REVIEW SUMMARY

PLANT ECOLOGY

How mycorrhizal associations drive plant population and community biology

Leho Tedersoo*, Mohammad Bahram, Martin Zobel

BACKGROUND: All vascular plants associate with fungi and bacteria—the microbiome. Root associations with mycorrhizal fungi benefit most plants by enhancing their nutrient access and stress tolerance. Mycorrhizal fungi also mediate plant interactions with other soil microbes, including pathogens and mycorrhizosphere mutualists that produce vitamins and protect against antagonists. Through these functions, mycorrhizal root symbionts influence the belowground traits of plants, regulate plant-plant interactions, and alter ecosystem processes. Extensive mycorrhizal networks physically connect conspecific and heterospecific plant individuals belowground, mediating nutrient transfer and transmission of phytochemical signals. Arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), ericoid mycorrhiza (ErM), and orchid mycorrhiza (OM) have a distinct evolutionary history, anatomy, and ecology, thereby differently affecting plant protection, nutrient acquisition, and belowground C and nutrient cycling.

ADVANCES: Mycorrhizal fungi are commonly the key determinants of plant population and community dynamics, with several principal differences among mycorrhizal types. We synthesize current knowledge about mycorrhizal effects on plant-plant interactions and ecological specialization. We conclude that mycorrhizal associations per se and fungal diversity and mycorrhizal types directly or indirectly affect plant dispersal and competition that shape plant populations and communities, and regulate plant coexistence and diversity at a local scale. Among AM plants, which represent nearly 80% of plant species globally, mycorrhizal associations and belowground hyphal networks tend to intensify intraspecific competition and alleviate interspecific competition by promoting the performance of inferior competitors. In AM systems, fungal diversity enhances plant diversity and vice versa, by providing species-specific benefits and suppressing superior competitors. Compared with other mycorrhizal types, EcM fungi provide substantial protection against soil-borne pathogens by ensheathing feeder roots and acidifying soil. Pathogen suppression leads to positive plant-soil feedback that promotes seedling establishment near adult trees, which can result in monodominant plant communities with a low diversity of various organism groups. Orchids produce millions of dust seeds with high dispersal potential to encounter compatible OM fungal partners, which nourish plants, at least in the seedling stage. Species of Ericaceae achieve competitive advantage and large population densities by shedding allelopathic litter and establishing ErM root symbiosis with selected groups of ubiquitous humus saprotrophs that have evolved efficient enzymes to access nutrients in recalcitrant organic compounds in strongly acidic environments.

OUTLOOK: Increasing evidence suggests that mycorrhizal fungi drive plant population biology and community ecology by affecting dispersal and establishment and regulating plant coexistence. Plant-fungal mycorrhizal associations per se and interlinking hyphal networks synergistically determine the functional traits and hence autecology of host plants, which is best reflected in the specialized nutrition and dispersal of orchids. Habitat patches dominated by either positive plant-soil feedback near EcM plants or negative conspecific feedback near AM plants may generate distinct regeneration patches for different plant species. Furthermore, niche differentiation both within and among mycorrhizal types enhances coexistence by leveraging interspecific competition through different rooting depths, foraging strategies, and soil nutrient partitioning. We still lack critical information about the mechanistic basis of several processes, such as interplant nutrient transfer through mycelial networks and the principles of carbon-to-nutrient exchange and trading in the mycorrhizal interface, as well as kin recognition and promotion. Understanding these processes will enable us to improve predictions about the impacts of global change and pollution on vegetation and soil processes and to elaborate technologies to improve yields in agriculture and forestry. ■

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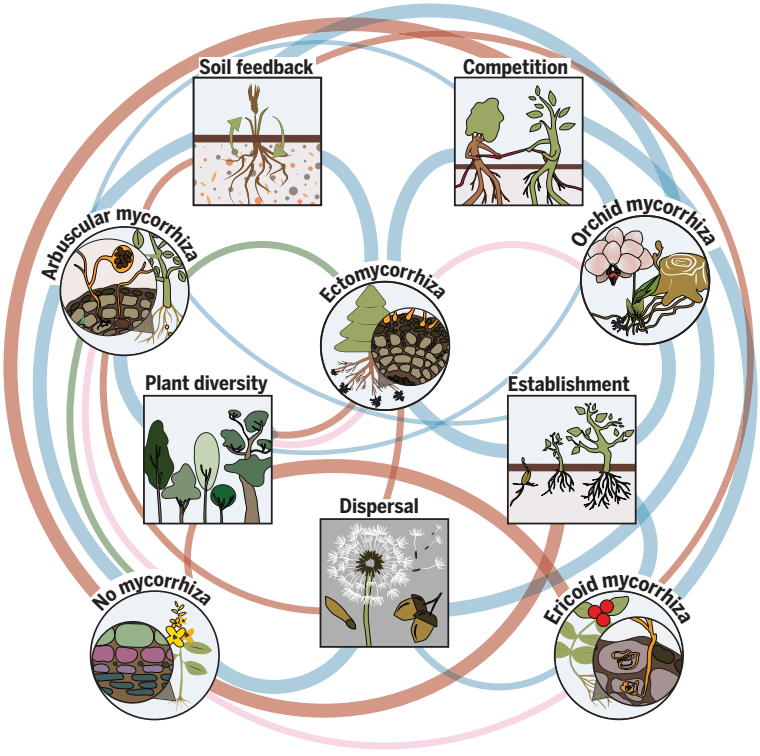

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Scheme indicating how mycorrhizal types (circles) differ in their effects on plant population- and community-level processes (squares). Blue lines, positive effects; red lines, negative effects; green lines, overlap of plant taxa among mycorrhizal types; pink lines, overlap of fungal taxa among mycorrhizal types. Line breadth indicates relative effect strength.

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REVIEW

PLANT ECOLOGY

How mycorrhizal associations drive plant population and community biology

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Mycorrhizal fungi provide plants with a range of benefits, including mineral nutrients and protection from stress and pathogens. Here we synthesize current information about how the presence and type of mycorrhizal association affect plant communities. We argue that mycorrhizal fungi regulate seedling establishment and species coexistence through stabilizing and equalizing mechanisms such as soil nutrient partitioning, feedback to soil antagonists, differential mycorrhizal benefits, and nutrient trade. Mycorrhizal fungi have strong effects on plant population and community biology, with mycorrhizal type–specific effects on seed dispersal, seedling establishment, and soil niche differentiation, as well as interspecific and intraspecific competition and hence plant diversity.

Plant ecology has traditionally focused on community responses to abiotic variables, competitive interactions among plant individuals, and aboveground herbivory (*1*). However, in recent decades, it has become clear that dispersal, speciation (*2*), and particularly symbiotic associations (*3*) also play important roles in plant population and community biology. Therefore, belowground interactions have been increasingly incorporated into species coexistence models (*4*). Herbivores, microbial antagonists, and mutualists differentially affect the fitness of individual plants and mediate intraspecific and interspecific competition and hence coexistence (*3*–*5*). Whereas the detrimental effects of parasites and pathogens can be relatively easily observed, the benefits of mutualistic microorganisms such as mycorrhizal fungi are not as immediately apparent in natural conditions (*5*), and consequently their effects on plant populations and communities are less well understood.

Mycorrhizal associations benefit most terrestrial plants by providing enhanced nutrient access and tolerance to abiotic and biotic stress (*6*, *7*). Mycorrhizal fungi mediate plant interactions with the soil microbiome, including pathogens and mycorrhizosphere mutualists that fix atmospheric nitrogen, take up phosphorus, produce vitamins, and/or protect against antagonists (*8*). Through these functions, mycorrhizal root symbionts drive the belowground traits of plants (*9*), regulate plant-plant interactions (*5*), and alter ecosystem processes (*10*) along with other biotic and abiotic drivers. Extensive common mycorrhizal networks (CMNs) physically connect conspecific and heterospecific plant individuals in soil, governing nutrient transfer into plants and transmitting phytochemical signals (*11*). There are four principal types of mycorrhiza—arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), ericoid mycorrhiza (ErM) and orchid mycorrhiza (OM)—which differ in their anatomy and evolutionary ecology (Table 1) (*6*, *12*). Recent studies have revealed substantial differences among mycorrhizal types in plant nutrient acquisition, soil C and nutrient cycling, and the capacity to protect against soil-borne pathogens (*10*, *13*) These differences have global-scale consequences for soil C sequestration and for mitigating N pollution and climate warming (*14*, *15*).

Several authors have reviewed the effect of mycorrhizas on plant community ecology, with a strong emphasis on AM in grassland ecosystems or OM (*5*, *16*). However, recently published controlled ecological experiments and comparative studies in ecophysiology, nutrient cycling, and plant-soil feedback (*17*–*20*) extend the mechanisms of mycorrhizal impact and suggest several key differences among mycorrhizal types.

Here we integrate results from experimental and observational studies from several disciplines and demonstrate that various stabilizing and equalizing mechanisms related to mycorrhizal associations regulate plant coexistence and diversity at local plant community and landscape levels (Fig. 1). We aim to answer two major questions: (i) What are the principal mechanisms by which mycorrhizal associations affect plant population and community ecology? and (ii) how do the mechanisms differ between mycorrhizal types? Finally, we provide a synthesis of mycorrhizal and mycorrhizal-type effects on plant biology.

Dispersal and establishment

To establish in a given community, viable diaspores first need to reach the target habitat. Plant distribution is often dispersal-limited; that is, not all potential community members reach suitable habitats (*21*). For many mutualistic associations, and in particular those involving plant taxa with negligible photosynthetic capacity, a plant individual has to encounter a fungal symbiont during the seedling establishment phase (*16*, *22*). Limitation of suitable partners may occur with higher probability when the host specificity of associations is high, which is relatively more common among OM and EcM associations than among other mycorrhizal types (*23*). For example, generalist EcM host plants were more efficient postglacial dispersers than specialists, perhaps owing to the better access to appropriate symbionts in new habitats (*24*).

Plant mycorrhizal types differ somewhat in their primary dispersal vectors: Nearly all ErM plants are animal- or wind-dispersed, and OM plants are wind-dispersed, but EcM and AM plants exhibit multiple dispersal strategies (*25*). Certain angiosperms such as orchids (all known species) produce dust seeds, which can disperse over long distances. At the same time, dust seeds lack energy reserves, and therefore seedlings rely strongly on symbiotic fungi during the early growth stages (*22*, *26*). Similarly, the dust-sized spores of pteridophytes disperse efficiently, and the gametophytes of some species may be mycoheterotrophic (receive much of the C from fungi), requiring a specific fungal partner (*22*). Among such groups, the presence of suitable fungi at a target site or codispersal of partners becomes a prerequisite for the maintenance and establishment of plant populations.

Although fungi produce microscopic diaspores, they may also be dispersal-limited (*27*). For example, dispersal limitation of EcM fungi and plants hampers their establishment in vegetation matrices dominated by AM or ErM species (*27*, *28*). Most species of EcM fungi have limited distribution ranges that are commonly shaped by those of their hosts (*29*). Conversely, the saprotrophic ErM fungal species exhibit cross-continental distributions, and their inoculum is present nearly everywhere (*30*). Similarly, many AM fungal taxa display nearly global distributions despite their relatively large propagule size—spores or root fragments colonized by hyphae—indicating efficient long-distance dispersal (*31*). Unlike the sexual spores of most other fungi, AM fungal glomerospores can tolerate seawater for >1 week (*32*).

To conclude, dispersal limitation is a common ecological phenomenon in both mycorrhizal plants and fungi, which may to a relatively greater extent affect establishment of plants with obligately mycorrhizal associations. Mycorrhiza-dependent dispersal limitation tends to be relatively more important in determining the establishment success and population dynamics of OM and EcM plants because of their generally high partner specificity.

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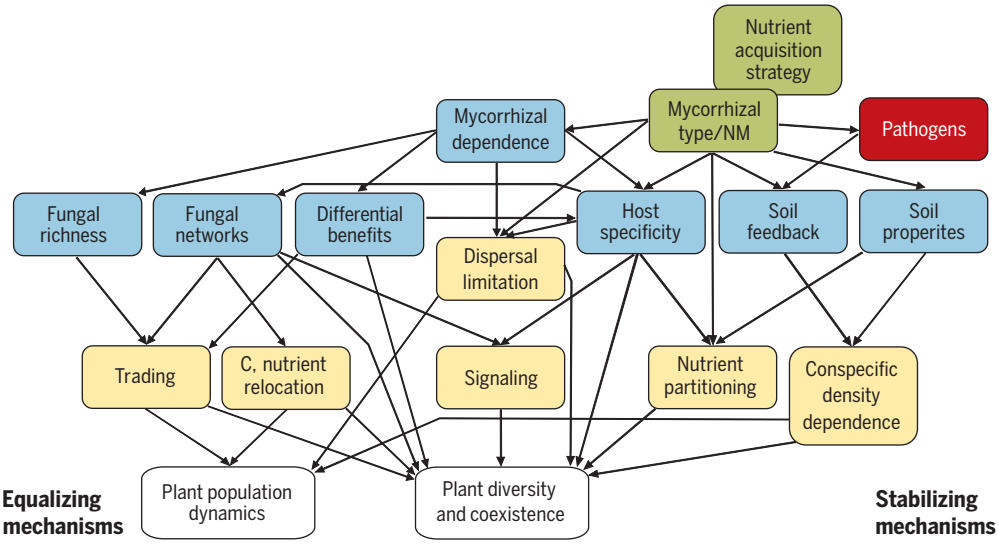

Fig. 1. Overview of stabilizing and equalizing mechanisms by which mycorrhizal associations promote plant coexistence and diversity and plant population dynamics. Mechanisms in the center have both stabilizing and equalizing aspects. Green, red, blue, and yellow boxes represent plants, various pathogens, direct mycorrhiza-related mechanisms, and mycorrhiza-associated processes, respectively. NM, nonmycorrhizal.

Belowground fungal linkages

The common mycelial network (CMN)

Genetic individuals of mycorrhizal fungi form CMNs in soil, connecting the root systems of conspecific and heterospecific plants of various ontogenetic stages (*11*). CMNs among plant species are strongly compartmentalized by mycorrhizal type (*33*) and to a lesser extent by association specificity (*23*). CMNs may redistribute carbon and nutrients among plants, enhance belowground signaling by plants, and regulate competition (*11*, *34*).

The mycelium of mycorrhizal fungi transports plant-derived carbon into soil in the form of sugars, amino acids, and polyols to sustain the mycorrhizosphere microbiome (*8*, *34*). The largest plant individuals with greatest net photosynthesis probably contribute most to the maintenance of mycorrhizal networks in AM and EcM symbioses. Besides maintaining the C demand of many nonphotosynthetic plants, the interconnecting mycelia transport C and macronutrients between photosynthesizing plants, representing 0 to 10% of net C movement (*11*). Using stable isotope labeling of carbon dioxide (CO_2) in a field experiment, Klein *et al.* (*35*) estimated that 40% of fine root carbon and 4% of total carbon originated from other trees.

Even if the rate of interplant C transfer is relatively low, it may be biologically important if it sustains the growth of shaded understory plants, especially seedlings at the stage of initial establishment. In EcM plants, Pickles *et al.* (*36*) demonstrated that relatively more C is transferred to kin than non-kin seedlings of *Pseudotsuga menziesii* by mycorrhizal networks. Although the mechanisms controlling carbon flow remain poorly understood, these results suggest that plants may be able to selectively provide their offspring with a competitive advantage in a way similar to promoting growth of root suckers in clonal plants. Enhancing kin seedlings relative to other conspecific seedlings may reduce genetic heterogeneity in plant populations, especially at fine scales.

Macro- and micronutrients also move between plants (*37*, *38*). N transfer may be biologically relevant in communities that comprise plants with large differences in N nutrition and N content, such as those containing actinorhizal and rhizobial plants. However, the net positive N transfer recorded from *Eucalyptus* sp. to the actinorhizal *Casuarina cunninghamiana* (*37*) runs counter to the hypothesis of nutrient movement from nitrogen-fixing plants to other plants and suggests that the mechanisms determining actual N transfer rates are not fully understood. Several other experiments demonstrated N or P flow via host-specific EcM fungi from a nonhost to a host plant (*38*, *39*). However, compared with mycorrhizal transportation, indirect nutrient transfer pathways, by root and leaf litter decomposition or uptake of root exudates, are estimated to be more important (*38*). Thus, it appears that AM and EcM fungi generally play a minor role in mutualistic interplant nutrient transfer.

Mycorrhizal fungi communicate with plants using organic acids, volatile organic compounds (VOCs), and phytohormones to initiate formation of the symbiosis (*40*) and to communicate warnings (*41*). AM and EcM CMNs are known to mediate plant-to-plant belowground signaling (*42*); and the same processes may, in theory, also occur through ErM, OM, and endophytic interactions. AM fungi deliver warning signals from pathogen- or herbivore-attacked plants to healthy individuals, inducing expression of defense-related genes and production of stress-related molecules (*42*–*44*), which lead to signal transfer via jasmonic acid and salicylic acid pathways (*44*). These warning systems may operate within species or at higher taxonomic levels (*43*). Besides providing warnings, AM and EcM fungi mediate plant kin recognition (and potentially self-recognition) in soil (*36*, *45*), which is probably communicated via root exudates (*46*). Efficient signal transmission may be under positive selection in both plants and fungi to maintain a stable environment and nutrient supply (*42*).

Taken together, signaling and nutrient transfer among plants are strongest between kin, which allows us to hypothesize that adult plants may support their direct offspring relative to other seedlings establishing in the rooting zone (Fig. 2). Conspecific non-kin and heterospecific plants from the same mycorrhizal type probably experience weaker communication and more variable costs and benefits from CMNs. Plants belonging to different mycorrhizal types are generally not connected by belowground signaling pathways and nutrient transfer, apart from occasional C or nutrient loss by means of parasitism.

Nutrient trade

Mycorrhiza can shape plant communities through its differential effects on plant species. Large plant individuals that contribute more C to mycorrhizal symbionts gain relatively more benefits from nutrient uptake by mycobionts (*47*), implying nutrient trading. Indeed, AM plants manipulate C flow to symbionts to promote root colonization by those fungi supplying most mineral P or N (*48*). Recently, the C-to-N trading model was extended to EcM symbiosis (*49*). For plants, the benefits of trading and partner selection are greater in conditions of nutrient limitation and high carbon availability (*48*).

Modeling studies indicate that both plants and fungi benefit from multiple trading partners that have no direct access to the resources limiting their performance (*50*). This leads to selection for more nutrition-specialist partners and thereby explains the rapid evolutionary loss of soil C acquisition capacity in mycorrhizal

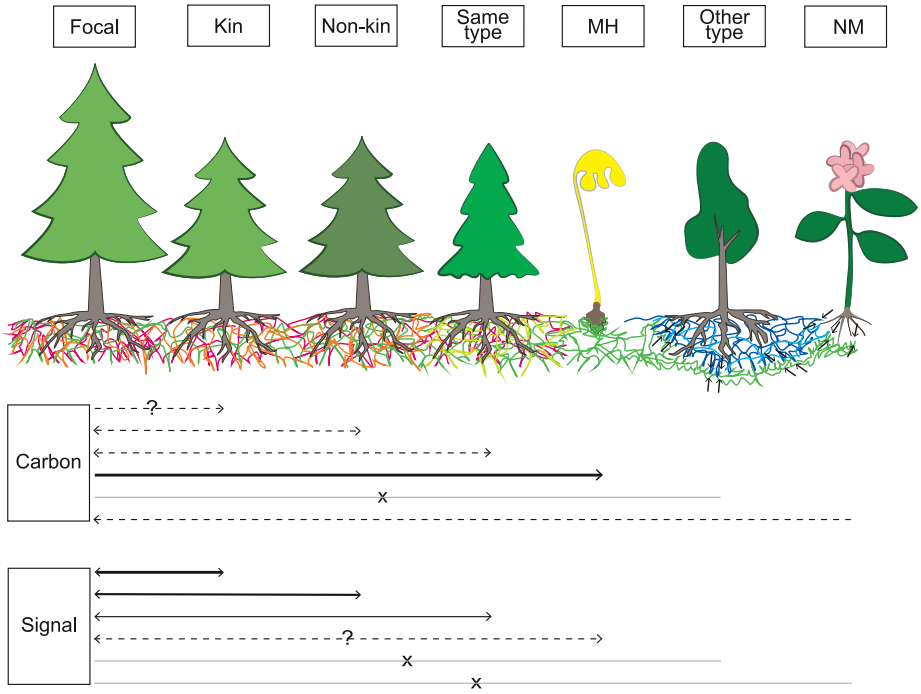

Fig. 2. Mycorrhizal network effects on carbon and signal transfer among plants. From left to right: focal (donor) plant; conspecific kin, conspecific non-kin, heterospecific but same mycorrhizal type, mycoheterotroph (MH; overlapping symbionts), heterospecific but other mycorrhizal type, and non-mycorrhizal (NM) plant. Colored lines indicate mycorrhizal fungal networks of different species or different mycorrhizal type (blue). Arrowheads depict potential antagonism among mycorrhizal fungi and plants of another mycorrhizal type or NM habit. Arrows indicate the direction of carbon and signal transfer; line width depicts the relative strength of transfer; dashed lines indicate weak and potentially biologically unimportant associations; gray, crossed-out lines indicate no association. Lines with question marks represent hypothetical flows that have not been studied.

fungi (*51*) and dominance of mycorrhizal plants in most terrestrial ecosystems (*12*). With an increasing number of fungal traders, nutrients become "cheaper" to plants (*52*). The presence of multiple trading partners also favors more cooperative symbionts and secures greater stability in the symbiosis (*48*, *50*).

Stabilizing mechanisms of plant coexistence

Stabilizing mechanisms of coexistence enhance negative intraspecific interactions relative to interspecific interactions. These mechanisms include resource partitioning among species, which results in relaxing interspecific competition, and frequency-dependent herbivory, resulting in greater losses of common species (*53*). Fluctuations in population densities and environmental factors in space and time may also contribute to resource partitioning and thus to species coexistence (*53*). However, classical coexistence theory does not address mutualistic relationships such as mycorrhiza. Here we outline how mycorrhizal associations contribute to stabilizing mechanisms.

Negative microbial feedback

Negative density dependence may arise not only from intraspecific competition but also from species-specific pathogens under their preferred hosts (*5*, *54*, *55*). In natural and experimental conditions, NM and AM plants experience more negative feedback from their soil biota compared with EcM plants, suggesting that EcM fungi protect plant root systems relatively more efficiently, compared with other mycorrhizal guilds (*13*, *17*, *18*). Indeed, AM plants accumulate relatively more pathogenic fungi in their mycorrhizosphere (*55*). Furthermore, in temperate and subtropical forests, EcM saplings and adult trees tend to exhibit positive density dependence, whereas AM trees show neutral density dependence (*55*–*57*). A combination of positive density dependence and differences in soil nutrition may lead to clustering of EcM tree seedlings around adult EcM trees and a lack of AM tree saplings around conspecific adult AM trees (*19*, *57*). Over time, aggregation of individuals belonging to a single species can lead to monodominance (>60% of basal area or stems belong to a single species), which is a particularly common phenomenon in EcM plant communities (*58*).

The magnitude of negative feedback may also differ within mycorrhizal types, depending on the level of root colonization. Plant species with potentially high growth rates and competitive ability tend to exhibit low AM root colonization and suffer most from negative soil feedback, compared with slow-growing species, which tend to experience high AM colonization and suffer less from negative feedback (*59*).

Exclusive partners

Potentially suitable partners represent a biotic niche space for plants and fungi that form mycorrhiza. Biotic niche differentiation is expected to reduce interspecific competition relative to intraspecific competition and hence enhance coexistence. Partner exclusivity (host specificity) is most common in mycoheterotrophic associations, where the EcM ("monotropoid" subtype) Ericaceae and OM Orchidaceae are highly dependent on specific, exploited fungal partners (*22*). In EcM systems, a few *Scleroderma* spp. are exclusive partners of the gymnosperm *Gnetum* spp. Conversely, EcM plant species of *Pinus*, *Alnus*, and *Pisonia* host multiple highly specific fungal species (*60*). The facultative nature of symbiosis for ErM fungi may disfavor specificity in ErM associations. In AM fungi, host specificity may be lacking because of asexuality and the presence of multiple heterogeneous nuclei in hyphae, which presents an obstacle to the synchronized evolution of specificity. Although there is currently no direct evidence for partner specificity favoring coexistence in mycorrhizal systems [but see (*61*)], specialization enhances coexistence in the plant-pollinator mutualistic system (*62*). Besides providing a stabilizing mechanism through biotic niche differentiation, specialist partners may enhance coexistence via enhanced benefits (see equalizing mechanisms).

Equalizing mechanisms of plant coexistence

Equalizing mechanisms reduce fitness differences between species and render interspecific plant competition more balanced (*63*). From this perspective, signaling and nutrient trading can be viewed partly as equalizing mechanisms in cases where inferior competitors linked to mycorrhizal networks are beneficiaries. Coexistence is enhanced if mycorrhiza benefits the competitively inferior species relatively more than fast-growing dominant species.

Mutualistic mycorrhizal types

Equalizing effects of mycorrhizal colonization have been demonstrated in multiple experimental systems with AM (*63*) and EcM (*64*) plants. However, there are also conflicting examples from studies of native and invasive plants, where mycorrhiza enhances dominant species and thus impedes coexistence (*65*).

Mycorrhizal dependency—the relative growth benefit of mycorrhizal association—differs among genotypes and species of plants belonging to all mycorrhizal types (*59*). In AM plants, early successional species and facultatively

mycorrhizal taxa exhibit lower growth responses than late successional taxa (65). These differences are usually enhanced in species mixtures compared with monocultures, resulting in enhancement of competitively inferior plant species (if these species are more mycorrhizal dependent) and thus promoting coexistence (59).

In nonspecific mycorrhizal associations, genotypes and species of mycorrhizal fungi benefit the growth of plant species differentially (65–67). Natural mycorrhizal fungal communities also differ in their effects on plant species (66, 67). This renders observed mycorrhizal colonization effects on plant performance variable and

Table 1. Evolutionary and functional differences among plant mycorrhizal types. Ma, millions of years ago; NA, not applicable.

	Arbuscular mycorrhiza	Ectomycorrhiza	Ericoid mycorrhiza	Orchid mycorrhiza	Nonmycorrhizal
Plant symbionts (percent of plant species) (12)	Most vascular plants (78%)	30 lineages of angiosperms and gymnosperms; mostly trees (2%)	Ericaceae, Diaspensiaceae (1.4%)	Orchidaceae (10%)	Several angiosperm groups (Brassicaceae, Proteaceae; 8%)
Typical habitat (15, 97)	Ubiquitous, particularly grasslands, croplands, temperate and tropical biomes	N-poor soils, mostly temperate and boreal forests, Mediterranean biomes, patchily in lowland rainforests	Highly acidic soils with mostly high organic content, usually cold tundra, boreal forests, and montane habitats	Ubiquitous but never dominant, including epiphytic habitats	Extreme: disturbed, early successional, nutrient-rich, P-starved, cold, aquatic habitats
Fungal symbionts (percent of described fungal species; our estimates)	Glomeromycota, Endogonomycetes (Mucoromycota); obligate mutualists (<0.5%)	>80 lineages of Basidiomycota, Ascomycota, and some Endogonomycetes; obligate mutualists (~15%)	Multiple lineages of Ascomycota and some Basidiomycota; free-living saprotrophs and root endophytes (<0.1%)	Ceratobasidiaceae, Serendipitaceae, Tulasnellaceae (all Basidiomycota), sometimes EcM fungi; free-living saprotrophs (<1%)	None, sometimes loose associations and nutritional benefits from free-living fungi
Anatomy (12)	Intracellular "arbuscules"	Intercellular "Hartig net," sheathing "mantle"	Intracellular "coils"	Intracellular "pelotons," their digestion	No specialized structures, sometimes AM hyphae
Extraradical hyphae (6)	Aseptate-multinucleate; few to abundant	Septate; few to abundant; may form rhizomorphs and high biomass	Septate; abundant	Septate; few to abundant	NA
Evolutionary history (12)	>450 Ma	150 to 180 Ma and onward	~100 Ma	~110 Ma	~110 Ma and onward
Nutrient acquisition (6, 10, 51)	Mostly P; low C biodegradation capacity	N and P; moderate C biodegradation capacity	N and P; strong C biodegradation capacity	N and P, some C; strong C biodegradation capacity	N and P; no C biodegradation capacity
Plant dispersal (25)	Variable	Variable	Zoochory, anemochory; efficient	Anemochory; dust seeds; highly efficient	Mostly anemochory; efficient
Seedling establishment	Seldom limited by mutualist availability	Often limited by mutualist availability; kin promotion (36)	Mutualists obtained from soil and roots of other plants (30)	Critically limited by specific mutualist availability (22)	Prefers mycorrhiza-free soil (12)
Plant soil feedback (13, 17, 18)	Negative or neutral	Positive or neutral	Not addressed	Positive (22)	Negative
Allelochemical production (79, 82)	Uncommon	Common	Very common	Not addressed	Variable (substantial in Brassicaceae)
Fungal diversity effects	Positive on plant diversity and productivity (78)	None or weakly positive (78)	Not addressed	Biotic niche to species (61)	Not addressed
Mycorrhizal means of altering plant co-occurrence and diversity (see text)	Differential benefits, hyphal networks, trading	None intraguild; suppresses overall plant diversity	None intraguild; suppresses overall plant diversity	Not addressed	Suppression via resource competition and parasitism

strongly dependent on the selection of experimental organisms (66). From an ecological perspective, species- or strain-specific benefits promote C for nutrient trading and partner selection. Hence, the availability of more fungal genotypes and species with complementary benefits may promote plant species coexistence and improve community productivity (68).

In mycorrhizal associations, specialist symbionts may provide enhanced benefits to their partners. If these partners are superior competitors, such as most large trees from the Pinaceae and Fagaceae families, their specialist fungi may promote interspecific competition. Conversely, inferior competitors, such as *Alnus* and *Salix* species, may potentially gain a competitive advantage. However, there is, as yet, no evidence that host-specific and nonspecific EcM fungi provide differential benefits. From an evolutionary perspective, host-specific mycorrhizal partners can be viewed as trapped, because they can only efficiently interact with a limited number of congeneric hosts and are therefore forced to be highly cooperative to survive. Although direct evidence is lacking, specific partners may have evolved more efficient communication and nutrient transfer mechanisms than their generalist competitors, which may somewhat relax the cost of cooperation. Laboratory experiments reveal that specialist fungi may deliver resources from nonhosts to hosts (39), but the occurrence and biological importance of this phenomenon require verification in natural conditions.

Mycoheterotrophs

Mycorrhizal networks play a fundamental role in equalizing interspecific plant competition in communities where mycoheterotrophs are found. A strategy of theft rather than fair trading has evolved among mycoheterotrophs, in which specialization reflects a host-parasite arms race, where the plant aims to gain greater control over a particular fungal "victim" (22). Fully or partly mycoheterotrophic plants tap into EcM or AM fungal networks and acquire some or all of their energy via mycorrhizal fungi from dominant plant individuals (22). All mycoheterotrophs are small and slow-growing, and most occur at low abundance; hence, drawing resources from overstory species allows them to coexist with more competitive species. Even when they occur at high abundance (e.g., Pyroleae), and despite sometimes displaying very high rates of transpiration, there is currently no evidence that mycoheterotrophs drain C in sufficiently large amounts to damage nurse trees (69).

Most mycoheterotrophs specialize on a particular fungal species, narrow group of species, or genus during the early germination and adult stages (22). Although there is evidence for coevolution between plants and fungi in some orchid genera, abrupt partner shifts are common in the mycoheterotrophic Orchidaceae and Ericaceae (70). Because of relatively specific symbiotic associations, mycoheterotrophs, including orchids, present a relatively high number of reproductively isolated sympatric races and low hybridization rates. Shifting fungal or pollinator partners in populations of orchid species may characterize these most common forms of specialization and underlie the hyperdiversity and ultrahigh diversification rates observed in Orchidaceae (22, 70). Biotic niche partitioning through association with different fungal symbionts promotes the coexistence of multiple orchid species (16). However, mycoheterotrophs have historically very high rates of extinction due to the evolution of multiple nonviable partner shifts and extinctions of intimate partners (70). Both mycoheterotrophic and autotrophic specialist plant and fungal species would themselves be extremely threatened by the extinction of their sole partner.

Initially, mutualistic fungal nursing of seedlings in small-seeded plants triggered the loss of photosynthesis, further seed size reduction, and autogamy in mycoheterotrophs to secure efficient dispersal (26). Increasing specialization toward fungal and pollinator partners has led to high ecological specificity and increased diversification rates at population and species levels, which underlie the high richness and sometimes strong contribution to local-scale plant diversity observed among orchids.

Partial mycoheterotrophy has long been considered an uncommon feature characteristic of certain orchids and EcM-associated ericaceous plants. However, recent stable isotopic evidence in natural plant communities suggests that this phenomenon may be widespread (>10% of plant species) among shade-tolerant AM herbs that develop hyphal coils rather than typical arbuscules in root cells (71). As these herbs are slow-growing, supplementary C from dominant AM trees and grasses received via

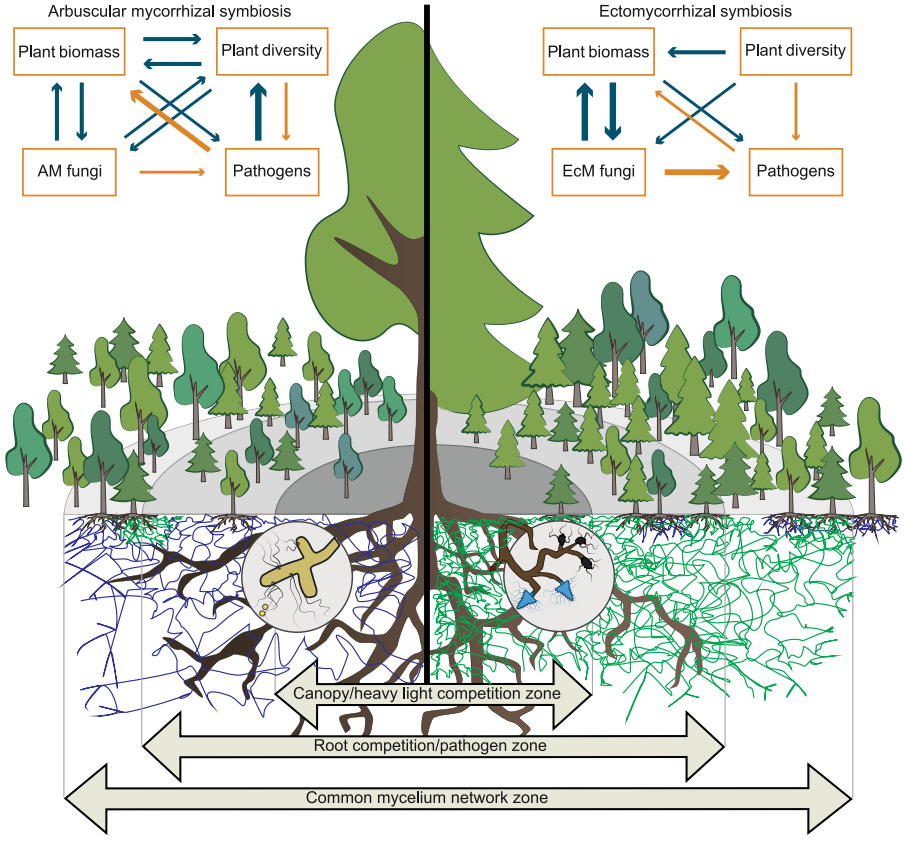

Fig. 3. Relative arbuscular mycorrhizal (left pane) and ectomycorrhizal (right pane) regeneration niches and the principal differences among mycorrhizal types in plant-mutualist-pathogen relationships (insets). The regeneration niche incorporates spatial heterogeneity in light competition (shade), root competition, the extent of common mycelial networks, conspecific versus heterospecific nurse plants and the same versus different mycorrhizal types. Symbol shapes indicate different mycorrhizal types ("spruce," ectomycorrhizal; "maple," arbuscular mycorrhizal); symbol colors indicate different species. Double-sized symbols indicate flourishing seedlings escaping from root competition and pathogens, and benefiting from common mycelial networks. In the insets, blue and orange arrows indicate positive and negative effects, respectively; arrow width depicts the relative importance of the effect; plant-to-plant diversity association is considered here as a productivity-to-diversity relationship.

CMNs may account for a previously unrecognized equalizing mechanism promoting plant coexistence.

Mycorrhizal fungi mediate competition

Mycorrhizal fungi regulate plant coexistence either by amplifying or equalizing plant competition. Classical plant ecology views competition either as direct interference between plant individuals or an indirect impact through resource depletion (*72*), but actual competitive interactions are much more complex owing to the involvement of antagonists and mutualists, including different mycorrhizal guilds.

Competitive effects of mycorrhizal fungi on plants

The availability of mineral nutrients may limit the growth of both plants and fungi in nutrient-poor ecosystems. In EcM ecosystems, nutrients are immobilized in fungal biomass to maintain mycelial structures and maximize reproductive effort. This may lead to a loss of nutrient-demanding AM plant species and reduced primary production (*73*).

Competitive interactions between plant individuals may be shaped by interactions with symbiotic fungi. For instance, EcM fungi reduce mycorrhizal root colonization of neighboring AM herbs (*74*) and enhance the competitive dominance of EcM trees over AM trees (*75*) by promoting litter accumulation and limiting access to nutrients (Fig. 3). Similarly, AM fungi were found to exacerbate iron deficiency in *Eucalyptus* seedlings and inhibit their establishment in Australian AM-dominated rainforest (*76*).

EcM and ErM fungi may reduce germination and growth of nonhost plants through direct interactions or allelochemicals (*77*). As yet there is no evidence for allelopathy in AM fungi (*78*). Nonetheless, in both laboratory and field experiments, AM fungi sometimes distort the root tissues of non-AM plants, hampering root development and functioning (*78*). Controlled experiments show that incompatible mycorrhizal interactions trigger defense mechanisms in nonhost plants and sometimes result in C loss to interacting fungi (*39*).

Competitive effects of plants on mycorrhizal fungi

Plant individuals can affect other plants by influencing the mycorrhizal fungi associating with their neighbors. By producing allelochemicals and VOCs, plants may inhibit the mycorrhizal fungi that associate with other plants. Ericaceae species are well known for producing phenolics-rich leaf litter that retards the growth of both AM and EcM fungi (*18*, *79*, *80*). By releasing allelopathic compounds or altering soil chemistry, AM shrubs reduce root length, root fungal colonization, and fungal richness of EcM plants (*81*). Conversely, EcM trees can suppress AM colonization of herbs via allelopathic litter or nutrient competition (*74*). The relative importance of allelochemicals in suppressing root colonization of other mycorrhizal types remains poorly understood owing to the design of experiments, which typically lack intraguild controls (i.e., testing the impact of allelochemicals on conspecific individuals or on other species from the same mycorrhizal type) in most experiments (*79*).

Much information on the effects of allelopathy comes from studies of aggressive invasive plants from the Brassicaceae and Chenopodiaceae families (*82*). These groups may have evolved the NM habit along with a high content of allelochemicals in their roots to suppress AM and EcM fungi and hence, indirectly, their mycorrhizal hosts (*79*). For example, the highly invasive NM herb *Alliaria petiolata* produces allelochemicals that severely reduce the local abundance of EcM and AM fungi and the degree to which they colonize other herbaceous plants and trees (*79*).

Competitive effects of plants on plants mediated by mycorrhizal fungi

Competition among plants may be related to plant mycorrhizal type and mycorrhizal dependence (the relative fungal benefits to plant species). For instance, ErM plants shed allelopathic and slowly decomposing litter, which hampers the development of other plants. ErM fungi with strong saprotrophic capacity render ericaceous plants highly competitive in acidic, nutrient-poor soils (*30*). Both AM and EcM fungi can protect their host plants from the detrimental effects of certain allelochemicals or extend their impact beyond the rhizosphere (*82*). In particular, AM fungi transport herbicides and allelochemicals to competing plants, hampering their growth up to 15 to 20 cm distant from roots (*83*). Such synergistic effects of plants and mycorrhizal fungi in alleviating and redistributing allelochemicals may well occur in other mycorrhizal types as well. Under certain conditions, NM plants may also have a competitive advantage. NM plants have evolved several strategies to avoid direct nutrient competition, such as nutrient acquisition from ultrapoor soils or early colonization of pioneer habitats where mycorrhizal competitors perform poorly, as well as allelopathic suppression of potential competitors (*84*).

Plant diversity and mycorrhiza

Experiments with AM plants and fungi have shown that simultaneous colonization and network formation by a diverse set of fungi can synergistically promote coexistence and diversity of plant species, compared to a system with a low diversity of fungi (*85*). Field studies in various natural ecosystems also suggest that mycorrhizal fungal and plant diversity are positively related (*86*, *87*). Besides increasing resource use complementarity (*88*), high fungal diversity may enhance nutrient trading (*50*), improve overall nutrient acquisition by plants, and promote primary productivity (*85*). In contrast to AM systems, experiments with EcM plants have revealed no fungal diversity effect on host performance or ecosystem services (*64*), despite some evidence for partitioning of organic P sources (*89*) and high functional complementarity among EcM fungal species (*10*, *51*). However, the lack of such effects may be related to studying seedlings over a short time.

Across geographic scales, EcM-dominated plant communities tend to be less diverse than AM-dominated communities (*90*, *91*). The above-described mechanisms related to altered nutrient availability (*10*) and accumulation of organic material and allelopathic compounds in EcM systems (*79*) provide plausible explanations. Alternatively, differences in plant diversity between EcM- and AM-dominated habitats may be related to plant-soil feedback. Because AM plants are relatively vulnerable to soil-borne pathogen attack and accumulate soil-borne pathogens, density-dependent accumulation of taxon-specific pathogens in the rhizosphere may suppress the abundance of prevalent AM plant species and hence contribute to the high plant diversity in AM-dominated communities (*5*, *73*, *92*). We suggest that these four mechanisms—access to organic nutrients, accumulation of organic material and allelopathic compounds, and positive plant soil feedback—act synergistically in EcM-dominated plant communities to maintain community monodominance over multiple generations.

Different mycorrhizal types

In many terrestrial ecosystems, three or more mycorrhizal types coexist, which may reflect different biological mechanisms. Fungi from all mycorrhizal types compete for mineral nutrients, but their differential capacity for organic nutrition enables a certain level of resource partitioning. In boreal and temperate forests, there is evidence for vertical niche partitioning among fungi belonging to different mycorrhizal types (*93*, *94*). For example, AM and ErM fungi specialize in uptake of different forms of P (*95*), whereas AM and EcM fungi partition sources of N (*96*). AM fungi can only access a subset of P forms available to EcM fungi (*20*), although this may be compensated by a lower C cost to AM fungi. Fine-scale disturbance and spatial heterogeneity of soil nutrients may further promote coexistence of plants associating with different groups of fungi (*6*, *97*). Such niche differentiation among plant mycorrhizal types potentially increases competition within mycorrhizal types, while enhancing coexistence of plants belonging to different mycorrhizal types.

Plant coexistence from a mycorrhizal perspective: Synthesis

Plant nutrient acquisition strategies and resistance to soil-borne pathogens strongly depend on mycorrhizal associations. Fungal partners belonging to different mycorrhizal types modify local soil conditions and generate habitat patches of differential quality, which affects offspring establishment of both host and nonhost plant species (*19*, *55*). EcM and ErM associations acidify soil by producing recalcitrant litter, deplete available nutrients, and produce allelochemicals (*10*, *82*, *97*), whereas AM systems accumulate relatively more soil-borne pathogens (*13*, *55*). Therefore, the size and distinctness of such habitat patches are a function of plant traits related to mycorrhizal associations, root and foliar chemistry, and competition. The resulting local abiotic and biotic heterogeneity creates specific regeneration niches for plants with different functional traits, including mycorrhizal type (*75*, *98*, *99*). Although most plants preferentially establish outside the zone of direct root competition and shade, establishment of EcM plants seems to depend most on the availability of preestablished CMNs (*19*, *100*). Orchids and most mycoheterotrophic groups require the presence of specific fungal species for germination and growth. Establishment of AM plants tends to fail under conspecific AM trees (*19*, *55*) and under EcM vegetation (*13*), their main regeneration niche being under heterospecific AM plants (Fig. 3).

To conclude, local-scale coexistence of plant species from *different* mycorrhizal types is enhanced by mycorrhiza-mediated resource partitioning. In EcM systems, positive soil feedback, build-up of recalcitrant organic material in topsoil, and access to nutrients in these organic layers enhance dominance and lead to lower diversity compared to AM systems. Conversely, negative soil feedback and differential mycorrhizal effects favor coexistence of AM plants, leading to high diversity of plants, soil microbes, and fauna.

Research needs

Despite insights from experimental mycorrhizal research conducted during more than a century, relatively little is known about the roles of mycorrhizal fungi in shaping plant communities. We identify three major unresolved issues and propose ways of addressing them.

Balanced incorporation of different mycorrhizal types in experimental research

The relative ease of manipulating herbaceous plants has favored use of AM symbiosis as a model mycorrhizal association in plant ecology (*78*), although difficulties in handling uncultured fungal taxa limit the range of possible experiments. We identified substantial functional differences among plants and fungi belonging to different mycorrhizal types, which invalidate generalization from AM-based models to other types of mycorrhiza. In particular, knowledge about the function and ecology of ErM associations needs to be improved. To disentangle the actual role of mycorrhiza in structuring plant communities, ecologists should address systems in which different mycorrhizal types are represented, such as temperate deciduous forests, Mediterranean shrublands, and tropical montane forests.

Mycorrhizal response to global change

Changes in climate, water, and nutrient availability, as well as invasions of plants and antagonists, trigger major shifts in vegetation and its associated microbiome (*15*). Changing abiotic and biotic environments may alter the costs and benefits of mycorrhizal associations and shift the competitive balance among mycorrhizal types and related ecosystem services. Information about the dispersal capacities and climatic tolerances of symbiotic fungi, and potential shifts in mycorrhizal functionality, would notably inform predictions about global change effects on agriculture, forestry, and conservation (*27*, *101*).

Role of the common mycelial network

CMNs represent one of the most fascinating features of mycorrhizal associations. Multiple studies have addressed C and nutrient redistribution among plants via CMNs and revealed the vital role of CMNs in the mycoheterotrophic lifestyle; yet the ecological importance of CMNs for autotrophic plants remains heavily debated (*11*, *35*, *78*). Novel tools such as -omics techniques; stable isotopes of O, K, and Ca; or nanoparticles offer real promise to trace the fate of resources in greater detail and in natural conditions (*102*–*104*). It has only recently been recognized that CMNs can transfer allelochemicals and transmit plant signals. Theoretically, hyphal networks could also represent pathways for virus transmission, given that several phytoviruses can infect fungi (*105*). If this were true, it would represent a new stabilizing mechanism promoting plant species co-occurrence and diversity, when abundant and fast-growing plant species, which usually invest little to defense systems, are affected most.

Conclusions

We posit that plant-fungal mycorrhizal associations per se and interlinking hyphal networks synergistically affect plant communities and ecosystem services through the altered functional traits and autecology of host plants. This is perhaps most clearly apparent in the specialized C nutrition of orchids and mycoheterotrophs. ErM plants but also some NM plants have evolved specific means of mineral nutrition in extremely nutrient-poor or otherwise extreme environmental conditions. Both high hyphal biomass and physical ensheathing of plant feeder roots may underlie the relatively strong protective benefits of EcM fungi to their host plants, which results in positive plant-soil feedback and high population densities and may, in the long term, lead to the development of low-diversity, potentially monodominant, ecosystems. The ways in which mycorrhizal plants and fungi modify the environment produce spatially distinct regeneration niches that favor establishment of plant species with different functional traits.

We recognize three ways in which different types of mycorrhiza influence plant population and community ecology: by affecting plant dispersal, establishment, and coexistence (the latter through stabilizing and equalizing mechanisms). Dispersal limitation of one or both symbiotic partners restricts the distribution of OM and EcM plants more than AM, ErM, and NM plants. Failure of either partner to arrive or establish in a given habitat may alter the diversity, as well as the taxonomic and mycorrhizal type composition, of plant communities. Stabilizing mechanisms via negative soil feedback are best understood in the context of AM systems. Niche differentiation both within and among mycorrhizal types enhances coexistence by leveraging interspecific competition via different rooting depths, foraging strategies, and soil nutrient partitioning. Equalizing mechanisms, which enhance weaker competitors, may operate through differential mycorrhizal benefits that elicit relatively stronger positive growth responses or enhancement of seedling establishment via CMNs. Although CMNs are important in AM, OM, and EcM associations, evidence that they enhance coexistence and diversity is so far limited to AM and OM systems. Species-specific benefits and resource trading may represent key mechanisms by which diversity begets diversity in plant-mycorrhizal fungi mutualistic systems.

REFERENCES AND NOTES

1. D. Tilman, *Resource Competition and Community Structure* (Princeton Univ. Press, 1982).
2. L. Götzenberger *et al*., Ecological assembly rules in plant communities—Approaches, patterns and prospects. *Biol. Rev. Camb. Philos. Soc.* **87**, 111–127 (2012). doi: 10.1111/j.1469-185X.2011.00187.x; pmid: 21692965
3. D. A. Wardle *et al*., Ecological linkages between aboveground and belowground biota. *Science* **304**, 1629–1633 (2004). doi: 10.1126/science.1094875; pmid: 15192218
4. J. D. Bever, Dynamics within mutualism and the maintenance of diversity: Inference from a model of interguild frequency dependence. *Ecol. Lett.* **2**, 52–61 (1999). doi: 10.1046/j.1461-0248.1999.21050.x
5. J. D. Bever *et al*., Rooting theories of plant community ecology in microbial interactions. *Trends Ecol. Evol.* **25**, 468–478 (2010). doi: 10.1016/j.tree.2010.05.004; pmid: 20557974
6. S. E. Smith, D. J. Read, *Mycorrhizal Symbiosis* (Academic Press, ed. 3, 2008).
7. S. Rasmann, A. Bennett, A. Biere, A. Karley, E. Guerrieri, Root symbionts: Powerful drivers of plant above- and belowground indirect defenses. *Insect Sci.* **24**, 947–960 (2017). doi: 10.1111/1744-7917.12464; pmid: 28374534

8. M. Buée, W. De Boer, F. Martin, L. van Overbeek, E. Jurkevitch, The rhizosphere zoo: An overview of plant-associated communities of microorganisms, including phages, bacteria, archaea, and fungi, and some of their structuring factors. *Plant Soil* **321**, 189–212 (2009). doi: 10.1007/s11104-009-9991-3
9. M. L. McCormack *et al*., Building a better foundation: Improving root-trait measurements to understand and model plant and ecosystem processes. *New Phytol.* **215**, 27–37 (2017). doi: 10.1111/nph.14459; pmid: 28295373
10. L. Tedersoo, M. Bahram, Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biol. Rev.* **94**, 1857–1880 (2019). doi: 10.1111/brv.12538; pmid: 31270944
11. S. W. Simard *et al*., Mycorrhizal networks: Mechanisms, ecology and modelling. *Fungal Biol. Rev.* **26**, 39–60 (2012). doi: 10.1016/j.fbr.2012.01.001
12. M. C. Brundrett, L. Tedersoo, Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytol.* **220**, 1108–1115 (2018). doi: 10.1111/nph.14976; pmid: 29355963
13. K. Kadowaki *et al*., Mycorrhizal fungi mediate the direction and strength of plant-soil feedbacks differently between arbuscular mycorrhizal and ectomycorrhizal communities. *Commun. Biol.* **1**, 196 (2018). doi: 10.1038/s42003-018-0201-9; pmid: 30480098
14. C. Terrer, S. Vicca, B. A. Hungate, R. P. Phillips, I. C. Prentice, Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science* **353**, 72–74 (2016). doi: 10.1126/science.aaf4610; pmid: 27365447
15. N. A. Soudzilovskaia *et al*., Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nat. Commun.* **10**, 5077 (2019). doi: 10.1038/s41467-019-13019-2
16. M. K. McCormick, D. F. Whigham, A. Canchani-Viruet, Mycorrhizal fungi affect orchid distribution and population dynamics. *New Phytol.* **219**, 1207–1215 (2018). doi: 10.1111/nph.15223; pmid: 29790578
17. J. A. Bennett *et al*., Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science* **355**, 181–184 (2017). doi: 10.1126/science.aai8212; pmid: 28082590
18. F. P. Teste *et al*., Plant-soil feedback and the maintenance of diversity in Mediterranean-climate shrublands. *Science* **355**, 173–176 (2017). doi: 10.1126/science.aai8291; pmid: 28082588
19. D. J. Johnson, K. Clay, R. P. Phillips, Mycorrhizal associations and the spatial structure of an old-growth forest community. *Oecologia* **186**, 195–204 (2018). doi: 10.1007/s00442-017-3987-0; pmid: 29086005
20. X. Liu *et al*., Partitioning of soil phosphorus among arbuscular and ectomycorrhizal trees in tropical and subtropical forests. *Ecol. Lett.* **21**, 713–723 (2018). doi: 10.1111/ele.12939; pmid: 29536604
21. J. A. Myers, K. E. Harms, Seed arrival, ecological filters, and plant species richness: A meta-analysis. *Ecol. Lett.* **12**, 1250–1260 (2009). doi: 10.1111/j.1461-0248.2009.01373.x; pmid: 19723285
22. V. Merckx, *Mycoheterotrophy: The Biology of Plants Living on Fungi* (Springer, 2013).
23. S. Põlme *et al*., Host preference and network properties in biotrophic plant-fungal associations. *New Phytol.* **217**, 1230–1239 (2018). doi: 10.1111/nph.14895; pmid: 29165806
24. J. Pither, B. J. Pickles, S. W. Simard, A. Ordonez, J. W. Williams, Below-ground biotic interactions moderated the postglacial range dynamics of trees. *New Phytol.* **220**, 1148–1160 (2018). doi: 10.1111/nph.15203; pmid: 29770964
25. M. Correia, R. Heleno, P. Vargas, S. Rodríguez-Echeverría, Should I stay or should I go? Mycorrhizal plants are more likely to invest in long-distance seed dispersal than non-mycorrhizal plants. *Ecol. Lett.* **21**, 683–691 (2018). doi: 10.1111/ele.12936; pmid: 29536599
26. O. Eriksson, K. Kainulainen, The evolutionary ecology of dust seeds. *Perspect. Plant Ecol. Evol. Syst.* **13**, 73–87 (2011). doi: 10.1016/j.ppees.2011.02.002
27. T. R. Horton, Spore dispersal in ectomycorrhizal fungi at fine and regional scales. *Ecol. Stud.* **230**, 61–78 (2017). doi: 10.1007/978-3-319-56363-3_3
28. K. G. Peay, M. Garbelotto, T. D. Bruns, Evidence of dispersal limitation in soil microorganisms: Isolation reduces species richness on mycorrhizal tree islands. *Ecology* **91**, 3631–3640 (2010). doi: 10.1890/09-2237.1; pmid: 21302834
29. H. Sato, R. Tsujino, K. Kurita, K. Yokoyama, K. Agata, Modelling the global distribution of fungal species: New insights into microbial cosmopolitanism. *Mol. Ecol.* **21**, 5599–5612 (2012). doi: 10.1111/mec.12053; pmid: 23062148
30. P. Kohout, Biogeography of ericoid mycorrhiza. *Ecol. Stud.* **230**, 179–193 (2017). doi: 10.1007/978-3-319-56363-3_9
31. J. Davison *et al*., Microbial island biogeography: Isolation shapes the life history characteristics but not diversity of root-symbiotic fungal communities. *ISME J.* **12**, 2211–2224 (2018). doi: 10.1038/s41396-018-0196-8; pmid: 29884829
32. R. E. Koske, J. N. Gemma, VA Mycorrhizae in strand vegetation of Hawaii: Evidence for long-distance codispersal of plants and fungi. *Am. J. Bot.* **77**, 466–474 (1990). doi: 10.1002/j.1537-2197.1990.tb13577.x; pmid: 30139163
33. H. Toju, P. R. Guimarães, J. M. Olesen, J. N. Thompson, Assembly of complex plant-fungus networks. *Nat. Commun.* **5**, 5273 (2014). doi: 10.1038/ncomms6273; pmid: 25327887
34. J. Leake *et al*., Networks of power and influence: The role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Can. J. Bot.* **82**, 1016–1045 (2004). doi: 10.1139/b04-060
35. T. Klein, R. T. L. Siegwolf, C. Körner, Belowground carbon trade among tall trees in a temperate forest. *Science* **352**, 342–344 (2016). doi: 10.1126/science.aad6188; pmid: 27081070
36. B. J. Pickles *et al*., Transfer of ^{13}C between paired Douglas-fir seedlings reveals plant kinship effects and uptake of exudates by ectomycorrhizas. *New Phytol.* **214**, 400–411 (2017). doi: 10.1111/nph.14325; pmid: 27870059
37. X. He, C. Critchley, C. S. Bledsoe, Nitrogen transfer within and between plants through common mycorrhizal networks (CMNs). *Crit. Rev. Plant Sci.* **22**, 531–567 (2003). doi: 10.1080/713608315
38. J. W. Munroe, M. E. Isaac, N_2-fixing trees and the transfer of fixed-N for sustainable agroforestry: A review. *Agron. Sustain. Dev.* **34**, 417–427 (2014). doi: 10.1007/s13593-013-0190-5
39. R. D. Finlay, Functional aspects of incompatible ectomycorrhizal associations. *Agric. Ecosyst. Environ.* **28**, 127–131 (1990). doi: 10.1016/0167-8809(90)90027-B
40. F. Martin, *Molecular Mycorrhizal Symbiosis* (Wiley-Blackwell, 2017).
41. S. Werner, A. Polle, N. Brinkmann, Belowground communication: Impacts of volatile organic compounds (VOCs) from soil fungi on other soil-inhabiting organisms. *Appl. Microbiol. Biotechnol.* **100**, 8651–8665 (2016). doi: 10.1007/s00253-016-7792-1; pmid: 27638017
42. M. A. Gorzelak, A. K. Asay, B. J. Pickles, S. W. Simard, Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. *AoB Plants* **7**, plv050 (2015). doi: 10.1093/aobpla/plv050; pmid: 25979966
43. Y. Y. Song, S. W. Simard, A. Carroll, W. W. Mohn, R. S. Zeng, Defoliation of interior Douglas-fir elicits carbon transfer and stress signalling to ponderosa pine neighbors through ectomycorrhizal networks. *Sci. Rep.* **5**, 8495 (2015). doi: 10.1038/srep08495; pmid: 25683155
44. D. Johnson, L. Gilbert, Interplant signalling through hyphal networks. *New Phytol.* **205**, 1448–1453 (2015). doi: 10.1111/nph.13115; pmid: 25421970
45. A. L. File, J. Klironomos, H. Maherali, S. A. Dudley, Plant kin recognition enhances abundance of symbiotic microbial partner. *PLOS ONE* **7**, e45648 (2012). doi: 10.1371/journal.pone.0045648; pmid: 23029158
46. M. Semchenko, S. Saar, A. Lepik, Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. *New Phytol.* **204**, 631–637 (2014). doi: 10.1111/nph.12930; pmid: 25039372
47. H. Ek, S. Andersson, B. Söderström, Carbon and nitrogen flow in silver birch and Norway spruce connected by a common mycorrhizal mycelium. *Mycorrhiza* **6**, 465–467 (1997). doi: 10.1007/s005720050148
48. J. D. Bever, Preferential allocation, physio-evolutionary feedbacks, and the stability and environmental patterns of mutualism between plants and their root symbionts. *New Phytol.* **205**, 1503–1514 (2015). doi: 10.1111/nph.13239; pmid: 25561086
49. S. Hortal *et al*., Role of plant-fungal nutrient trading and host control in determining the competitive success of ectomycorrhizal fungi. *ISME J.* **11**, 2666–2676 (2017). doi: 10.1038/ismej.2017.116; pmid: 28731478
50. G. A. K. Wyatt, E. T. Kiers, A. Gardner, S. A. West, A biological market analysis of the plant-mycorrhizal symbiosis. *Evolution* **68**, 2603–2618 (2014). doi: 10.1111/evo.12466; pmid: 24909843
51. A. Kohler *et al*., Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nat. Genet.* **47**, 410–415 (2015). doi: 10.1038/ng.3223; pmid: 25706625
52. A. Argüello *et al*., Options of partners improve carbon for phosphorus trade in the arbuscular mycorrhizal mutualism. *Ecol. Lett.* **19**, 648–656 (2016). doi: 10.1111/ele.12601; pmid: 27074533
53. P. Chesson, Updates on mechanisms of maintenance of species diversity. *J. Ecol.* **106**, 1773–1794 (2018). doi: 10.1111/1365-2745.13035
54. A. Packer, K. Clay, Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature* **404**, 278–281 (2000). doi: 10.1038/35005072; pmid: 10749209
55. L. Chen *et al*., Differential soil fungus accumulation and density dependence of trees in a subtropical forest. *Science* **366**, 124–128 (2019). doi: 10.1126/science.aau1361; pmid: 31604314
56. I. A. Dickie, N. Koele, J. D. Blum, J. D. Gleason, M. S. McGlone , Mycorrhizas in changing ecosystems. *Botany* **92**, 149–160 (2014). doi: 10.1139/cjb-2013-0091
57. T. Sasaki *et al*., Role of mycorrhizal associations in tree spatial distribution patterns based on size class in an old-growth forest. *Oecologia* **189**, 971–980 (2019). doi: 10.1007/s00442-019-04376-2; pmid: 30919108
58. K. S. Peh, S. L. Lewis, J. Lloyd, Mechanisms of monodominance in diverse tropical tree-dominated systems. *J. Ecol.* **99**, 891–898 (2011). doi: 10.1111/j.1365-2745.2011.01827.x
59. M. Moora, M. Zobel, Arbuscular mycorrhizae and plant-plant interactions, in *Positive Plant Interactions and Community Biology*, F. Pugnaire, Ed. (CRC Press, 2010), pp. 79–98.
60. P. G. Kennedy, J. K. M. Walker, L. M. Bogar, Interspecific mycorrhizal networks and non-networking hosts: Exploring the ecology of host genus *Alnus*. *Ecol. Stud.* **224**, 227–254 (2015). doi: 10.1007/978-94-017-7395-9_8
61. M. W. Waud, P. Busschaert, B. Lievens, H. Jacquemyn, Specificity and localised distribution of mycorrhizal fungi in the soil may contribute to co-existence of orchid species. *Fungal Ecol.* **20**, 155–165 (2016). doi: 10.1016/j.funeco.2015.12.008
62. A. Pauw, Can pollination niches facilitate plant coexistence? *Trends Ecol. Evol.* **28**, 30–37 (2013). doi: 10.1016/j.tree.2012.07.019; pmid: 22951227
63. S. Stanescu, H. Maherali, Arbuscular mycorrhizal fungi alter the competitive hierarchy among old-field plant species. *Oecologia* **183**, 479–491 (2017). doi: 10.1007/s00442-016-3771-6; pmid: 27848080
64. D. A. Perry *et al*., Mycorrhizal fungi in mixed-species forests and other tales of positive feedback, redundancy and stability, in *The Ecology of Mixed-Species Stands of Trees*, M. G. Cannell *et al*., Eds. (Blackwell, London, 1992), pp. 151–179.
65. D. C. Hartnett, G. W. T. Wilson, Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* **80**, 1187–1195 (1999). doi: 10.1890/0012-9658(1999)080[1187:MIPCSA]2.0.CO;2
66. J. D. Hoeksema *et al*., Evolutionary history of plant hosts and fungal symbionts predicts the strength of mycorrhizal mutualism. *Commun. Biol.* **1**, 116 (2018). doi: 10.1038/s42003-018-0120-9; pmid: 30271996
67. C. Hazard, L. Kruitbos, H. Davidson, A. F. S. Taylor, D. Johnson, Contrasting effects of intra- and interspecific identity and richness of ectomycorrhizal fungi on host plants, nutrient retention and multifunctionality. *New Phytol.* **213**, 852–863 (2017). doi: 10.1111/nph.14184; pmid: 27636558
68. B. Bachelot, M. Uriarte, K. L. McGuire, J. Thompson, J. Zimmerman, Arbuscular mycorrhizal fungal diversity and natural enemies promote coexistence of tropical tree species. *Ecology* **98**, 712–720 (2017). doi: 10.1002/ecy.1683; pmid: 27984646
69. L. Tedersoo, P. Pellet, U. Kõljalg, M.-A. Selosse, Parallel evolutionary paths to mycoheterotrophy in understorey Ericaceae and Orchidaceae: Ecological evidence for mixotrophy in Pyroleae. *Oecologia* **151**, 206–217 (2007). doi: 10.1007/s00442-006-0581-2; pmid: 17089139
70. D. L. Taylor *et al*., Progress and prospects for the ecological genetics of mycoheterotrophs, in *Mycoheterotrophy*, V. Merckx, Ed. (Springer, 2013), pp. 245–266.
71. P. Giesemann, H. N. Rasmussen, H. T. Liebel, G. Gebauer, Discreet heterotrophs: Green plants that receive fungal

carbon through *Paris*-type arbuscular mycorrhiza. *New Phytol.* nph.16367 (2019). doi: 10.1111/nph.16367; pmid: 31837155
72. E. T. Aschehoug, R. Brooker, D. Z. Atwater, J. L. Maron, R. M. Callaway, The mechanisms and consequences of interspecific competition among plants. *Annu. Rev. Ecol. Evol. Syst.* **47**, 263–281 (2016). doi: 10.1146/annurev-ecolsys-121415-032123
73. O. Franklin, T. Näsholm, P. Högberg, M. N. Högberg, Forests trapped in nitrogen limitation—An ecological market perspective on ectomycorrhizal symbiosis. *New Phytol.* **203**, 657–666 (2014). doi: 10.1111/nph.12840; pmid: 24824576
74. K. M. Becklin, M. L. Pallo, C. Galen, Willows indirectly reduce arbuscular mycorrhizal fungal colonization in understorey communities. *J. Ecol.* **100**, 343–351 (2012). doi: 10.1111/j.1365-2745.2011.01903.x
75. M. G. Booth, J. D. Hoeksema, Mycorrhizal networks counteract competitive effects of canopy trees on seedling survival. *Ecology* **91**, 2294–2302 (2010). doi: 10.1890/09-1139.1; pmid: 20836451
76. D. P. Janos, J. Scott, C. Aristizábal, D. M. J. S. Bowman, Arbuscular-mycorrhizal networks inhibit *Eucalyptus tetrodonta* seedlings in rain forest soil microcosms. *PLOS ONE* **8**, e57716 (2013). doi: 10.1371/journal.pone.0057716; pmid: 23460899
77. V. Rinaudo, P. Bàrberi, M. Giovannetti, M. G. A. van der Heijden, Mycorrhizal fungi suppress aggressive agricultural weeds. *Plant Soil* **333**, 7–20 (2010). doi: 10.1007/s11104-009-0202-z
78. C. Wagg, R. Veiga, M. G. A. van der Heijden, Facilitation and antagonism in mycorrhizal networks. *Ecol. Stud.* **224**, 203–226 (2015). doi: 10.1007/978-94-017-7395-9_7
79. A. Javaid, Allelopathic interactions in mycorrhizal associations. *Allelopathy J.* **20**, 29–42 (2007).
80. P. Kohout *et al*., Ericaceous dwarf shrubs affect ectomycorrhizal fungal community of the invasive *Pinus strobus* and native *Pinus sylvestris* in a pot experiment. *Mycorrhiza* **21**, 403–412 (2011). doi: 10.1007/s00572-010-0350-2; pmid: 21161550
81. K. A. Meinhardt, C. A. Gehring, Disrupting mycorrhizal mutualisms: A potential mechanism by which exotic tamarisk outcompetes native cottonwoods. *Ecol. Appl.* **22**, 532–549 (2012). doi: 10.1890/11-1247.1; pmid: 22611852
82. D. Cipollini, C. M. Rigsby, E. K. Barto, Microbes as targets and mediators of allelopathy in plants. *J. Chem. Ecol.* **38**, 714–727 (2012). doi: 10.1007/s10886-012-0133-7; pmid: 22585095
83. E. K. Barto *et al*., The fungal fast lane: Common mycorrhizal networks extend bioactive zones of allelochemicals in soils. *PLOS ONE* **6**, e27195 (2011). doi: 10.1371/journal.pone.0027195; pmid: 22110615
84. M. C. Brundrett, Global diversity and importance of mycorrhizal and nonmycorrhizal plants. *Ecol. Stud.* **230**, 533–556 (2017). doi: 10.1007/978-3-319-56363-3_21
85. M. G. A. van der Heijden *et al*., Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* **396**, 69–72 (1998). doi: 10.1038/23932
86. I. Hiiesalu *et al*., Species richness of arbuscular mycorrhizal fungi: Associations with grassland plant richness and biomass. *New Phytol.* **203**, 233–244 (2014). doi: 10.1111/nph.12765; pmid: 24641509
87. L. Tedersoo *et al*., Tree diversity and species identity effects on soil fungi, protists and animals are context dependent. *ISME J.* **10**, 346–362 (2016). doi: 10.1038/ismej.2015.116; pmid: 26172210
88. H. Maherali, J. N. Klironomos, Influence of phylogeny on fungal community assembly and ecosystem functioning. *Science* **316**, 1746–1748 (2007). doi: 10.1126/science.1143082; pmid: 17588930
89. J. Köhler *et al*., Ectomycorrhizal fungal diversity increases phosphorus uptake efficiency of European beech. *New Phytol.* **220**, 1200–1210 (2018). doi: 10.1111/nph.15208; pmid: 29770963
90. E. B. Allen *et al*., Patterns and regulation of mycorrhizal plant and fungal diversity. *Plant Soil* **170**, 47–62 (1995). doi: 10.1007/BF02183054
91. M. Gerz, C. G. Bueno, M. Zobel, M. Moora, Plant community mycorrhization in temperate forests and grasslands: Relations with edaphic properties and plant diversity. *J. Veg. Sci.* **27**, 89–99 (2016). doi: 10.1111/jvs.12338
92. R. Bagchi *et al*., Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* **506**, 85–88 (2014). doi: 10.1038/nature12911; pmid: 24463522
93. B. D. Lindahl *et al*., Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. *New Phytol.* **173**, 611–620 (2007). doi: 10.1111/j.1469-8137.2006.01936.x; pmid: 17244056
94. H. Toju, O. Kishida, N. Katayama, K. Takagi, Networks depicting the fine-scale co-occurrences of fungi in soil horizons. *PLOS ONE* **11**, e0165987 (2016). doi: 10.1371/journal.pone.0165987; pmid: 27861486
95. M. F. Ahmad-Ramli, T. Cornulier, D. Johnson, Partitioning of soil phosphorus regulates competition between *Vaccinium vitis-idaea* and *Deschampsia cespitosa*. *Ecol. Evol.* **3**, 4243–4252 (2013). doi: 10.1002/ece3.771; pmid: 24324874
96. S. Luo, B. Schmid, G. B. De Deyn, S. Yu, Soil microbes promote complementarity effects among co-existing trees through soil nitrogen partitioning. *Funct. Ecol.* **32**, 1879–1889 (2018). doi: 10.1111/1365-2435.13109
97. D. J. Read, Mycorrhizas in ecosystems. *Experientia* **47**, 376–391 (1991). doi: 10.1007/BF01972080
98. L. Gómez-Aparicio *et al*., Spatial patterns of soil pathogens in declining Mediterranean forests: Implications for tree species regeneration. *New Phytol.* **194**, 1014–1024 (2012). doi: 10.1111/j.1469-8137.2012.04108.x; pmid: 22428751
99. E. Laliberté, H. Lambers, T. I. Burgess, S. J. Wright, Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytol.* **206**, 507–521 (2015). doi: 10.1111/nph.13203; pmid: 25494682
100. I. A. Dickie, S. A. Schnitzer, P. B. Reich, S. E. Hobbie, Spatially disjunct effects of co-occurring competition and facilitation. *Ecol. Lett.* **8**, 1191–1200 (2005). doi: 10.1111/j.1461-0248.2005.00822.x; pmid: 21352443
101. W. H. van der Putten *et al*., Plant-soil feedbacks: The past, the present and future challenges. *J. Ecol.* **101**, 265–276 (2013). doi: 10.1111/1365-2745.12054
102. R. H. Nilsson *et al*., Mycobiome diversity: High-throughput sequencing and identification of fungi. *Nat. Rev. Microbiol.* **17**, 95–109 (2019). doi: 10.1038/s41579-018-0116-y; pmid: 30442909
103. F. Z. Teng, N. Dauphas, J. M. Watkins, Non-traditional stable isotopes: Retrospective and prospective. *Rev. Mineral. Geochem.* **82**, 1–26 (2017). doi: 10.2138/rmg.2017.82.1
104. M. D. Whiteside *et al*., Mycorrhizal fungi respond to resource inequality by moving phosphorus from rich to poor patches across networks. *Curr. Biol.* **29**, 2043–2050.e8 (2019). doi: 10.1016/j.cub.2019.04.061; pmid: 31178314
105. M. J. Roossinck, Evolutionary and ecological links between plant and fungal viruses. *New Phytol.* **221**, 86–92 (2019). doi: 10.1111/nph.15364; pmid: 30084143

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How mycorrhizal associations drive plant population and community biology

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The pervasive power of mycorrhizas

Associations between plants and symbiotic fungi—mycorrhizas—are ubiquitous in plant communities. Tedersoo *et al.* review recent developments in mycorrhizal research, revealing the complex and pervasive nature of this largely invisible interaction. Complex networks of mycorrhizal hyphae connect the root systems of individual plants, regulating nutrient flow and competitive interactions between and within plant species, controlling seedling establishment, and ultimately influencing all aspects of plant community ecology and coexistence.

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