Opinion

Symbiotic control of canopy dominance in subtropical and tropical forests

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Subtropical and tropical forests in Asia often comprise canopy dominant trees that form symbioses with ectomycorrhizal fungi, and species-rich understorey trees that form symbioses with arbuscular mycorrhizal fungi. We propose a virtuous phosphorus acquisition hypothesis to explain this distinct structure. The hypothesis is based on (i) seedlings being rapidly colonised by ectomycorrhizal fungi from established mycelial networks that generates positive feedback and resistance to pathogens, (ii) ectomycorrhizal fungi having evolved a suite of morphological, physiological, and molecular traits to enable them to capture phosphorus from a diversity of chemical forms, including organic forms, and (iii) allocation of photosynthate carbon from adult host plants to provide the energy needed to undertake these processes.

The structure of tropical and subtropical forests: the race to the top

Subtropical and tropical forests are some of the most species-rich plant communities on Earth, but they are at risk from pressures of climate and land-use change (e.g., logging, deforestation) [1]. Understanding the factors that maintain plant diversity and structure in these forests is needed from a conservation and restoration perspective, as well as informing our knowledge of fundamental ecological processes. Various hypotheses have been suggested to explain high plant diversity in these biomes, including the role of micro-topographic niches, trade-offs in survivorship and growth in responses to niches, Janzen–Connell effects, and negative density-dependence [2]. However, a key feature of many subtropical and tropical forests is their distinct structure. In many locations the canopy is dominated by a limited number of tree species – for example, **dipterocarps** (see Glossary) and members of the Fagaceae **–** that form symbioses with **ectomycorrhizal fungi**, and an understorey comprising many species of plants that mainly form symbioses with **arbuscular mycorrhizal fungi** (Box 1). The factors that generate this distinctive structure have received less attention. While the nutrient-foraging activities and the physiological and molecular mechanisms regulating the activity of ectomycorrhizal and arbuscular mycorrhizal fungi have been well studied, usually these studies have been done in isolation with little attempt to consider their capacity to affect co-occurrence of host plants supporting each type of mycorrhiza. In addition, the net effects of the presence of mutualistic mycorrhizal fungi and pathogens have also been rarely considered as a driver of forest community structure.

The nutritional benefits to host plants of supporting mycorrhizal fungi, regardless of type, are well known [3]. It is increasingly recognised that many plant communities are either limited or co-limited by phosphorus, a situation that is likely to become more widespread due to the deposition of atmospheric reactive nitrogen. Nonglaciated soils in tropical and Southern hemisphere biomes are particularly depleted in phosphorus [4,5], and the availability of this element provides a strong control of community composition in these regions [6]. A key selective force on mycorrhizal plants and fungi in these environments is likely to be the ability to evolve mechanisms to acquire phosphorus [7]. The organic pool in soil is usually dominant, and individual groups of molecules are

Highlights

In many species-rich subtropical and tropical forests, the canopy is dominated by trees that form symbioses with ectomycorrhizal fungi, while understorey trees typically form symbioses with arbuscular mycorrhizal fungi.

We propose a virtuous phosphorus acquisition hypothesis to explain this structure. This hypothesis is based on evidence that ectomycorrhizal fungi are better equipped than arbuscular mycorrhizal fungi to acquire growth-limiting phosphorus from organic forms in soil through the production of enzymes and exudates.

Ectomycorrhizal saplings also gain more benefit from the formation of fungal networks with neighbouring adult plants, which also suppress infection by pathogens. Canopy dominance provides plants with the opportunity to capture more carbon from the atmosphere and fuel these below-ground nutrient-foraging activities.

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also highly diverse: for example, there are over 40 variants of the abundant molecule **inositol phosphate** [8], usually a dominant organic form in soil. Thus, we propose that natural selection will have generated adaptations to enable foraging mycorrhizal fungi to acquire functional groups of phosphorus forms in soil, with consequences for the structure of forest communities.

In this opinion article we therefore integrate recent work on the role of plant–soil interactions in determining the growth and fitness of trees in subtropical and tropical forests. We propose that a 'virtuous phosphorus acquisition hypothesis' maintains canopy dominance of ectomycorrhizal host plants in phosphorus-limited or co-limited systems. The hypothesis is based on a positive feedback loop involving rapid colonisation of seedlings by ectomycorrhizal fungi, generation of positive feedback with ectomycorrhizal fungi, resistance to pathogens, ability to capture phosphorus from a diversity of chemical forms, and allocation of photosynthate carbon below ground to fuel these processes (Figure 1).

Allocation of carbon to mycorrhizal fungi: the energy driving nutrient acquisition

Mycorrhizal fungi are dependent on host plants for their supply of energy (carbon). Although ectomycorrhizal fungi have some capacity for saprotrophy, the ready availability of carbon from host plants is far more likely to drive their activity compared with decomposition of organic compounds. The amount of carbon allocated to mycorrhizal fungi can range from 1% to 30% of the carbon photosynthesised by plants [3]. The large range of values reported in the literature reflects the variability generated by specific combinations of mycorrhizal plants and fungi, and interaction with a plethora of abiotic and biotic factors (e.g., herbivory, pathogens, temperature, water availability, soil fertility). Overall, ectomycorrhizal plants tend to allocate proportionately more carbon to mycorrhizal fungi than plants with **arbuscular mycorrhizas**, although there is overlap. Clearly, high rates of photosynthesis unlock the full potential of mycorrhizal fungi by maximising available energy from plants. In many circumstances, the growth and reproduction of trees is linked to the vertical light gradient in forests, which creates strong selection for rapid height growth to maximise carbon gain for potential allocation to fungi. However, photosynthesis is often strongly linked to leaf nitrogen and phosphorus concentrations, and availability of light, and so the potential to reach the canopy and to acquire growth-limiting nutrients is vital to maintain this luxury supply of carbon.

A key feature of carbon allocation below ground to mycorrhizal fungi is the rapidity at which it occurs. In ectomycorrhizal systems, carbon was observed to accumulate faster in the growing

Figure 1. Graphical summary of the virtuous phosphorus acquisition hypothesis. (A) Ectomycorrhizal fungi supported by adult plants provide established absorptive fungal networks that rapidly colonise roots of (B) seedlings, increasing their survival and growth. (C) Production of extracellular enzymes by ectomycorrhizal fungi, fuelled by carbon from adult plants, facilitates access to a large pool of (D) chemically diverse forms of phosphorus, including monoesters, inositol phosphates, nucleic acids, and orthophosphates. (E) Phosphorus acquired by ectomycorrhizal fungi is translocated to host plants which increases primary production, enables plants to dominate the canopy, and (F) upregulate photosynthesis. This provides the energy to drive below-ground processes generating positive feedback. By contrast, (G) arbuscular mycorrhizal seedlings gain fewer benefits from common mycorrhizal networks associated with adults, are more susceptible to (I) root pathogens, and have access to (H) smaller pools of soil phosphorus primarily comprising inorganic orthophosphates. Figure produced with BioRender.com.

fronts of the **extraradical mycelium** compared to roots [9]. *In situ* pulse-labelling of ectomycorrhizal trees also demonstrates rapid allocation to root tips in the field [10]. A second feature is the ability of ectomycorrhizal plants to direct carbon to specific regions of their root systems and subsequently to spatially explicit parts of the mycorrhizal mycelium [9]. This ability means that carbon can be directed to where it is needed most, for example in relation to nutrient foraging activities or for defence.

We propose that allocation of carbon to mycorrhizal fungi is critical in enabling plants to access the key growth-limiting nutrients, notably phosphorus, in tropical and subtropical forests, and that differences between arbuscular and ectomycorrhizal fungi in the underlying mechanisms of nutrient acquisition contributes to their relative dominance of Asian subtropical and tropical forests. The production of the suite of enzymes capable of degrading organic forms of phosphorus – such as phytases, phosphodiesterases, and phosphomonoesterases – requires energy, and so fungi that produce these enzymes extracellularly likely have a high demand for carbon. In general, the activity of phosphorus-degrading enzymes is greater in ectomycorrhizal fungi than in arbuscular mycorrhizal fungi [11,12].

Recent studies suggest a close link between allocation of recent assimilate from plants and the activity of enzymes responsible for nutrient acquisition in the rhizosphere of Norway spruce [13]. Moreover, carbon allocation to ectomycorrhizal fungi and its release as exudate [14] is a key pathway of energy into free-living microorganisms [15] that may stimulate phosphorus mineralisation (Figure 2). Free-living saprotrophic microorganisms capable of degrading organic phosphorus or solubilising inorganic forms can associate closely with ectomycorrhizal fungal hyphae, and this may reflect a degree of co-dependency (or even symbiosis) related to nutrient acquisition. For example, the bacteria *Burkholderia* spp. can solubilise fluorapatite when growing with the ectomycorrhizal fungus *Laccaria bicolor* [16]. Localised death of foraging mycelium may also serve to stimulate microbial activity [17] and help promote efficient recycling of nutrients contained within fungal mycelium. Indeed, multitrophic interactions throughout the soil food web may be a key driver of phosphorus dynamics in soil [18].

If carbon allocation does play a critical role in driving phosphorus dynamics and niche partitioning, then any factor that modifies this process (positively or negatively) could have important effects on the ecology of forest structure and dynamics. For example, increases in atmospheric carbon dioxide concentrations generally lead to greater allocation of carbon below ground, including to mycorrhizal fungi [19]. We therefore suggest that the relationships between climate change factors and phosphorus dynamics requires further attention.

Accessing phosphorus from soil

Total phosphorus concentrations in soil vary considerably across the globe. This variation is partly driven by the composition of parent material [20] but also by environmental (biotic and abiotic) and climate drivers. In addition, there are myriad forms of phosphorus in soil comprising inorganic phosphates and organic forms such as monoesters, diesters (e.g., phospholipids), and phytates [21,22]. These forms interact with the soil matrix in different ways, which contributes to their accessibility as nutrient sources. This variation in amount and diversity of phosphorus in soils provides opportunities for natural selection to generate contrasting affinities and mechanisms of uptake, as seen for other growth-limiting resources such as nitrogen [23,24]. Temperate forests dominated by ectomycorrhizal trees tend to result in soil where organic phosphorus cycling is more prominent than in soils under arbuscular mycorrhizal trees [12]. It has been hypothesised that niche partitioning of soil phosphorus may therefore play a key role in regulating the composition of plant communities in situations where phosphorus limits or co-limits growth [7]. Increasingly, this hypothesis has generated empirical support [25–27]. It has been demonstrated that ectomycorrhizal dipterocarp and Fagaceae saplings produced more biomass when supplied with inositol phosphate (phytate) as a sole phosphorus source, but were also able to grow on a simple monoester (glucose 6-phosphate) and inorganic phosphate [28]. By contrast, arbuscular mycorrhizal tropical saplings grew best on inorganic phosphate and performed poorly on phytate. These findings provide evidence that the early phase of growth of
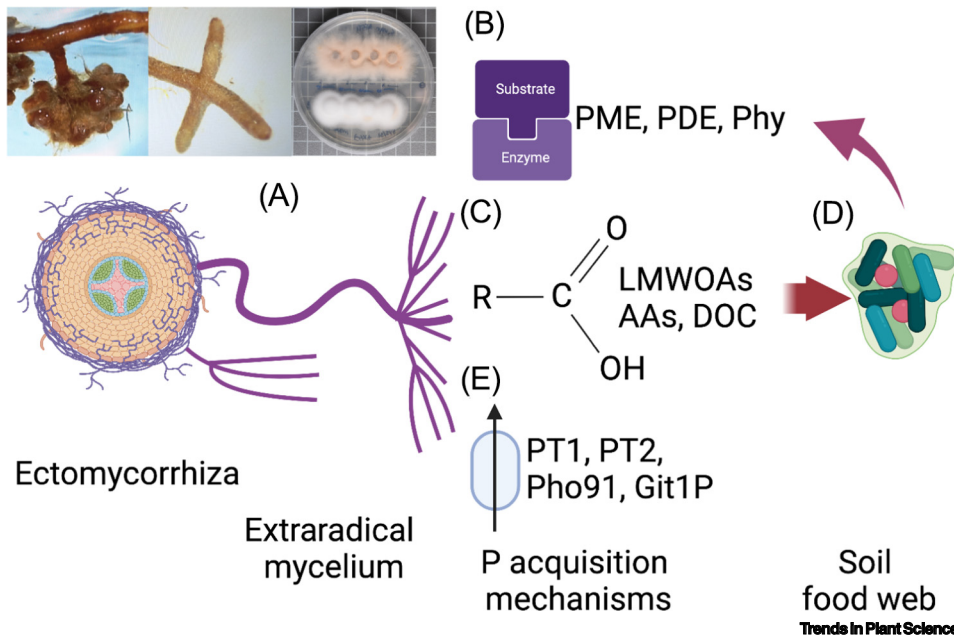
Figure 2. Morphological, physiological, and genetic traits of ectomycorrhizal fungi facilitating their role in efficient uptake and transport of phosphorus from soil, and increasing the competitive ability of canopy-dominant host plants. (A) Photographs showing the varied morphology of ectomycorrhizas extracted from soil and fungal isolates growing in pure culture on Petri dishes. Extraradical mycelium is absent in some ectomycorrhizal fungi, while others produce hyphae of various lengths including long-distance transport types with thick rhizomorphs, and proliferation of highly branched fine foraging hyphae. The extraradical mycelium enables fungi to explore and penetrate soil pores, and contains apparatus for phosphorus (P) acquisition, including (B) extracellular phosphorus-degrading enzymes – phosphomonoesterase (PME), phosphodiesterase (PDE), and phytase (Phy) – and (C) low-molecular-weight organic acids (LMWOAs) that dissolve inorganic phosphates, and together with amino acids (AAs) and other dissolved organic carbon (DOC), feed soil food webs to stimulate further phosphorus mineralisation, and (E) a range of high-affinity (PT1, PT2, Pho91, and Git1P) and low-affinity phosphate transporters [36]. Photographs by Dr Fay Voller. Figure produced with BioRender.com.

seedlings can be strongly regulated by their affinity for different phosphorus forms, and this is a key component of our hypothesis (Figure 1).

What was not determined [28] were the forms of phosphorus taken up, and whether the fungi themselves were directly involved. We suggest that the type of mycorrhiza with which plants associate (i.e., **ectomycorrhiza** versus arbuscular mycorrhiza) has a direct role because their traits (Figure 2), discussed later, reflect contrasting affinities for organic and inorganic forms of phosphorus. One fascinating possibility is that simple organic phosphorus forms could be taken up intact [29]. This mechanism would place ectomycorrhizal plants and fungi at a major advantage because they 'short-circuit' the reliance on mineralisation of organic forms extracellularly, which is open to competition from other organisms. Indeed, there is clear evidence of direct uptake of organic nitrogen by ectomycorrhizal fungi [30], and it seems reasonable to assume that this mechanism could evolve for phosphorus. To test this hypothesis requires sophisticated targeted 'tracer' experiments using non-sterile soil combined with inoculation techniques or the use of physical methods to separate extraradical mycelium from bulk soil [31]. Such tracer experiments are difficult because of the possibility of detecting phosphorus that has been hydro-lysed and transported, rather the intact molecule [32].

Further evidence of direct roles of ectomycorrhizal fungi on the acquisition of phosphorus from organic forms comes from analyses of their physiology and molecular biology (Figure 2). Many

ectomycorrhizal fungi can produce extracellular enzymes responsible for degradation of organic molecules such as monoesters and phytate [33,34], and the activities of these enzymes are typically greater and more widespread than for arbuscular mycorrhizal fungi. In addition, a relationship between the acquisition of ^{32}P from phytate and fungal growth in pure culture was found [34]. Recent advances in interrogation of fungal genomes also revealed that ectomycorrhizal fungi possess the genes necessary for phosphorus scavenging from organic molecules [35] and the subsequent transport of inorganic phosphorus [18,36]. For example, **basidiomycetes** possess a suite of high-affinity phosphorus transporters – including the organic phosphorus transporter Git1P not present in arbuscular mycorrhizal fungi [36] – and both basidiomycetes and **ascomycetes** contain similar numbers of genes coding for secreted phosphatases as saprotrophic fungi. Further coupling of molecular analysis of fungal genomes with their ability to grow on specific phosphorus compounds may give us a greater insight into the evolutionary origins and mechanisms of acquisition of phosphorus from organic forms.

Inorganic phosphorus can be tightly bound to surfaces and become insoluble, particularly when associated with calcium. One widespread strategy to overcome this problem is the exudation of low-molecular-weight organic acids (LMWOAs) that raise the pH and solubilise phosphates. Several ectomycorrhizal fungi produce LMWOAs in pure culture [37] and in symbiosis [14], and so it is possible that this dissolution mechanism may contribute to phosphorus nutrition of host plants. In addition, ectomycorrhizal plants and fungi tend to produce greater amounts of exudates compared to arbuscular mycorrhizal plants and fungi [38].

A final consideration concerns the role of mycorrhizal fungal diversity in regulating phosphorus dynamics in soil and subsequent uptake by plants. As noted above, ectomycorrhizal fungi possess morphological, physiological, and molecular traits that likely make them highly competitive in acquiring phosphorus from diverse sources. However, individual fungi vary substantially in nutrient-acquiring traits both within (intraspecific) and among (interspecific) species [39–41]. Most plants associate with communities of mycorrhizal fungi, and the diversity of these communities is therefore likely to influence the efficiency of phosphorus acquisition by hosts [42].

Our hypothesis also needs to be reconciled with a recent meta-analysis of leaf and root nutrients that showed strong separation in nitrogen concentration between arbuscular mycorrhizal and ectomycorrhizal trees in temperate biomes, reflecting the respective reliance of these mycorrhizal types on 'fast' and 'slow' cycling of nitrogen [43]. However, no such differences were seen in the case of tropical tree species for either nitrogen or phosphorus. One explanation is that phosphorus cycling remains broadly 'slow' under both ectomycorrhizal and arbuscular mycorrhizal trees in tropical and subtropical forests, such that phosphorus is never available in luxurious quantities (for the reasons stated previously) that would generate distinctive leaf or root tissue concentrations; instead the key mechanism is around partitioning of the diversity of chemical forms.

Response of seedlings to fungal networks

A fascinating feature of mycorrhizal fungi is their ability to colonise multiple plants of the same or different (compatible) species to form **common mycorrhizal networks (CMNs)** [44]. The presence of a physical connection between plants introduces the possibility that the fungi could be a conduit for resources and materials (e.g., mineral nutrients, carbon, water, infochemicals, viruses) from plant to plant, as well as from soil distant to a new recruit to the CMN. Laboratory experiments clearly demonstrate movement of carbon and mineral nutrients to seedlings via CMNs [45,46], and classic field experiments – albeit undertaken in a limited number of locations – also suggest that net transfer of carbon can occur between saplings [47]. Despite these studies, *in situ* evidence for such effects occurring in forests in multiple habitats and biomes

is very limited and often overstated, in part due to the difficulty of designing experiments that manipulate the presence solely of CMNs [48]. Nonetheless, given the abundance of mycorrhizas on natural vegetation, the expectation is that CMNs are frequently formed [49], and we propose that the differential response of arbuscular and ectomycorrhizal seedlings to common mycorrhizal networks, and networks of pathogens, supported by surrounding adult plants could be a critical step shaping the structure of subtropical and tropical forests (Figure 1).

Our hypothesis is based partly on recent studies that have tested how the potential for seedlings to integrate into CMNs (and nonmycorrhizal fungal networks, notably pathogens) impacts the performance of seedlings in situations where different mycorrhizal types coexist. In subtropical forests, naturally regenerating arbuscular mycorrhizal seedlings tend to have significantly greater pathogen loads on their roots than ectomycorrhizal seedlings [50,51], which might offset positive effects of integrating into a CMN comprising arbuscular mycorrhizal fungi. This observation may partly reflect the nature of the colonisation: ectomycorrhizas comprise a dense sheath of fungal mycelium around infective root tips that may physically prevent pathogens from entering roots. Other parts of ectomycorrhizal host roots are also better protected due to their woody nature. By contrast, arbuscular mycorrhizal roots allow access to fungi throughout their length, and there is limited opportunity for physical exclusion of pathogens capable of lysing plant cell walls.

In field manipulations, ectomycorrhizal seedlings also gain greater biomass and have greater survivorship when they have the potential to form CMNs with conspecific adults [50]. Integration into a CMN could have significant positive effects on the growth of the newly recruited member of the network through access to resources available to the fungus (either from the soil or from other plants), and via protection from pathogens. Whether such effects [50] are a direct consequence of nutrient resource allocation from neighbouring trees is unknown and remains to be tested in tropical and subtropical forests, although as noted previously, this phenomenon can occur both in nature and in the laboratory. Our hypothesis, however, is based on the more likely scenario that integration of seedling roots into an established fungal network, constructed and sustained by carbon from adult plants, gives ectomycorrhizal seedlings access to a ready-made absorptive structure whereupon it can gain immediate nutritional benefit. Nonetheless, this hypothesis requires additional exploration, notably in understanding how both plants and fungi control resource distribution throughout mycelial networks. There is evidence for asynchrony in resource transfer to different plants in CMNs in arbuscular mycorrhizal plants [52], and it is possible that some mycorrhizal fungi may effectively act as parasites by diverting resources to other host plants in a network. Additionally, broader, more holistic benefits of integration into CMNs may have a role in driving a differential response of ectomycorrhizal and arbuscular mycorrhizal plants, including distribution of water and pest-alert signals [49,53].

While the above processes have been discussed at an individual level, some of these processes likely operate at the community level to generate differential impacts on ectomycorrhizal and arbuscular mycorrhizal plants. For example, field experiments revealed that root mycorrhizal colonization of ectomycorrhizal saplings was significantly affected by conspecific density to a greater extent than for arbuscular mycorrhizal saplings, while pathogen infection on fine roots was density-dependent for arbuscular mycorrhizal but not ectomycorrhizal saplings [51]. In another subtropical forest in east China, mycorrhizal type mediated the accumulation rates of different fungal guilds and tree neighbourhood interactions at the community level [54].

Concluding remarks and future perspectives

We propose a 'virtuous phosphorus acquisition hypothesis' to explain the structure of subtropical and tropical forests, which tend to be associated with phosphorus-deficient soils. Whilst this

Outstanding questions

How do expression of genes and production of extracellular phosphorus-degrading enzymes relate to rates of phosphorus acquisition by trees?

Can ectomycorrhizal plants and fungi can acquire organic forms of phosphorus directly, without resorting to mineralisation of the molecule? This question is technically challenging due to the potential to detect transfer of labelled phosphorus that has been cleaved from an organic form.

What is the impact of global climate change factors, such as elevated atmospheric carbon dioxide concentrations and drought, on phosphorus acquisition rates by ectomycorrhizal and arbuscular mycorrhizal plants?

What is the contribution of the virtuous phosphorus acquisition hypothesis relative to other factors (such as gap formation, herbivory) in shaping forest structure?

hypothesis is supported by various strands of independent evidence, a more holistic test is required. In addition, the hypothesis proposed here is largely derived from experiments and observations in Asia. It remains to be seen whether our hypothesis holds in other tropical regions such as Africa and south America, where the structure of forests often differs from those in Asia. Moreover, we highlight the need to integrate novel physiological experiments using tracers with the rapidly emerging analyses of genome assembly and function of mycorrhizal fungi. Finally, the hypothesis states a strong connection between below-ground carbon supply from host plants to ectomycorrhizal fungi and their phosphorus acquisition activities; this connection requires robust testing under conditions that can, as far as possible, replicate the natural environment (such as the use of mature plants). We also need to consider how the impact of changes in carbon supply in response to global climate change factors (notably elevated atmospheric carbon dioxide concentrations) may disrupt phosphorus dynamics and competitive abilities of coexisting plants (see Outstanding questions).

Declaration of interests

No interests are declared.

References

1. Gibson, L. *et al.* (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381
2. Wright, J.S. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130, 1–14
3. Smith, S.E. and Read, D.J. (2008) *Mycorrhizal Symbiosis* (3rd Edn), Elsevier
4. Vitousek, P.M. *et al.* (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* 20, 5–15
5. Yokoyama, D. *et al.* (2018) Characteristics of phosphorus fractions in the soils derived from sedimentary and serpentinite rocks in lowland tropical rain forests, Borneo. *Soil Sci. Plant Nutr.* 64, 218–221
6. Condit, R. *et al.* (2013) Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc. Natl. Acad. Sci. U. S. A.* 110, 5064–5068
7. Turner, B.L. (2008) Resource partitioning for soil phosphorus: a hypothesis. *J. Ecol.* 5, 713–723
8. Saiardi, A. (2017) Has inositol played any role in the origin of life? *Life* 7, 24
9. Leake, J.R. *et al.* (2001) Rates and quantities of carbon flux to ectomycorrhizal mycelium following ^{14}C pulse labeling of *Pinus sylvestris* seedlings: effects of litter patches and interaction with a wood-decomposer fungus. *Tree Physiol.* 21, 71–82
10. Högberg, M.N. (2010) Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytol.* 187, 485–493
11. Antibus, R.K. *et al.* (1997) Root surface phosphatase activities and uptake of P-32-labelled inositol phosphate in field-collected gray birch and red maple roots. *Mycorrhiza* 7, 39–46
12. Rosling, A. (2016) Phosphorus cycling in deciduous forest soil differs between stands dominated by ecto- and arbuscular mycorrhizal trees. *New Phytol.* 209, 1184–1195
13. Zhou, J. *et al.* (2022) Ectomycorrhizal and non-mycorrhizal rhizosphere fungi increase root-derived C input to soil and modify enzyme activities: a ^{14}C pulse labelling of *Picea abies* seedlings. *Plant Cell Environ.* 45, 3122–3133
14. Van Hees, P.A.W. *et al.* (2006) Oxalate and ferricrocin exudation by the extramatrical mycelium of an ectomycorrhizal fungus in symbiosis with *Pinus sylvestris*. *New Phytol.* 169, 367–377
15. Deslippe, J.R. (2016) Stable isotope probing implicates a species of *Cortinarius* in carbon transfer through ectomycorrhizal fungal mycelial networks in Arctic tundra. *New Phytol.* 210, 383–390
16. Fontaine, L. *et al.* (2016) Phosphate-solubilizing bacteria isolated from ectomycorrhizal mycelium of *Picea glauca* are highly efficient at fluorapatite weathering. *Botany* 94, 1183–1193
17. Drigo, B. *et al.* (2012) Rapid incorporation of carbon from ectomycorrhizal mycelial necromass into soil fungal communities. *Soil Biol. Biochem.* 49, 4–10
18. Becquer, A. *et al.* (2014) From soil to plant, the journey of P through trophic relationships and ectomycorrhizal association. *Front. Plant Sci.* 5, 548
19. Keel, S.G. *et al.* (2006) Canopy CO_2 enrichment permits tracing the fate of recently assimilated carbon in a mature deciduous forest. *New Phytol.* 172, 319–329
20. Porder, S. and Ramachandran, S. (2013) The phosphorus concentration of common rocks – a potential driver of ecosystem P status. *Plant Soil* 367, 41–55
21. Redel, Y. *et al.* (2008) Phosphorus fractions and phosphatase activity in an Andisol under different forest ecosystems. *Geoderma* 145, 216–221
22. Turner, B.L. and Engelbrecht, B.M.J. (2011) Soil organic phosphorus in lowland tropical rain forests. *Biogeochemistry* 103, 297–315
23. McKane, R.B. (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415, 68–71
24. Ashton, I.W. *et al.* (2010) Niche complementarity due to plasticity in resource use: plant partitioning of chemical N forms. *Ecology* 91, 3252–3260
25. Steidinger, B.S. *et al.* (2015) Variability in potential to exploit different soil organic phosphorus compounds among tropical montane tree species. *Funct. Ecol.* 29, 121–130
26. Ceulemans, T. *et al.* (2017) Phosphorus resource partitioning shapes phosphorus acquisition and plant species abundance in grasslands. *Nat. Plants* 3, 16224
27. Ahmad-Ramli, M.F. *et al.* (2013) Partitioning of soil phosphorus regulates competition between *Vaccinium vitis-idaea* and *Deschampsia cespitosa*. *Ecol. Evol.* 3, 4243–4252
28. Liu, X. (2018) Partitioning of soil phosphorus among arbuscular and ectomycorrhizal trees in tropical and subtropical forests. *Ecol. Lett.* 21, 713–723
29. Rennenberg, H. and Herschbach, C. (2013) Phosphorus nutrition of woody plants: many questions – few answers. *Plant Biol.* 15, 785–788
30. Näsholm, T. *et al.* (1998) Boreal forest plants take up organic nitrogen. *Nature* 392, 914–916

31. Johnson, D. *et al.* (2001) Novel in-growth core system enables functional studies of grassland mycorrhizal mycelial networks. *New Phytol.* 152, 555–562

32. Rest, B. *et al.* (2002) Glycerophosphocholine metabolism in higher plant cells. Evidence of a new glyceryl-phosphodiester phosphodiesterase. *Plant Physiol.* 130, 244–255

33. Cairney, J.W.G. (2011) Ectomycorrhizal fungi: the symbiotic route to the root for phosphorus in forest soils. *Plant Soil* 344, 51–71

34. Antibus, R.K. *et al.* (1992) Phosphatase-activities and phosphorus uptake from inositol phosphate by ectomycorrhizal fungi. *Can. J. Bot.* 70, 794–801

35. Miyauchi, S. *et al.* (2020) Large-scale genome sequencing of mycorrhizal fungi provides insights into the early evolution of symbiotic traits. *Nat. Commun.* 11, 5125

36. Plassard, C. *et al.* (2019) Phosphorus transport in mycorrhiza: how far are we? *Trends Plant Sci.* 24, 794–801

37. Plassard, C. *et al.* (2011) Diversity in phosphorus mobilisation and uptake in ectomycorrhizal fungi. *Ann. For. Sci.* 68, 33–43

38. Tedersoo, L. and Bahram, M. (2019) Mycorrhizal types differ in ecophysiology and alter plant nutrition and soil processes. *Biol. Rev.* 94, 1857–1880

39. Johnson, D. *et al.* (2012) The importance of individuals: intraspecific diversity of mycorrhizal plants and fungi in ecosystems. *New Phytol.* 194, 614–628

40. Hazard, C. *et al.* (2017) Contrasting effects of intra- and interspecific identity and richness of ectomycorrhizal fungi on host plants, nutrient retention and multifunctionality. *New Phytol.* 213, 852–863

41. Hazard, C. *et al.* (2017) Strain identity of the ectomycorrhizal fungus *Laccaria bicolor* is more important than richness in regulating plant and fungal performance under nutrient rich conditions. *Front. Microbiol.* 8, 1874

42. Hazard, C. and Johnson, D. (2018) Does genotypic and species diversity of mycorrhizal plants and fungi affect ecosystem function? *New Phytol.* 220, 1122–1128

43. Averill, C. *et al.* (2019) Global imprint of mycorrhizal fungi on whole-plant nutrient economics. *Proc. Natl. Acad. Sci. U. S. A.* 116, 23163–23168

44. Leake, J.R. *et al.* (2004) Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. *Can. J. Bot.* 82, 1016–1045

45. Finlay, R.D. and Read, D.J. (1986) The structure and function of the vegetative mycelium of ectomycorrhizal plants. 1. Translocation of ^{14}C-labeled carbon between plants interconnected by a common mycelium. *New Phytol.* 103, 143–156

46. Finlay, R.D. and Read, D.J. (1986) The structure and function of the vegetative mycelium of ectomycorrhizal plants. 2. The uptake and distribution of phosphorus by mycelial strands interconnecting host plants. *New Phytol.* 103, 157–165

47. Simard, S.W. *et al.* (1997) Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* 388, 579–582

48. Karst, J. *et al.* (2023) Positive citation bias and overinterpreted results lead to misinformation on common mycorrhizal networks in forests. *Nat. Ecol. Evol.* 7, 501–511

49. Gilbert, L. and Johnson, D. (2017) Plant–plant communication through common mycorrhizal networks. In *How Plants Communicate with their Biotic Environment. Advances in Botanical Research* (Vol. 82) (Becard, G., ed.), pp. 83–97, Academic Press

50. Liang, M.X. *et al.* (2020) Soil fungal networks maintain local dominance of ectomycorrhizal trees. *Nat. Commun.* 11, 2636

51. Liang, M.X. *et al.* (2021) Soil fungal networks moderate density-dependent survival and growth of seedlings. *New Phytol.* 230, 2061–2071

52. Walder, F. *et al.* (2012) Mycorrhizal networks: common goods of plants shared under unequal terms of trade. *Plant Physiol.* 159, 789–797

53. Gilbert, L. and Johnson, D. (2015) Plant-mediated 'apparent effects' between mycorrhiza and insect herbivores. *Curr. Opin. Plant Biol.* 26, 100–105

54. Chen, L. *et al.* (2019) Differential soil fungus accumulation and density dependence of trees in a subtropical forest. *Science* 366, 124–128