facilitate seedling establishment. ECM seedlings growing near adult plants have symbionts more similar to those of the adults and grow better than do isolated seedlings [19,20,46,47]; however, absence of growth benefits has also been reported [21]. In a temperate forest, unequal isotopic fractionation during photosynthesis in canopy and understorey individuals showed that adults in the canopy contributed most of the carbon to the ECM network: the $^{13}C:^{12}C$ ratio of ECM fungi was closer to that of the canopy trees, indicating that the latter contributed 57–100% of the fungal carbon [48]. More directly, *Quercus rubra* seedlings planted near congeneric ECM *Quercus* species had improved establishment, growth, mineral nutrition and symbiont diversity compared with seedlings near AM *Acer rubrum* [49]. A trenching experiment demonstrated that an ECM network improved growth of shade-intolerant ECM *Pinus strobus* seedlings, but not of shade-tolerant ECM *Betula allegensis* or *Tsuga heterophylla* [50]. There is little evidence, however, for carbon flow through ECM networks to seedlings [51]. Facilitation of seedling establishment is less clear in AM than in ECM networks [34]. AM networks facilitate the establishment of connected seedlings by increasing their biomass and phosphorus nutrition in grassland microcosms [52], but performance of seedlings linked to an AM network in pot experiments was inferior to that of isolated mycorrhizal seedlings and equal to that of non-mycorrhizal seedlings [53]. An AM network also negatively affected the growth of tropical tree seedlings *in situ* [54].

Differences in CMN feedbacks among species or experimental conditions could be influenced by soil fertility, plant–fungus species interactions and the age of adult plants [21,41,44,52]. The greater abundance of soil pathogens near conspecific adults (the so-called 'Janzen–Connell effect' [49]) can outweigh the positive effects of CMNs. Moreover, experiments examining CMNs often report on growth and mineral nutrition that are only indirectly related to fitness. Given that mycorrhizal fungi also affect plant reproduction [1], questions about the effects of CMNs on plant fitness remain.

Evolution of common mycorrhizal networks
CMNs linking plants of the same and different species are common, and affect plant community structure by the modulation of plant–plant interactions and, in some cases, by nutrient transfers (Box 1). Plants entering a CMN are thus at risk of helping their competitors: CMNs thus appear as 'dangerous' and somewhat paradoxical relationships. Here, we review possible evolutionary mechanisms that could drive plants to enter CMNs.

A neutral view
CMNs could exist as a consequence of fungal biology, without significant cost to either partner, especially to the plants, of attaching to a network. Even for plant–plant carbon transfers via the CMN, the cost to the donor plant might be negligible [6], such as when large trees support small mycoheterotrophic plants [14] (Box 1). Simard *et al.* [30] showed that five times more carbon was transferred through ECM networks than through direct soil pathways, without a measurable cost to the donor plant. In addition, if transfer is bidirectional and if the direction of net transfer changes over time (Box 2), costs could be shared more among linked plants than is so far thought. In an AM network including vernal herbs and deciduous trees bearing leaves in summer, carbon flux reversed over the growing season, with the herb serving as a donor in spring but as a receiver in summer [31], suggesting that the net outcome could be neutral for each partner. Where net neutral cooperation exists between plants, the risk persists over time of selecting a larger carbon sink and (even without nutrient transfers) plants abusing positive feedback in CMNs. Maintaining neutrality thus requires that CMN plant partners control the costs of symbiosis. If plants strongly control costs of their fungal associates, this indirectly counterselects plants overexploiting CMNs, so that interplant cooperation remains nearly neutral or is arrested. Although the reduction of mycorrhizal colonization in highly fertile soils shows that plants can regulate the association [55], further direct evidence of plants selecting against costly partners is required [2].

Are plants favoring common mycorrhizal networks?
Entering CMNs might help seedling establishment. At the intraspecific level, helping seedlings through CMNs could be selected if seedlings are genetically related to surrounding adults (help to kin) and/or undergo heavy shade, and thus cannot pay carbon to their fungi. This scenario [56] is relevant for ECM plant species that have large seeds limiting their dispersal and regenerate under closed conspecific canopies (such as *Fagus* or *Quercus* spp.): congruently, support to seedlings appears to be more common in ECM [48–50] than in AM [53,54] networks. At the interspecific level, having non-specific fungal associates and entering a CMN supported by other species enables seedlings to establish where no conspecific adults grow [57]; any CMN cost would thus be a by-product of this selective advantage. Assuming this, two predictions can be made. First, pioneer species could evolve more-specific symbionts: indeed, the pioneer ECM *Alnus* or *Larix* trees associate with very specific fungi [1]; such specific fungi could even slow down successional replacement by other plant species needing CMNs. Second, old monospecific forests should recruit more-specific fungi to avoid cooperation with (and invasion by) competing plant species. Congruently, specific fungi accumulate with time in ECM networks [58], but some generalist fungi persist [1,58], and it is unclear whether this increased specificity is driven by the hosts or by environmental changes alone.

Are fungal partners selecting CMNs?

A non-exclusive view is that selection favors CMN-forming fungi. CMN-mediated resource equalization between plants (especially among seedlings) might improve plant survival and thus provide future carbon sources for the fungus [56]. This particularly applies where priority effects (i.e. first come, first served) determine the outcome of interfungal competition, as suggested for competing ECM fungi in experimental conditions [59,60]: for a fungus, 'helping' plants that it has already colonized might be more secure than searching for new hosts. Similar 'insurance' reasons could also explain why fungi link several plant species: generalist fungi colonize ecosystems with variable plant communities or subject to frequent disturbances more successfully than do specialist fungi [56]. Congruently, the greater specificity observed among ECM as compared with AM fungi could relate to the greater longevity and larger population sizes of ECM host plants, reducing environmental disturbances [61]. Comparatively, AM fungi generally associate with hosts that are more short-lived and more scattered in plant communities. Unfortunately, our ignorance of fungal lifespan limits discussions of the 'stability' of their environments.

Competitive exclusion

The coexistence of plant species within a CMN relates more broadly to the problem of competitive exclusion. Hypotheses accounting for the coexistence of organisms sharing the same ecological niche could be relevant [55]: for example, the razor–scissor–paper model accounting for coexistence of competitors [62] can also predict the co-occurrence of plant species in CMNs. Imagine a simple CMN-linked plant community with three plant species, A, B and C, where A benefits from B, B benefits from C and C benefits from A, with each benefit mediated by the CMN. Balanced selection would favor a dynamic equilibrium [62], where A, B and C coexist, and survive only if they remain in the CMN. Modelling of CMNs (Box 3) could enable further testing of hypotheses about factors that maintain CMNs in ecosystems and in evolutionary terms.

Liaisons dangereuses, open to investigation

CMNs update our notion of mycorrhizal symbioses, once considered as a 'one plant–one fungus' relationship, to an ecologically relevant web of interactions. Strikingly, the mycocentric view of CMNs (networks of fungi linked by shared trees, Box 3) is absent from the literature, reflecting how terrestrial ecology is phytocentric.

Our understanding of the ecological role and evolution of CMNs is still impaired by our limited knowledge of fungal biology, and the effects of CMNs on partner fitness, partner-imposed sanctions and partner choice in mycorrhizae [2]. Even in the extreme case of mycoheterotrophs (Box 1), costs to fungal and plant donors remain unknown. Although CMNs are less tractable than other diffuse mutualisms, such as pollination or cleaning mutualisms, they can have profound effects on plant communities and ecosystem function, compelling further studies on these intriguing *liaisons dangereuses*.

Box 3. Common mycorrhizal networks as typical biological networks

How CMNs integrate competing plant and fungal sinks remains largely unclear, although it is now known that many biological structures are embedded in networks of interactions [69]. The CMN concept includes hypotheses on the arrangement of plants and mycorrhizal fungi in a plant–fungus–soil continuum. The architecture of such arrangements in CMN should be amenable to mathematical or engineering network theories and could share properties with other networks, such as food webs, or networks of neurons, transportation, telecommunication and even social networks. Theoretically, a network is a system of nodes connected by links. Nodes are generally discrete structures, objects, or stable intersections, whereas links can be tangible physical structures, biological reactions, or social interactions. The architecture of a network includes, among other things, the number of links per node (degree or connectivity), the degree distribution or probability that a node has a certain number of links, the directionality of links, and the path length or average number of links traversed between two given nodes. The characteristics of degree distributions in networks are typically either random or scale-free [69,70] (Figure I), with scale-free networks capable of having nodes of extremely high degree.

Network theory has been applied tentatively to determine whether the architecture of a potential mycorrhizal network is random or scale-free [71]. Given that mycorrhizae are two-way interactive symbioses between plants and fungi, distribution patterns of ECM morphotypes with their associated *Quercus garryana* trees can be correlated from two perspectives [71]. Using trees as nodes and fungi as links, the phytocentric view demonstrates that the distribution of potential mycorrhizal links, as measured by the number of ECM morphotypes on trees, is random (Figure Ib), suggesting that all individual oak trees are more or less equal in linking to fungi in a potential ECM network. Using fungi as nodes and trees as links, however, the mycocentric view reveals that the distribution of tree links to fungi is scale-free (Figure Ic), indicating that certain fungus species act as hubs with frequent connections to a potential ECM network. From the viewpoint of evolutionary stability, the implication of this study is that an individual tree is relatively equivalent whereas a keystone fungus might have a more crucial role in sustaining the function of an ECM network. Such approaches provide opportunities to explore network theory or computer modelling to link functions and evolutionary stabilities of mycorrhizal networks under realistic conditions.
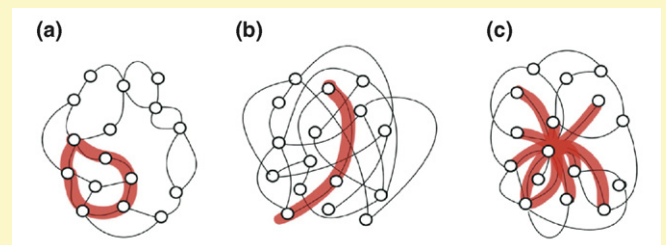
Figure I. Diversity of networks: the same set of nodes can be linked in many different ways. **(a)** A regular network, where nearest neighbors are connected, tends to have local groups of highly interconnected nodes. **(b)** A random network is easily traversed because the number of steps between any two nodes is relatively small. **(c)** Scale-free networks, distinguished by the presence of a few highly connected nodes, have local interconnected groups and are easily traversed. The red lines highlight sets of connections illustrating the distinctive feature of each network type: local connections (regular) (a), long-range connections (random) (b), and a combination of the two (scale-free) (c). Reproduced, with permission, from [70].

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