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Viewpoints

Maintenance of host specialisation gradients in ectomycorrhizal symbionts

Summary

Many fungi that form ectomycorrhizas exhibit a degree of host specialisation, and individual trees are frequently colonised by communities of mycorrhizal fungi comprising species that fall on a gradient of specialisation along genetic, functional and taxonomic axes of variation. By contrast, arbuscular mycorrhizal fungi exhibit little specialisation. Here, we propose that host tree root morphology is a key factor that gives host plants fine-scale control over colonisation and therefore opportunities for driving specialisation and speciation of ectomycorrhizal fungi. A gradient in host specialisation is likely driven by four proximate mechanistic ‘filters’ comprising partner availability, signalling recognition, competition for colonisation, and symbiotic function (trade, rewards and sanctions), and the spatially restricted colonisation seen in heterorhizic roots enables these mechanisms, especially symbiotic function, to be more effective in driving the evolution of specialisation. We encourage manipulation experiments that integrate molecular genetics and isotope tracers to test these mechanisms, alongside mathematical simulations of eco-evolutionary dynamics in mycorrhizal symbioses.

Specificity in symbioses

Symbioses prevail in nature through mutualistic, parasitic or commensalistic interactions and are responsible for regulating numerous ecosystem functions, are involved in the maintenance of biodiversity, and in driving speciation (Gilbert *et al.*, 2012). An intriguing feature of many symbioses is the varying degrees of specificity exhibited by partners. For example, a high degree of specificity has been reported in ant–plant protective associations (Heil & McKey, 2003), phytophagous insects (Jaenike, 1990), insect pollination (Bronstein *et al.*, 2006) and ectomycorrhizal (ECM) fungi and plants (Cullings *et al.*, 1996), the focus of this perspective.

The historical view that mycorrhizal fungi were often considered to exhibit limited host plant specificity was strongly influenced by the globally widespread and abundant arbuscular mycorrhizal (AM) fungi, where *c.* 300 AM fungal species associate with *c.* 300 000 compatible host plants (Öpik *et al.*, 2013; Öpik & Davison, 2016).

But even in AM associations, there is evidence of strong host ‘preferences’, with co-existing AM plants harbouring distinct communities of AM fungi (e.g. Vandenkoornhuyse *et al.*, 2002; Martinez-Garcia & Pugnaire, 2011; Martinez-Garcia *et al.*, 2015) and mutual benefits can vary considerably among individual host/fungus associations (Johnson *et al.*, 2012). Despite these findings, there is no doubt that specialisation on fully autotrophic plants is much more common in ECM fungi than in AM fungi.

There are *c.* 20 000–25 000 species of fungi that can form ectomycorrhizas, from a wide taxonomic range of groups but predominantly from the Basidiomycota and Ascomycota groups (Rinaldi *et al.*, 2008; Tedersoo *et al.*, 2010). By contrast, there are only *c.* 6000–7000 species of host plants, which are mainly trees, that exclusively form ECM (Brundrett & Tedersoo, 2018). Molecular methods have provided new insights into the diversity of ECM fungi at scales from individual root tips to biomes, and these datasets raise many intriguing questions concerning their preferences for hosts. In particular, it is increasingly apparent that some ECM fungi only associate with a restricted range of plants, while others are cosmopolitan generalists with, apparently, no specific requirements (Roy *et al.*, 2008; van der Linde *et al.*, 2018). Communities of ECM fungi invariably comprise taxa which exist along a gradient of specialisation and host generalist and specialist ECM fungi coexist, often in close proximity, on a single section of root on an individual tree. Despite these observations, the mechanisms that enable gradients in host specialisation to evolve and be maintained are unresolved.

Here, we first provide a brief overview of specialisation in ECM symbioses before addressing how host specialisation may be maintained. We propose that the heterorhizic root systems characteristic of ECM host plants is key to specialisation. Heterorhizic root systems comprise ‘long roots’, from which ‘short roots’ develop laterally with limited apical growth to form discrete root tips, which become colonised by ECM fungi to form ectomycorrhizas (Kúbiková, 1967; Brundrett *et al.*, 1990). Specifically, the formation of spatially explicit root tips or small sections of root colonised by ECM fungi provides opportunities for mechanistic ‘filters’ to be more effective than would otherwise be the case, and which enable gradients in host specialisation to occur and persist.

Are ECM host specialists special cases?

Detailed analyses of long-term ECM sporocarp data and molecular analysis of roots both provide evidence that a gradient of host specialisation is established in nature. We analysed sporocarp data from Boletoid and Agaricoid ECM fungi in Scandinavia and northern Europe (Knudsen, 2018) and found that 54% of ECM fungi associated with two or fewer host plant genera (Fig. 1). This analysis supports previous work, mainly in North America, where

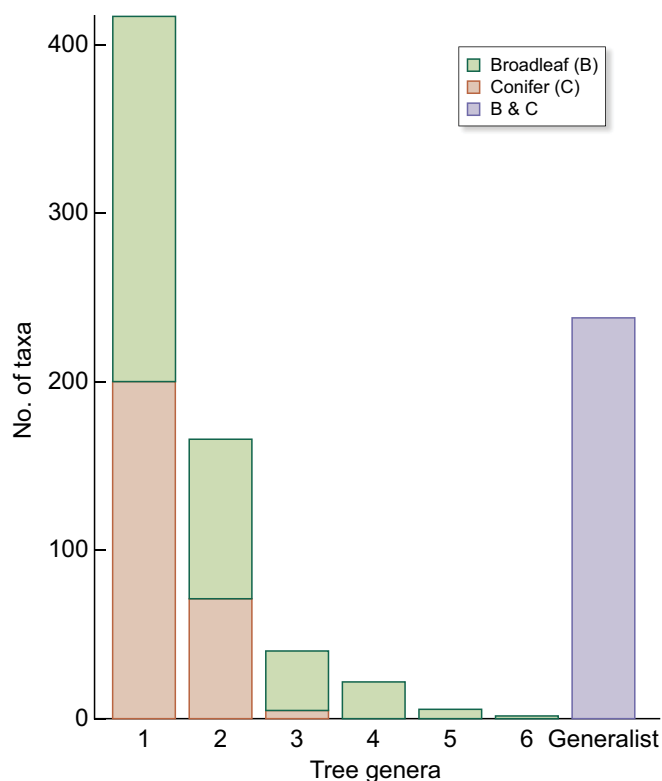


Fig. 1 Number of fungal taxa that associate with one–six broadleaf or coniferous tree genera, or have no preference. Based on fungal species present in Funga Nordica (Knudsen, 2018) for which associations are known.

40% of epigeous basidiomycete genera associated exclusively with a single host genus (Molina *et al.*, 1992). Reliance on sporocarp data to suggest host association may be open to interpretation, but more recent molecular analysis of ECM root tips also reveals similar patterns of specificity. In mixed conifer–broadleaf forests in Japan, Ishida *et al.* (2007) found that 40% of ECM fungal taxa were associated with a single genus of host plants. Similarly, in an extensive survey of ectomycorrhizal fungi in European woodlands, *c.* 12% of the most abundant ECM fungal taxa were unique to just one species of host plant (van der Linde *et al.*, 2018). These data support a host specialisation gradient by the fungi, but these patterns may also involve host selection. Nonetheless, host selection itself may encompass a suite of mechanisms that ultimately lead to specialisation (see below).

In addition to these community-level gradients of specificity, there are some hosts that only associate with highly specialised ECM fungal communities, most notably *Alnus* spp. (Tedersoo *et al.*, 2009; Rochet *et al.*, 2011; Roy *et al.*, 2013). Indeed, understanding how *Alnus* spp. interact with ECM fungi (e.g. Ardanuy *et al.*, 2021) may provide important insights that can be tested in situations where plants can host both generalist and specialist fungi simultaneously. *Alnus* is also interesting in that it forms symbioses with actinorhiza, which fix atmospheric nitrogen in a symbiosis that evolved subsequent to ectomycorrhiza (Wang *et al.*, 2022). One further line of inquiry is whether the molecular basis of specialisation is shared between ECM fungi and actinorhiza in *Alnus* and indeed with other nitrogen-fixing microbes in other host plants.

Collectively, the analyses above provide insight on the prevalence of a specificity gradient in temperate and boreal forest ecosystems. In the tropics, however, the situation is less clear, partly because of a relative lack of detailed analyses. Some plants (and fungi) are highly selective with a narrow symbiont range; for example, the *Scleroderma* clade containing *S. sinnamariense* has a strong host preference for the gymnosperm genus *Gnetum* (Bechem & Alexander, 2012; Tedersoo & Põlme, 2012). The data from south east Asian tropical systems point towards weak evidence for host specialisation (Peay *et al.*, 2015), despite claims in older literature, often reiterated, that ECM fungi exhibit narrow species-level specialisation in dipterocarps (e.g. Smits, 1983). Nonetheless, recent work suggests that host preferences exist that can improve survival, colonisation and growth benefits for ECM seedlings beneath conspecifics or close relatives (Liang *et al.*, 2020, 2021; Segnitz *et al.*, 2020).

Host specialisation operates across genetic, taxonomic and functional variables

While it is clear that host specialisation is prevalent, it remains difficult to provide an unequivocal definition of host specialisation. This is because host specialisation occurs along a gradient across genetic, functional (i.e. traits) and taxonomic levels of hosts (Molina & Horton, 2015; Fig. 2a).

Previous work has generally considered specialisation solely from the perspective of the taxonomy of hosts (e.g. from taxonomic species to divisions; Fig. 2a), but host genetic and trait variation may also be associated with a gradient of host specialisation: indeed, the traits of plants are key for driving the evolution of pathogen specificity (Lacaze & Joly, 2020) and in regulation of plant–soil feedback in nonwoody species (Semchenko *et al.*, 2022). Trait variation may encompass specific changes in single traits through to complex variation in trait syndromes (Valverde-Barrantes *et al.*, 2018; Fig. 2a). For example, the highest degree of specialisation in ECM fungi is seen with *Pinus*, where species of the fungal genus *Suillus* associate uniquely with two-, three- and five-needle pines (Kretzer *et al.*, 1996; Liao *et al.*, 2016; Nguyen *et al.*, 2016). By contrast, many ECM fungi associate uniquely with either conifers or broadleaves (Fig. 1).

Specialisation may also reflect gradients in genetic variation from single nucleotide substitutions to large sections of genomes subject to horizontal transfer, that is genomic islands (Fig. 2a; Dobrindt *et al.*, 2004). There are no known ECM fungi that associate uniquely with only one species of host plant (from multispecies genera). The degree of fungal specialisation most commonly observed is at the genus level (but see *Pinus* below). Where ectomycorrhizal plant genera are represented by single species over large geographic areas, for example *Fagus sylvatica* in western Europe, it can appear that there are ECM fungal species which are restricted to that single host species. However, these same fungal species associate with *F. orientalis* in eastern Europe (A. Taylor, pers. obs.). The extreme specialisation in symbioses would refer to associations at an intraspecific or genetic level between particular genotypes of host plants and fungi, reflected at the very finest scale as single nucleotide substitutions (Kirzinger & Stavrindes, 2012). At present, there is no evidence for such extreme

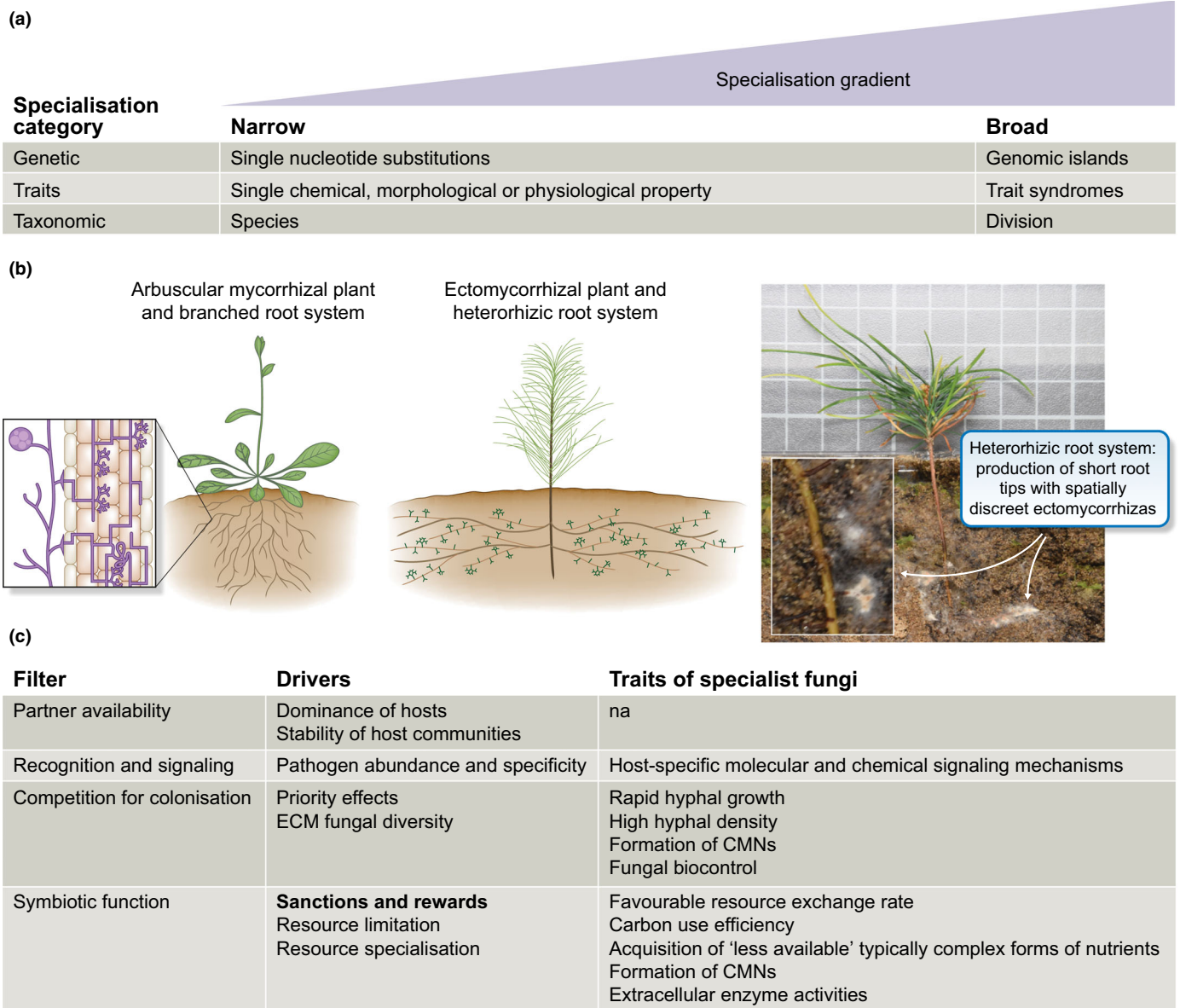


Fig. 2 Host specialisation can be conceptualised as a gradient and can be driven by the morphology of roots and other factors. (a) Host specialisation represented as a continuum encompassing genetic, functional (i.e. traits) and taxonomic elements. (b) The key feature of ectomycorrhizal (ECM) hosts driving specialisation is the production of heterorrhizic root systems that (potentially) enables precise allocation of carbon to specific ectomycorrhizas. (c) Additional mechanistic filters are also required to be overcome for specialisation to occur in ECM fungi (Photos by D. Johnson).

genetic specialisation within ECM symbionts but there is increasing recognition of the importance of genotypic diversity of mycorrhizal plants and fungi in shaping the functioning of the symbiosis (Johnson *et al.*, 2012; Hazard *et al.*, 2017). Fast- and slow-growing clones of Norway spruce have been shown to support different ECM fungal communities, but the mechanisms behind this phenomenon remain unclear (Velmalu *et al.*, 2013). Host specialisation is therefore best represented by a series of continuous variables (Fig. 2a).

The morphology of ECM root systems is key to the evolution of specialisation

The architecture of roots is vital in regulating a plethora of biotic interactions, including localised immune responses and changes in

cell wall chemistry. These localised changes can even enable roots to become colonised by nonpathogenic bacteria, or resist pathogenic species (Kawa & Brady, 2022). Yet, the morphology of root systems has yet to be considered in detail in discussions of host specialisation by ECM fungi. A striking feature of many ECM host plants is their propensity to form heterorrhizic root systems (Fig. 2b); by contrast, ericaceous and AM plants do not have this heterorrhizic morphology. While root morphology can be influenced by molecular or chemical 'cross-talk' between plants and ectomycorrhizal fungi (e.g. Plett & Martin, 2011), the production of 'short roots' characteristic of heterorrhizic roots is key to the formation of ectomycorrhizas (Tarkka *et al.*, 1998).

Support for the role of root morphology in specialisation is also gleaned from nonwoody species that form mycorrhizas with ECM

fungi. For example, shrubs such as *Arctostaphylos* spp., which do not have heterorhizic root systems, have been shown to support a wide range of fungi traditionally considered to be specialised on ECM trees (Molina & Trappe, 1982; Krpata *et al.*, 2007), providing preliminary evidence that specialisation is driven by the host and not the fungus. However, there are some situations where this generalisation fails, for example trees such as *Salix* and *Populus* have long sections of unsuberised fine roots that can become colonised by specialist or generalist ECM or AM fungi along their length. Thus, further empirical work is needed to test whether both root morphology and host are the principal drivers of host specialisation gradients in ECM fungi, and this work clearly needs to focus on comparing the molecular mechanisms underpinning the formation of mycorrhizas by specialists and generalists. Nonetheless, theoretical analyses lend support to our hypothesis. Hoeksema & Kummel (2003) developed a spatially explicit model that suggested acceleration of the mortality of root tips colonised by less beneficial (or even detrimental), but more competitive ECM fungi, could explain persistence of mutualism.

We argue that the spatially discreet nature of ECM fungal colonisation on heterorhizic root systems enables more effective fine-scale control by host plants and facilitates sanctioning, akin to the idea of ‘compartmentalisation’ recently put forward to explain cooperation across several symbioses (Chomicki *et al.*, 2020), compared with root systems that do not have this feature. As a result, we hypothesise that this is a key mechanism that has driven specialisation *and* speciation, leading to *c.* 25 000 ECM fungal species along a gradient of host specificity. While there is some evidence for host control of spread of fungal colonisation in roots (e.g. Lauressergues *et al.*, 2012), colonisation of individual roots by AM fungi is typically widespread comprising multispecies communities (Deveautour *et al.*, 2021). By contrast, speciation of AM fungi is limited and there are only *c.* 300 species described.

Mechanistic filters maintaining gradients of host specialisation

Gradients of host specialisation occur via four proximate, nonmutually exclusive mechanistic ‘filters’ comprising: (1) partner availability; (2) signalling recognition; (3) competition for colonisation; and (4) symbiotic function (trade, rewards and sanctions). These mechanisms (Fig. 2c) are not necessarily specific to heterorhizic root systems, but we emphasise that this root morphology greatly facilitates the efficacy and ability of Mechanisms 3 and 4, in particular, to drive specialisation.

Mechanism 1: partner availability

Partner availability at both temporal and spatial scales is critical to maintain a gradient of specialisation. High temporal stability of both host plants and host environment is a requirement for the evolution of specialisation in ectomycorrhiza. In stable environments, host plants that maintain specialist ECM fungi on their roots are protected against loss of specialists or changes in their effectiveness (Bogar *et al.*, 2022). Plants may benefit from specialists by hedging their bets by associating with both generalists

and specialists. This bet-hedging might explain why tree hosts associate with generalists yet also support communities comprising specialist ECM fungi (Horton *et al.*, 2005; Roy-Bolduc *et al.*, 2015). Similarly, generalist fungi that maintain this lifestyle are protected against loss of a specific host tree species or genera for the same reasons. The heterorhizic root system permits ECM fungi from across a specialisation gradient to form ectomycorrhizas on spatially proximal root tips of the same host.

Stable environmental conditions should therefore select for the evolution of specialists. If nutrient exchange varies between seasons in temperate and boreal biomes (Högberg *et al.*, 2010), then the expectation would be for more specialists in the less seasonal tropics, but this appears not to be the case (Peay *et al.*, 2015). Geological timescale may provide the environmental stability needed and glacial refugia can provide the conditions for speciation of ectomycorrhizal species (Sánchez-Ramírez *et al.*, 2015). Co-evolution is hypothesised to have led to the specialisation of several ECM partnerships with *Pseudotsuga* spp. (Murata *et al.*, 2013; Mujic *et al.*, 2019) indicating the importance of evolutionary time to specialisation. Some specialist fungal taxa such as Suilloids have dormant propagules that only form ECM when a suitable host is present, and this strategy may reduce the cost of being a host specialist (Bruns *et al.*, 2002).

The spatial structure and dominance of host plants is a key component allowing the evolution of interspecific mutualism (Doebeli & Knowlton, 1998). Stand longevity can also increase dominance of more specialist fungi (Horton *et al.*, 2005; Rudawska *et al.*, 2018), indicating that stability over decades can affect the presence of specialist fungi. Lankau & Keymer (2016) postulated that specialists may decrease towards the edge of the realised niche of a host species. However, the dearth of information on tree partner range for many fungal species means this hypothesis could not be explicitly tested, and so we recommend this to be a key gap to fill.

Mechanism 2: recognition and signalling

Signalling and recognition is a critical mechanism underpinning specialisation: a classic example is in nitrogen-fixing bacteria *Rhizobium* which produce *Nod* factors that are recognised by specific receptor kinases in the plant, which leads to the formation of nitrogen-fixing nodules on the root. In the legume symbiosis, there is a cascade of signalling processes between *Rhizobia* and plants that are localised on host root systems (Murray *et al.*, 2007), and in the arbuscular mycorrhizal symbiosis, the fungi are stimulated to grow when exposed to strigolactones produced by plant hosts, although these tend to be produced more or less systemically rather than at defined locations on the root (Lanfranco *et al.*, 2018). We hypothesise that the heterorhizic root system of ECM plants permits highly targeted recognition and signalling between host plant and symbiotic partner on a single root tip basis. Certainly, there is much evidence for localised changes in cell functioning, morphology and gene expression in colonised short roots compared with noncolonised roots (e.g. Tarkka *et al.*, 1998, 2001; Sebastiana *et al.*, 2014), but it is currently difficult to disentangle a specific role played by heterorhizic root morphology in facilitating such local responses.

One key driver for the evolution of host-specific signalling is the need for plants to defend themselves against pathogens, while at the same time promoting colonisation by mutualists. Specialisation of ECM fungi could therefore reflect the need for plants to invoke more sophisticated recognition strategies to counteract the effects of high pathogen densities that tend to accumulate beneath parental plants (Janzen, 1970; Connell, 1971). Negative feedback of local soil conditions on offspring fitness may be more likely in long-lived plants such as trees where pathogens can accumulate during the lifespan of the host. Comparative genomic analysis has revealed that the often host-specific genus *Lactarius* use similar proteases to pathogenic fungi to interact with their host (Lebreton *et al.*, 2022) but whether this holds for other genera remains to be determined.

Increased abundance of pathogens could lead to greater degrees of specialisation required by ECM fungi. A shift along the ECM specialisation gradient with ECM fungal species on seedlings under conspecifics and a decrease in the generalist ECM fungus *C. geophilum* (Deniau *et al.*, 2017) could reflect this selective pressure. Merges *et al.* (2018) also found higher abundances of specialist fungal pathogens and a specialist ECM fungus in closer proximity to the host plant, indicating that promotion of specialist mutualists may counteract the effect of pathogen accumulation. Liang *et al.* (2020, 2021) found that productivity and survival of ECM seedlings was greater when they grew alongside and had potential to form common mycorrhizal networks (CMNs) with ECM adults, especially of the same genus. The same situation did not occur with AM plants, and these plants also harboured more pathogens compared with ECM seedlings. Laliberté *et al.* (2015) proposed that more work is needed to resolve whether the home advantage of conspecific plants could be due to ECM protecting against soil pathogens. This idea could be developed further to test the hypothesis that specialist ECM fungi confer more protection against pathogens, or have greater ability to offset negative effects of pathogens, compared with generalists in a home field situation.

Metatranscriptomics offers new opportunities to test for signalling mechanisms between host plants and fungi. This technique has revealed that gene expression varies between compatible and incompatible host–fungus interactions (Liao *et al.*, 2016; Plett & Martin, 2018). Yet, when hosts are compatible, there is conflicting evidence of the degree to which fungi alter gene regulation in the host. *Cenococcum geophilum* does not demonstrate host-specific gene regulation (de Freitas-Pereira *et al.*, 2018), whereas another host generalist fungus, *Laccaria bicolor* has over 1000 genes which are differentially regulated in interactions with diverse host plants (Plett *et al.*, 2015). Gene clusters linked to host specificity are enriched in host specialist ECM fungi compared with other ECM fungi (Lofgren *et al.*, 2021), and the gene class sedolins have been linked to specificity (Lebreton *et al.*, 2022), but more work on the specificity of transcriptomes of other ECM fungi in different circumstances is required. Finally, volatile organic compounds (VOCs) produced by mycorrhizal fungal species differ from those produced by other fungal guilds (Guo *et al.*, 2021) but a possible role for VOCs as a means of recognition between plants and ECM fungi remains to be determined.

Mechanism 3: competition for colonisation

Competition for colonisation, often mediated via priority effects, shapes fungal community structure (Kennedy *et al.*, 2009). Priority effects are driven by three distinct niche components, namely: overlap, impact and requirement (Vannette & Fukami, 2014). Niche overlap primarily concerns arrival time, but the latter two components are both likely driven by interactions taking place with plants, including the exchange of resources (Johnson, 2015). Thus, competitive outcomes of priority effects can occur on short roots and these processes may contribute to generating gradients in host specialisation. For example, gradients in host specialisation may have evolved to reduce competition that might otherwise occur when colonising multiple host plant species, but thus far the evidence is equivocal. The ECM fungal communities associated with *Alnus* are structured by neutral or positive, rather than competitive, interactions (Kennedy *et al.*, 2014). Yet for other situations, competition is known to impact ECM fungal community structure (Pickles *et al.*, 2012), including on mature plants (Thoen *et al.*, 2019). Parlade & Alvarez (1993) found that generalists were better competitors for hosts than specialists in pairwise interactions, and other work showed that the *Pinus* specialist *Rhizopogon occidentalis* was less competitive than the generalist *Tomentella sublilacina* (Lilleskov & Bruns, 2003).

The production of secondary metabolites by fungi, which are known to cause antagonistic effects and drive competition in saprotrophic fungi (Rangel *et al.*, 2021), may also be an important mechanism that could drive host specialisation gradients. In addition, inoculation experiments have demonstrated that timing of colonisation is important for competition and the speed of spore germination may be an important competitive trait (Kennedy *et al.*, 2020). The bioassay approaches used in these studies may be a useful way to screen multiple ECM plants and fungi under different environmental contexts to determine whether general patterns or key functional traits emerge.

When associated with pine, the specialist *Suillus pungens* had greater extracellular enzymatic activity and was less abundant than *Thelephora terrestris*, which can associate with both conifer and broadleaf trees (Moeller & Peay, 2016). Moeller & Peay (2016) hypothesised that there is a trade-off between competition for host roots and production of nutritionally important extracellular enzyme activities. It remains to be tested whether a similar trade-off could explain the apparently weaker competitive abilities of specialist fungi. For example, while generalists may have superior ability to colonise plants, specialists may have greater capacity to access key growth-limiting nutrients, which influences ‘terms of trade’ (see also section below) maintaining a host specialisation gradient. This capacity will have different trade values depending on the environmental context (section below).

Mechanism 4: symbiotic function (trade, sanctions and rewards)

Once associated with plant roots, mycorrhizal fungi engage in reciprocal exchange of nutrients and reduced carbon with the host. Indeed, ‘reciprocation’ of growth-limiting resources was identified

as a fundamental tenet of the evolution of cooperation in early classic experiments using game theory (Axelrod & Hamilton, 1981). Subsequent advances in theoretical models highlight that returns in partner investment greatly help to maintain mutualisms (Doebeli & Knowlton, 1998). Thus, it seems reasonable to assume that host specialisation is related to the cost and benefits of reciprocation. For example, do host specialist ECM fungi supply plants with more mineral nutrients for a given amount of host-derived carbon compared with host generalists? In other words, is the 'resource exchange ratio' favoured for plants supporting specialists? It has been hypothesised that preferential allocation of carbon may contribute to ECM diversity (Dickie, 2007), and in both nitrogen-fixing nodules and AM fungi, sanctioning of plant-derived resources is thought to be a key mechanism to control symbiotic function (Kiers *et al.*, 2003, 2011). While sanctioning may also occur in AM systems (Kiers *et al.*, 2011), evidence suggests this is unlikely to occur within individual root sections or cells (Bever *et al.*, 2009). By contrast, the heterorhizic root system of most ECM plants is far more suited for fine-scale sanctioning compared with AM host plants. Recent experiments highlight how bidirectional exchange of resources (i.e. carbon from plant to fungus and mineral nutrients, notably nitrogen, from fungus to plant) is affected by fungal identity (and nitrogen status of soils) in ECM systems (Bogar *et al.*, 2022). Unfortunately, there are no data quantifying resource exchange ratios between ECM host plants and specialist and generalist fungi, and this is a key gap in knowledge to fill. The ability to quantify and visualise fine-scale patterns of the activity of radioisotopes (such as carbon and phosphorus) in individual ectomycorrhizas (e.g. Rosling *et al.*, 2004) offers potential to explore resource exchange with fungi along a gradient of specialisation.

A further consideration in this mechanistic filter is the extent to which ECM fungi can control resource exchange, that is consideration of a mycocentric view in driving a specialisation gradient. For example, what are the traits of ECM fungi that may enable fungi to overcome the need for plant C allocation? One key trait may be mantle hydrophobicity: ECM fungi with hydrophilic mantles enable nitrate to be transferred via the apoplast directly to host plants at no cost to the fungus. Despite this, plants perceive the nutrient and allocate C to the fungus, so the fungus gains energy for no cost (Nygren *et al.*, 2008). As a result, ECM fungi with hydrophilic mantles proliferate in forests that have been fertilised or subjected to large inputs of atmospheric nitrogen. Obviously, a sudden pulse of nutrients resulting from artificial fertilisation cannot be considered a driver of specialisation gradients but the phenomenon suggests that mobile nutrients such as nitrate may routinely bypass the requirement to be taken up by ECM fungi with hydrophilic mantles before being 'passed' onto the host plant. Such a mechanism would clearly be advantageous.

The evolution of gene families involved in interaction with the host indicates that there may be control in the interaction by the ECM fungi (Lofgren *et al.*, 2021; Lebreton *et al.*, 2022). There is compelling evidence that in nitrogen-limited systems, such as the Boreal forest, ECM fungi may enforce nitrogen limitation by immobilising nitrogen in their biomass (Högberg *et al.*, 2017) despite receiving carbon from hosts without detriment to the host

plant (Corrêa *et al.*, 2008, 2011). The explanation is that an individual ECM fungus rarely, if ever, is the sole coloniser of a host plant, and individual fungi have potential to colonise multiple plants to form CMNs (Beiler *et al.*, 2010), which likely prevail in nature, despite the lack of unequivocal field data supporting such a view (Gilbert & Johnson, 2017; Alaux *et al.*, 2021; Karst *et al.*, 2023). In this situation, the CMN is akin to the 'commons' in the classic 'tragedy of the commons' scenario (Hardin, 1968). Acquisition of nitrogen by the connected host plant community may saturate or even decrease in proportion to carbon supplied to the fungi, but acquisition of nitrogen by the individual plant remains in proportion to the amount of carbon supplied to the fungus (Henriksson *et al.*, 2021). Whether host specialists and generalists modify such patterns remains to be tested. One key factor relevant to the ideas presented by Henriksson *et al.* (2021) is the extent to which host generalists and specialists form CMNs in nature. One key fungal trait to quantify is whether there is systematic difference in the ability of specialists and generalists to form CMNs. The fitness consequences of the formation of CMNs may be particularly advantageous to specialists because of the (potentially) restricted number of individuals available to colonise, and this could generate more efficient mechanisms of CMN formation.

A further factor is the key role played by environmental context in regulating resource exchange, especially when mineral nutrients such as nitrogen and phosphorus are limited. In addition, there is a need to be mindful of how measurements of resource exchange translate into fitness. Although it is reasonable to assume allocation of resources between mycorrhizal plants and fungi has some bearing on fitness, the underpinning evidence remains weak (Helgason & Fitter, 2009) and limited by the ability to define fitness for ECM fungi. Most theoretical analyses of host specialisation use fecundity as a proxy of fitness, and the shape of the fitness curve between specialists and generalists is one of the key factors regulating their coexistence (Levins, 1962; Wilson & Yoshimura, 1994). Of particular importance is: (1) quantifying the relationship between fitness and resource exchange ratio under varying growth-limiting environmental conditions; (2) understanding how fitness is related to absolute amounts of resources acquired from each partner; and (3) how these parameters vary in host specialist and generalist fungi. For example, it may be that the resource exchange ratio remains broadly constant but that specialists and their hosts exchange more resources.

Increased symbiotic function acting via nutrient exchange may also be related to specialisation on resources of the host leading to positive feedbacks with fungal partners akin to ideas developed in AM fungal systems (Bever *et al.*, 2009). For example, selection for genes that regulate enzymatic capabilities may enable specialists to more effectively recycle resources from litter of host plant species compared with generalists.

Indeed, the ability to acquire and trade particular resources (i.e. resource specialisation) is thought to be a key evolutionary stable strategy for mycorrhizal symbioses (Schwartz & Hoeksema, 1998). Other functions should also be considered as targets of selection for specialisation, and these may relate to specific environmental contexts. For example, ECM may enhance plant defence (Palermo *et al.*, 2003) and resistance to attack, water uptake (Marjanovic *et al.*, 2005), trace element capture (Gil-Martinez *et al.*, 2018) and

resistance to toxic pollutants (Gil-Martinez *et al.*, 2018; Branco *et al.*, 2022).

Finally, evolution of host specialisation gradients may also be driven by exchange of non-nutritional molecules, such as those related to defence and immunity, but which are likely linked to the provision of energy (carbon) by hosts. For example, recent evidence shows that ECM fungal colonisation rewires plant immunity both locally and systemically (Dreischhoff *et al.*, 2020). The spatially explicit changes in plant immunity seen in the nonmycorrhizal plant *Arabidopsis* in response to challenges from bacteria (Emonet *et al.*, 2021) must surely be more effective in heterorhizic root systems with spatially discreet units of ECM colonisation. Indeed, in eucalyptus, provision of carbon to ECM fungi was not correlated with the number of colonised root tips, but rather to the expression of defence- and stress-related genes in the plant. These findings suggest that carbon acquisition by ECM fungi involves individual fungal demand for carbon and defence responses of the host (Stuart *et al.*, 2023). It would be fascinating to test whether such responses are related to host specialisation gradients in ECM fungi.

Reversing the trend?

A gradient of host specialisation by ECM fungi is supported by both sporocarp occurrence data and belowground community studies directly on ectomycorrhizal root tips. High prevalence of specialists could suggest a strong evolutionary driver to become more specialised to a particular host genus or group via one or more of the mechanisms discussed above. However, it may also partly reflect evolutionary pathways to mycorrhiza formation and the relative balance of generalist to specialist taxa. Ectomycorrhizal fungi are considered to have evolved on multiple occasions from free-living saprotrophic fungi (Tedersoo & Smith, 2017; Strullu-Derrien *et al.*, 2018). Generalist litter decay fungi could have evolved into generalist ECM fungi associated with multiple hosts, which in turn via host specialisation and subsequently divergence separate into specialist species. Thus, one generalist would lead to multiple specialists, thereby increasing the relative representation of specialists globally. Conversely, a single specialist would, most likely, revert back to being a single generalist, and these bidirectional evolutionary processes would support the maintenance of a host specialisation gradient. One further mechanism that maintains host specialisation and diversifies host specialists in pathogenic fungi is 'host jumping' (Thines, 2019). For example, fungi may jump hosts if the efficiency of colonisation is poor, either in the lifetime of a symbiont or across evolutionary time. An intriguing question therefore is whether such processes occur in ECM fungi that fall along a gradient of host specialisation?

There are few well-supported examples of a specialist ECM fungus reverting back to being more of a generalist. Lofgren *et al.* (2021) stated that specialisation on a given host is not an evolutionary irreversible state, including evidence of one reversion between host groups in the *Suillus* phylogeny. Den Bakker *et al.* (2004) undertook a detailed analysis of the ECM fungal genus *Leccinum*, the species of which are all well-known as having genus-level host associations. They found that one taxon, *L. aurantiacum*, associated with a range of hosts, including Fagaceae,

Populus and *Betula*, and had most likely evolved from a host specialist associated with *Populus*. The lack of reversals may partly reflect a lack of detailed analyses but may also suggest that the evolutionary steps involved in reversals are considerable.

Future work and outlook

Our hypothesis is based on the assumption that root morphology, namely the ability to produce heterorhizic root systems (Fig. 2), is key to maintaining host specialisation gradients in mycorrhizal fungi particularly via competition for colonisation and trade, rewards and sanctions. We encourage experiments to provide more rigorous testing of this basic principle, alongside resolving how the four mechanistic filters may maintain host specialist gradients in ECM fungi. The consideration of resource exchange in this context may require a broader question to be tackled: does resource exchange ratio vary among different ECM genotypes, regardless of their classification into one type or another? If specialisation is plant-driven and differential allocation of carbon is a factor driving it, we might expect to see variation in resource exchange ratio between genotypes of ECM fungi and plants.

Knowledge on the molecular mechanisms by which carbon, nitrogen and phosphorus is exchanged or traded between plant and fungus is still lacking (Stuart & Plett, 2020). This expanding area of research will help determine the importance of trade in specialisation by fungal species. Analysis of the metabolomes and transcriptomes expressed by mycorrhizal plants and fungi in different environments together with analyses of trait syndromes will help unveil interactions between fungi acting along a gradient of specialisation. Moreover, omic analyses coupled with isotopic analyses on individual ectomycorrhizas (*sensu* Stuart *et al.*, 2023) may help identify 'good partners' and potential rewards to host and fungus. Most models to date focus on the amount and rate of trade of resources that may be attributed to host specialization. Yet, ECM fungi are known to provide other benefits such as defence signalling, pathogen protection and tolerance to contaminated soil and drought, and these wider benefits must also be considered in future work.

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Competing interests

None declared.

Author contributions





DJ conceived the work; DJ and AFST secured the funding; AA and AFST analysed data; DJ led the writing with contributions from FV, AA and AFST.

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Data availability

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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