# An examination of the ecology and influence of mycorrhizal fungi in UK woodlands using modelling, field studies and restoration experiments

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# Declaration

Declaration: I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Petra Guy

# Acknowledgements

It was a dream of mine for sometime to return to research, and particularly to research the subject of woodlands and mycorrhizal fungi, I therefore want to especially thank Brian Pickles, not only for offering me this amazing opportunity, but for his clear and calm guidance throughout my studies, particularly those times when things got a bit difficult, as they inevitably do during PhD research. Thank you also to my co-supervisors Mark Tibbett and Richard Sibly for their straightforward advice and support, which was always available when needed. I would like to thank Neil Humphries for their help, not only lugging trees and poles around, but also for constructive thoughts and feedback. Tarmac Ltd also offered funding and support for some of the work carried out in this thesis.

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# Abstract

This work presents several topics on the role of mycorrhizal fungi in woodland ecosystem function. We start with an exploration of the subset of ectomycorrhizal fungi (EMF) with a limited host range, referred to as specialists. Although empirical data demonstrates the existence of specialist and generalist EMF, we do not fully understand the functional differences between them. We therefore use game theory to explore the question, 'what is a specialist EMF?' Mycorrhizal fungi play a fundamental part in plant soil dynamics; they influence plant interactions and are major contributors to plant nutrition and health. However, the role of mycorrhizal fungi in woodland conservation and management is still not fully appreciated. We have therefore carried out an in-depth study of the mycorrhizal type of British woody plants which will be accessible to woodland specialists, but perhaps not mycorrhizal specialists, in the hope that this will make decisions involving mycorrhizal type straightforward and accessible. We also show the importance of knowing the mycorrhizal type of woodland plants by demonstrating the relationship between the mycorrhizal type of trees and understory species richness. Detailed data of the distribution of EMF is still sparse, we therefore also carried out extensive field work to ascertain the taxa associated with oaks (*Quercus robur, Q. petraea*) in Britain. Further, we used multi-site generalised dissimilarity models to explore the drivers of turnover of these communities and how they differed for rare and common species. We show that, whilst species richness of EMF was positively correlated with soil potassium, atmospheric pollutants were the most important drivers of community change. Soil translocation is often used as a means to enhance biodiversity in the restoration of ancient woodlands, however, little is known about the potential of this process as a supply of EMF inoculum. We therefore conducted a pilot study into the potential use of bait trees as a means to examine the the EMF inoculum in these soils by measuring the colonisation rate of saplings planted in a restoration woodland. The study allowed us to isolate several important elements for improvement in the experimental method, as well as several additional components which would allow more precise information regarding inoculum potential of these soils.

# Contents

# Chapter 1

# Introduction

## 1.1 Abstract

The overarching theme of this thesis is the role of mycorrhizal fungi in woodland ecosystem functioning. Mycorrhizal fungi are fundamental to woodland health, being the major supplier of nutrients to plants. The fine mycelium of these symbionts is able to access smaller soil pores than plant roots, hence increasing a plant's access to water and soil nutrients. Moreover, they can synthesise enzymes allowing access to nutrients locked up in organic forms which would otherwise be unavailable to their plant hosts. Mycorrhizal fungi mediate many important plant soil feedbacks that are essential for ecosystem services and functions such as soil fertility, carbon storage and biodiversity gain. In temperate woodlands, most trees are colonised by ectomycorrhizal fungi (EMF), but most understory plants, woody shrubs and some tree species are colonised by arbuscular mycorrhizal fungi (AMF). These two different types of fungi engender different plant soil feedbacks. For instance, arbuscular and ectomycorrhizal trees exhibit contrary conspecific density dependence, whilst it is thought that arbuscular mycorrhizal trees in broadleaved woodlands facilitate understory species richness. We therefore explored this relationship between the proportion of arbuscular mycorrhizal type trees and understory species richness in British woodlands using the Centre for Ecology and Hydrology's Bunce dataset. This dataset contains over and understory plant species in 103 broadleaved woodlands across Britain. Using this data we were able to confirm for the first time in British woodlands a positive effect on herb species richness due to the proportion of arbuscular mycorrhizal tree types. This information is important for woodland planning and management.

During the course of the data analysis above, we discovered that robust empirical data describing the mycorrhizal associates of many British woody plants was lacking. That is, we cannot be certain whether some plants host EMF or AMF. We therefore conducted a substantial literature review of the empirical data describing the mycorrhizal associations for all British woody plants. This review has allowed

us to produce a robust dataset in which the mycorrhizal type is detailed, as well as quantifying the strength of evidence behind each association. This review demonstrated that evidence of mycorrhizal type is weak for more than half of British woody plants, and we were able to highlight specific species requiring further study.

The total number of mycorrhizal fungal taxa is unknown, but may be as high as half a million based on current estimates. Therefore, although many landscape scale studies of mycorrhizal fungal species have been carried out, there is still a lack of baseline biological records. Without this data, we cannot answer questions such as which mycorrhizal species are rare? Or which are associated with particular hosts or habitats? This lack of data therefore hampers our ability to assess habitats, for example, whether they are species poor, or conversely, a refuge for rare species. This means that, whilst afforestation is currently an important part of tackling biodiversity loss and climate change we are unable to fully understand the health of these new woodlands. Further, we cannot comment on the the success of procedures such as soil translocation for the mitigation of loss of ancient woodlands, without more data regarding the species we expect to find in those ancient woods. Therefore, as part of this research we carried out a large landscape scale study in which we sampled the EMF of oak (*Quercus petraea, Q. robur*), an important British tree. Our field work revealed fifty species which had not been previously recorded as associates of oak. In addition we sampled soils in oak woodlands across Britain and explored drivers of ectomycorrhizal community change. We found evidence that anthropogenic pollution is the main driver of change across oak woodlands in Britain, particularly oxidized nitrogen. Further, we show for the first time that atmospheric deposition of calcium and magnesium cations are an important filter of community structure. We also show that drivers of rare and common species may differ. In addition, we demonstrate that the species richness of EMF of oaks may be considerably larger than previously thought.

Soil translocation is used in ecological restoration as a means of increasing biodiversity in restoration woodlands when ancient woodlands are lost. However, there is very little literature reporting the efficacy of this process for translocating EMF propagules and inoculating new woodlands. We hypothesised that bait trees planted in translocated soil would become colonised by pioneer species of EMF and that the richness of the community would be lower than that of bait trees planted in an ancient woodland, since these would also be colonised via live hyphal networks. In addition, we thought that we could use data from our landscape scale survey above, to compare the community of the bait trees with that of mature trees and hypothesised that these communities would differ, since EMF have been observed to exhibit succession - pioneer communities differ from those found in mature woodlands. We therefore conducted an initial pilot study into the use of bait trees as a means to address these hypotheses. We found that the high colonisation rate of EMF already

present on the bait trees when they were obtained from the nursery means that aseptically grown trees would be required. We also found that we were unable to eliminate dispersal as a method of inoculum supply and suggest that spore traps would be a useful addition to a future experiment. In addition, all bait trees showed very little root growth, potentially limiting EMF colonisation. This was probably due to a mix of factors, such as low light, restricted water and compacted soil. The use of bait trees would therefore be maximised if these issues were addressed, for example, planting holes could be better prepared.

A requirement of this PhD research set by the QMEE DTP was an initial six month project with a mathematical focus. That project generated several counter-intuitive consequences of specialism and generalism from the perspective of both hosts and fungi and led to a more in-depth analysis. Specialist EMF tend to be found almost exclusively in association with certain host trees, for example, *Lactarius quietus* is often found with oaks. Generalists, on the other hand, can be found colonising a wide range of tree species. Whilst empirical data demonstrates that these two guilds exist in nature, their expected traits are not clearly defined. We therefore used evolutionary game theory to explore specialism in ectomycorrhizal communities in order to, in part, answer the question: "What is a specialist EMF?" Our modelling allowed us to define traits we expect to see in a specialist, for example, a specialist may be better at obtaining carbon from its host plant compared to a generalist, but will not, in return, promote the growth of their host trees; on the contrary, the growth of their host trees will be best promoted by generalists.

## 1.2 What are mycorrhizal fungi?

Mycorrhizal fungi are symbiotic organisms which colonise plant roots, enhancing plant nutrient uptake and receiving carbon in return (Tibbett & Sanders, 2002; Smith & Read, 2009; Pritsch & Garbaye, 2011; van der Heijden *et al.*, 2015; Becquer *et al.*, 2019). Although there are more than ten different types of mycorrhizal fungi currently recognised, composed of different species and forming different structures when colonising plant roots (Kariman *et al.*, 2018), there are two main types which are of interest to this work, arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF). Arbuscular mycorrhizal fungi are the most common root symbiont and are formed by fungi in the phylum glomeromycota (Smith *et al.*, 2009). Arbuscular mycorrhizal fungi are recognised by the presence of nutrient exchange organs which can be in the form of arbuscules, hyphal coils or something intermediate between these, and sometimes vesicles which act as nutrient storage organs (Smith *et al.*, 2009). Arbuscular mycorrhizal fungi tend to dominate ecosystems in which nitrogen is available in the form of nitrate (as opposed to being locked up in more complex forms in organic matter) and phosphorus is the growth limiting nutrient (Read,

1991). Hence they are associated with grassland ecosystems, but also occur in temperate woodlands as symbionts of understory plants, as well as some tree species (Read & Perez-Moreno, 2003). Ectomycorrhizal fungi are much less common, but are the major symbiont of trees in temperate woodlands, and hence of particular relevance for woodland ecosystems in the UK. Ectomycorrhizal fungi are made up of fungi belonging to the phyla basidiomycota, ascomycota and mucoromycota (Rinaldi *et al.*, 2008; Yamamoto *et al.*, 2017). They are recognised structurally by a mantle of hyphae which surrounds the root and a Hartig net, made up of hyphae which penetrate between the cortical root cells. The extramatrical mycelium can spread to distances of millimetres or metres through the soil depending on the species (Agerer, 2001). Whilst AMF produce small, below ground spores, EMF produce a variety of epigeous bodies such as mushrooms, branching coraline structures and crusts as well as hypogeous truffles. AMF infection can only be seen with a high power microscope microscope after root staining. EMF colonisation however, is visible to the naked eye, because the root morphology is often altered and the mantle formed by different species may be clearly observed. In some species the mantle is characteristic, however many species are cryptic and molecular analysis is required to distinguish these. Along with many other nutrients, such as potassium and phosphorus (Becquer *et al.*, 2019), EMF have been shown to access nitrogen in organic or inorganic forms (Finlay *et al.*, 1992; Tibbett *et al.*, 2000; Nicolás *et al.*, 2018; Pellitier & Zak, 2021), and are therefore important symbionts of trees in temperate forests which tend to have organic soils with a slowly decomposing litter layer (Read, 1991).

Many mycorrhizal fungi display the trait of specialism, in which host species is a strong factor influencing the mycorrhizal community. This host specificity is often explored for EMF (Molina *et al.*, 1992; Lang *et al.*, 2011; Rosinger *et al.*, 2018) however, host effect may be equally strong for AMF (Koziol & Bever, 2016; Põlme *et al.*, 2018; Sepp *et al.*, 2019), although this is still a matter of debate (van der Heijden *et al.*, 2015). Empirical data demonstrates that host is a strong driver of mycorrhizal communities, (Ishida *et al.*, 2007; Rasmussen *et al.*, 2017; Boeraeve *et al.*, 2018). Evolutionary game theory is an approach to exploring mutualisms which allows us to predict possible host or symbiont traits. Using this technique Steidinger & Bever (2014) predicted, for example, that host trees with different abilities to select mycorrhizal partners can coexist due to negative feedback on their mycorrhizal associates. This implies that host trees may also display different traits, those which discriminate less and have many fungal partners, and those which discriminate more and have fewer. This negative feedback is seen in the arbuscular mycorrhizal symbiosis, where the growth of *Plantago* was promoted by a mycorrhizal partner that tends to associate with a different plant species, *Panicum sphaerocarpon* (Bever, 2002b). Although we know that specialism occurs, and we have some evidence as to

how it occurs, that is, chemical signalling stimulates spore germination (Fries *et al.*, 1987; Kikuchi *et al.*, 2007), the benefits to either the host or the symbiont are not clear (Bruns *et al.*, 2002).

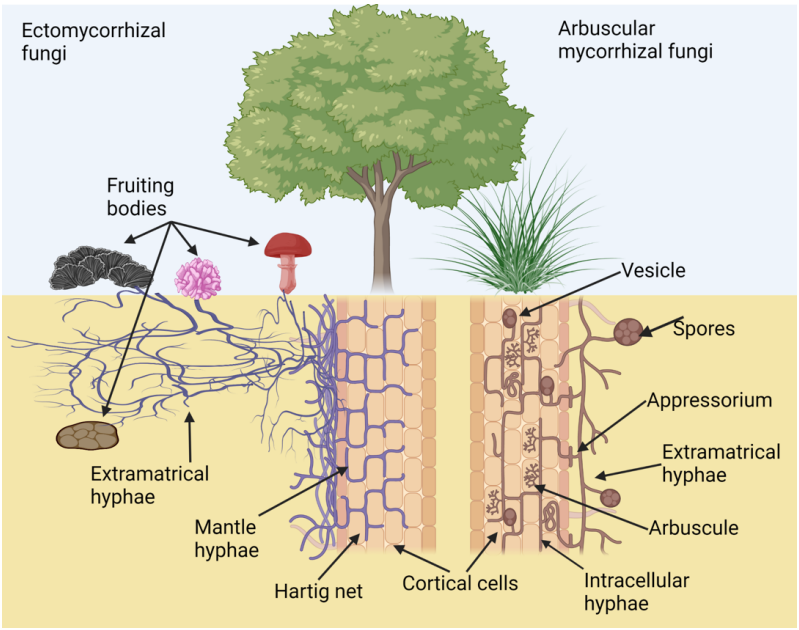


Figure 1.1: Graphic highlighting some structural and functional features of EMF and AMF. EMF are the main mycorrhizal associates of trees in temperate woodlands. They are characterised as comprising a Hartig net, which is the growth of fungal hypahe between the cortical cells within the root, a fungal mantle surrounding the root and hyphae penetrating into the surrounding soil. EMF have different types of fruiting bodies, both hypogenous truffles and epigeous bodies such as mushrooms, crusts and coralline branching structures. AMF are the main symbionts of herbaceous plants and woody understory shrubs, but also some temperate trees. They do not produce fruiting bodies, although the do produce large spores

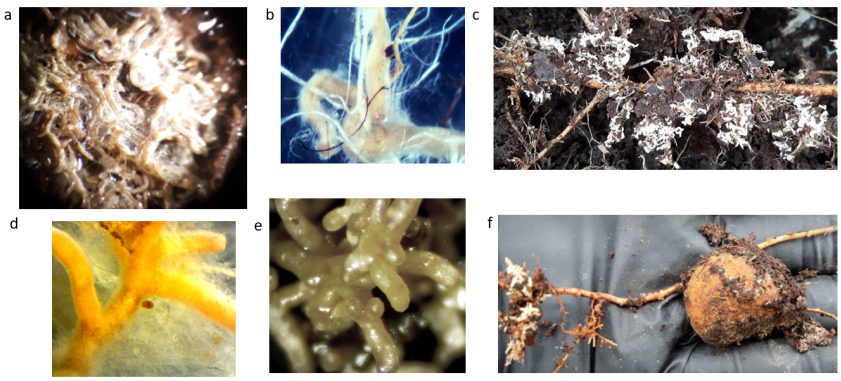


Figure 1.2: Images showing different ectomycorrhiza morphologies. Images a, b, d, e show roots collected during field work for this thesis. All roots are oak (*Quercus petraea, Q. robur*, but notice that in a) the root morphology has been altered to a dense curling mass. Image b) shows a species with thick rhizomorphs. Species d) has fine hyphae and distinctive orange mantle whereas the species in image e) produces a smooth mantle. Images c) and f) show that often the mycorrhizal structures are clearly visible to the naked eye. Image e) shows a hypogenous fruiting body

## 1.3 How mycorrhizal fungi contribute to woodland ecosystem functioning

As well as providing access to nutrients, colonisation by mycorrhizal fungi can result in changes which provide plants with increased disease resistance. For example, inoculation with AMF was found to increase the tolerance of olive trees against infections caused by the fungal pathogen *Verticillium dahliae* (Boutaj *et al.*, 2021), whilst colonisation rates of EMF in *Pinus tabulaeformis* has been found to correlate positively with survival of seedlings in the presence of the fungal pathogen *Fusarium solani* (Zhang *et al.*, 2017). Mycorrhizal fungi can also provide increased resistance against insect herbivory. Babikova *et al.* (2013) demonstrated that AMF mycelial networks transferred stress signalling compounds between *Vicia faba* seedlings. Similarly, it has been shown that insect defoliation of *Pinus ponderosa* or *Pseudotsuga menzeisii* leads to transfer of stress signalling compounds to neighbours via connecting EMF mycelial networks (Song *et al.*, 2015). Mycorrhizal colonisation can also improve seedling survival. Nara (2005) for example, demonstrated that seedlings grown in pots together with a mycorrhizal 'mother' plant had higher survival rates than those that were grown with non-mycorrhizal controls. In field conditions, positive plant interactions driven by mycorrhizal fungi allow the establishment of secondary species. For instance, it has been found that *Quercus ilex* seedling establishment is facilitated by the presence of *Arbutus unedo*, with which it shares many EMF (Richard *et al.*, 2009). Similarly, *Arctostaphylos* spp promote the establishment of *Pseudotsuga menziesii* (Horton *et al.*, 1999). Mycorrhizal fungi can also improve drought tolerance of their host plants (Pickles *et al.*, 2017) by increasing the surface area of water absorbing organs and penetrating smaller soil pores than plant roots (Johnson *et al.*, 2017). Further, mycorrhizal fungi are important drivers of woodland diversity. It has been observed that temperate broadleaved woodlands which contain a higher proportion of trees which associate with AMF, have higher understory species richness (Veresoglou *et al.*, 2017; Grünfeld *et al.*, 2020; Guy *et al.*, 2022). This important plant soil feedback is thought to be the result of increased AMF inoculum supply which facilitates the establishment of a more species rich herbaceous understory.

## 1.4 Importance of woodlands

Woodlands are recognized as important components of healthy landscapes, specifically, providing carbon sequestration, flood reduction and improvements to air quality as well as being important for biomass production, such for bioenergy (Beckett *et al.*, 1998; Brainard *et al.*, 2009; Ciccarese *et al.*, 2012; Burton *et al.*, 2018; Cooper *et al.*, 2021). Woodlands also offer ecosystem services to many woodland specific

taxa, such as plants, bats, butterflies, birds and hoverflies (McKay, 1991; Tudor *et al.*, 2004; Newson *et al.*, 2009; Boughey *et al.*, 2011; Fuentes-Montemayor *et al.*, 2013; Kimberley *et al.*, 2013; Fuller *et al.*, 2018). Therefore, woodlands are important habitats in the drive to maintain and increase biodiversity. Carbon dioxide removal, in particular, receives much attention and is a major driver of new woodland development (Lezaun *et al.*, 2021). The carbon sink of forests globally was estimated to be about 2.4 petagrams per year for the years between 1990 and 2007 (Pan *et al.*, 2011). It is estimated that natural regeneration (as opposed to planting schemes) in Scotland could remove nearly 7 million tons of carbon dioxide per year (Fletcher *et al.*, 2021). As part of the Net Zero strategy (Gov.UK, 2008) and the 25 Year Environment Plan (Gov.UK, 2018) the UK government intends to increase UK woodland cover, with planting schemes aiming for 50,000 ha/yr by 2035. Several large forests are currently being planted, such as the Heart of England forest (heartofenglandforest.org) and the Northern Forest (thenorthernforest.org.uk).

## 1.5 Problems faced by woodlands

Woodlands offer many ecosystem services and woodland diversity is important for the optimal provision of these (Aerts & Honnay, 2011). However, biodiversity worldwide continues to decline (Butchart *et al.*, 2010; Tittensor *et al.*, 2014; Forister *et al.*, 2019), implying potential reductions of ecosystem function, stability and resilience (Loreau *et al.*, 2001; Gaston & Spicer, 2008; Jucker *et al.*, 2014; Hutchison *et al.*, 2018). For example, forests with greater tree diversity have greater productivity (Zhang *et al.*, 2012) due to reduced competition through niche partitioning (Loreau & Hector, 2001). Greater tree diversity also leads to greater below ground diversity of soil microbes (Thoms *et al.*, 2010). Similarly, forests with low diversity are less resilient due to a lack of interspecific buffering (Aussenac *et al.*, 2019). Woodlands in the UK show multiple signs of degradation, such as loss of diversity, increasing homogeneity, eutrophication and loss of ground flora species richness, (Kirby *et al.*, 2005; Keith *et al.*, 2009). Woodland specialist birds, moths, beetles and butterflies continue to show decreases in abundance (Brereton *et al.*, 2019; Homburg *et al.*, 2019; Stagg & Ward, 2020), in some cases, this occurs despite increases in habitat availability (Blumgart *et al.*, 2022). As woodlands become degraded, their ability to provide ecosystem services is reduced (Aerts & Honnay, 2011; Policelli *et al.*, 2020).

Tree disease is an additional major problem affecting forests around the world. In the USA, for example, anthropogenically introduced pests cause tree mortality rates which are significantly greater than background (Fei *et al.*, 2019), while *Buxus* spp in Europe are threatened by the box tree moth, *Cydalina perspectalis* and the fungus *Calonectria pseudonaviculata* (Mitchell *et al.*, 2018). Tree disease is likewise causing high tree mortality in the UK, (Freer-Smith & Webber, 2017). Specifically,

*Fraxinus excelsior*, which makes up a large proportion of tree cover is in decline due to the fungal disease *Hymenoscyphys fraxineus*. Oaks are threatened by the oak processionary moth *Thaumetopoea processionae*, Oak mildew, *Erisyphe flexuos* and Oak Decline; a term for a syndrome of decline brought about by a combination of negative agents which would not affect healthy trees, but can cause death in trees weakened by other factors. For example, trees weakened by drought which are then attacked by predatory insects. These diseases have changed the shape of woodland communities (Rackham, 2008) and will continue to do so. Reductions in abundance of trees which form a large proportion of woodland canopies will have a cascading negative effect on neighbouring trees and the species which depend on them (Mitchell *et al.*, 2019). For instance, the loss of ash *Fraxinus excelsior* and oaks *Quercus petraea, Q. robur* in UK woodlands has potential impacts on over 500 associated taxa (Mitchell *et al.*, 2022). This problem is also thought to be exacerbated by the lack of functional redundancy, that is, other tree species are not present in woodlands which might go some way to offering alternative niches. Mathematical models suggest that the loss of ash could lead to 115 other species being at risk of extinction due to high levels of obligacy (Hultberg *et al.*, 2020).

## 1.6 Three areas of interest in this work

### 1.6.1 Afforestation schemes

Large tree planting schemes are currently underway with more planned, as discussed above. Planting the appropriate tree is recognised as important and encapsulated by the phrase 'right tree, right place'. This means, not only are the surrounding habitat and soil conditions important when considering which trees to plant, but also the ecosystem services offered by trees in return, such as flood protection or habitat for invertebrates. However, the role of mycorrhizal fungi is still not well known and does not currently form part of tree planting strategies. Similarly, whilst a response is being considered to the problem of Ash Dieback, such as replacement tree species, the mycorrhizal type of those trees has not yet been included as part of the important suite of traits under consideration (Iverson *et al.*, 2016; Broome *et al.*, 2019; Palik *et al.*, 2021)

### 1.6.2 Current woodland management

We have discussed above how many woodlands in the UK are suffering degradation such as homogenization and biodiversity loss. Although the direct effects of this degradation may be difficult to quantify, it has been pointed out that there is a need to improve habitats to prevent, for instance, further insect decline, before we fully understand the complex suite of drivers causing it (Forister *et al.*, 2019). It is

clear, however, that the loss of some woodland practices are related to reductions in woodland taxa. Coppicing, for example, has been shown to increase insect diversity through the introduction of larval and food plants which flourish under higher light conditions (Nilsson *et al.*, 2008; Fartmann *et al.*, 2013). This also shows that the diversity of plant and non-plant taxa is entwined. Hence, knowledge regarding the drivers of plant diversity are of paramount importance. Mycorrhizal fungi have been shown to be drivers of understory species richness (Veresoglou *et al.*, 2017; Guy *et al.*, 2022), but their role in woodland management is not yet fully appreciated.

### 1.6.3 Restoration woodlands on translocated soil

Ancient woodlands are a specific woodland habitat, the conservation of which is of particular concern in the UK. Ancient woodlands are classified as areas which have been continuously wooded since 1660 in Ireland, since 1750 in Scotland and since 1600 in England and Wales. Ancient woodlands are thought to be of particular ecological importance due their tendency for greater species richness (Thomas *et al.*, 1997) and occurrence of specific taxa with poor dispersal (Kimberley *et al.*, 2013) which flourish where disturbance is low (Goldberg *et al.*, 2007). Approximately 2% of woodland in the UK is designated as ancient, amounting to about 585 thousand hectares. Despite this low coverage, ancient woodlands in the UK are regularly lost to building and infrastructure projects. Various processes are sometimes carried out in order to mitigate this loss, for example, the planting of new woodlands on soils translocated from the lost ancient woodland site. However, there is no literature which examines the result of ancient woodland soil translocation on mycorrhizal fungi in the UK. Lessons may be learnt from mining restoration processes in other parts of the world, where some studies of the trajectory of mycorrhizal fungal communities have taken place. Several reports have been published regarding EMF communities in woodlands restored after bauxite mining in Australia (Gardner & Malajczuk, 1988; Glen *et al.*, 2008). However data is sparse, moreover, we do not know whether we will see similar results here as elsewhere. The restored Australian woodlands cited above occur within a well connected floristically diverse habitat, which is not the case in the UK. Restored woodlands in the UK are small and isolated and hence dispersion of fungi into these woodlands may be limited. Given the importance of mycorrhizal fungi to woodland processes, it is essential that we understand the effect of soil translocation on mycorrhizal fungi in the UK. The hypothesis behind soil translocation is that the diversity of the restoration woodland will be enhanced due to the addition of soil flora and fauna, and that this flora and fauna will be beneficial to woodland establishment. In the case of mycorrhizal fungi, we hope that fungal propagules will be preserved and hence colonise newly planted trees, but this has not as yet been monitored. This is of particular interest because we know that EMF exhibit succession (Visser, 1995; Jumpponen *et al.*, 1999; Nara

*et al.*, 2003; Twieg *et al.*, 2007). Hence we would not necessarily expect to see the same EMF community in ancient woodlands as we would on younger trees or in early successional habitats.

## 1.7 Knowledge gaps

Specialist and generalist EMF species have been identified through empirical research (Ishida *et al.*, 2007; Tedersoo *et al.*, 2008a; Lang *et al.*, 2011). However, the costs or advantages of specificity to hosts or symbionts is not clear (Bruns *et al.*, 2002). In chapter 2, we sought to explore the dynamics of specialists and generalists in woodlands and thereby highlight important counter-intuitive concepts regarding the nature of these two guilds. We attempt to answer the question 'what is a specialist?' and by using evolutionary game theory we are able to predict the traits of generalism and specialism in broad terms. We incorporate into this model the concept that trees may also display the traits of high and low receptivity as suggested by Steidinger & Bever (2014) and explored by Pither *et al.* (2018).

Above, we highlighted the importance of the distribution of plants of different mycorrhizal type (whether plants are colonised by AMF or EMF) in woodlands, and the effect of this distribution on woodland diversity. However, data identifying the mycorrhizal associations of different plant taxa is lacking (Brundrett, 2009; Bueno *et al.*, 2019a). This means that researchers relying on published databases for knowledge of type may be utilising unreliable data (Dickie *et al.*, 2007; Brundrett & Tedersoo, 2019). Without robust data regarding mycorrhizal type, we cannot fully explain the plant diversity of different habitats, nor can we use this information to influence woodland diversity in our current woodlands through appropriate planting of trees with different mycorrhizal type. In chapter 3 we conducted an in-depth review of the mycorrhizal type of British woody plants. This provides detailed information regarding the distribution of plants of different mycorrhizal type, and highlights areas for future study where data is sparse.

Plant soil feedbacks mediated by mycorrhizal fungi influence woodland diversity though the supply of suitable inoculum to the understory species. This is of great relevance in temperate broadleaved woodlands where the majority of the plant diversity is due to that understory, particularly since we see a continued loss of plant diversity in our woodlands. However, there is very little data confirming this understory response to tree type. In chapter 4 we therefore explore the response of the understory species richness in 103 broadleaved woodlands across the UK.

Baseline biogeographical data of EMF species is lacking (van der Linde *et al.*, 2018; Clubbe *et al.*, 2020), which is unsurprising given the number of mycorrhizal fungal species (van der Heijden *et al.*, 2015). This means that we cannot, for example, estimate expected mycorrhizal species richness in healthy woodlands or predict

expected mycorrhizal communities of specific habitats, such as ancient woodlands. In addition, the drivers of EMF communities are not well known. For example, whilst some studies indicate that soil pH is significant (Suz *et al.*, 2014; Tedersoo *et al.*, 2014; Suz *et al.*, 2017; Rosinger *et al.*, 2018), others do not (Jarvis *et al.*, 2013; Pena *et al.*, 2017). Without this knowledge we cannot fully understand how environmental factors, such as rainfall or soil type, might change a community, nor can we anticipate anthropogenically generated changes, such as pollution or climate change. Without these baseline comparisons, assessing the health of mycorrhizal fungal communities in woodlands is not possible. Therefore, currently, it is difficult to judge how mycorrhizal communities of existing woodlands, new planting schemes or restoration woodlands might naturally be related to one another. In chapter 5 we address this issue through a large landscape scale survey of the ectomycorrhizal community of oaks, an important British native tree. We determined the EMF community of mature trees as well as exploring the drivers of EMF richness and community structure.

Soil translocation is a significant mitigation procedure carried out during the loss of ancient woodland, However, the lack of data regarding the outcome of soil translocation means that the success of this process is unknown. There are therefore several questions that must be addressed in soil translocation schemes. Firstly, are EMF propagules preserved by this process, do they include a wide diversity of EMF, including later successional species, or, over time as the restoration woodlands develop, do their EMF communities approach those of the ancient woodlands which they have replaced? In chapter 6, we describe a pilot study undertaken with an industry partner in order to explore methods which could be used to assess the potential of soil translocation as a source of ectomycorrhizal inoculum in restoration woodlands. To do this we compare the community of EMF on saplings planted in a translocated soil to saplings planted in an ancient woodland and to the community we found on mature trees as part of the landscape scale survey mentioned above.

The graphic shown in 1.3 summarises the knowledge gaps described above which we hope to address, and also outlines how the questions we hope to answer here are essential if we are to understand mycorrhizal mediation of ecosystem functions in a variety of woodland habitats.

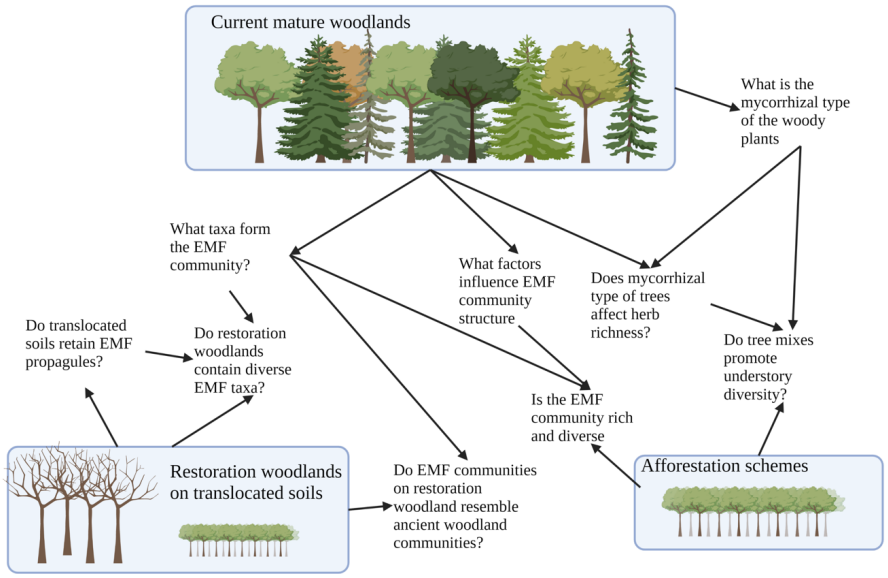


Figure 1.3: Graphic summarising the knowledge gaps which we hoped to address in this research and their applications to woodland ecosystems.

# Chapter 2

# Using game theory to model the dynamics of specialisms in ectomycorrhizal fungal communities

## 2.1 Abstract

In mature temperate woodlands, most tree roots are colonised by ectomycorrhizal fungi (EMF) which supply nutrients and receive carbon from their host trees. Some specialist EMF have a limited host range and tend to be found in association with a small number of tree species, whilst other generalist EMF are ubiquitous and can be found in association with almost any tree species. Similarly, some evidence suggests that trees display different traits in relation to their EMF association, with some high receptivity trees hosting many more species than other low receptivity trees. It has been suggested that specialist EMF may have co-evolved with their hosts to provide more nutrients and to receive more carbon. However, if specialists and high receptivity trees have co-evolved in this manner, why would they not have out-competed generalists and low receptivity trees? It is known that negative feedbacks within mutualisms allow partners of various qualities to co-exist. In this analysis, we model trees and EMF as belonging to one of two guilds, low and high receptivity trees and generalist and specialist EMF. We use replicator equations to express fitness relationships between the guild members which allow both guilds of trees and fungi to co-exist in a steady state. We review literature in support or contradiction of these results and discuss these fitness relationships in relation to functional aspects of mutualisms in order to better understand woodland dynamics. In addition we suggest areas of future work required to validate these models and give a hypothesis as to the functionality of specialist EMF.

## 2.2 Introduction

### 2.2.1 What is specialism?

Some EMF are more likely to be found in association with certain host trees than others (Molina *et al.*, 1992). These EMF are referred to as specialists and are said to have a narrow host range (Molina *et al.*, 2015). For example, Lang *et al.* (2011) found that *Fagus, Tilia* and *Carpinus* in mixed forests shared 10% of all EMF detected, but 61% of EMF were specific to one host. In an experiment in which native *Betula pendula* and *Quercus spp.* were planted in conspecific dominant stands Newton (1991) found that oak seedlings were colonised with 21 different EMF species, birch with 15, but that only three species were common to both trees. The EMF *Suillus pungens* associates almost exclusively with only two species of pine (Bruns *et al.*, 2002). Rasmussen *et al.* (2017) found that in mixed woodlands of oak and pine, of 120 EMF species detected, only ten species were common to both tree types. In mixed conifer/broad leaved forests Ishida *et al.* (2007) found over 70% of EMF species are associated with only one genus. Mixed evergreen forests in California, United States, are dominated by the conifer *Pseudotsuga menzeisii* and the broad leaved evergreen *Lithocarpus densiflora*, in these woodlands Kennedy *et al.* (2003) found 30% of EMF species were common to both hosts while 48% were specific to *P. menzeisii* and 21% to *L. densiflora*.

Some ecosystems appear to show lower levels of specificity. In a conifer dominant dune ecosystem Roy-Bolduc *et al.* (2016) find low levels of host specificity, reporting 10% of taxonomic units as specialists. Ryberg *et al.* (2011) found no host specificity between willow species in arctic tundra ecosystems. Lack of specificity has also been found between native and non-native species. In a study in China, Ning *et al.* (2019) found that only one species of *Suillus* tended to associate with the native *Pinus massoniana* whereas all other EMF found were shared between the native and an introduced species. Similarly, in Yellowstone National Park, USA, 5% of EMF were found to show some host preference with the native *Pinus contorta*, all other species were common to the native and the non-native *Picea englemannii* (Cullings *et al.*, 2000).

Early successional ecosystems can contain a limited number of EMF, some display a dominance of specialists of the invading early successional tree species (Twieg *et al.*, 2007; Collier & Bidartondo, 2009) whilst others contain mainly generalists (Nara *et al.*, 2003). Generalists are clearly important for the establishment of new tree species, for example Horton *et al.* (1999) show that Douglas-fir colonises patches of *Arctostaphylos* scrub where the tree seedlings are colonised by EMF shared between the two plants. Moreover, propagule banks can contain a small number of ubiquitous pioneer species (Taylor & Bruns, 1999; Miyamoto & Nara, 2016). As woodlands mature, species richness of EMF generally increases to include a mixture

of generalists and specialists (Keizer & Arnolds, 1994; Ishida *et al.*, 2007; Twieg *et al.*, 2007; Lang *et al.*, 2011; Rasmussen *et al.*, 2017). Observations of mature woodlands appear to show a trend for a greater species richness of EMF with some degree of host preference or host specificity (Kennedy *et al.*, 2003; Ishida *et al.*, 2007; Lang *et al.*, 2011; Rasmussen *et al.*, 2017) but a greater abundance of generalists (Kennedy *et al.*, 2003).

### 2.2.2 What is generalism

Some EMF can be found in association with many different tree species and are said to have a wide host range, or referred to as generalists. In a study in Corsica Taudiere *et al.* (2015) found *Amanita panthera, A.rubescens, A. vaginata, Clavulina cinera, C coralloides, Humaria hemisperica, Inocybe geophylla* and *Thelophora terrestris* in association with more than 69% of tree species. In Lang *et al.* (2011)'s study mentioned above, another species of *Amanita*, *A. rubescens*, is common to the three trees sampled. Work by Roy *et al.* (2008) suggests that *Laccaria amethystina* can be found in association with at least seven different tree hosts. Massicotte *et al.* (1999) report *Wilcoxina mikolae* in association with all 5 tree species in their study of forests in southwestern Oregon, United States. *Paxillus involutus* has been reported to associate with *Betula pendula, Carpinus betulus, Tilia cordata, Quercus robur* and *Pinus sylvestris* (Newton, 1991; Trocha *et al.*, 2012; Rudawska *et al.*, 2019), whilst many studies show that *Cenococcum geophilum* can be found on many temperate tree species (Newton, 1991; Massicotte *et al.*, 1999; Lang *et al.*, 2011; Trocha *et al.*, 2012; Roy-Bolduc *et al.*, 2016; Rasmussen *et al.*, 2017; Rudawska *et al.*, 2019).

Although some EMF can demonstrate a very narrow host range, sometimes being found in association with a single tree species, the converse is not usually true. For example, while Lee & Kim (1987) found *Suillus grevillei* only in stands of *Larix leptolepis*, the larch was found to host 31 other EMF species. *Pseudotsuga menziesii* is thought to harbour around 250 host specific EMF (Molina *et al.*, 1992).

### 2.2.3 Tree receptivity

There is some evidence that trees also display different mycorrhizal association traits; those which host many EMF species (high host receptivity) and those which host fewer (low host receptivity). Molina *et al.* (1992) introduced the term host receptivity and highlighted the range in the number of symbionts of certain tree species. However, Molina *et al.* (1992) specifically mentions the genus *Alnus*, which is something of a special case (Tedersoo *et al.*, 2009) and *Dipterocarp* species. The authors also point out that lack of study could lead to misleading conclusions, indeed, more recent empirical data from tropical forests, may suggest that EMF species diversity for dipterocarps is higher than originally believed (Brearley, 2012). In Taudiere *et al.*

(2015) study of Corsican trees and EMF, some tree species such as *Corylus avellana* and *Betula pendula* were found to associate with fewer EMF, while others such as *Quercus ilex* hosted significantly larger populations. Similarly, through detailed search of the UNITE fungal sequence database (UNITE, 2022) Pither *et al.* (2018) found that *Carya* and *Betula* tended to host fewer EMF, whilst *Fagus* and *Castanea* hosted many. We also carried out review of thirteen studies of oak (*Quercus robur, Q. petraea*) and ten studies of birch (*Betula pendula*). We found 259 EMF species associated with two species of oak, (table D.2 in appendix D3) but only 86 species associated with birch (table A.1 in appendix A1).

### 2.2.4 Fitness benefits conferred to hosts

What fitness benefits could be conferred to the host trees associating with EMF displaying the traits of specialism or generalism? Molina *et al.* (1992) suggest that specialists could convey an advantage to their hosts by reducing facultative epiparasitism. That is, specialists help reduce competition between plants because one plant is unable to indirectly parasitize another through connected hyphae. There is some evidence that specialists transfer more nutrients to their hosts than generalists. Gorissen & Kuyper (2000) found that specialists transferred more nitrogen to hosts than generalists, but the division between the behaviour of specialists and generalists is not clear cut. Colpaert *et al.* (1996) found that whilst the generalist *Scleroderma citrinum* retained significantly more nitrogen than two other EMF species examined, the remaining two species, a specialist and a generalist, retained similar amounts. In a later work Colpaert *et al.* (1999) found no difference in the phosphorus concentration of the host tree when associated with generalists or specialists. Similarly, Duñabeitia *et al.* (2004) report greater growth of *Pinus radiata* with pine specialist *Rhizopogon* compared to the generalist *Scleroderma citrina*. However, in this study, only one species of Rhizopogon, *R. roseolus* was correlated with significantly higher shoot length, the results for *R. luteolus* were similar to those for the generalist EMF.

Ectomycorrhizal fungi confer other benefits to plants, such as disease resistance and drought tolerance (Chakravarty & Unestam, 1987; Whipps, 2004; Pickles & Simard, 2016; Zhang *et al.*, 2017; Yin *et al.*, 2018; Sebastiana *et al.*, 2019). Parke *et al.* (1983) showed a specialist to confer improved drought tolerance compared to generalists. A study on resistance to pine wilt disease showed mortality was lowest for plants associated with a specialist compared to a generalist (Chu *et al.*, 2019). However, not all specialist EMF examined in this study conferred equal benefits and studies in which the comparative benefits of different EMF species are compared are limited.

Generalists mycorrhizal fungi potentially allow multiple plant hos species to access a common mycorrhizal network (Simard *et al.*, 2012). Although this could lead

to facultative epiparasitism, it can also increase plant fitness (van der Heijden & Horton, 2009; Gorzelak *et al.*, 2015) by allowing transfer of nutrients (Pickles *et al.*, 2017) and signalling compounds (Song *et al.*, 2010; Babikova *et al.*, 2014) which protect against predators. If neighbouring trees are heterospecific, this network relies on fungi which are to some extent generalists (Kennedy *et al.*, 2003). However, many mature forests are dominated by a single tree species, or a limited number of tree species. For example, the National Vegetation Classification for woodlands in the UK, which groups woodlands according their most abundant tree species (Hall *et al.*, 2004), describes many woodland habitats as dominated by one or two tree species. These would include the vegetation type W18, describing native Scottish pine woods, which consist almost entirely of *Pinus sylvestris*. Similalry, W14 describes beech woods (*Fagus sylvatica*). Although beech is often abundant, other species can occur, but these are generally limited to *Betula pendula, Quercus robur* and limited numbers of *Fraxinus excelsior* and *Acer pseudoplatanus*. Indeed plant soil feed-backs tend to generate monospecific stands within woodlands (Liang *et al.*, 2020; McQuire, 2007; Teste *et al.*, 2009; Pickles *et al.*, 2017; Rog *et al.*, 2020). Moreover, a monospecific stand still allows access to a common mycorrhizal network.

### 2.2.5 Fitness benefits conferred to EMF

What about the advantage conferred to fungi showing the traits of specialism or generalism? Using the example of the specialist *Suillus pungens*, which is confined to two species of pine Bruns *et al.* (2002) suggest that specialists are adapted to derive more nutrients from their hosts. *S. pungens* produces abundant sporocarps compared to other species within its habitat whilst at the same time it is not an abundant coloniser of roots. The authors hypothesise that the most likely explanation is that the specialist EMF is better adapted to obtain greater amounts of carbon from the host. Gorissen & Kuyper (2000) found that under elevated carbon dioxide, a specialist EMF (*Suillus bovinus*) incorporated the increased $CO_2$ into root growth, leading to increased root dry mass, growth whilst a generalist EMF (*Laccaria bicolor*) did not. The authors suggest that the increased mass could be due to increased fungal mass such as more root tips, thicker fungal sheath and more mycelium. This supports the hypothesis that specialist EMF are able to take up more carbon from their hosts compared to generalist EMF.

If it is the case that generalists are not adapted to obtain extra nutrients, why are they not out competed by specialists? Since generalists do not require host specific germination, they facilitate establishment of different tree species and allow succession of species within woodlands (Baar *et al.*, 1999; Horton *et al.*, 1999; Collier & Bidartondo, 2009). Their ability to survive with many different tree types could be a factor in their continued persistence.

In summary, specialists and generalists are so called due to their physical rather

than their functional traits. In other words, specialists are defined as such due to data suggesting their preferential occurrence on a limited number of tree types, but the functional parameters of specialism, although hypothesised, is not yet well known (Bruns *et al.*, 2002). In this analysis we hope to be able to supply more information as to the functional traits that define specialism in EMF.

## 2.3 Methods

Replicator equations describe the rate of change of the proportions of a population which exhibit different behaviours. In our case, whether an EMF is a specialist or a generalist is such a behaviour. In replicator dynamics, the growth rate of the proportion of the population with a behaviour is assumed to be proportional to the difference between the fitness resulting from that behaviour, and the average expected fitness of the entire population. (Maynard Smith, 1974; Taylor & Jonker, 1978; Hofbauer & Sigmund, 1998; Schuster, P.and Sigmund, 1982). Replicator dynamics offers a means to explore the fitness relationships between guilds of trees and fungi which would generate a stable population of both. Similar analysis using systems of nonlinear differential equations has been used to explore mutualistic interactions, but these analyses usually focus on the potential for parasitism in symbiotic relationships. Neuhauser & Fargione (2004) used the Lotka-Volterra predator prey model to examine potential changes from mutualism to parasitism and found that increased soil fertility could favour parasitic interactions. This result is confirmed, for instance, by the lack of mycorrhizal associations for plants in low competitive, high phosphorus environments (Lambers & Teste, 2013), and the ability of some arbuscular mycorrhizal fungi to parasitically infect ruderal, non-mycorrhizal species (Veiga *et al.*, 2013).

Similarly, the potential for non-beneficial mutualisms was explored by Steidinger & Bever (2014). In this work, replicator equations are used to represent the rate of change of beneficial versus non-beneficial symbionts depending on the ability of hosts to discriminate between fungal partners. The authors were considering a range of fungal behaviour from beneficial to cheating. The model suggests that within the tree community, we will find hosts with different abilities to discriminate. Hosts with a low ability to discriminate will facilitate the survival of many different fungal species, including those which might supply fewer nutrients. This analysis therefore, also suggests a dynamic in which two types of tree host exist.

Ezoe (2019) used the replicator equations to demonstrate that there can be a stable state with both mutualists and non-mutualists, if hosts can adjust the number of associating symbionts. We know that tree hosts can select EMF, both by stimulating spore germination (Fries *et al.*, 1987; Miller *et al.*, 1993) and penalizing low nitrogen supply (Hortal *et al.*, 2017; Bogar, 2019) which could therefore contribute

to the stable state described by Ezoe (2019). The general format for Ezoe (2019)'s model is similar to the application explored here. In that paper two strains of fungi are modeled which could be taken to represent a specialist EMF which gains fitness when in association with its host tree, but not when in association with a non-host tree. Ezoe (2019) finds that both strains of fungi can exist in a stable equilibrium if host partner preference is weak. This would appear to be the case in mature woodlands where we see that although fungi may have a very strong partner preference (a very narrow host range), trees in general, do not.

### 2.3.1 Application of the replicator equations

In this chapter, the application of the replicator equations to an equilibrium of specialists and generalists and trees hosting a low or high number of EMF is explored in more detail. The full derivation of the results using the replicator equations can be found in appendix A2. In summary, the replicator equations allow us to evaluate the rate of change of the proportions of specialists and generalists and high and low receptivity trees in terms of their fitness. The rate of change of the proportion of each guild is related to the difference between the fitness of that guild and the fitness of the entire population. The rate of change of generalist EMF, for example, is proportional to the difference between the fitness of generalist EMF and all EMF. Generalist fitness will depend on the number of times they encounter high or low receptivity hosts. By summarising these scenarios for EMF and trees we create a pair of simultaneous differential equations which express the rate of change of proportions of trees and EMF in relation to their fitness as they host or partner different guild members. We can assume that, in general, a steady state occurs in woodlands in which both guilds of trees and fungi coexist, that is, we do not find woodlands in which only specialists or generalist occur, or only high or low receptivity trees. These rates of change must then be zero. By setting the pair of differential equations to zero we can solve them and generate two possible fitness relationships, one of which is depicted in figure 2.1.

## 2.4 Summary of model results - asymmetry between host plants and EMF

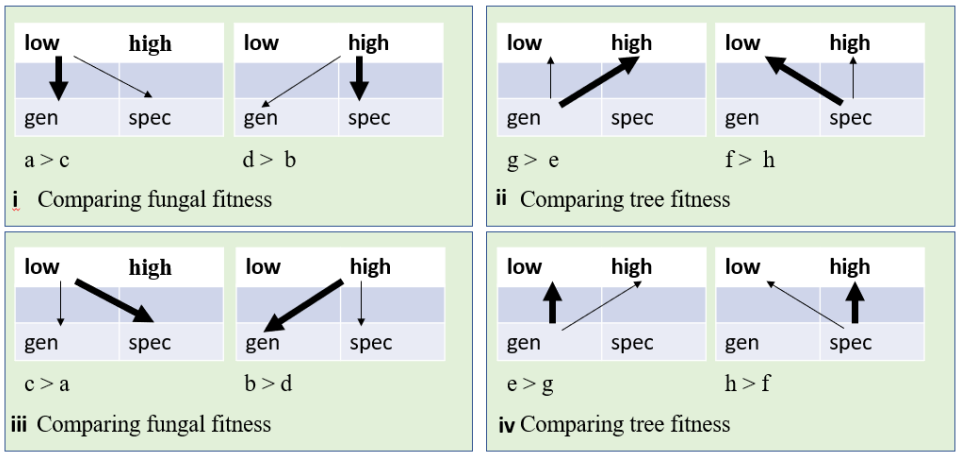


Figure 2.1: Depiction of outcomes of the steady state, after Bever (2002b). The arrows depict the direction of the fitness relationship and the arrow sizes indicate the relative magnitude of the fitness. The top plates show the results for one solution to the steady state, while the bottom plates are the converse solution. The plates on the left depict results for comparisons of fungal fitness, and those on the right summarise comparisons for tree fitness. For example, i) shows that if generalist EMF are fitter than specialist EMF when in association with low receptivity trees, then specialist EMF are fitter than generalist EMF with high receptivity trees. ii) depicts the result that if low receptivity trees are fitter than high receptivity trees when hosting specialist EMF, then generalist EMF confer greater fitness to high receptivity trees than they do to low receptivity trees. Note that either plates i and ii are true or plates iii and iv

The results of the replicator equations summarised in the top panel of 2.1 depict the scenario in which a generalist EMF is fitter with low receptivity trees than a specialist EMF. From this it might seem natural to infer, conversely, that low receptivity trees are fitter with generalists, but this is not the result described by the steady state. The equations do not tell us about the fitness of host trees when colonised by one fungal type or the other. Instead, we learn that what follows is that low receptivity trees would be fitter than high receptivity trees when hosting specialists. Panel b describes the result that if specialists are fitter than generalists when associating with high receptivity trees, then high receptivity trees are fitter than low receptivity trees when hosting generalist EMF. All of these relationships are one solution to the replicator equations.

This situation is described by Bever (1999) as an asymmetric relationship between host plants and mutualistic fungi. That is, if a particular fungal symbiont is fitter with a certain plant type, that plant type is fitter with another symbiont. Bever (2002b) sought empirical evidence to confirm this relationship using the arbuscular mycorrhizal fungal (AMF) symbiosis between two different plant species

Table 2.1: Summary of ecological implications of equation results for the replicator equations solved for two guilds of trees and EMF. Note that the converse of each of these arguments could also be true, the solution to the replicator equations allows two opposing scenarios.

| Implications of the replicator equations | Replicator equations DO NOT tell us |
|---|---|
| Low receptivity trees are fitter than high receptivity trees when in association with specialists | Whether specialists are fitter with low receptivity trees or high receptivity trees |
| High receptivity trees are fitter than low receptivity trees when in association with generalists | Whether generalists are fitter with high or low receptivity trees |
| Specialist EMF are fitter than generalists when in association with high receptivity trees | Whether high receptivity trees are fitter with specialists or generalists |
| Generalist EMF are fitter than specialists when is association with low receptivity trees | Whether low receptivity trees are fitter with generalists of specialists |

and an AMF that could be considered as a specialist for one of the plants but not the other. In agreement with the above statements, they found that the AMF which grew best in association with *Plantago* did not promote the growth of that plant - instead the growth of *Plantago* was most promoted by the AMF which grew best in association with *Panicum sphaerocarpon*.

The replicator equations suggest potential fitness relationships between EMF and trees when we compare:

- Fitness of different EMF with the same tree types
- Fitness of different tree types with the same EMF

The replicator equations do not give us information about the same EMF types with different tree types, or the same tree types with different EMF types. The results for one possible set of relations are summarised in table 2.1. Another important result here is that if, for example, we see that specialists are fitter than generalists with high receptivity trees, the converse, the high receptivity trees are fitter with specialists than they are with generalists, does not need to be true. This is assuming that the steady state depicted by the top panel of 2.1 is true. Therefore, a trait of specialists may be that they are better at extracting carbon from their host trees compared to generalists, but not that they provide more nutrients compared to generalists. Therefore whilst we require consistent data demonstrating that when we compare specialists with a single host tree, we can expect a range of outcomes if we compare a single host tree with a range of specialist EMF.

Note that the solution to the steady state results in two opposing asymmetric scenarios, either of which could be true. A simple way to summarise this information is using the game theory matrix shown in figure 2.2. We also introduce this figure as

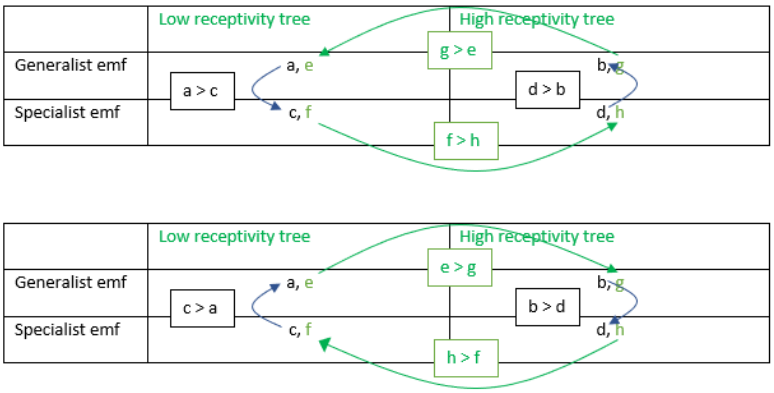


Figure 2.2: a,b,c,d represent the fitness of EMF when associating with low or high receptivity trees. e,f,g,h, represents the fitness of high or low receptivity trees when associated with specialist or generalist EMF. For instance, a is the fitness of generalist EMF in association with a low receptivity tree; h is the fitness of a high receptivity tree in association with a specialist EMF. The arrows describe the direction of the relationship, green arrows apply to trees and black to EMF. For example, the green arrows in the upper figure show that a high receptivity tree is fitter than a low receptivity tree when associated with a generalist. The replicator equations allow either of the opposing scenarios depicted to be true.

a more straightforward means to summarise literature reviewed in the next section. In the figure, a,b,c,d refer to the fitness of EMF when in association with low or high receptivity trees. e,f,g,h refers to tree fitness when hosting different guilds of EMF. The green arrows depict fitness relationships between tree types, that is, the arrow from g to e describes the replicator equation result that high receptivity trees must be fitter than low receptivity trees when hosting generalist EMF.

The fitness statements depicted by this diagram are:

1. $a > c \implies g > e \implies f > h$ and $d > b$ or
2. $c > a \implies e > g \implies h > f$ and $b > d$

That is, item one says, if generalists are fitter than specialists with low receptivity trees, then high receptivity trees are fitter than low receptivity trees with generalists, low receptivity trees are fitter than high receptivity trees with specialists and specialists are fitter than generalists with high receptivity trees. Item two is the converse. We hope that empirical data will validate one of these scenarios, either one or the other could be true, not both.

## 2.5 Supporting literature

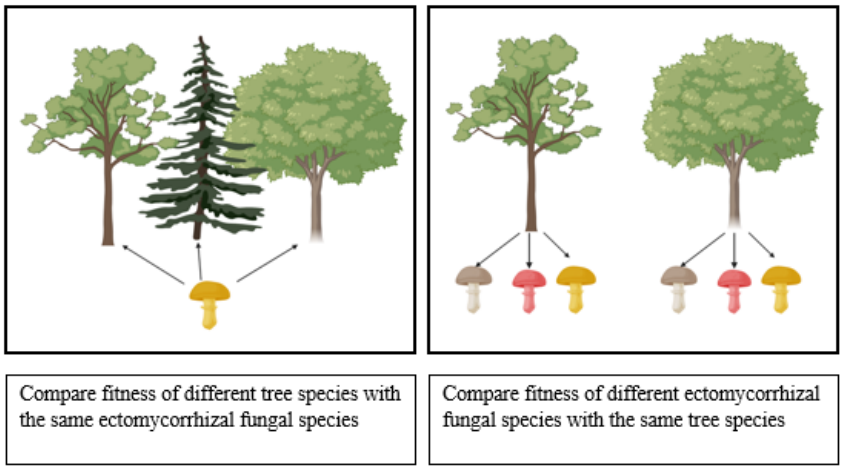


Figure 2.3: Illustrates the fitness relationships we require to validate the model. We are interested comparisons of tree fitness with single fungal species and different fungal species with the same tree species. For example, the left hand panel depicts experiments in which the fitness of different tree species, low and high receptivity hosts, is compared when colonised by a single fungal species. Experiments would be repeated with a range of different EMF. The right hand panel depicts experiments in which the fitness of different EMF, specialist EMF and generalist EMF is measured when colonising the same tree species. The experiments would be repeated with a range of different trees.

For the purposes of model validation, we require data showing the difference in fitness of generalists versus specialists with either high or low receptivity trees. We are not concerned with the comparisons in fitness of generalists alone with the two different tree types, or specialists alone with two different tree types. This is depicted in the right hand panel of 2.3. In addition, we are looking for data showing the fitness of different tree types when grown with the same fungal types. For example, low or high receptivity trees grown with only generalists or only specialists. We do not require the comparison of the same tree type with different fungal types, for instance, high receptivity trees with either specialist or generalist fungi. This is depicted in the left hand panel of figure 2.3.

Very few pieces of research measure fitness, in the sense that they do not record number of surviving offspring. These data would be very difficult to record for both trees and fungi. Proxies might be the number of fruiting bodies or number of viable seeds. But in any case, most of the literature is not concerned with fungal or host tree fitness, but rather with nutrient absorption and transfer. We will therefore use alternative data, such as plant yield, plant or fungal nitrogen content or mycelial mass. This literature is summarised chronologically below. Note that we refer back to the abbreviations found in figure 2.2 for fitness.

### 2.5.1 Comparing different EMF guilds with single hosts, (a to c, d to b)

Dosskey *et al.* (1990), found that *Rhizopogon* act as a greater sink for photosynthate when in association with *Pseudotsuga menziesii* than two species of generalist EMF. Using carbon transferred to the EMF as a proxy for fitness, this work suggests that specialists are fitter with the high receptivity Douglas-fir than the generalists, (d>b). When $CO_2$ levels were increased, the shoot to root ratio decreased for *Pinus sylvestris* in with association with the specialist *Suillus bovinus* compared to the generalist *Laccaria bicolor*. This could indicate that the specialist was better able to take up and use the carbon from the host than the generalist (d>b) (Gorissen & Kuyper, 2000). Bruns *et al.* (2002) hypothesised that specialist EMF may be able to extract more carbon from their hosts than generalists. This statement was based on the observation that several species of specialists often produce abundant sporocarps, but are rarely found on tree roots (d>b) (Gardes & Bruns, 1996). This data is persuasive as it is based on field observations in natural mature woodlands.

### 2.5.2 Comparing different host trees with single EMF guild, (e to g, f to h)

Abuzinidah & Read (1986) record the yield and nitrogen content of four different tree species when grown in the non-mycorrrhizal state or with the generalist EMF *Hebeloma crustuliniforme*. The benefit to the plants was most marked for *Betula pendula*, suggesting that the generalist confers more benefit to the low receptivity tree than it does to the high receptivity trees (e>g). Shi *et al.* (2017) found that the competitive advantage (measured as relative biomass of plants) for trees of different successional stages depended on the EMF species. For example, *Cenococcum geophilum* gave a competitive advantage to the mid-successional tree *Quercus serrata* over the early successional *Pinus massoniana* while *Pisolithus tinctorius* did not. The authors also report that *P. tinctorias* conferred a much greater competitive advantage to the later successional *Cyclobalanopsis glauca* than to the early successional *P. massoniana* than *Paxillus involutus* or *Laccaria bicolour*. Since all the EMF species here could be considered generalists, this work suggests that later successional trees have a competitive advantage over early successional trees when in association with generalists, but this effect is not equal among generalists. However, it is difficult to determine whether the tree species in this experiment are high or low receptivity due to lack of data of species richness of EMF associated with them. We have seen that early successional trees may have lower receptivity (Taudiere *et al.*, 2015). If that observation held for the trees in this biome (subtropical forest in southeastern China), then this work would support the relationship g>e. However, that would imply that *P. massoniana* has lower receptivity than *Lithocarpus glaber*,

this seems unlikely as pines, in general, tend to host a high diversity of specialist and generalist EMF. However, this data is interesting as it does imply a difference in outcomes conferred to different tree types.

### 2.5.3 Experiments which tell us about redundant fitness relationships

Since the experiments in the literature are not designed to address the modelling we have explored here, in many cases they reveal relationships that are not helpful in this analysis. However, these are still of interest since we might expect to see a range of potentially conflicting outcomes. Some results may suggest that a high receptivity host tree is conferred greater fitness when hosting specialist EMF, whilst other data may contradict this (h to g, e to f).

Parke *et al.* (1983) found that the specialist Rhizopogon was more successful at promoting growth of *Pseudotsuga meziesii* when compared to two other generalist EMF (Chu-Chou & Grace, 1985) (h>g). Abzinadah *et al.* (1986) measure yields and nitrogen content of the high receptivity tree *Pinus contorta* when in association with three different EMF using two different nitrogen sources. The yield and nitrogen content of the plant was increased compared to the non-mycorrhizal state when in association with either of the specialists *Suillus bovinus* or *Rhizopogon roseolus* when protein was used as the nitrogen source (h>g). When ammonium was used, the specialists were found to increase yield (h>g) but no EMF were found to increase nitrogen content. This work suggests some increase in fitness conferred to the plant as measured by yield or nitrogen content, when in association with a specialist, if nitrogen is available in inorganic form. *Pinus sylvestris* has been reported as having higher nitrogen content when in association with the specialist *Suillus bovinus* compared to the generalist *Laccaria bicolor* (h>g) (Gorissen & Kuyper, 2000). The ratio of $^{15}$N to $^{14}$N, $\delta$N, provides information about nitrogen transfer between plants and EMF. Preferential transfer of $^{14}$N by fungi means that EMF can be depleted in this isotope but retain $^{15}$N. Whilst plants may have less enriched $^{15}$N than depleted $^{14}$N. Hence $\delta$N can be decreased in mycorrhizal plants compared to non-mycorrhizal plants and a reduction in $\delta$N between mycorrhizal plants could imply the EMF is transferring less N overall to its host. Hobbie *et al.* (2005) found the ratio $\delta$N was higher for specialists than generalists, suggesting that specialists may transfer more (h>g). Dosskey *et al.* (1990) found no significant difference in the nutrient content of Douglas-fir hosting either the specialist *Rhizopogon vinicolor* or the generalist *Laccaria laccata* (g = h). Colpaert *et al.* (1996) found that there was no significant difference in shoot weight or nitrogen content of *Pinus sylvestris* when inoculated with the generalist *Thelephora terrestris* or the specialist *Suillus bovinus* (g = h). In a later work, the same authors found no significant difference in shoot phosphorus for Scots pine inoculated with four different EMF, two generalists and two specialists

(Colpaert *et al.*, 1999) (g = h). While Duñabeitia *et al.* (2004) found that *Pinus radiata* inoculated with the specialist *Rhizopogon lutelous* had the greatest shoot weight (h>g), they also found no significant difference in shoot weight between plants grown with specialist *Rhizopogon luteolus* or the generalist *Sceloderma citrinum* (g = h). Chu *et al.* (2019) considered the effect of EMF on the mortality of *Pinus tubularformis* when infected with pine wilt disease. Although trees inoculated with the pine specialist *Suillus laricinus* showed the lowest mortality this was not constant for other *Suillus* species and pines hosting *S. tomentosus* showed a higher mortality than uninoculated control trees, (h>g, h<g). In other words, the pine specialist, *Suillus* conferred different mortality outcomes.

Table 2.2: Summary of literature

| **Fitness relationship** | **Finding** | **References** |
|---|---|---|
| d>b | Higher photosynthetic rate with specialist, reduced shoot to root ratio under high $CO_2$ for specialist, Greater sporocarp production with low colonisation abundance | (Dosskey *et al.*, 1990; Gorissen & Kuyper, 2000; Gardes & Bruns, 1996) |
| h>g | Host tree recovered more quickly from water stress with specialist, Greater plant dry weight and nitrogen content with specialist, specialists have higher $\delta$N | (Parke *et al.*, 1983; Abzinadah *et al.*, 1986; Gorissen & Kuyper, 2000; Hobbie *et al.*, 2005) |
| e>g | Increase in nitrogen content and plant dry weight greater for *Betula pendula* than for *Picea marana, P. sitchensis* or *Pinus contorta* | (Abuzinidah & Read, 1986) |
| a - c | no data found | |
| f - h | no data found | |

## 2.6 Discussion

The results of the literature review are summarised in table 2.3. We searched for data which consistently supported both statements - the scenarios depicted in the upper or lower panel of figure 2.2. Several pieces of work supported the relationship d>b (Dosskey *et al.*, 1990; Gorissen & Kuyper, 2000; Gardes & Bruns, 1996) but this was not unequivocal (Colpaert *et al.*, 1996, 1999). Similarly, several studies

demonstrated that h>g, (Parke *et al.*, 1983; Abzinadah *et al.*, 1986; Gorissen & Kuyper, 2000; Hobbie *et al.*, 2005). However, this is not a relationship we need in order to validate this model. Only one piece of work was found which could suggest that e>g (Abuzinidah & Read, 1986). No work was found which could give information regarding the fitness of generalists compared to specialists when in association with low receptivity trees, or the comparative fitness of low and high receptivity trees when in association with specialists.

The results of Chu *et al.* (2019), which show a variety of outcomes for a host tree when colonised by a range of specialist and generalist EMF, may be in agreement with the results from the steady state which suggest that whilst specialist EMF may be fitter with the host trees compared to generalists, when we look at the converse relationship - the fitness conferred to a host by different EMF species, we may see a range of outcomes. This may be expected if a specialist EMF is a greater carbon sink, it may weaken a host tree to a greater extent than an EMF which has lower carbon requirements. This may have deleterious effects on smaller plants already weakened by disease.

Besides the lack of available literature, the literature cited may be unreliable for the purposes of validating this model for several reasons. Firstly, most of the data comes from pot experiments using a pairing of one species of host with a single EMF, such results may not be applicable to multi-species settings. Perry *et al.* (1989) demonstrated that seedling biomass of ectomycorrhizal *Pseudotsuga menziesii* increased when it was grown in mixture with *Pinus ponderosa* compared to in a monoculture. Therefore, although single species experiments are important (Kennedy, 2010), multiple species experiments are also required. Secondly, the data summarised comes from a limited number of EMF and tree species. The data from pot experiments in table 2.3 comes from less than ten generalist and specialist EMF, and within each study, usually only three or four taxa tend to be used. This is problematic because we know we can expect a range of outcomes within each guild. For example, Abuzinidah *et al.* (1989a) found yield and nitrogen content of *Betula pendula* infected with three different EMF, *H. crustiliniforme, Amanita muscari* and *P. involutus* changed depending on the species; being greatest with *H. crustiliniforme* and least with *P. involutus*. All these EMF are considered generalists. Ectomycorrhizal fungi are also known to display intraspecies variation (Tibbett *et al.*, 1998, 2000). Cairney (1999) discusses many examples of intraspecific variation in EMF and raises the issue of the potential problem of attempting to understand ecological functionality based on experiments on a limited number of isolates. This indicates the need for experiments using not only more EMF species, but several isolates of each species. Experiments required broadly fit into two categories, firstly, those which look at community structure, and then use this to infer fitness. This would include studies of above and below ground EMF abundance for example. Secondly,

those which examine the mechanisms which could lead to fitness, such as nutrient transfer (Bengtsson *et al.*, 1994; Kennedy, 2010).

## 2.7 Future work

### 2.7.1 Fitness of mycorrhizal guilds

We need experimental designs that specifically address the following questions:

Are generalists or specialists fitter when in association with low receptivity trees (fitness relation ship a-c)
Are generalists or specialists fitter when in association with high receptivity trees (fitness relationship b-d)

Notice that the results of the replicator equations suggest that there are only two combinations for the fitness relationships. For example, if generalists are fitter than specialists with low receptivity trees (a>c), then it follows that d>b, g>e and f>g. Therefore, if we accept that the replicator equations model the fitness relationships between guilds of trees and ectomycorrhizal fungi, we could look to confirm only one of these relationships. Of course, it would be interesting to confirm more than one and to thereby also ascertain that the replicator equations do in fact model this symbiosis.

Many experiments are designed to assess the benefit to the plant of the mycorrhizal symbiosis, for instance, the amount of nitrogen or phosphorus transferred to the host. In order to validate the model, we are instead interested in the benefit to the EMF, and in particular, do some EMF gain more benefit than others. Ideally, we want to measure fungal fitness. This is difficult for many organisms, but particularly for fungi which have complicated life cycles, may not reproduce sexually and have a blurred concept of the individual (Helgason & Fitter, 2009). Pringle & Taylor (2002) argue that a single measure of fitness, such as mycelial growth rate, might be an appropriate metric if we know how that measure is correlated with fitness. For example, in pot experiments Bever (2002a) found second generation arbuscular mycorrhizal communities were correlated with spore counts. Since fitness is related to reproductive success, fruit body abundance might be a suitable metric. Sporocarp abundance is relatively easy to measure, although species with inconspicuous or hypogeus fruiting bodies may be overlooked and this does not account for the fact that many EMF propagate vegetatively.

Several studies have been carried out of above and below ground EMF communities, for example (Dahlberg *et al.*, 1997; van der Heijden *et al.*, 1999; Jonsson *et al.*, 1999a; Smith *et al.*, 2007; Rudawska *et al.*, 2011; Spake *et al.*, 2016). Further analysis of these results and further similar studies might allow comparison

of the abundance of fruiting bodies and mycorrhizal root tips (Gardes & Bruns, 1996). Consistent patterns whereby specialists are more common above than below ground, would add strength to the argument that specialists obtain greater amounts of carbon from their host (Bruns *et al.*, 2002) and use this for sporocarp production. However, we learn nothing of fungi which do not produce easily detected sporocarps. If carbon transferred to the EMF is considered a proxy for fitness, then pot experiments could be used to access data on a wider range of species and strains. The cost of the mutualism is likely to be greater for EMF that transfer more nutrients (Bever, 2015), therefore carbon sink strength as ratio of nutrient transfer (Bidartondo *et al.*, 2001) is probably a better estimate for EMF fitness.

Experimental design must differentiate between EMF guilds when in association with a single host type. For instance, a range of different specialist EMF in association with a high receptivity tree such as *Quercus robur, Pinus sylvestris* or *Fagus sylvatica* and a range of different generalist EMF when in association with low receptivity trees such as *Betula pendula* or *Corylus avellan.* The difference in carbon received and nitrogen transferred could be considered as the cost of the symbiosis to the EMF, and EMF with lower costs, i.e. those that receive more carbon per unit nitrogen, could be considered as fitter because potentially they have more carbon available for reproduction and growth. For example, Bidartondo *et al.* (2001) show that *Paxillus involutus* transferred more ammonium per mg of mycorrhizal mass than two species of *Suillus*, but the ratio of the percentage of carbon allocated to mycorrhizas to the amount of ammonium transferred was greatest for a species of *Rhizopogon.*

### 2.7.2 Fitness of host guilds

In this analysis we model trees as if they belong to one of two guilds: those with high receptivity and those with low receptivity. However, this pattern could be due to lack of data. In our literature review which appears to show relatively few EMF on *Betula pendula*, the studies tended to be smaller compared to large landscape scale studies of oak, for example. Moreover, the number of symbionts could be a function of the habitat. Early successional habitats contain a limited number of fungal propagules (Baar *et al.*, 1999; Taylor & Bruns, 1999; Collier & Bidartondo, 2009), and therefore, if some tree species are more frequently sampled in those settings, they would appear to have low host receptivity, however, the receptivity would be a function of habitat rather than a trait of the host. For example, in old growth forests in Estonia similar species richness of EMF for *Picea abies* and *Betula pendula* are reported (Tedersoo *et al.*, 2008b). Since we are modelling the steady state of mature woodlands, we are interested in whether trees found to have fewer EMF partners in early successional settings still exhibit that behaviour in mature woodlands. If so, then host receptivity is a functional tree trait and is not linked

to environmental factors such as EMF dispersal or edaphic conditions. Therefore, a more in-depth review of the literature is required in order ascertain host receptivity across a broader range of geographical locations. Additional sampling of putatively low receptivity trees in mature woodlands in different biomes is also required.

Assuming trees in mature woodlands show different traits in relation to their EMF receptivity, we then wish to answer the following questions:

Are high or low receptivity trees fitter when in association with generalists.(fitness relationship g-e)
Are high or low receptivity trees fitter when in association with specialists. (fitness relationship f-h)

Again, note the two possible fitness combinations. For example, if low receptivity trees are fitter than high receptivity trees with generalist EMF (e>g), then high receptivity trees will be fitter than low receptivity trees with specialists.

Although plant fitness may be easier to define than fungal fitness, it is still problematic to measure (Primack & Kang, 1989). For example, if we record number of surviving offspring, then at what age are they recorded, do we consider the entire life cycle of the tree and include vegetative propagation? Undoubtedly a proxy such as growth rate or seed quantity must be used.

In pot experiments many factors can be measured which would contribute to survival of hosts, such as drought tolerance, nutrient content, growth rate and disease resistance. Trees representing the two guilds need to be grown either with only specialist EMF or with only generalist EMF. As discussed above, tree growth in mixture may differ from that of trees grown in isolation, therefore single as well as mixtures of co-occurring low and high receptivity trees should be used. Using trees from British woodlands as an example, the fitness of *Betula pendula* could be compared with *Quercus robur* when grown with a generalist such as *Hebelome crustuliniforme*. The fitness of the same trees would then be compared when grown with specialists such as *Lactarius pubescens* (birch specialist) and *Lactarius quietus* (oak specialist).

Seed weights play an important part in outcomes of EMF symbiosis, for example seed weight along with host receptivity have been shown to be important in determining post-glacial tree migration rates (Pither *et al.*, 2018). Plants with low seed weights could benefit more from early mycorrhizal colonisation due to a lack of nutrient reserves. Pioneer plant species tend to have smaller seed weights (Salisbury, 1944; Cornelissen, 1999). Seed weight may also influence outcomes of both greenhouse and field experiments. For example, when looking at the difference in dry weight and nitrogen content for four species of mycorrhizal and non-mycorrhizal trees, the difference was most marked for the tree species with the lowest seed weights

(Abuzinidah *et al.*, 1989b). We have seen that there may be a correlation between successional stage and host receptivity (Taudiere *et al.*, 2015). In other words, if low receptivity trees tend to have smaller seed weights, then EMF colonisation may more significantly affect plant growth compared to trees with larger seeds. However, our model implies that low receptivity trees are fitter with either specialists or generalists. For example, if low receptivity trees are fitter with specialists than high receptivity trees, then high receptivity trees are fitter with generalists than low receptivity trees. If this difference in fitness is due to seed weight, in what way would this be affected by the EMF guild? Why would only specialists provide benefit to low seed weight trees and not generalists, or vice versa. This may be related to differences in nutrients supplied and the carbon sink strength of the EMF, which is likely to be more important at the seedling stage when carbon is more of a cost to the plant. The table below shows seed weights for 17 British woodland trees (Kew, 2008). As expected, the trees with the lowest seed weights tend to be pioneer trees. We require more data in order to confirm whether they also display low receptivity in non-pioneer settings.

Table 2.3: Seed weights for ectomycorrhizal British trees

| **Tree species** | **Seed weight (g per 1000 seeds** |
|---|---|
| Salix aurita | 0.0718 |
| Salix caprea | 0.129 |
| Salix fragilis | 0.14 |
| Betula pendula | 0.6 |
| Betula pubescens | 0.72 |
| Corylus avellana | 2.4 |
| Pinus sylvestris | 35.1 |
| Tilia cordata | 42 |
| Carpinus betulus | 1063.3 |
| Fagus sylvatica | 2311 |
| Quercus petraea | 2342.2 |
| Quercus robur | 3378 |
| Castanea sativa | 9944 |

## 2.8 Conclusion

We used the replicator equations to explore the fitness relationships between trees of low and high receptivity and specialist and generalist EMF. We discussed the possibility that trees may display these different functional traits in the mycorrhizal relationship, that is, demonstrating high or low receptivity, and reviewed the current evidence for this. Although this is an intriguing idea, and there is some evidence of a pattern in the receptivity of trees (Steidinger & Bever, 2014; Taudiere *et al.*, 2015; **?**), this needs further empirical data and we suggested some areas where this could take place.

By considering the fitness relationships which give rise to a steady state we found that an asymmetric relationship can occur which leads to the continued coexistence of trees and fungi displaying both traits. The mathematics of the model did not indicate the direction of the fitness relationships, and two alternatives were possible. Considering one possible result, we can conclude that if high receptivity trees promote the fitness of specialists more than generalists, then specialists will promote the growth of low over high receptivity. In addition, we should then observe that low receptivity trees will promote the growth of generalists over specialists, and in turn, that the fitness of high receptivity trees will be best promoted by generalists.

We saw that the steady state of the replicator equations allows us to speculate regarding the fitness of different fungal guilds when hosted by the same tree guild, or, different tree guilds when hosting the same mycorrhizal guild. This is important since we might infer that if, for example, a high receptivity tree confers greater fitness to its specialist mycorrhizal fungi than it does to its generalists, then the converse is true. That is, specialists confer greater fitness to high receptivity trees than generalists. However, the steady state is not influenced by this converse relationship, and therefore we could potentially see a range of different behaviours when we compare different fungal guilds and a single host tree. This allows us to assign potential traits to specialist EMF. Again, limiting the example to one result of the steady state, we can say that a specialist is and EMF which is better at extracting carbon from its host (given that we accept that this is a proxy for fitness), but it is not a trait of specialism to promote the fitness of high receptivity trees anymore than a generalists might.

We reviewed the literature in order to validate the model. Some data was found to support the result that specialist EMF are fitter than generalist EMF when in association with high receptivity trees, however, the data was sparse and inconclusive. We high lighted reasons why the current literature may not be appropriate for the purposes of validating this model and suggested alternative experiments and community data that would be required.

Previous authors have demonstrated how negative feedback mechanisms maintain diversity in the symbiosis between arbuscular mycorrhizal fungi and herbaceous

plants. This work extends modelling of mycorrhizal symbiosis to EMF and demonstrates how the same feedback mechanism can be extended to include two guilds of trees and EMF fungi.

# Chapter 3

# Mycorrhizal type of British woody plants - current knowledge, future directions and patterns within the landscape

## 3.1 Abstract

Knowledge of the mycorrhizal type of plants is important for understanding habitat functioning, such as plant soil feedbacks between the over and understory in temperate woodlands. Whilst databases exist which summarise mycorrhizal type for many species, this data may be sparse or lacking for many plants. In this chapter we conduct an in-depth review of this knowledge as it pertains to British woody plants, and demonstrate that robust data is lacking for more than half of them. We sought to allocate mycorrhizal type to 190 woody plants in all, and found two of more pieces of empirical data for only 35% of species. We identify eight species which may be facultatively mycorrhizal and two possibly non-mycorrhizal taxa. We suggest that more data is urgently required for *Salix* spp, which we show to both be lacking in data and having high cover. We also show that, whilst nearly half of woodland cover is made up of arbuscular mycorrhizal type woody plants, these tend to be light loving, understory species, suggesting that as woodlands succeed, ectomycorrhizal plants will be more abundant with potential repercussions for understory herb richness.

## 3.2 Introduction

While the majority of plants form associations with mycorrhizal fungi there is some variation in their mycorrhizal status. Most plants are always colonised (obligately mycorrhizal, OM). Under the right soil conditions some plants are capable of healthy

growth without or with low levels of colonisation (facultatively mycorrhizal, FM) (Smith *et al.*, 2009). For example, Brundrett & Kendrick (1987) report *Sambucus nigra* to be colonised in the summer months, but not later in the year. A few plants are never found to host mycorrhizal fungi (non-mycorrhizal, NM) and have lost symbiotic ability (Lambers & Teste, 2013; Kamel *et al.*, 2017; Cosme *et al.*, 2018). The mycorrhizal type of a plant is the functional trait describing the type of mycorrhizal fungi which the plant hosts. Arbuscular mycorrhizal (AM) type plants, which form associations with AM fungi (AMF) are the most common and it is these that can vary in status between OM and FM. Ectomycorrhizal (EM) type plants are less common but they are the major type of association for the woodland over-story in temperate woodlands and are thought to be always obligate (Moora, 2014). Knowledge of mycorrhizal type is essential because it influences ecosystem dynamics. For example, boreal or temperate woodland soils, dominated by EM and ericoid plants, tend to store more carbon per unit of nitrogen than grassland or tropical forests where AM plants are more common (Averill *et al.*, 2014). AM and EM type trees have been shown to accumulate soil pathogens at different rates (Chen *et al.*, 2019), this can lead to a difference in density with EM type trees tending to have a positive density dependence in contrast to AM type trees, (Bennett *et al.*, 2017; Liang *et al.*, 2020; Segnitz *et al.*, 2020). Further, lack of inoculum may inhibit the establishment of AM type trees in EM dominant woodlands or vice versa (Haskins & Gehring, 2005) or contribute to reduced under-story diversity of AM herbs in EM dominant woodlands (Veresoglou *et al.*, 2017).

There are several resources and published databases which list mycorrhizal type of herbaceous plants, trees and shrubs. One of the earliest lists detailing mycorrhizal type for EM type plants was published by Trappe (Trappe, 1962). As well as summarising the knowledge to date of the effects of mycorrhizal fungi on their host plant, Trappe (1962) discussed specificity (the tendency for some EMF to associate with one host over another) and compiled a list of all known associations for EMF at that time. Harley & Harley (1987) is a huge compilation of mycorrhizal associations of British plants based on literature going back to around 1900. That work serves as a summary of studies that had mentioned mycorrhizal associations in the period 1875-1986. Wang & Qiu (2006) incorporated works such as Harley  Harley (1987) and extended them to compile a worldwide list of mycorrhizal associations for the purpose of exploring evolutionary patterns in mycorrhizal symbioses. These authors added associations for bryophytes and incorporated newer studies. Akhmetzhanova *et al.* (2012) published a database of over 7000 records based on the work of Ivan Selianov in the former Soviet Union. The data is purely field based summarising work on nearly 3000 plant species from 154 different sites in the former Soviet Union. This represents a valuable resource since often multiple species within the same genus are sampled, in the field and across different habitat types. Hempel

*et al.* (2013) compiled a list focussing on Central European flora in order to model plant traits, whilst Bueno *et al.* (2017) summarise data for 1442 plant species of Europe. Later databases, such as Bueno (2017), often offer improvements on older sources, because they both review earlier sources, incorporate new data and offer a focus on a particular region.

FungalRoot (Soudzilovskaia *et al.*, 2020) is a recent comprehensive summary of over 36000 records of published literature. FungalRoot is probably the largest and most up to date compilation of mycorrhizal type information. It also offers important features, such as expert opinion on assignments and information as to whether all mycorrhizal types were examined. MycoDB Chaudhary2016 is a different resource in that it is a summary specifically of studies of inoculation experiments of EMF and AMF with clearly defined selection criteria.

However, caution must be exercised when extracting mycorrhizal type from type databases. These issues have been thoroughly reported elsewhere (Brundrett & Tedersoo, 2019; Tedersoo *et al.*, 2019; Brundrett & Tedersoo, 2020; Bueno *et al.*, 2019a, 2021; Brundrett, 2021), therefore we will only present a brief summary of some of the main points. Some databases are simply summaries of the literature, such as Harley  Harley (1987) and Wang  Qui (2006) and are not intended for use without critical consultation of the source material, errors can therefore arise in their use when, for example, the data is sparse or based on sporocarp studies alone. Sporocarp studies are not typically suitable for assigning mycorrhizal type since fungal mycelia can extend some distance from a host tree. Sparse data can lead to incorrect conclusions about mycorrhizal type. Dickie *et al.* (2007) highlights the incorrect assignment of type to *Buddleja davidii* because it was based on a single piece of data. Harley  Harley (1987) reported a non-mycorrhizal plant; later work however, observed AM colonisation. Hawthorn (*Crataegus monogyna*) is also an interesting case. As a member of Rosaceae it would be expected that this plant is AM type. However some authors report both EMF and AMF colonisation (Kovács & Bagi, 2001; Kovács & Szigetvári, 2002; Maremmani *et al.*, 2003). Taken alone, these observations might be considered an error, either through roots being traced to incorrect trees, or incorrect recognition of root morphology. However, more recent studies in which roots are carefully traced to trees and molecular methods used to identify fungi colonising the root, still find evidence of EMF in hawthorn roots (Boeraeve *et al.*, 2021). This suggests that the mycorrhizal type of some plants needs more careful consideration and more empirical data. Another point to be aware of when consulting published databases, is that mycorrhizal type may be based on experiments involving inoculation of seedlings. Glasshouse studies such as this are an essential part of the suite of information required to understand mycorrhizal type, but on their own, they may not reflect the expected state of mature trees as there is evidence that seedlings of some putatively EM trees will associate with AM fungi

when stressed, or when EM fungal inoculum is in short supply (Cázares & Trappe, 1993; Smith *et al.*, 1998).

Mycorrhizal type appears to be conserved to some extent in many plant families or genera (Tedersoo & Brundrett, 2017; Brundrett & Tedersoo, 2018, 2020). However, it has been shown that this taxonomic approach to the assignment of type should be exercised with caution. Bueno *et al.* (2018) found that only 46% of plant families have the same mycorrhizal type across all species and this number decreases further amongst plant families with more species studied. This highlights the importance of quantity of empirical studies and suggests that we might not always be able rely on phylogeny to assign mycorrhizal type where data is sparse. Moreover, it is important to be aware how much data has been used to make an assignment of type. Deviations from status within family are more likely for some families than others. For example, Albornoz *et al.* (2021) highlights the fact that Fabaceae, and AM family, contains several non-mycorrhizal genera, therefore sparse data may be more important for AM plants as mycorrhizal status can vary. Similarly, although Ericacea are a diverse family with relatively little data, it is likely that mycorrhizal type is conserved across similar species which co-occur across the same habitat, such as in the restricted data set of British plants which we consider here (Vohník, 2020; Albornoz *et al.*, 2021).

Definition of mycorrhizal type is generally based on the structures formed by the colonising fungus within plant roots (Kariman *et al.*, 2018). For example, EMF form a Hartig net within the root cortical cells and a sheath around the root tip, both of which are diagnostic for EM type plants. This partially explains why some EM diagnosis can be erroneous. Unless a Hartig net is observed, which requires root dissection and high power microscopic analysis, only the sheath is visible. Therefore, root changes or infections of non-mycorrhizal fungi which give the appearance of a sheath or Hartig net could lead to the the plant being interpreted as EM type. Some EM designations made in early research have been questioned as it is thought that dark septate fungi were confused with *Cenococcum geophilum* infection, hyphal networks around a root, perhaps of a saprophytic fungus, may have been mistaken as an EM mantle, alternatively, phi thickening in cortical roots may be confused with a Hartig net (Tedersoo & Brundrett, 2017; Brundrett & Tedersoo, 2020).

Definition of AM type generally implies observing arbuscules (Brundrett & Tedersoo, 2019). However, observations of roots colonised by glomeromycotan fungi can include roots with a combination of arbuscules, vesicles or hyphae, (Brundrett, 2009; Cosme *et al.*, 2018). Discussions as to a strict definition of AM type are ongoing (Brundrett & Tedersoo, 2019; Bueno *et al.*, 2019a, 2021). This means that plants defined as AM type in literature may fit a range of criteria because strict definitions have not been followed. In addition, some AM type plants are facultatively mycorrhizal. If limited research is available, observations of uncolonised plants may lead

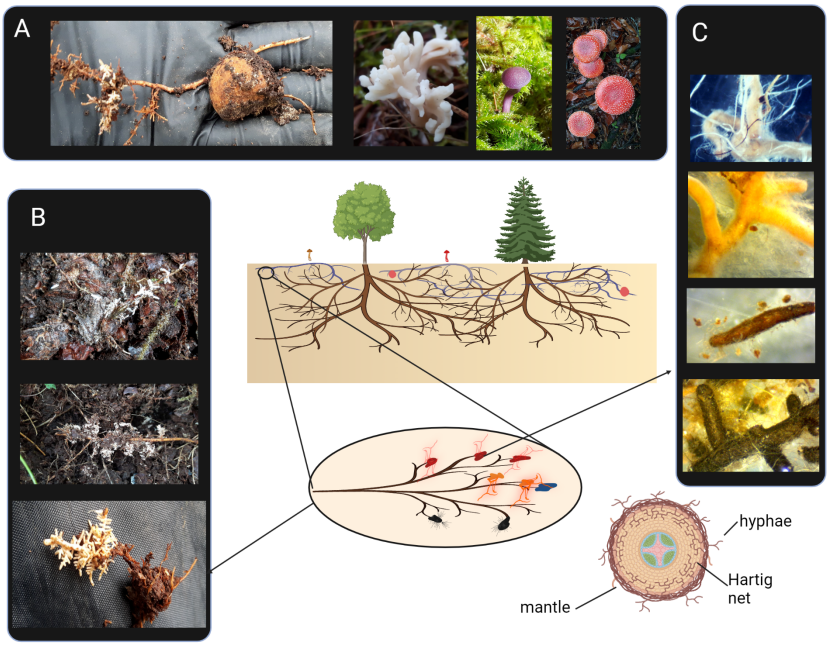


Figure 3.1: Ectomycorrhizal fungi mainly associate with trees and other woody plant. They form a sheath around the root tips often visible to the naked eye (see plate B). The root morphology is often altered, and the mantle formed around the tip can can be colourful (see plate C). Hyphae can extend long distances through the soil. EMF form above and below ground fruiting bodies (See plate A). The EMF penetrates between the cell walls of the root cortex where the pattern of penetrating hyphae is referred to as a Hartig net.

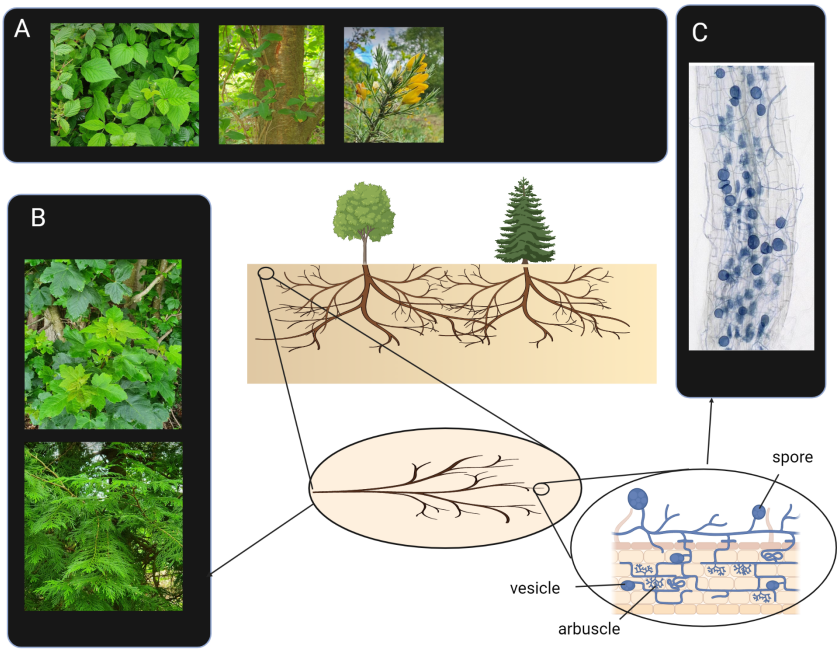


Figure 3.2: Arbuscular mycorrhizal fungi associate with trees, woody shrubs and most herbaceous plants (See plates A and B). The root appears unchanged and colonisation cannot be seen with the naked eye. The fungi form small spore within the soil and penetrate into cells forming an arbuscule which is the site of nutrient exchange. Vesicles are also formed within the roots and act as nutrient storage organs (See plate C).

to an incorrect conclusion of NM status.

Finally, much modern research is based on molecular analysis of root material, in which case, unless microscopic analysis is also carried out, physical features which define mycorrhizas will not be observed, and therefore molecular analysis alone strictly only gives evidence of AMF or EMF in roots, and not of mycorrhizal symbiosis.

The issues outlined above become less important as more consistent, repeated empirical data becomes available. Some data may confirm root structures, whilst others may demonstrate growth benefits. However, currently, data is often lacking and it is therefore advisable to be wary of assignments of type where evidence is sparse.

In this work, we aim to provide a focused resource which summarises the latest information on the mycorrhizal type of British woody plants using field-based data. In addition, we summarise the number of sources for individual plant species in order to highlight areas where caution may be required and where future study would be useful. We also highlight plant species for which data is sparse in relation to their cover and further, summarise a set of plants for which data is lacking, but which form an important part of the UK landscape due to their high cover, and therefore suggest the most important areas for future work. Finally, we use this data to explore the mycorrhizal type of British landscapes.

## 3.3 Methods

Our approach was to use the FungalRoot database (Soudzilovskaia *et al.*, 2020) as a starting point. We scrutinised all citations and did not include papers which could not be easily accessed, for example through Google Scholar or via a university subscription. This is not intended as any comment on the quality of the work, but because we wanted to make it as straightforward as possible for any work cited here to be available to others for scrutiny. We also do not include work involving seedlings or glass house experiments. In addition, we sought more evidence where research was scarce.

We have not attempted a detailed critique of the methods used, although in our discussion we highlight papers where authors do not specify their selection criteria (see appendix). Rather, we seek to summarise and review as much modern empirical data as is currently available. The papers we reference may use molecular or microscopic techniques or both. Therefore, strictly, the assignment of type here could imply that mycorrhizal colonisation was observed, or that mycorrhizal fungi were detected in roots through molecular analysis. We also summarise how many pieces of data were used for each allocation. Despite the large number of entries in FungalRoot and the additional work we sourced, there were still several important plant species for which data was weak. We have, in general, assumed type is

conserved within genus.

We have restricted our sources for assignment of type to research carried out in the field specific to the species. This excludes work which may offer some additional context. We therefore provide two values which readers can use to assess the confidence of our allocation. Firstly, we list the number of field studies we found for the specific plant species (num field studies). Secondly, we scored our assignments based on the number of entries in FungalRoot since 1990 which agree with our assignment, for all plants within the same genera (confidence score). For example, we found no work looking at the mycorrhizal type of *Sambucus racemosa* (num field studies = 0). In other words, we find no work studying this plant in natural habitats that is also easily accessible via usual search engines. However, we assigned AM type based on other members of the genus. Consulting FungalRoot, we find 14 pieces of work on *Sambucus* spp. since 1990 (confidence score 14). By quantifying these two values (number of field studies, confidence score) we aim to highlight two points. Firstly, how many plant species in the UK have not been studied in the field. This is important because we know that for some genera, type is not conserved, and moreover, it is possible that as more data becomes available, we may find more species for which type is not conserved (Bueno *et al.*, 2018, 2019b). Secondly, in many cases sufficient data is not available, and some extrapolation of type may be a useful interim measure. Taxonomic extrapolation is only advised for the genus level (Bueno *et al.*, 2021), and therefore we only use the sum of genus level data for this confidence score rather than family level.

To make the assignment of mycorrhizal type transparent, we include a detailed discussion of all papers reviewed. This allows readers to understand how we have determined the mycorrhizal type, the breadth, or dearth, of data and allows straightforward critique of those decisions.

In a small number of cases, some research finds AMF colonisation whilst other work finds none, suggesting FM status. We have allocated these as AM type, since if there is any colonisation, will be by AMF. However, it will be the case that colonisation rates for these plants can be low or fluctuating. A few plants do not form mycorrhizal associations and are therefore strictly NM. This differs from the situation above where a plant may show low levels of colonisation, in that the normal state of the plant is to remain uncolonised.

To generate a list of British trees and woody shrubs we used Plantatt (Hill *et al.*, 2004). Plantatt lists attributes of all UK plant species, including natives, archaeophytes and neophytes and supplies additional traits such as broad habitat, Ellenberg values and ultimate height. Ellenberg values classify plant species according to their niche along an environmental gradient. Ellenberg values exist for moisture tolerance, preferred pH, soil fertility, salt tolerance and shade tolerance. A plant with a low Ellenberg L, for example, will tend to be more shade tolerant than one with a high

Ellenberg L. We use these additional traits to explore patterns of mycorrhizal type within the landscape, with a particular focus on woodlands.

## 3.4 Results and discussion

We sought to allocate mycorrhizal type to 190 plant species defined as woody plants in Plantatt. Most UK woody plants are AM type (62%), with 20% being EM type and 7% are ericoid, which includes heathland species such as heather (*Erica* spp.). The percentages of each mycorrhizal type for UK woody plants is shown in figure 3.3. We highlight eight species which were allocated as potentially facultatively mycorrhizal, detailed in table 3.2. For a full list of species see table B.1 in the appendix. We found that for more than half the UK species there was little or no empirical data according to our criteria. Figure 3.4 summarises the distribution for the number of field studies found for UK woody plants.

When we ignored taxonomic conservation of type and glasshouse experiments we found 125 species, 66% of UK woody plants, were lacking in data, that is, we found 1 or no recent field studies. For many of these species, the assumptions of conservation of type within genus may indeed be robust. For example, although we found no recent field work for *Potentilla fruticosa*, there are 76 other pieces of work for different members of the genus which find AM type. However, as Bueno *et al.* (2019a) point out, *Pulsatilla patens* may be EM type when other members of the genus have so far been found to be AM type (Hoeksema *et al.*, 2018). Similarly, there is some evidence that *Crataegus monogyna* may host EMF despite other members of Rosaceae being AM type (Boeraeve *et al.*, 2018). If we relax our criteria and assume type is conserved within genus, then we reduce the number to nineteen species for which data is sparse, see table 3.1.

If mycorrhizal type assignments are to be used for modeling ecosystem functioning, then plants with greater cover are likely to be more important since they have a higher probability of occurring in the ecosystems being studied. *Buxus sempervirens*, for example, although native and a common horticultural plant, has limited range outside gardens. Therefore, in deciding where to focus future work, cover of the species with sparse data is important. Column two of table 3.1 shows the cover in hectads (10km x 10km) for species with sparse data. Willows (*Salix* spp.) are notable as both lacking in data, and having high cover in the landscape.

### 3.4.1 Facultatively mycorrhizal plants

*Atriplex portulacoides* and *Suaeda vera* are coastal plants found in salt marshes. Although AMF do colonise plants in these habitats (Carvalho *et al.*, 2004), the AMF species may be limited and levels of colonisation vary between species, with some showing little or no colonisation (Carvalho *et al.*, 2001) and soil sodium levels

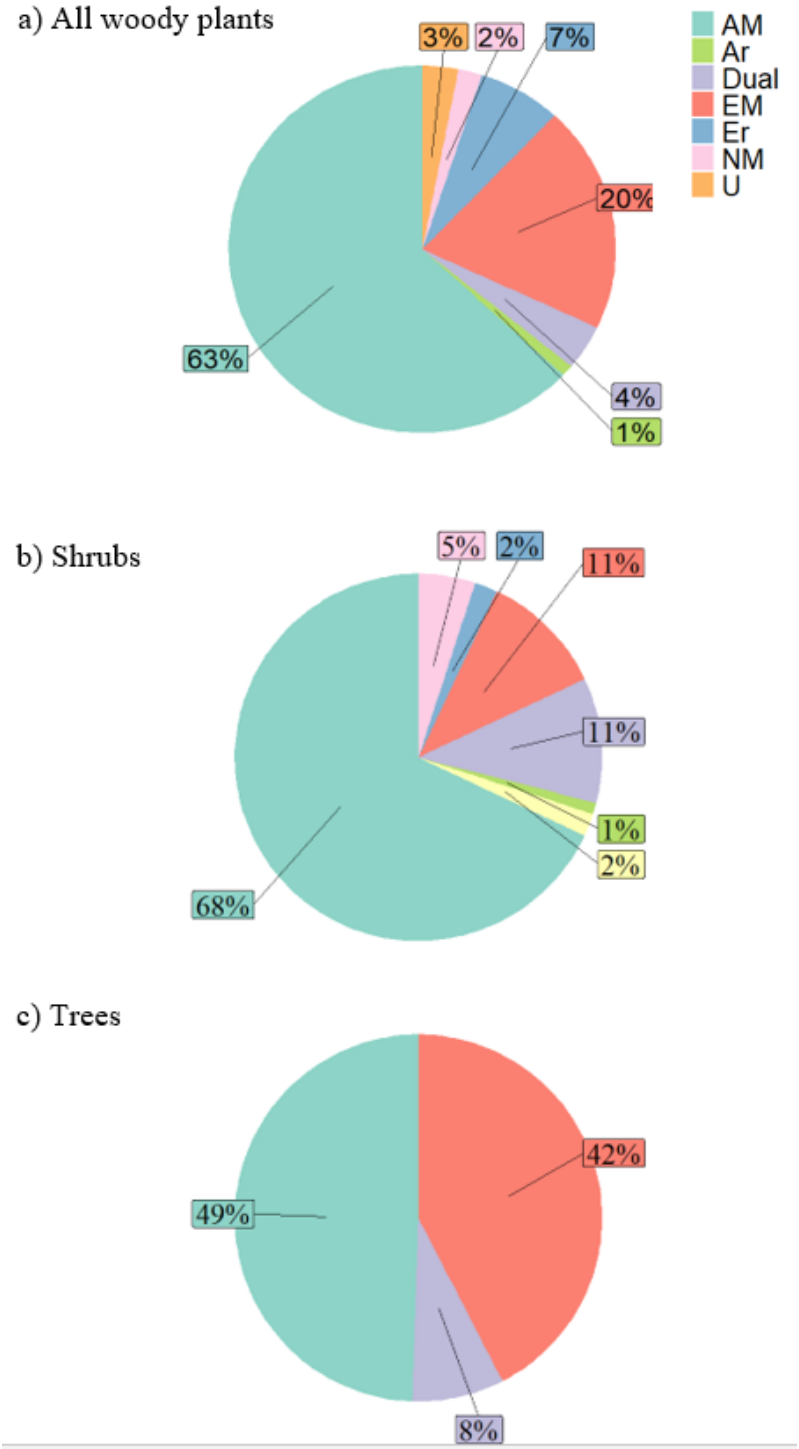


Figure 3.3: Proportion of mycorrhizal types of UK woody plants. The plots show the proportion of plants for each mycorrhizal type in relation to the total number of UK woody plants a) All woody plants, b)Shrubs only, which here are defined as woody plants with height $\leq$ 8m. The majority of shrubs are AM type but also include ericoid, EM and arbutoid species. c) Trees are defined as woody plants of height $>$ 8m.

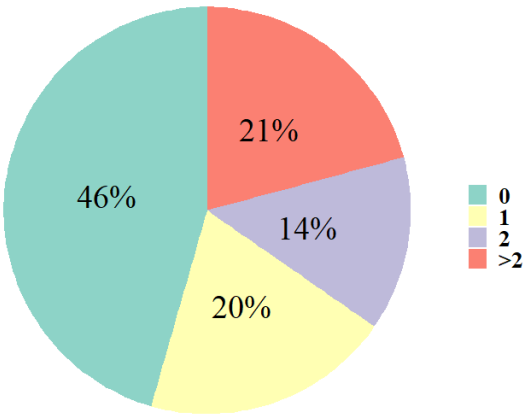


Figure 3.4: Number of field studies found for each species. The coloured sections denote the number of field studies found on which the assignment of types was based. The green section indicates that no field studies were found for 46% of the species under consideration. For a fifth of species, only 1 study was found (the yellow segment). We found one or no piece of field work for for more than half of UK woody plants

Table 3.1: Species for which data is sparse. The first column shows the species and the second the cover in hectads (10km x 10km squares) for that species as listed in Plantatt (Hill *et al.*, 2004), the final column is the assigned mycorrhizal type. (AM = arbuscular mycorrhizal, EM = ectomycorrhizal, U = unknown, we were not able to assign type). For these species, we found one or less field studies and two or less pieces of work on other members of the same genus. In many cases only one family member is lacking in data, with Salicaceae and Fabaceae being notable exceptions. This is particularly interesting as mycorrhizal type is not conserved within either of these genera and therefore empirical data at species level is vital.

| Species | Cover(hectads) | Type |
|---|---|---|
| Acaena novae-zelandiae | 82 | AM |
| Buxus sempervirens | 2 | U |
| Colutea arborescens | 166 | U |
| Fuchsia magellanica | 367 | AM |
| Laburnum anagyroides | 1119 | U |
| Lavatera arborea | 188 | AM |
| Leycesteria formosa | 418 | U |
| Lupinus arboreus | 341 | NM |
| Mahonia aquifolium | 991 | AM |
| Mespilus germanica | 98 | AM |
| Salix arbuscula | 48 | U |
| Salix lanata | 15 | EM |
| Salix lapponum | 101 | EM |
| Salix myrsinifolia | 276 | U |
| Salix myrsinites | 78 | EM |
| Salix purpurea | 1189 | AM |
| Salix viminalis | 2194 | EM |
| Taxus baccata | 1881 | AM |

Table 3.2: Species for which may be facultatively mycorrhizal. Some work definitively demonstrates fluctuating levels of colonisation in *Sambus nigra*, similar studies on the other species listed would be beneficial. Full discussion for each species can be found in the appendix

| Species | Comment |
|---|---|
| *Sambucus nigra* | Fluctuating levels of colonisation have been demonstrated |
| *Sambucus racemosa* | |
| *Atriplex portulacoides* | Low and fluctuating levels of colonisation found |
| *Suaeda vera* | Low and fluctuating levels of colonisation found |
| *Laurus nobilis* | Other members of the genus show low levels of colonisation. Limited work for this species |
| *Lavatera arborea* | Uncolonised plants reported |
| *Rhamnus cathartica* | Some reports show no or low colonisation for members of this genus, although Akhmetzhanova (2012) show 13 of 15 *Rhamnus* spp., to be AM type |
| *Buddleja davidii* | Although an early record states no colonisation (Harley and Harley, 1987), there is strong evidence of AM colonisation for this plant (Dickie *et al.*, 2007), but more work would be useful. |

has been found to negatively correlate with AMF colonisation rates (Wang *et al.*, 2021). However, there are some reports of AMF colonisation (Akhmetzhanova *et al.*, 2012). In addition, *Atriplex nummularia* collected in the field in South Australia have been found to have colonisation rates which varied greatly between plants collected from the same location, (Asghari *et al.*, 2005), and even low levels of colonisation have been found to result in positive growth responses (Asghari *et al.*, 2005; Plenchette & Duponnois, 2005). This suggests that these plants may be FM. As with *A. portulacoides*, colonisation levels seem to vary for *Suaeda vera* with both high and low colonisation reported (Sengupta & Chaudhuri, 1990; Wang *et al.*, 2004; Chaudhry *et al.*, 2005; Sonjak *et al.*, 2009; Chaudhry *et al.*, 2009). Half the entries in FungalRoot for this genus suggest a lack of colonisation. Agwa & Abdel-Fattah (2002) find no colonisation in *S. vera* sampled from the Mediterranean coast of Egypt. However, since colonisation levels appear to fluctuate in this genus, this one study may be insufficient to allocate mycorrhizal status as NM. We found very little work for *Laurus nobilis* (Maremmani *et al.*, 2003) and although Lauraceae tend to be AM type (Soudzilovskaia *et al.*, 2020), there are several studies which fail to find colonisation in members of this genus (Weimin *et al.*, 1994; Cooke & Lefor, 1998; Brundrett, 2009). No work was found for *Lavatera arborea* and both mycorrhizal and non-mycorrhizal plants are reported for *Lavatera* spp (Koske *et al.*, 1992; Allsopp & Stock, 1993; Nobis *et al.*, 2015). There are various reports on the mycorrhizal type for *Rhamnus* spp. (Weimin *et al.*, 1994; Kovács & Bagi, 2001;

Çakan & Karataş, 2006; Akhmetzhanova *et al.*, 2012). *Sambucus* spp. a common understory shrub, appear to demonstrate fluctuating colonisation rates. Brundrett & Kendrick (1987) noticed that *Sambucus pubens* was well colonised by AMF in the spring, but most senesced by the autumn while.Malloch & Malloch (1982) find a third of this same *Sambucus* species sampled colonised.

### 3.4.2 Non-mycorrhizal plants

The only plants found to have non-mycorrhizal status here are *Myrica gale*, *Carpobrotus edulis* and *Lupinus arboreus*. *Myrica gale* produces cluster roots as a mechanism for nutrient uptake and plants of this type generally do not associate with mycorrhizal fungi (Lambers & Teste, 2013). Two studies of *Carpobrotus edulis* in Australia and South Africa, both would indicate that the plant is not mycorrhizal in its native habitats (Logan et al., 1989, Allsopp and Stock, 1993), although data is sparse. *Lupinus arboreus* has been shown to resist colonisation in greenhouse experiments (Oba *et al.*, 2001)

### 3.4.3 No assignments of type made

For six species (*Buxus sempervirens, Colutea arborescens, Laburnum anagyroides, Leycesteria formosa, Salix arbuscula, S. myrsinifolia* ) we did not assign type since no field data was found and either no data was available for the genus on which to make an estimate, or, for two willow species, mycorrhizal type is not conserved within genus.

### 3.4.4 *Salix spp.*

Data was extremely sparse for willows (*Salix* spp.). Willows are considered dual (van der Heijden, 2001; Teste *et al.*, 2019), that is, they can host both AMF and EMF, as with other members of the Salicaceae such as poplars (*Populus* spp.), (Teste *et al.*, 2009). Therefore, field studies which look for both types of colonisation are particularly important, and lacking, for this genus. In our review we found little evidence of dual status for UK native willows, with the majority of the UK species being allocated as EM. However, this allocation is generally based on two or fewer studies and is therefore not robust. We allocated *S. purpurea* as AM, based on one piece of data, but note that Akhmetzhanova *et al.* (2012) state EM type for this willow. We assigned *S. repens* as dual based on three pieces of field work and glasshouse experiments demonstrating positive growth responses for low levels of AMF colonisation. Other authors have collected large amounts of data on some willow species, for example *S. caprea* and *S. phylicifolia*. These are shown in FungalRoot as unpublished data of EM type, but the authors specifically state that only EM colonisation was explored.

### 3.4.5 Patterns of mycorrhizal type in the landscape - focus on woodlands

Mycorrhizal type is not distributed evenly throughout the landscape. As figure 3.5 shows, different habitats are dominated by plants of different mycorrhizal type. Woodland woody plants include a large number of AM and EM type plants; hedgerows, however, are dominated by AM woody shrubs. This is important in terms of habitat fragmentation, since it implies that hedgerows might not provide a means of dispersal of EMF inoculum throughout the landscape. Mycorrhizal fungal spores are dispersed by insects, small mammals and wind. In the case of EMF, sporocarps are designed for wind dispersal, although dispersal distances may not be large (Galante *et al.*, 2011). It has been shown that EMF spore richness is halved 1km from forests (Peay *et al.*, 2010) and that some species are better dispersers than others (Peay *et al.*, 2012). Tree seedlings in heathland have been shown to have limited EMF colonisation compared to nearby woodlands (Collier & Bidartondo, 2009). This suggests that actively encouraging EMF type trees within linear landscape features could be positive for connectivity. Coastal and waterside habitats feature many dual plants as this is where you would find poplar (*Populus* spp.) and alder (*Alnus* spp.). Heathland, bog and fen and montane habitats have a large proportion of ericoid mycorrhizal plant cover, such as heather (*Erica* spp., *Calluna vulgaris*) and bilberry (*Vaccinium* spp).

Temperate woodlands are known to be dominated by an over-story of EM type plants (Read & Perez-Moreno, 2003), since many temperate tree species are EM type, such as beech (*Fagus sylvatica*), oak (*Quercus robur, Q. petraea*) or birch (*Betula pendula*). Figure 3.5, however, shows that there is a high cover of AM type woody plants in UK woodlands. In order to explore this further, we looked at how mycorrhizal type in woodlands was shared between the canopy and the under-story. Figure 3.6 breaks down the cover into 10m height groups. This demonstrates that the cover of AM type woody plants in woodlands is concentrated in the under-story, with the majority of over-story cover being made up of EM type plants. Note that over a third of the AM cover of trees in the 20m to 30m height category is made up of ash (*Fraxinus excelsior*), which is currently in decline due to the invasive emerald ash borer (*Agrilus planipennis*) and Chalara ash dieback (*Hymenoscyphus fraxinus*) Because trees making up the tallest height categories are EM type, as woodlands mature, AM plant cover will reduce, unless the AM under-story plants are shade tolerant. Note that, apart from *Thuja plicata*, Plantatt may not account fully for some tall, and potentially later successional, AM tree types. The tallest trees occurring in Plantatt are the EM types *Pseudotsuga mensiesii* and *Picea sitchensis*. The non-native AM type conifers *Sequoia sempervirens* and *Sequoiadendron giganticum* are also found in the UK. However they are not common (2000 records shown in NBN Atlas, (NBNatlas, 2022).

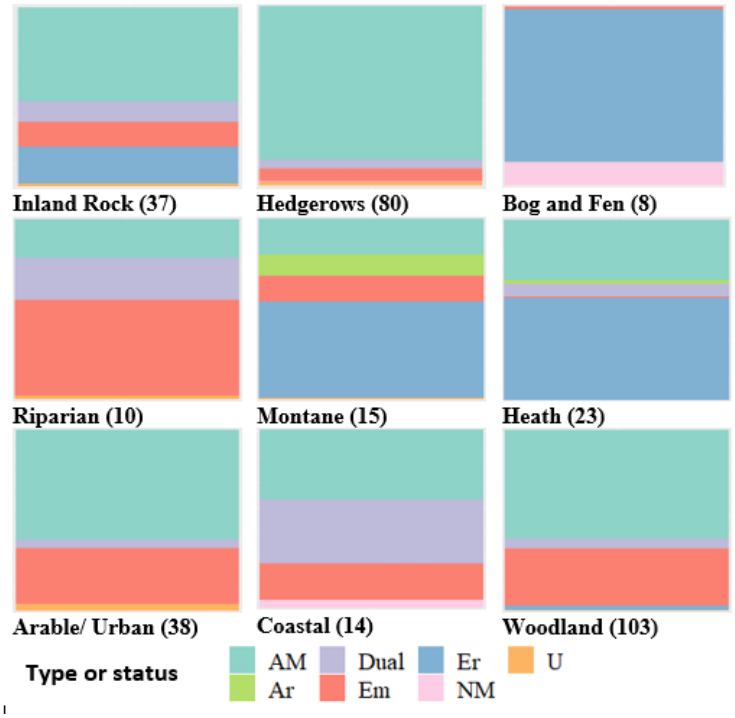


Figure 3.5: Proportions of different mycorrhizal type plants if different habitats by cover (hectatds). The habitats are derived from the broad habitat codes found in Plantatt (Hill *et al.*, 2004). Some plants may occur in more than one habitat and are included in both. The numbers after the habitat name refer to the number of species linked with that habitat

Figure 3.7 shows the under-storey (height <=10m) by Ellenberg L value. The species richness of shade tolerant AM woody plants is less than half that of more light demanding species, with the most shade tolerant being only the ericoid shrub *Gaultheria shallon*, which may partially explain its successful invasion of some woodlands. Therefore, as woodlands mature, in the absence of canopy opening disturbances, the richness of AM woody shrubs will decrease, shifting the ecosystem to one in which EM type plants are more common. This sort of disturbance is exemplified by the 1987 storm across the south east of England after which species richness of broad leaved woodlands was estimated to have increased by 32% (Smart *et al.*, 2014).

Since the species richness of the herbaceous under-story has been shown to correlate with the proportion of AM type woody plants (Veresoglou *et al.*, 2017; Guy *et al.*, 2022), this shift to an EM dominant over-story could contribute to a loss in woodland diversity. Woodland management interventions, such as selective felling or coppicing in order to introduce more light and hence encourage the more light demanding AM type species, and selective planting of AM type trees as replacements for ash could mitigate this loss.

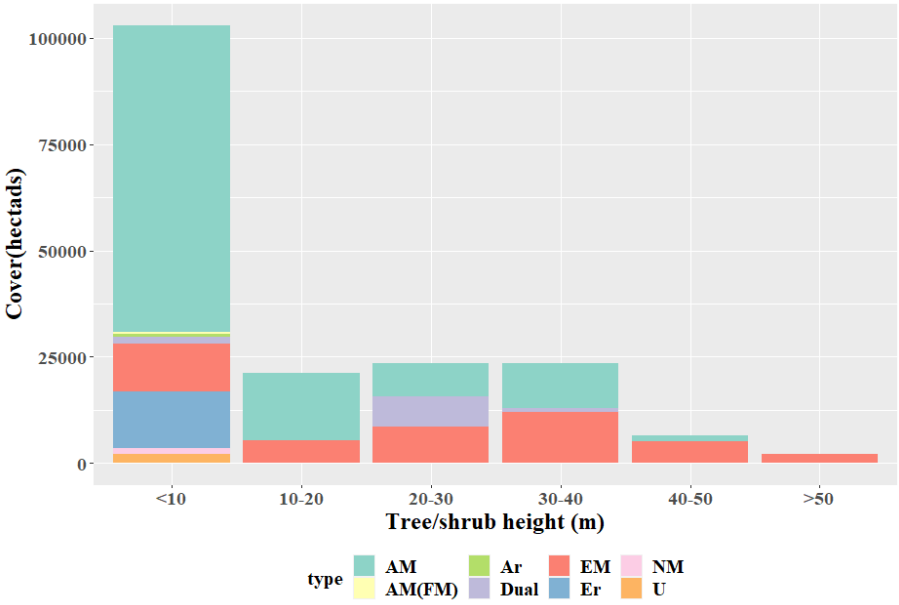


Figure 3.6: Cover of woodland plants at different canopy heights. Heights were taken from Plantatt (Hill *et al.*, 2004) in which details for the derivation of heights is given, but briefly, they represent the heights to which the trees may reach, not heights recorded in the landscape. The stacked bars show the proportions of cover for different mycorrhizal type for different heights. The majority of AM type plants are in the under-story (height less than 10m).

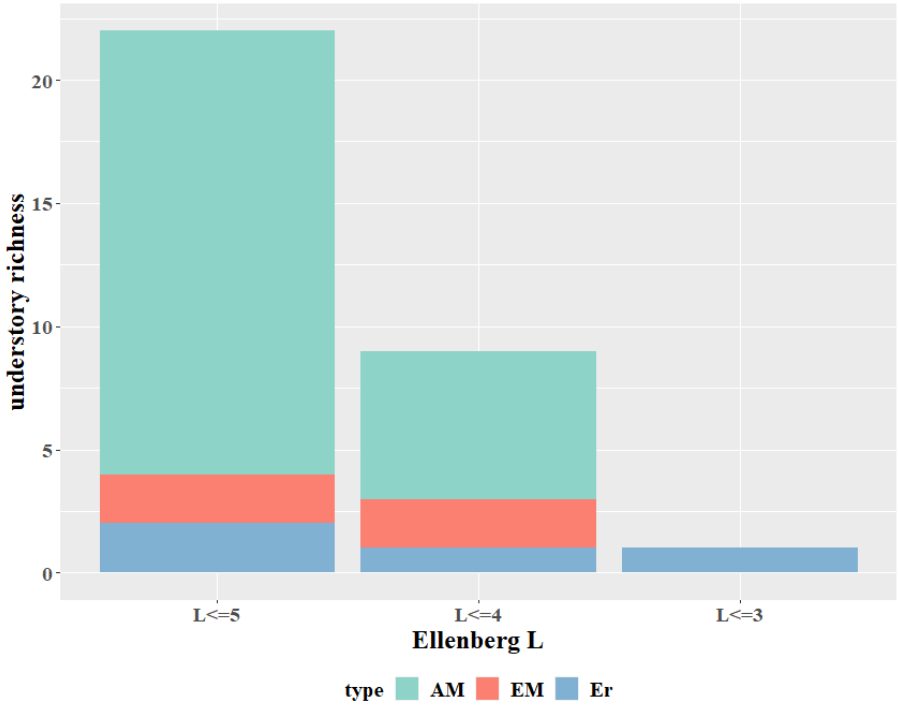


Figure 3.7: Species richness of under-story (ultimate height $< 10$m) woody plants at different Ellenberg L values. The stacked bars show the proportions of mycorrhizal type for light values. A low Ellenberg L value is given to more shade tolerant species

## 3.5 Conclusions

Using two or more pieces of field work we allocated mycorrhizal type to 65 out of 190 UK woody plant species. We found no pieces of work which matched our criteria for 87 (46%) British woody plant species. Relaxing our criteria to assume mycorrhizal type is conserved with genus reduces the number of species with sparse data to eighteen, (10%). Based on cover (hectads), we recommend more empirical data is required for *Salix* spp., especially work in which AM and EM colonisation is examined coincidentally in the same plant. We recommend that the mycorrhizal type of willows assigned here is treated with some caution until more data is acquired. We highlight eight species which are potentially FM and require further data to confirm that state. We found data that suggests that only two UK woody species are NM.

By exploring mycorrhizal type within different habitats, we demonstrated that the majority of hedgerow cover is made up of AM type plants, which may have implications for the dispersal of EM inoculum given the highly fragmented nature of most British forests and woodlands. We also show that, whilst the majority of woodland cover of woody plants is made up of AM type species, these form the under-story species, with a reduced number of AM species being found in the canopy or being shade tolerant. This implies a shift from AM to EM type plants as woodlands mature, with potential consequences for woodland diversity. In addition, a significant proportion of AM over-storey currently consists of ash (*Fraxinus excelsior*) which will likely be lost, and therefore replanting schemes may need to consider the inclusion of a suitable AM type later successional tree, such as *Acer pseudoplatanus*, in order to maintain a higher proportion of AM type woody plants in mature woodlands.

# Chapter 4

# Mycorrhizal type of woody plants influences understory species richness in British broad leaved woodlands

New Phytologist

Research

# Mycorrhizal type of woody plants influences understory species richness in British broadleaved woodlands

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## Summary

- Mature temperate woodlands are commonly dominated by ectomycorrhizal trees, whereas understory plants predominantly form arbuscular mycorrhizal associations. Due to differences in plant–fungus compatibility between canopy and ground layer vegetation the 'mycorrhizal mediation hypothesis' predicts that herbaceous plant establishment may be limited by a lack of suitable mycorrhizal fungal inoculum.
- We examined plant species data for 103 woodlands across Great Britain recorded in 1971 and in 2000 to test whether herbaceous plant species richness was related to the proportion of arbuscular mycorrhizal woody plants. We compared the effect of mycorrhizal type with other important drivers of woodland plant species richness.
- We found a positive effect of the relative abundance of arbuscular mycorrhizal woody plants on herbaceous plant species richness. The size of the observed effect was smaller than that of pH. Moreover, the effect persisted over time, despite many woodlands undergoing marked successional change and increased understorey shading.
- This work supports the mycorrhizal mediation hypothesis in British woodlands and suggests that increased abundance of arbuscular mycorrhizal woody plants is associated with greater understory plant species richness.

## 4.1 Introduction

Temperate forests and woodlands are significant repositories of biodiversity, which is currently in decline due to human activity and climate change. Within woodlands, a greater diversity of tree species has been shown to buffer the negative effects of drought (Gazol & Camarero, 2016; Aussenac *et al.*, 2019) and increase tree productivity (Fichtner *et al.*, 2017), whilst plant diversity more broadly is an essential component of ecosystem health, productivity, and resilience to multiple types of disturbance (Loreau *et al.*, 2001; Loreau & Hector, 2001; Hector *et al.*, 1999; van der Plas, 2019). Hence a major goal in ecology is to understand the mechanisms that determine the diversity and composition of plant communities and their stability over time.

Plant community structure and diversity are linked by complex plant-soil feedback (PSF) mechanisms (Bever *et al.*, 1997; van der Heijden *et al.*, 1998; van der Heijden & Horton, 2009) that influence both above and below-ground assemblages of organisms (Hartnett & Wilson, 2002; Wardle *et al.*, 2004; Johnson *et al.*, 2005; van der Putten *et al.*, 2013; Kardol *et al.*, 2015; Ke *et al.*, 2015; Tedersoo *et al.*, 2020). For example, tree species which acquire pathogenic root fungi at a greater rate than mutualistic fungi are more likely to suffer from negative density dependence (Chen *et al.*, 2019). An important trait that influences PSFs is the mycorrhizal type of plants (Moora, 2014).

Mycorrhizas are an ancient association between plants and mycorrhizal fungi (Lutzoni *et al.*, 2018; Strullu-Derrien *et al.*, 2018) in which host plants provide the fungi with photosynthate in exchange for access to soil nutrients and other services (van der Heijden *et al.*, 2015). An increasing number of different mycorrhizal types are now recognised (Kariman *et al.*, 2018) but temperate trees and other woody plants are typically either ectomycorrhizal (EM) hosts (colonised by EM fungi), or arbuscular mycorrhizal (AM) hosts (colonised by AM fungi), although some plant species can associate with both (dual-mycorrhizal; Teste *et al.* (2019)). Many of these fungi can colonise multiple individual plants, forming a common mycorrhizal network (CMN) (Leake *et al.*, 2004; Simard & Durall, 2004; Simard *et al.*, 2012) capable of transferring nutrients and defence signals, and potentially providing other benefits such as drought tolerance (Finlay & Read, 1986; Gorzelak *et al.*, 2015; Gehring *et al.*, 2017; Pickles *et al.*, 2017) . These CMNs mediate plant community structure (Booth, 2004; McQuire, 2007; Simard, 2009) by increasing seedling survival through access to compatible mycelium growing on adjacent conspecific or heterospecific host trees (Simard *et al.*, 1997, 2012; Selosse *et al.*, 2006; McQuire, 2007; van der Heijden & Horton, 2009; Liang *et al.*, 2020).

A growing body of evidence indicates that mycorrhizal associations and CMNs tend to produce different responses in their hosts, with EM associations commonly generating positive to neutral PSFs and AM associations neutral to negative PSFs

(van der Heijden & Horton, 2009; Bennett *et al.*, 2017; Teste *et al.*, 2017; Kadowaki *et al.*, 2018). Haskins & Gehring (2005) demonstrated that pinyon pine (Pinus edulis) seedlings, an EM host, were less colonised by EM fungi when growing near AM type trees. In other words, the sources of EM fungal inoculum were limited in soil in which AM type hosts were dominant. Similarly, the successful colonisation of AM-dominated grasslands (Thiet & Boerner, 2007) and heath (Collier & Bidartondo, 2009) by EM type seedlings may be limited by low levels of EM fungal inoculum. Weber *et al.* (2005) demonstrated that AM type trees (western redcedar; Thuja plicata) could be excluded from forest areas dominated by EM type trees due to a lack of AM fungal inoculum. Kovacic *et al.* (1984) found a lack of AM fungal inoculum under live EM type pines (ponderosa pine; Pinus ponderosa) compared to dead pines and observed a higher abundance of AM type understorey plants beneath dead rather than live pines. Similarly,Barni & Siniscalco (2000) found that AM fungal inoculum was reduced in sites which had succeeded to predominantly EM type trees. Notably, they found that AM fungal inoculum was still high in the early stages of succession when AM type trees were abundant. Hence the establishment of plants can be influenced by the supply of compatible AM or EM fungal inoculum, with the potential to affect range dynamics of trees over sufficient timescales (Pither *et al.*, 2018).

The "mycorrhizal mediation hypothesis" proposed by Veresoglou2017 suggests that AM associated woody plants will facilitate the establishment, and therefore potentially increase the species richness, of AM associated herbaceous plants. The relationship between AM trees and herbaceous plant species richness was first explored over thirty years ago. Newman & Reddell (1988) found a strong positive correlation between the relative abundance of AM trees and the species richness of herbaceous plants in a study of plant communities in the Great Smoky Mountains, Tennessee (USA). More recently, Veresoglou2017 speculated that this positive relationship was due to mycorrhizal mediation through inoculum supply. Using data from 77 mixed broadleaf woodlands in north-western Germany, they found that the richness and abundance of herbaceous plants was positively correlated with the abundance of AM trees and woody shrubs. In a subset of the same woodlands, increasing AM tree cover (%) was not found to be related to the diversity of AMF soil communities (Grünfeld *et al.*, 2021), but did appear to influence the colonisation rate of understory AM plant species Grunfeld2019a. This suggests that mycorrhizal mediation between trees and herbaceous plants may be an important driver of herbaceous plant species richness in woodlands.

Most broadleaved woodlands in Great Britain are dominated by EM rather than AM hosts (see figure C.1 in appendix C1). According to the National Forest Inventory (NFI), only a quarter of broad-leaved tree cover in 2011 was provided by AM hosts (National Forest Inventory, 2012). Much of this (44%) was formed by

ash (Fraxinus excelsior), which is currently in decline due to the invasive emerald ash borer (Agrilus planipennis) and Chalara ash dieback (Hymenoscyphus fraxinus). Therefore, if herbaceous plant species richness is related to AM tree cover, this may have important consequences for woodland ecology and management in Britain.

Here we provide the first comprehensive examination of the mycorrhizal mediation hypothesis in British woodlands using the Bunce survey (Wood *et al.*, 2015). The Bunce survey has so far taken place twice, in 1971 and again in 2000. The data set has been thoroughly reviewed elsewhere (Kirby *et al.*, 2005; Smart *et al.*, 2014) and much is already known about the change in British woodlands over the past 70 years Hopkins2007,Keith2009. For example, a lack of management has tended to change the structure of woodland into more mature high forest with an increase in tree basal area, a reduction in the number of trees with small stems, and a homogenisation of plant species. In other words, a smaller number of shade-loving species have increased, and a much larger number of light-loving species have been lost, with increases in understory trees such as holly ( *Ilex aquifolium* ) which shades out the understory and can lead to a reduction in diversity. A noticeable exception to this trend was the 1987 storm in the southeast of the UK, which introduced open areas and resulted in increased herbaceous plant species richness (Smart *et al.*, 2014). However, overall, understorey species richness decreased between the surveys. Soil pH has also tended to increase between the surveys in line with national trends due to reduced sulphur deposition (Kirk *et al.*, 2010). No changes were found in mean soil organic matter, although some sites saw significant increases and fewer plots showed low levels of soil organic matter.

In general, climatic gradients are known to influence plant richness, with a general trend towards increased species richness in the south of the UK driven by energy related variables Albuquerque2011 although these are likely to be modified by local topographic effects (O'Brien, 2000). Whilst edaphic data is part of the Bunce survey and is highly precise to the plots at 200 m2 resolution, climate data would be at a much lower resolution of 5 km grid squares and would not therefore be able to explain any of the within-site, between-plot variation in the response, possibly leading to a fatally under-powered analysis. Moreover, soil pH and carbon content integrate many distal effects including climate, topography, elevation and pollutant deposition. Therefore, whilst climate would be a coarse estimate which may be the same for several sites, edaphic variables are precisely aligned with the plant data. We therefore asked whether the abundance of AM trees and shrubs influenced herbaceous species richness, and whether this effect was detectable over the 29 years between surveys and across a uniquely large-scale but fine-resolution sample of both less shaded and more shaded, mature woodlands. Additionally, we examined the additive and interactive effects of shading, soil organic matter, and soil pH along with the relative abundance of AM trees and shrubs to compare the effect size of

the latter to these other important predictors. Our primary aim was to determine whether the relative abundance of AM trees and shrubs in British woodlands has a positive effect on herbaceous plant species richness, using long-term, large-scale monitoring data gathered across Great Britain in 1971 and again in 2001. If true, this would provide an important and independent confirmation of previous work on the mycorrhizal mediation hypothesis (Veresoglou *et al.*, 2017; Grünfeld *et al.*, 2020). Furthermore, our approach would enable a novel exploration of the strength of any mycorrhizal mediation between trees and herbaceous plants in woodlands as a driver of herbaceous plant species richness, relative to other important factors, and whether any such effect persists over time.

## 4.2 Materials and Methods

### 4.2.1 Sources of data

We used the Bunce survey (Wood *et al.*, 2015), which recorded all plant species in 16 randomly placed square permanent 200 m2 plots in each of 103 broadleaved semi-natural woodlands across Great Britain. The Bunce survey is the only survey of its type in the UK, incorporating long-term monitoring of multiple woodlands across England, Scotland, and Wales. The survey includes both biotic and abiotic data for 103 woodlands, originally selected as being a representative subset of over 2000 sites and are therefore considered to be characteristic of native British woodlands. The herbaceous plant richness comes from the recording of ground cover, which lists all plant species and seedlings of trees and shrubs (defined as individuals below 25 cm in height). Tree species in each plot are recorded separately with diameter at breast height (DBH) and number of stems in each DBH class. Additionally, soil organic matter content (SOM) and soil pH (pH) were measured from a 5 x 15cm soil sample removed from the centre of each plot. The assignment of mycorrhizal type of the trees and woody shrubs was made after thorough scrutiny of sources cited in available trait databases (Akhmetzhanova *et al.*, 2012; Soudzilovskaia *et al.*, 2020) together with additional sources where data was scarce or lacking for British species. The methods of assignment of type are discussed in chapter 3, the table of mycorrhizal types of British woody plants can be found in table B.1 in appendix B2 and a detailed discussion of the assignment of type to each plant appears in appendix B1.

### 4.2.2 Statistical analysis

The species richness ($\alpha$-diversity) for the ground flora was calculated for each 200 m2 plot. The total woody canopy cover was calculated as the sum over the DBH classes multiplied by the number of stems in that class. This value was used as

a proxy for shading (shading: cm). The subset of AM type trees and shrubs was extracted and the AM overstory cover was calculated. The relative abundance of AM type trees and shrubs (RelAm: dimensionless ratio) was then the AM cover divided by the total cover. In order to estimate the inoculum potential of each plot, we use the correlation between shoot and root biomass. In a meta-analysis of over 786 studies a positive linear correlation was found between shoot and root biomass in woodlands (Mokany *et al.*, 2006). Since most fine roots will be colonised by mycorrhizal fungi, a larger tree implies a larger fine root mass and a higher fungal colonisation. Hence a larger tree has greater inoculum potential, that is, it is more likely to have more fungal material to produce propagules, whether those propagules are mycelium or spore containing bodies. In addition, larger trees are generally expected to produce more carbon through photosynthesis and will be more capable of supporting larger mycorrhizal fungal communities. Therefore, based on these aboveground-belowground links, we considered that the aboveground measure of DBH x stem count was a reasonable way of estimating the belowground contribution of AM type trees to AM fungal inoculum potential. One large tree may have the same inoculum potential as several smaller shrubs but will also increase shading and therefore may have a negative impact on plant richness, hence our inclusion of the shading term. Soil pH (pH: negative log of H+ activity) and soil organic matter content (SOM: % dry matter lost on ignition) were also extracted from the data.

To account for the nested structure of the data of plots within sites, mixed effects models were used (Gelman & Hill, 2007; Zuur *et al.*, 2009; Schielzeth & Nakagawa, 2013). The 'lme4' package in R (Bates *et al.*, 2015) was used for generalized linear mixed effects model (GLMM) analysis. We did not seek here to create a model which incorporated all known effects since prediction of woodland responses to a wider range of plausible drivers was not our goal. Instead, our approach was to use the mixed model to generate effect sizes to allow comparison of a limited set of important drivers.

Site was fitted as a random intercept with pH, shading, SOM, RelAm, and year as fixed effects. In a small number of cases (5 sites in year 1 and 6 sites in year 2) there were strong correlations between explanatory variables when examined within groups (Spearman correlation $> |0.80|$). These sites were removed from the analysis, which reduced the between variable correlations to $|0.26|$ (See figure C.2). Since the response variable was a count data, a Poisson distribution and log link was initially used. However, this resulted in an over-dispersed model (Gelman & Hill, 2007; Bolker *et al.*, 2009) and therefore a negative binomial model was used after confirming the lack of over-dispersion. All possible combinations of variables of a global model were explored including interaction terms between i) year and pH, shading, and RelAm and ii) shading and RelAm. The dredge function of the 'MuMIn' package (Barton, 2020) was used to extract the model with the lowest Akaike

Information Criteria (AIC). We used the 'performance' package (Lüdecke *et al.*, 2021) to extract the conditional and marginal $R_2$ (Nakagawa & Schielzeth, 2013,?) of the lowest AIC model. Regression coefficients were standardised and used to assess variable importance (Nakagawa & Cuthill, 2007; Gelman, 2008; Schielzeth, 2010). Significant variables were those whose regression parameters had 95% confidence intervals that did not include zero. We also considered the square of pH since plant species richness has been shown to have a unimodal response to soil pH in woodlands (Gould & Walker, 1999; Peppler-Lisbach & Kleyer, 2009), and see figure C.3 in appendix C3. Holly (Ilex aquifolium) and hawthorn (*Crataegus monogyna*) are two of the most common tree species found in British woodlands, and assignment of mycorrhizal type was considered weak for these plants. We therefore conducted a sensitivity analysis where the mycorrhizal type was varied between AM and EM for hawthorn and AM and unknown for holly. In each instance the modelling process described above was repeated.

Spatial autocorrelation was tested by examining spline correlograms of the fitted model Pearson residuals (Ba *et al.*, 1991; Zuur *et al.*, 2009). The residuals showed no increase in spatial autocorrelation at short distances, see figure C.4 in appendix C4.

## 4.3 Results

### 4.3.1 Effect of canopy mycorrhizal type on understory herbaceous species richness

The AIC "best" model (lowest AIC) of understory herb $\alpha$-diversity contained pH, RelAm, SOM, year and the interaction between year and pH (Figure 1); details of all six models with $\Delta\text{AIC} < 2$ are provided in C.5 in appendix C5. The relative abundance of AM trees and shrubs (RelAm) had a significant positive effect on understory herb species richness as did the soil pH whereas the effect due to SOM was not significant. The effect of year, and the interaction between year and pH were both negative and significant. In the set of six candidate models (models within $\Delta\text{AIC} < 2$ of the AIC "best" model) the same effects and interaction term were always significant, and neither SOM nor shading were statistically significant. Using the transformation of pH to pH2 did not decrease AIC or increase $R_2$ in any model. The effect size for the random effect of site was larger than that of the explanatory variables ($3.24 \pm 0.042$) indicating that unknown site-specific factors explained variation in understorey richness in addition to the fixed effects. Sensitivity analyses revealed that the models were not sensitive to changes in the mycorrhizal status of *Ilex aquifolium* or *Crataegus monogyna*, and changes in the mycorrhizal type did not alter the variable set in the model with the lowest AIC (see table C.6 in appendix

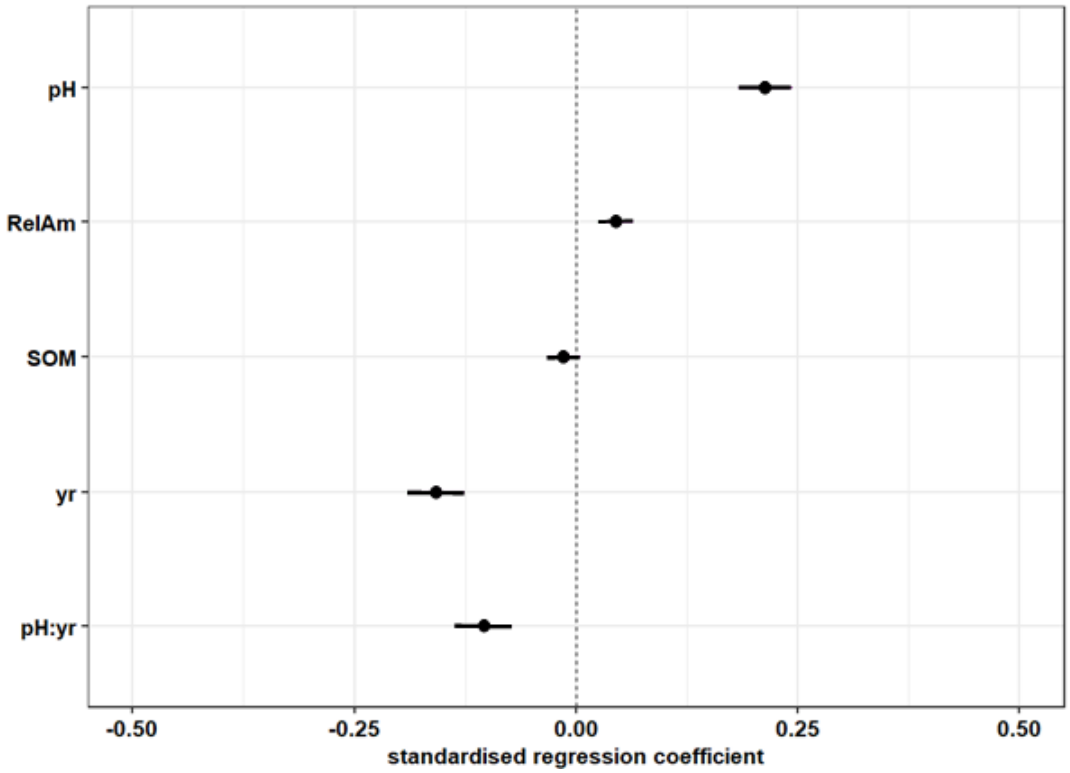


Figure 4.1: Effect of key explanatory factors on the understory richness of herbaceous plants using standardised regression coefficients with 95% confidence intervals. The explanatory variables were centred such that a 1 standard deviation (sd) change in the variable results in the effect size change in the response (sd pH = 1.22, sd RelAm = 0.34). The relative abundance of AM trees and shrubs (RelAm) has a significant positive effect, as does soil pH (pH). The effect of soil organic matter (SOM) is not significant. The effect of year (yr), and the interaction between year and pH (pH:yr) are negative. Conditional $R^2$ 0.492, marginal $R^2$ 0.114.

C6).

## 4.4 Discussion

We asked whether the proportion of AM type trees and woody shrubs affects herbaceous plant species richness in British broadleaved woodlands. We found that, in agreement with the mycorrhizal mediation hypothesis (Veresoglou *et al.*, 2017), the proportion of AM type trees and shrubs had a positive effect on herbaceous plant species richness. An important outcome of our approach was that it revealed the temporal consistency of this positive effect over the three decades between surveys. We were also able to show, for the first time, how the strength of the effect due to woody plant mycorrhizal type compared to other factors known to influence herbaceous plant species richness.

In this analysis we considered shading, soil organic matter content, and soil pH. Soil pH had the strongest effect, and a negative interaction with year. The positive effect of soil pH is seen because woodlands tend to have a pH below that which is

optimal for plant richness. In the Bunce woodlands for example, the median soil pH is around pH 4.75, whereas maximum plant richness is seen at between pH 5.5 and 6.0. Therefore, any increase in soil pH would correlate with an increase in plant richness. The negative interaction with year indicates that the positive effect of soil pH decreased across the two years of the survey. This is probably due to increased shading in the woodlands. As woodland shading increases, the plant community shifts to more shade tolerant species. Therefore, any richness response to soil pH occurs within this limited community. This could have the effect of suppressing herbaceous plants response to pH variability.

The significant negative effect of year on understory plant species richness was expected and reflects the general reduction in herbaceous richness seen in these woodlands between the two Bunce survey years. In our models, the interaction terms between the relative abundance of AM type trees and soil pH, year, or shading, were either not contained in or were not significant in any models within $\Delta$AIC $<$ 2, demonstrating that the RelAm effect was robust despite the successional changes in these woodlands. In previous explorations of the mycorrhizal mediation hypothesis, a significant positive correlation between AM type woody plants and herbaceous species was found in mature ancient woodlands (Veresoglou *et al.*, 2017). We found that the effect of the mycorrhizal type of the canopy was more important than shading, in both mature and less mature woodlands suggesting that mycorrhizal mediation affects understory richness of both shaded and unshaded plant communities.

In our study we quantified the amount of AM type woody plants in order to link above ground plant abundance with below ground AM fungal inoculum potential, and thereby build on previous work to address the mycorrhizal mediation hypothesis (Veresoglou *et al.*, 2017). However, if the abundance of woody plants does indeed imply greater abundance of AM fungi, it may in turn imply greater AM fungal richness, assuming richness is positively correlated with abundance. AM plant diversity has been shown to correlate with AM fungal diversity through differential resource acquisition (van der Heijden *et al.*, 1998; Kernaghan, 2005). For example, grassland plant richness has been found to be positively correlated with AM fungal richness(Hiiesalu *et al.*, 2014). We note that this effect is not consistent, other studies have found no relationship between above ground plant richness and AM fungal diversity (Öpik *et al.*, 2008) or found a significant relationship with plant diversity rather than plant richness (Mirzaei & Moradi, 2017). Alternatively, a negative relationship between plant richness and mycorrhization has been found in temperate grasslands (Leon *et al.*, 2022). Plant responses to AM fungi vary, so any plant diversity response may depend on soil conditions and AM fungal species identity (Vogelsang *et al.*, 2006). We cannot ascertain in this work whether the PSF mechanism driving understory richness is inoculum potential through AM fungal

abundance or niche exploitation through AM fungal richness, therefore future work could examine empirical data on both AM fungal richness and inoculum potential and explore correlations between AM woody plant cover and AM fungal richness. Interestingly, Mirzaei & Moradi (2017) measured spore density and found a significant relationship between AM fungal spore density and plant diversity, but not plant richness. In that work, plant richness was only significantly correlated with AM fungal colonisation, which could also be considered as a measure of inoculum potential.

In our analysis, the effect size for the random intercept was greater than that of any of the fixed effects, suggesting that historical legacies and local landscape scale effects are likely to have been important drivers of woodland plant species richness. The importance of these factors in British woodlands has been demonstrated by several authors. For example, (Peterken & Game, 1984) found that ancient woodlands in Lincolnshire, in the east of England, had greater understorey species richness, as did newer woods connected to ancient woodlands, whereas isolated newer woodlands were species poor. Woodland species tend to have poor dispersal characteristics (Kimberley *et al.*, 2014), implying that, unless habitat connectivity is high, these species may fail to colonise new woodlands. Similarly, (Petit *et al.*, 2004) found that woodland plant species richness in England is correlated with woodland patch size, however, the authors also found that this effect did not persist for upland woods, where light and soil pH were more important. Other factors known to influence woodland plant richness include disturbance (Boch *et al.*, 2013) or windthrow (Smart *et al.*, 2014), nitrogen deposition, shading, habitat heterogeneity, and land use around the woodland (Dzwonko & Loster, 1988; Petit *et al.*, 2004; Brudvig *et al.*, 2009). All these factors will increase the between site variance and contribute to the effect size of the random intercept.

The positive effect of the proportion of AM trees and shrubs on herb species richness supports previous findings (Newman & Reddell, 1988; Veresoglou *et al.*, 2017) and further strengthens the case for the mycorrhizal mediation hypothesis by demonstrating this effect for the first time across over 100 British woodlands and 30 years. The importance of identifying tree mycorrhizal type as a driver of understory species richness is that, unlike edaphic or climatic properties for example, it is a factor over which we can exert control in woodland management. If management plans depend on natural regeneration, then in a fragmented landscape, and in woodlands dominated by a low diversity of EM type trees, AM type trees could be excluded with a negative effect on herbaceous plant species richness. This work suggests that the relatively straightforward practice of interplanting AM type hosts may be a tractable approach to increase woodland biodiversity. Or, when planning to plant new woodlands, the proportion of AM type and EM type hosts could be considered from the perspective of their influence on understory plant biodiversity.

## 4.5 Conclusion

We have shown that herb species richness is positively associated with the proportion of AM type trees and shrubs in British woodlands, and for the first time we show that this effect is robust across thirty years of woodland succession. Our study builds on and expands previous work which has shown a link between overstorey mycorrhizal type and understorey species richness (Newman & Reddell, 1988; Veresoglou *et al.*, 2017; Grünfeld *et al.*, 2020). Finally, our results demonstrate that the effect due to AM type trees and shrubs is significant when compared with other important drivers of woodland plant species richness across a large-scale national gradient of climate, soil and woodland type.

# Chapter 5

# Ectomycorrhizal fungal communities of Oak (*Quercus robur, Q.petraea*) in British woodlands

## 5.1 Abstract

Ectomycorrhizal fungi (EMF) are fundamental to ecosystem functioning, they provide trees with the majority of their nutrient needs and increase drought tolerance and resistance to pathogens and herbivory. Detailed DNA-sequence based landscape scale data is sparse but essential for understanding EMF communities. Oak form the largest single species component to standing volume in British broad-leaved woodlands and therefore knowledge of their EMF community is of particular interest. We analysed EMF communities of oak in 19 woodlands across Britain and find 125 species. We have collated a review of current literature of EMF found with *Q. robur* and *Q. petraea* to generate an up to date reference for EMF associates of oak. We also considered the impact of environmental variables on EMF communities. We found that EMF richness increased with increasing soil K, but was not correlated with other environmental or edaphic variables tested. Atmospheric pollutants were the most important factor influencing EMF communities and drivers may differ between rare and common species. Indicator species were identified for edaphic and climatic properties of the sites, as well as soil types and atmospheric pollutants. We also suggest that these two native oak species could support as many as 250 EMF species.

## 5.2 Introduction

Woodlands supply an important range of ecosystem services, such as pollution removal (Beckett *et al.*, 1998; Tallis *et al.*, 2011), carbon sequestration (Brainard *et al.*, 2009; Ostle *et al.*, 2009) and flood reduction (Burton *et al.*, 2018; Murphy *et al.*, 2021). UK wood product exports were valued at £1.7 billion in 2019 (Stagg & Ward, 2020) with the value of total ecosystem services provided by woodlands in the UK valued at £3.3 billion in 2017 (ONS, 2020). Further, wooded areas provide cultural benefits including improvements to mental health (Coles & Bussey, 2000; O'Brien, 2005; Acton & Carter, 2016; Cook, 2020). Woodlands in the UK experience multiple stresses and many show signs of degradation, such as reductions in understory richness (Kirby *et al.*, 2005), loss in biodiversity of woodland taxa (Amar *et al.*, 2006; Keith *et al.*, 2009; Brereton *et al.*, 2019; Ellis & Coppins, 2019) and increases in tree disease (Freer-Smith & Webber, 2017). Parts of the UK are very densely populated which also puts woodlands under great pressure from recreational use, which can damage ground flora and soils due to trampling and soil compaction (Littlemore & Barker, 2001; Summers *et al.*, 2007; Kozlowski, 2008) and disturb bird populations, (Fernández-Juricic, 2000; Banks & Bryant, 2007). Soil compaction also reduces fine root tip abundance and ectomycorrhizal colonisation rates and abundance (Amaranthus *et al.*, 1996; Hartmann *et al.*, 2014) with potential health implications for the host trees. Declines in other woodland species have also been found, such as lichens, (Ellis & Coppins, 2019). Other factors are also indicated in declines in woodland diversity such as lack of woodland management and habitat fragmentation Dzwonko & Loster (1988); Honnay *et al.* (1999); Brudvig *et al.* (2009); Boch *et al.* (2013); Petit *et al.* (2004); Thiele *et al.* (2018). As woodlands become degraded, their ability to provide ecosystem services is reduced (Aerts & Honnay, 2011; Policelli *et al.*, 2020).

EMF are drivers of plant population dynamics such as plant diversity, (van der Heijden *et al.*, 1998; Tedersoo *et al.*, 2020) and hence an essential component of woodland ecosystem function (Wagg *et al.*, 2014). They play a fundamental role in tree health providing plants with nutrients protecting against drought, pathogens and insect herbivory (Song *et al.*, 2010; Pickles *et al.*, 2017; Chen *et al.*, 2019). With EMF community assemblages likely to be in flux due to anthropogenic influences such as climate change and nitrogen deposition and with currently observed deterioration in tree health (Mitchell *et al.*, 2019) and nutrition (Jonard *et al.*, 2015), gathering data on EMF communities and what shapes them is of paramount importance.

### 5.2.1 Oaks in British woodlands

The UK has a limited tree flora; the Global Tree Portal (BGCI, 2021) lists 85 native species, less than France, 126, Germany, 99 or Italy, 156. Numbers of trees species

in the UK would be similar to Scandinavian countries (Norway 54, Sweden, 52) if not for the large number of rare endemics in the *Sorbus* complex which make up nearly half the UK species. Woodland area in the UK in 2020 was estimated to be 3.2 million hectares, 13% of the area of the UK, with that area being split roughly equally between broad-leaved trees and conifers, where conifer generally means non-native conifer plantations, (Stagg & Ward, 2020). The only native conifers are *Pinus sylvestris* and *Juniper communis*. Woodlands in the UK have been influenced by human activity for thousands of years and therefore old growth, undisturbed forests, such as those found in the western United States, do not exist. Perhaps the most undisturbed woodland habitats in the UK are the remnants of Atlantic hazel forests on the west coast of Ireland and Scotland and the fragments of Caledonian pine forest in Scotland (Coppins & Coppins, 2012). Some woodlands in the UK are referred to as 'ancient'. This means that there is a record of continuous wooded cover since 1750 (in Scotland) or since 1600 (England, Northern Ireland and Wales). These dates were chosen as this is when records for these woodlands began, but woodlands themselves may be much older. Although these ancient fragments have seen continuous wooded cover for several hundred years at least, this does not mean that they are undisturbed, pristine habitats. Woodlands in the UK have a long and complex history of management (Rotherham, 2022). They have been managed and worked by mankind for hundreds of years. For example, trees have been coppiced and certain species favoured over others for their usefulness (Rackham, 2008), such as oaks for charcoal. Hence in the UK, there is no comparison for woodland communities between undisturbed and anthropogenically altered woodlands, since all of British woodlands are affected by humans in some way, either in the past or currently. Therefore, there is no baseline for an undisturbed EMF community of oak against which other woodlands can be compared. Instead, data from a range of woodlands across an environmental and geographic gradient is required.

Britain has two native oak species, *Quercus robur* and *Q. petraea*, although several other species are now established, such as the evergreen neophyte *Q. ilex*, the Turkey oak *Q. cerris* and *Q. rubra* is also becoming more common. Oak comprises 16% of woodland cover and 28% of standing volume of wood in broad-leaved woodlands, see figure 5.1, making oaks one of the most common tree species by cover, second only to birch, but being the most important species in terms of growing volume. The two native species are often undifferentiated in mycorrhizal fungal studies (Courty *et al.*, 2008; Leski *et al.*, 2009; Suz *et al.*, 2014). The two species interbreed freely and often co-occur with a range of intermediate morphologies. Although careful study of leaf shape does allow species separation (Kremer *et al.*, 2002), and there are clearly morphological differences, as well as differences in wood anatomy (Feuillat *et al.*, 1997) and metabolites (Buche *et al.*, 2021), Kelleher *et al.* (2005) found that in Irish populations although species could be morphologically separated,

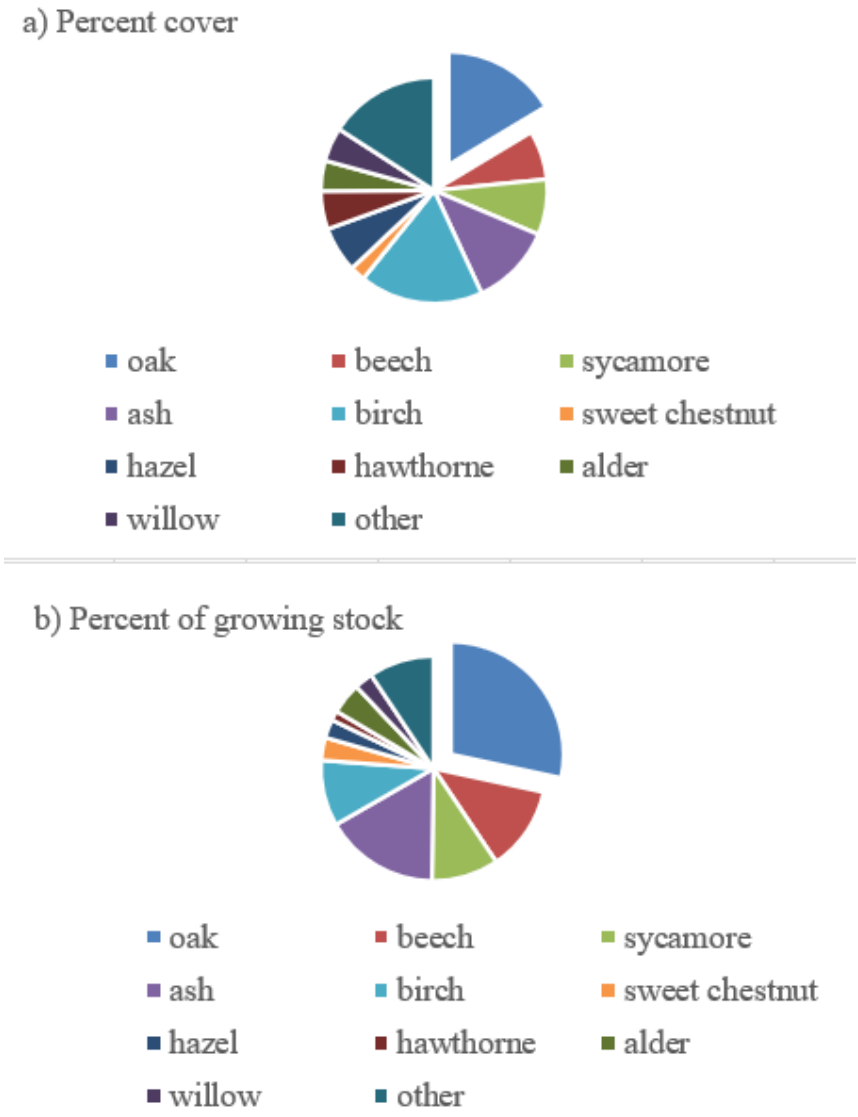


Figure 5.1: a) Percentage cover and b) percentage volume of growing stock as a fraction of total broad-leaved species in the UK.(Stagg & Ward, 2020). Oaks are second only to birch in percent cover, but form the largest fraction of growing stock by volume in broad-leaved woodlands in the UK.

molecular variation was stronger between populations than it was between species.

Oaks support high diversity across many taxonomic groups. In Kennedy & Southwood (1984) summary of biological records of insects and mites from nearly twenty different sources collected between 1932 and 1981 on twelve different tree species, oaks host one of the highest numbers of insects, matched only by willows, see figure 5.2. In a recent review 2300 species were found to associate with oak (Mitchell *et al.*, 2019), comprising birds, bryophytes, fungi, invertebrates, lichens and mammals; nearly 14% of these are obligate oak species demonstrating the ecological importance as well as the economic value of oaks in our landscape.

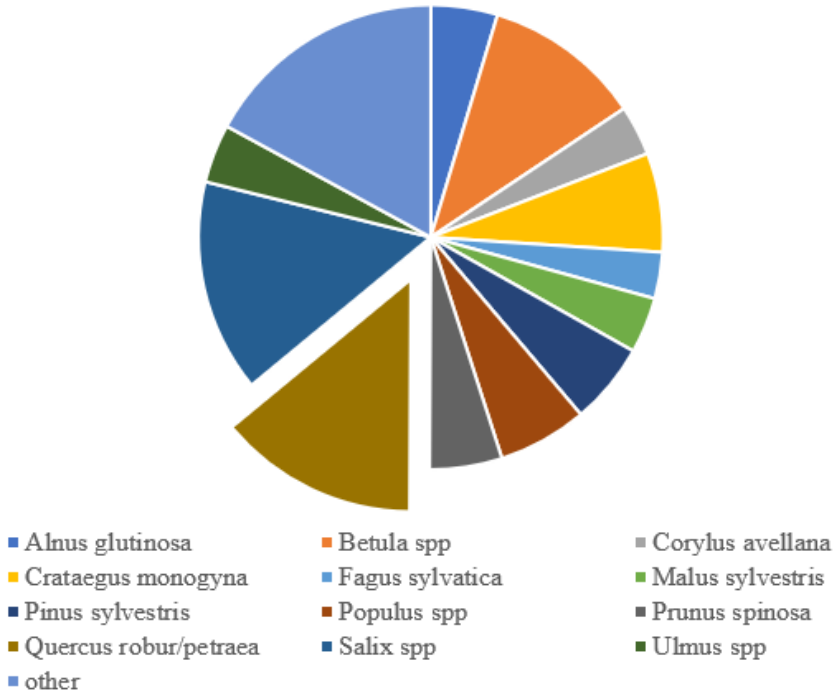


Figure 5.2: Summary of numbers of insect species associating with British trees,taken from (Kennedy & Southwood, 1984). The authors comment that host tree abundance is the best predictor of associated insect species richness. Oaks are one of the UKs most abundant broad-leaved tree which partially explains their importance as a host.

### 5.2.2 Review of EMF of oak

Two initial studies of the EMF of oak were sporocarp records taken in Sweden and Germany. Tyler (1992) counted sporocarps in pure stands in 175 forests in Sweden in order to compare the affinity for different fungi with different tree species, for both EMF and saprotrophic fungi, finding some degree of host preference in around half the species recorded. Keizer & Arnolds (1994) studied roadside verges planted with oaks of different ages in order to assess succession and comment that, unlike forest trees which tend to have a peak in richness, the number of EMF species for roadside trees continued to increase into old age. Obviously these studies will not account for the full community of EMF as they will not include hypogeous species, however, they still contribute to the body of knowledge concerning oak associating EMF.

Several pieces of work consider the issue of the communities of declining oaks. Mosca *et al.* (2007) ask whether reduction in competition by thinning can alleviate stress in *Q. robur* in Italy. The authors found, contrary to their expectations, that thinning did not increase the abundance of ectomycorrhizal or healthy root tips and speculate that one reason for this could be due to local conditions whereby the thinning exacerbated anoxic conditions in a damp soil. Bzdyk *et al.* (2019) studied declining oaks in Poland and found that mycorrhizal root tip abundance is negatively correlated with declining tree health, whilst EMF diversity was highest

in trees least affected by decline. In a recent study in England, diversity was not associated with decline, but the frequency of healthy root tips was (Barsoum *et al.*, 2021).

EMF communities have been shown to demonstrate temporal and vertical variation. Courty *et al.* (2008)'s study in France examined changes in EMF community at different depths within the soil and and different times through the year. The authors found that the relative abundance of species changed with both time and sampling depth. Different species with the same genus can also show vertical partitioning. *Rhizopogon vesiculous* has been found to be more common in mineral soil horizons than *R. vinicolor* (Beiler *et al.*, 2012). Other studies have also found a differentiation of species by soil horizon (Dickie *et al.*, 2002; Rosling *et al.*, 2003; Baier *et al.*, 2006), this is to be expected due to niche differentiation; the soils at different depths will display different chemical properties, although competition between species with a similar niche could play a part (Mujic *et al.*, 2016). Additionally, Courty *et al.* (2008) found changes in the abundance of species with time and certain species were only detected at certain times, for instance, *Clavulina* spp., were only found in the winter. These results have importance implications for sampled species richness. In order to approach real richness values, repeated sampling of the same locations throughout the year is required, as well as sampling at different soil depths. In addition, when comparing sites sampled at different times, conclusions might be drawn about differences in community which are potentially due to temporal effects.

Trocha *et al.* (2012) compared native EMF of *Q. robur* with non-native *Q. rubra* and found the EMF community of the native oak to be higher than that of the non-native. In contrast, the authors found the community of native *Pinus sylvestris* to be lower than a non-native pine. Schirkonyer *et al.* (2013) compare EMF diversity of five tree species in Germany. Of the five trees examined, *Fagus sylvatica* and *Q. petraea* had the highest species richness with 20 and 18 species identified respectively, while *Larix decidua* had the lowest with 14 species. Suz *et al.* (2014) conducted a large study of 22 plots across nine European oak forests. The authors found nitrogen deposition, soil pH and mean precipitation all had some influence on EMF communities, with nitrogen deposition, soil pH and root density explaining a quarter of the variance in the data. Martinová *et al.* (2016) compare oaks across an urban gradient from street trees through parks to forests. The authors found that soil pH was the most important factor influencing the EMF community and also demonstrated that the species richness of street trees was about half that of their park or forest counterparts.Molecular methods were used to determine EMF species in all the above studies.

The species found in association with oaks in the above studies and listed to species level are shown in table D.2 in the appendix to this chapter. The combined

studies show that *Lactarius quietus, Russula ochroleuca, Cenococcum geophilum, Paxillus involutus, Scleroderma citrinum, Russula nigricans, Laccaria amethystina, Thelephora terrestris* and *Tomentella sublilacina* are likely to be found with oaks, being reported in six or more of the studies. Many studies have shown that *Lactarius quietus* is found in association with many oak species, not just the two of interest to this work , but also *Q. ilex, Q. crispula, Q. suber, Q. pyrenica, Q. faginea* and *Q. dentata* (Gebhardt *et al.*, 2007; Ortega *et al.*, 2010; Toju *et al.*, 2013), and is a common sporocarp seen in oak woodlands (O'Hanlon & Harrington, 2012). The other common species are generalist EMF found in association with many other tree species (Cuvelier, 1991; Tyler, 1994; Matsuda & Hijii, 1998; Gardes & Bruns, 1996; Jonsson *et al.*, 1999b; Roy *et al.*, 2008; Blom *et al.*, 2009; Baptista *et al.*, 2010; Sarsekova *et al.*, 2020; Wilgan *et al.*, 2020; Santolamazza-Carbone *et al.*, 2021). In our review, which included sporocarp surveys as well as molecular analysis, a total of 232 taxa were reported to species level, with more than half of the species only reported in one study. The large number of rare species in each study is expected from species abundance distributions, and highlights the importance of repeated empirical studies for obtaining full community data for EMF. For instance, gaining knowledge as to which EMF are generalists and which are specialists, the importance of which was highlighted in chapter 2.

## 5.3 Drivers of EMF communitie structure and richness

There is some variability across studies as to the drivers of EMF community structure and species richness. For example, whilst soil pH is found to be significant in many studies (Suz *et al.*, 2014; Tedersoo *et al.*, 2014; Suz *et al.*, 2017; Rosinger *et al.*, 2018; van der Linde *et al.*, 2018; Defrenne *et al.*, 2019) this is not always the case (Jarvis *et al.*, 2013; Pena *et al.*, 2017). Similarly, some studies find precipitation important (Jarvis *et al.*, 2013; Defrenne *et al.*, 2019), whilst in a meta analysis of 98 sites across Europe, rainfall was not found to be significant (Rosinger *et al.*, 2018). Many studies find soil type find is significant (Suz *et al.*, 2014; Pena *et al.*, 2017; Suz *et al.*, 2017), as is location (longitude/latitude) and sampling time (Courty *et al.*, 2008). Community shifts are also reported due to liming - the addition of calcium or calcium and magnesium containing amendments to treat acidification in forest soils. Liming increases soil pH and therefore improves cation exchange capacity and hence tree health. Increases in soil pH due to liming have been shown to correlate with increases in the number of mycorrhizal root tips and also turnover in EMF communities (Erland & Söderström, 1990; Bakker *et al.*, 2000). For example, Rineau & Garbaye (2009) found ectomycorrhizas of *Russula ochroleuca* to be absent from limed plots which were dominated by *Lactarius subdulcis* and *Tomentella sublilacina*.

Woodland management and understory diversity (Pena *et al.*, 2017), anthropogenic activity (Tedersoo *et al.*, 2012), habitat connectivity (Jarvis *et al.*, 2013) and litter and humus depth (Suz *et al.*, 2017) have also been found to significantly affect EMF community composition.

Nitrogen deposition (N-dep) is associated with reduced EMF colonisation of root tips (de Witte *et al.*, 2017) and has been consistently shown to have a significant impact on EMF richness and community (Cox *et al.*, 2010; Kjøller *et al.*, 2012; Lilleskov *et al.*, 2019). However the response is not equal for all species with some showing an increase in abundance, such as *Paxillus involutus, Scleroderma citrinum, Tomentella, Tomentella sublilacina* and *Thelephora terrestris*, whilst others decrease in abundance (Brandrud, 1995; Lilleskov *et al.*, 2002).

When different tree species are used for studies, host is an important factor determining community composition (Bahram *et al.*, 2011; Pena *et al.*, 2017; van der Linde *et al.*, 2018; Rosinger *et al.*, 2018; Barsoum *et al.*, 2021).

The predictors of species richness are also variable. A unimodal response to temperature, soil pH and stand age have been reported (Tedersoo *et al.*, 2012; Rosinger *et al.*, 2018), as well as negative correlations with altitude, soil moisture and anthropogenic disturbance (Tedersoo *et al.*, 2012; Suz *et al.*, 2017). Positive correlations are reported for litter pH, soil K and soil pH (Suz *et al.*, 2014, 2017). Both negative and positive responses have been found for rainfall (Tedersoo *et al.*, 2012; Pena *et al.*, 2017).

Some of this variability may be accounted for by regional versus local effects. For instance, Bahram *et al.* (2011) found that mean annual temperature was the main driver of richness at a local scale, whereas precipitation was the main driver at regional scales. In addition, the gradients of the predictors vary across studies such that the predictors may be important only when the range is sufficiently large (Suz *et al.*, 2014). Alternatively, the affects could be confounded, such as rainfall with edaphic properties such as water-saturated soils (Tedersoo *et al.*, 2012).

Differences in modelling approaches may also play a part. For instance Glassman *et al.* (2017) demonstrated that different conclusions could be reached when using techniques such as Mantel and ADONIS tests compared with using a non-linear method, generalised dissimilarity modeling (Ferrier *et al.*, 2007). Furthermore, drivers of community turnover in some organisms have been shown to differ between common and rare species (Latombe *et al.*, 2018b; Ascensão *et al.*, 2020; Krasnov *et al.*, 2020).

Since there is concern that lack of empirical data on diversity and drivers of EMF communities inhibits the understanding of ecosystem processes (Lilleskov *et al.*, 2016; Arraiano-Castilho *et al.*, 2021; Suz *et al.*, 2021), our aim in carrying out this work was to contribute to baseline data on EMF species and drivers of EMF communities of oak. By limiting our community analysis to oaks we both gather

data on an important British species, whilst also focusing on edaphic and climatic affects on community composition and eliminating changes due to host. Only two studies have been carried out providing information regarding EMF communities of oaks in the UK, (Suz *et al.*, 2014; Barsoum *et al.*, 2021), but these sampled a smaller number of sites in England. Our survey adds to and expands this data by sampling oaks in a large number of British woodlands across a wide geographical and environmental gradient. Knowledge of the EMF communities found in mature woodlands is important as a target for future forests, especially currently as many new woodlands are planned in the UK. However, we lack sufficient baseline data as to the diversity and richness of EMF in our current woodlands. In addition, we wanted to know if there was an ancient woodland community, or indicator species associated with that habitat. Finally we asked whether we could identify key factors influencing EMF communities of oak, and whether these were consistent across rare and common species.

## 5.4 Materials and Methods

### 5.4.1 Site details

Nineteen woodland sites were selected across Britain. The location of the woods is shown in figure 5.3.

Mono-specific oak woodlands were preferentially sought, but this was not possible in all cases and about half the woodlands were mixed species. The sites were a combination of privately owned land and those managed by conservation charities such as the Woodland Trust, the National Trust or the Wildlife Trust. Appropriate permissions were obtained before accessing the sites. At most sites the oak species was *Quercus petraea* with *Q. robur* occurring at five sites. The majority of the woods (15) were classed as ancient, the youngest was planted within the last 50 years. The understory vegetation varied with the soil type and location from continuous carpets of *Vaccinium myrtillus* on acid soils to *Rubus fruticosus* and *Urtica dioica* on more fertile clay soils. The range limit of the sites was 57.05° to 50.54 ° N and -0.04° to -5.63° E. Across this geographical range maximum monthly average summer temperatures varied from approximately 20° to 28°C, whilst the minimum temperatures varied between about 6° and -4°C. The most southeasterly parts of the UK tend to be very dry and average daily rainfall in sites in the south was around 50mm. Sites on the north west coast of Scotland are much wetter with average daily rainfall closer to 150mm. Three of the sites had very heavy clay soils, (LL, LW, HP), whilst others were sandy (SP) or highly organic (WW). The fine root density in the upper soil was noticeably reduced at sites with heavier soils compared to those on lighter soils or those that had a light organic layer. Most woodlands in the UK are heavily grazed by deer, in addition, some of the sites were grazed by sheep or cattle

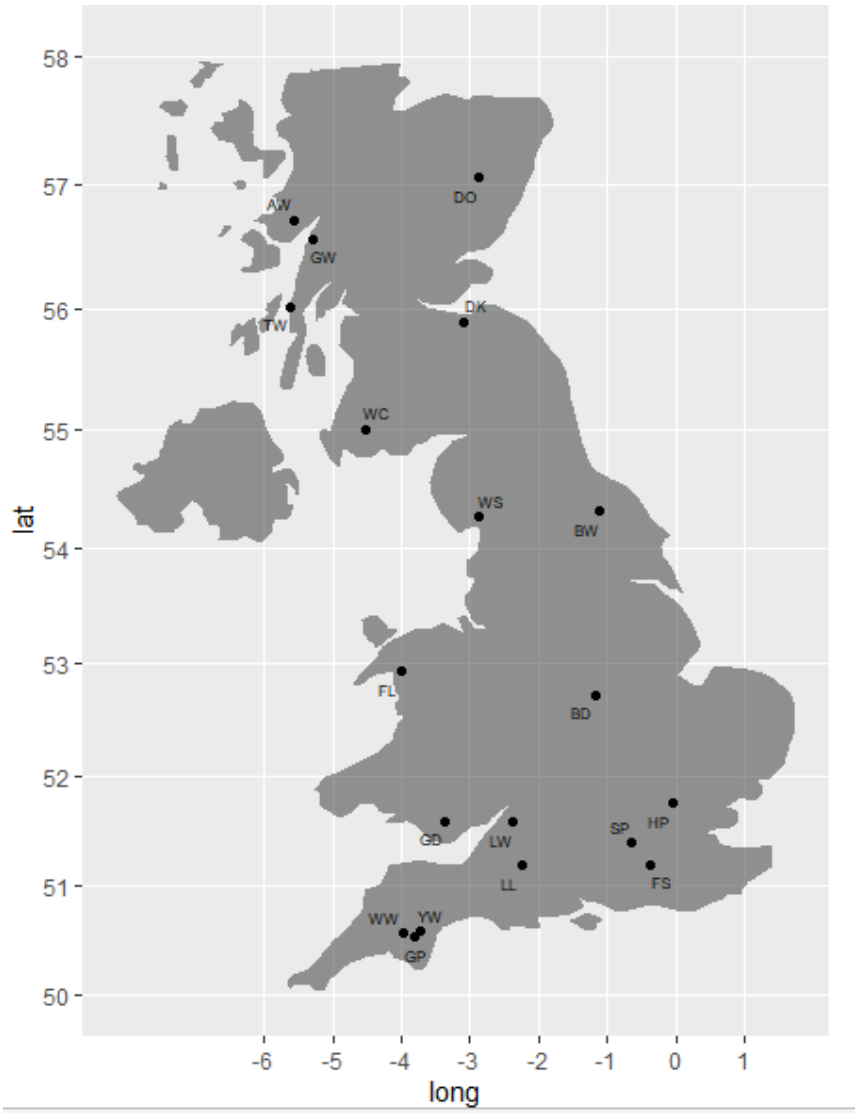


Figure 5.3: Map indicating locations of sampled woodlands, the letters indicate codes used to identify each site.

(WW, LL). A few sites were fenced and showed denser understory vegetation and lack of grazing (GD, WS). Field work was carried out between 11$^{th}$ June and 28$^{th}$ September 2019, with the more northerly woodlands sampled latest.

### 5.4.2 Site biographies

In the UK woodlands are classified according to the vegetation which is common and most abundant. Generally, this phytosociological classification follows as a result of factors such as soil type or geology (Hall *et al.*, 2004). Oak woodlands generally fall into two categories, W16 and W17. Both of these are both typified by very acidic soil which can be either very free draining or those occurring in the wetter northwest of the country and show a large amount of humus build up. This is reflected in the sites surveyed in this work. The upper quartile of soil pH in this study was pH 4.1. One site had a high pH of 5.7, but this was unusual as it was one of only 2 sites with clay soil. The sites varied between monospecific oak woods

Figure 5.4: Ariundle Oakwood in northwest Scotland.

Figure 5.5: Soil at Ariundle Oakwood in northwest Scotland: in some locations the illuvial layer was deep and a dark red brown.

to mixed, with eleven different tree species observed at Grey Park in Devon, south west England: *Fraxinus excelsior, Ulmus glabra, Fagus sylvatica, Sorbus aucuparia, Castanea sativa, Aesculus hippocastrum, Ilex aquifolium, Pinus sylvestris,Corylus avellana, Acer pseudoplatanus*. Average total daily rainfall is around 150 mm for sites in the north west, but a third of that for sites in the south east. Below are brief summaries of five sites in order to demonstrate the variety between the oak woods.

**Ariundle Woodland** is an example of Atlantic oak rain-forest, the soils are moist and precipitation is high. Referred to as ancient woodland, these woods were still shaped by human activity and demand for charcoal has contributed to a dominance of oak which was coppiced for fuel. As figure 5.4 shows, oaks are the only species over large areas of the site. The soil was a podzol with a defined organic layer and a gravelly or sandy yellow or rich red brown illuvial layer which was up to a metre deep. The ground flora consisted of deep mounds of *Rhytidiadelphus* with grasses and ferns. Although the woodland was open, with plenty of light reaching the floor, as with most sites, no evidence of oak regeneration was seen, despite the area being deer fenced.

Figure 5.6: Soils at Ariundle Oakwood in northwest Scotland: In some areas the illuvial layer was shallow and lighter in colour.

Figure 5.7: Longleat, in south west of England, younger trees surrounded by grass to the trunk.

**Longleat** was unusual in that the oaks sampled were in a parkland setting rather than woodland. Longleat is a stately home comprising large areas of farmland, working forest and landscaped parkland. Many of the oaks in the parkland are ancient trees which would have been contained within the surrounding forest before it was cleared to create landscaped parkland in the eighteenth century. The soil at Longleat is clay and tended to be compacted beneath the trees by machinery and grazing animals. In one case, grass had been cleared from the trunk and mulch applied, see figure 5.8, and the abundance of fine roots was much greater for this tree than the others sampled. For most of the trees sampled, the dense sward resulted in dense mesh of grass roots below the soil surface, in which fine tree roots were not found. Therefore, the root samples from this site, rather than being in the top organic layer, were from deeper in the soil, below the grass roots.

**Friday Street** is an area on the North Downs in the south east of England. Due to its location it is one of the warmest and driest woodlands sampled. Tree

Figure 5.8: Longleat, in south west of England. This tree had grass cleared and mulch applied. Fine roots were much more abundant compared to those with grass to the trunk.

Figure 5.9: Friday Street in south east England.

cover is mainly resitricted to oaks, Scots pine, (*Pinus sylvestris*) and birch, (*Betula pendula*). The soil is sandy and acidic with a light litter layer of oak leaves, see figure 5.10. The ground flora comprises bracken and bilberry (*Pteridium aquilinum, Vaccinium myrtillus*), see figure 5.9

**Witherslack** is a small, fifty year old Wild Life Trust plantation of oaks. The soil was very thin on shale and showed little variation across the site. The plantation included some self seeded birch and sycamore, (*Betula pendula, Acer pseudoplatanus*) as well as a couple of yew, (*Taxus baccata*) and some small holly, (*Ilex aquifolium*). Otherwise the plantation consisted entirely of oak with sparse ground flora, see figure 5.11. Fruiting bodies of *Elaphomyces muricatus* were also found on several trees at this site, see figure 5.12

Figure 5.10: Soils at Friday Street are very sandy with humus layer and litter of recalcitrant oak leaves

**Whistmans Wood** is a small oak wood on Dartmoor, in the southwest of England. At 392m it was the highest wood sampled. The soil is a shallow umbrisol around large granite boulders. Litter had accumulated around the edge of the boulders and fine roots and ectomycorrhizas could be found in these thin, litter layers, see figure 5.14. Between the boulders, pockets of wet organic soil occurred, but few fine roots were evident outside the litter layers. The trees are small and stunted. There was very little ground cover as a result of sheep grazing. The sheep roam freely into the wood from the adjacent moorland. Confirmation that grazing is the main cause of lack of undergrowth was demonstrated by an exclosure in which ground flora was abundant.

### 5.4.3 Root sampling

At each site, five trees were selected for sampling. The trees were spread across the sites and none of the sampled trees were adjacent. The mean distance between trees was 441m with a minimum distance of 14m and a maximum of 2.5km. At sites containing mixed species, the trees were additionally chosen to be distant from heterospecific neighbours and usually stands of oak occurred within these mixed woodlands such that root identity was not in doubt. Samples were taken within 2m of the trunk. This simplified sampling because fine root density was high, it reduced the probability of sampling roots from other species and, in addition, allowed roots to be traced to the trunk if there was any doubt of root identification. Loose litter was swept away and fine roots taken from the upper organic layer by gently moving the soil with a small fork and snipping roots with secateurs. In order to capture more species, roots were collected at three points around each tree located as far apart as possible, approximately every 120°. Samples were placed in bags and frozen at -18°C on site using a portable freezer. A total of 570 samples were collected (19 sites, 5 trees per site, 3 samples per tree at 2 soil depths). Material was then

Figure 5.11: Plantation of approximately fifty year old trees at Witherslack, Cumbria, north west England

Figure 5.12: Fruiting body of *Elaphomyces muricatus* and ectomycorrhizas of a different fungal species

Figure 5.13: Stunted oaks growing amongst granite boulders on Dartmoor, south west England

stored at -18°C for up to 9 months while processed. Due to the presence of fungal tree diseases (*Hymenoscyphus fraxineus, Phytophthora ramorum* and *Phytophthora kernoviae*), soil was removed from footwear and tools and both were cleaned with Virkon between sites.

### 5.4.4 Root preparation

The roots were removed from the freezer and washed over a fine sieve. The loose soil was saved and added to soil samples (see below). The roots were randomly split into smaller subsections and fine roots randomly selected from each of these groups. Root tips were cleaned under a microscope and colonised tips selected and placed in a 1.5 ml Eppendorf tube until 100 tips were collected. Whilst examining root tips, if a selection was heavily colonised by a single morphotype, another sample would be chosen, and within each selection, as many different morphotypes as possible were sought. Note that the intention behind this procedure is to maximize species richness. The tubes were then frozen at -18°C until root processing was complete. We pooled the samples from the upper soil layers for each tree so that ultimately 95 samples were sent for molecular analysis (19 sites, 5 trees in each site).

### 5.4.5 Molecular analysis of EMF

DNA extraction and sequencing was carried out by Novogene, Cambridge, UK according to Novogene protocol as follows; DNA extraction was carried out using EchoLUTION Plant DNA kit. A total amount of 200ng of DNA was used for PCR amplification with corresponding primers set to target the fungal ITS re-

Figure 5.14: Ectomycorrhizal roots mainly found in poorly decomposed litter layers

Table 5.1: Summary of woodland characteristics. Whether the wood was grazed was a subjective observation for evidence of grazing, such as lack of understory, but also dependant on observation of deer fencing. In general, all unfenced woodland in the UK will be heavily grazed by deer. Soil type was taken from the UKSO, http://mapapps2.bgs.ac.uk/ukso/home.html.

| Site code | Name | Long | Lat | Ancient | Mono-specific | Grazed | Soil type |
|---|---|---|---|---|---|---|---|
| AW | Ariundle | 56.72 | -5.55 | yes | yes | no | podzol |
| BD | Buddon Wood | 53.73 | -1.17 | yes | yes | yes | stagnosol |
| BW | Birch Wood | 54.32 | -1.13 | yes | no | yes | stagnosol |
| DK | Dalkeith | 55.90 | -3.08 | yes | no | yes | cambisol |
| DO | Dinnet | 57.05 | -2.87 | yes | yes | yes | umbrisol |
| FL | Coed Felinrhyd | 52.93 | -4.00 | yes | yes | yes | umbrisol |
| FS | Friday Street | 51.20 | -0.39 | no | no | yes | podzol |
| GD | Coed Gelli-draws | 51.59 | -3.34 | yes | no | yes | umbrisol |
| GP | Grey Park | 50.54 | -3.8 | no | no | yes | umbrisol |
| GW | Glasdrum | 56.56 | -5.28 | yes | no | no | umbrisol |
| HP | Hoddesdon Park | 51.76 | -0.41 | yes | no | no | stagnosol |
| LL | Longleat | 51.19 | -2.24 | yes | yes | yes | cambisol |
| LW | Lower Whitmore | 51.59 | -2.37 | yes | no | yes | stagnosol |
| SP | Silwood Park | 51.41 | -0.65 | no | no | yes | luvisol |
| TW | Taynish | 56.02 | -5.63 | yes | no | no | umbrisol |
| WC | Wood of Cree | 55.01 | -4.53 | yes | yes | yes | histosol |
| WS | Witherslack | 54.28 | -2.87 | no | yes | no | cambisol |
| WW | Whistman's Wood | 50.58 | -3.96 | yes | yes | yes | umbrisol |
| YW | Yarner | 50.59 | -3.72 | yes | yes | yes | podzol |

gion; ITS3(5'- GCATCGATGAAGAACGCAGC-3') and ITS4 (5- TCCTCCGCTTATTGATATGC -3). Each primer set was ligated with a unique barcode set. PCR products were then selected for proper size and purified for library preparation. The same amount of PCR product from each sample was pooled, end polished, A-tailed, and ligated with adapters. After purification, the library was analyzed for size distribution, quantified using real-time PCR, and sequenced on NovaSeq 6000 SP flowcell with PE250. BLAST searches were carried out using the UNITE public sequence database (https://unite.ut.ee/). Sequences were assigned to species names when BLAST matches showed scores of 97% or higher. Genus level assignments only were made when either no species level matches were found or multiple species matches at 97% and above within the same genus.

### 5.4.6 Environmental data

Rainfall and temperature data were taken from the Met Office historic station data for the years 2014 to 2019 (https://www.metoffice.gov.uk/research/climate/maps-and-data/historic-station-data). This data set contains the mean daily maximum and minimum temperatures and the total daily rainfall for weather stations located across the UK. Data was chosen for stations closest to the site sampled. For temperature variables we used five year average of the maximum monthly temperatures, (temp:°C). For rainfall we took the average of total daily rainfall between 2014 and 2018, (precipitation:mm). Pollutant deposition data was taken from UK Centre for Ecology and Hydrology UK deposition data. The data provides three year average of concentration based estimates of wet and dry deposition of oxidised nitrogen, reduced nitrogen, non-marine sulphur and calcium and magnesium cations (nox,nhx,nms,camg:keq $ha^{-1}year^{-1}$) at 5km $^2$ resolution. Specifically, we used the data set covering forest habitats for 2017-2019 (Levy *et al.*, 2021). Site elevations (elevation, m) were obtained from FreeMapTools (https://www.freemaptools.com/elevation-finder.htm). For each site we also recorded several binary categorical variables: ancient woodland, grazed, whether the woodland was mixed or solely oak, and the oak species (*Quercus robur, Q petraea*).

### 5.4.7 Soil sampling and analysis

At each tree sampled lose litter was removed and a soil sample ring was used to select the volume of soil, this soil was weighed and used for soil density estimation. Since soil density is simply the weight scaled by the volume, and values were scaled before analysis, the soil weight was used as a proxy for density. Soil was also collected adjacent to each root sampled, this was combined with rhizoshpehere soil and soil used for density analysis. This mixed pooled sample was used for soil nutrient analysis. Soils were dried at 50°C for 24 hours. Soil was split into batches for

analysis of pH, carbon to nitrogen ratio and nutrient content.

Estimates of soil pH (pH: negative log of H+ activity) were based on measurements of 2g of soil mixed with either 5ml, 10ml or 15ml of water, depending on soil type, and recorded with a Thermoscientific Orion Star A211 pH probe. In order to account for different water quantities required for different soil types, calibration curves were constructed for a range of different samples and the average gradient used to estimate the pH at 5ml for every soil sample. Readings were repeated until three constant consecutive values were obtained. For some soils this required repeat readings over several hours. Carbon and nitrogen content was measured by combustion using a LECO CH 628 elemental analyser. Soil nutrients (K, Mg and P, $mgKg^{-1}$) were estimated from inductively coupled plasma optical emission spectroscopy of Mehlich 3 extractants.

### 5.4.8 Statistical analysis

Estimated richness of EMF of oak across the UK was calculated using the Chao2, Jackknife and Bootstrap estimators and visualised with species rarefaction curves generated using the vegan package in R (Oksanen *et al.*, 2019). Potential correlations between continuous variables were explored using Spearman rank correlations Influence of environment on richness was visualised using scatter plots together with observation of the goodness of fit and p value of univariate linear models. Multivariate models were not constructed due to lack of strong correlations.

We explored patterns in species turnover using zeta diversity ($\zeta$) (Hui & McGeoch, 2014) using the zetadiv package in R (Latombe *et al.*, 2018a). Traditional diversity metrics use pairwise combinations, and therefore commonly reflect a combination of turnover due species with low occupancy rates and richness differences between pairs of sites (Anderson *et al.*, 2011). Zeta diversity extends traditional diversity metrics to include multiple sites by calculating the average number of species shared between n sites. $\zeta_2$ is the average of the species shared between ${}^{n}C_2$ combinations of 2 sites, $\zeta_3$ is the average number of the species shared between ${}^{n}C_3$ combinations of 3 sites, and so on, where n is the total number of sites sampled. Low and high orders of zeta therefore reflect diversity of rare and common species respectively (Latombe *et al.*, 2019). Plotting increasing orders of zeta against the order number (zeta decline curves) indicates how species are distributed in the landscape by exposing patterns of rare and common species. For instance, sharp declines indicate that turnover is mainly dependant on rare species, (Latombe *et al.*, 2018b; McGeoch *et al.*, 2019).

We also examined the parametric form of the zeta decay curve.The ratio of subsequent zeta values (retention rate) is the probability of species shared between $i$ sites also being shared by $i + 1$. If these values are equal for all zeta orders, then species are randomly disbursed in the landscape, perhaps due to high dispersal and

the zeta decay curve is exponential. If the ratio is not constant the decay curve takes the form of a power law, indicating that the chance of finding a common species in the next site is higher than the chance of finding a rare one. This suggests the communities are shaped by environment or niche (Hui & McGeoch, 2014; Latombe *et al.*, 2018b; McGeoch *et al.*, 2019). Further, the exponent of the power law relationship can be extracted and used to estimate species richness (Hui & McGeoch, 2014; Hui *et al.*, 2018). Zeta diversity modelling also offers a method to examine spatial autocorrelation through distance decay calculations which regress different orders of zeta against Euclidean distance and therefore reveal whether distance influences species at different orders of zeta. A negative value for the distance decay at an order of zeta expresses a relationship where the greater the distance between sites, the fewer the number of shared species. If this value is large, this suggests some spatial autocorrelation between sites.

In order to explore the effect of environment, we carried out multisite generalised dissimilarity modeling (MSGDM) (Latombe *et al.*, 2017, 2018b, 2019; Ascensão *et al.*, 2020; da Fonte *et al.*, 2021) using the zetadiv package in R (Latombe *et al.*, 2018a). MSGDM is a technique for expressing nonlinear relationships between environmental and spatial variables and orders of zeta. Recent work using MSGDM suggest that drivers of compositional turnover can differ between high and low occupancy species and across environmental gradients (Krasnov *et al.*, 2020; da Fonte *et al.*, 2021), therefore this technique offers an important extension to methods such as generalised dissimilarity models which use only pairwise dissimilarity. The environmental variables are transformed using Isplines and the relationship between these Isplines and orders of $\zeta$ is fitted using a generalised linear model with a log link function. The maximum values of the Isplines indicate the relative importance of the explanatory variables, whilst the slope of the Ispline curve across the scaled environmental variable indicates how changes in the environmental variable relate to changes in species assemblages at different points along an environmental gradient (Latombe *et al.*, 2017). A greater gradient at lower values of altitude, for example, would indicate that elevational changes are important at lower altitudes, if the slope for that variable decreased toward the upper end of its range, this would indicate that the same change in altitude at higher elevations has less affect on species composition. Distance can be included in the MSGDM and hence the relative influence of environment or distance can seen. MSGDM requires that $\zeta$ values are normalized according to Sørensen or Simpson calculations (that is, by dividing by mean or minimum richness of the n sites). We chose the latter as this method tends to highlight variables more important to compositional turnover as opposed to those related to richness (Latombe *et al.*, 2018b). To check the influence of variable correlation we generated models with and without the most highly correlated variables (nms and nox, K and Mg, Spearman correlation 0.75 and 0.78 respectively). In either case,

the variable importance was not altered and we therefore used all variables in the model. To increase computational speed, 1000 random combination of the 19 sites were used. This means that incomplete sampling occurs for $\zeta$ orders above 4 ($^{19}C_4$ = 3876). Therefore the models were repeated 100 times and the mean value of the explained deviance and Isplines was taken. We plot the mean value of the Isplines across the 100 replicates to evaluate the relative importance of the environmental drivers and how changes in environmental variables may affect species turnover. Models were assessed using Pearsons $R^2$ between the predicted and observed $\zeta$ as the explained variance of the model.

Finally, indicator species analysis was carried out using the indicspecies package in R (Cáceres & Legendre, 2009) using the phi coefficient (Chytrý *et al.*, 2002). The phi coefficient varies between -1 and 1, where -1 implies that a species is not found under particular environmental conditions and 1 indicates that is is always found.

## 5.5 Results

### 5.5.1 Fungal OTUs

We sampled roots from 95 trees at 19 sites across Britain. Of 1145 BLAST matches 125 EMF were saved at the 97% sequence similarity rate, 115 of these to species level. 86% of species belonged to Basidiomycota. (See Table D.1) The data was dominated by rare species with 75% of the species found in fewer than 18 samples. Fifty species were recorded for the first time on oak, to our knowledge (see Table D.2 for summary of EMF found on from a review of 12 studies). *Russula* was the most common genus, forming 17.6% of the species, followed by *Cortinarius* (14.4%). The oak specialist *Lactarius quietus* occurred in 92 out of 95 plots and the generalists *Cenococcum geophilum, Lactarius amethystina, L. tabidus, Russula ochroleuca, R. fragilis* and , were present at 90% of trees sampled.

### 5.5.2 Response of EMF richness to environmental variables

Species rarefaction curves did not show a tendency towards a zero gradient (see figure 5.15), suggesting that sampling was incomplete. Species richness estimation made using the Chao, Jacknife one and two and Bootstrap estimators predict a landscape richness for EMF of oak of between 136 and 154 species. Average site-scale richness was 42 species, ranging from 18 at Friday Street, a dry sandy site in the south east of England, to 63 at Yarner Wood, a site on Dartmoor National park to the south west. Zeta diversity declines from $\zeta_1 = 42$, the average number of species shared between all sites to $\zeta_{15} = 8$, the number of widespread species (see figure 5.17a). The rapid decline indicates that turnover is predominantly due to rare species. The increasing retention rate (5.17b) reflects a power law relationship in the parametric form of the

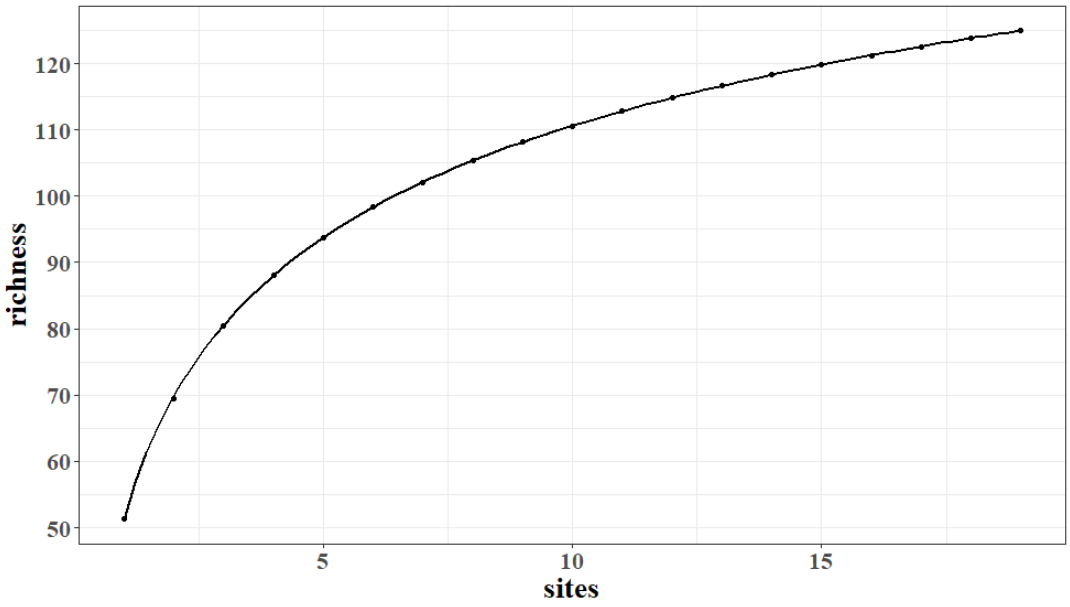


Figure 5.15: Species rarefaction curve for EMF species in nineteen woodlands across Britain. The curve shows that saturation was not reached and suggests a greater species richness of EMF of oak in British oak woodlands than was found in this study

zeta decline curve indicating non-stochastic species turnover. The coefficient of the power-law relationship was -0.59, giving an extrapolated species richness of around 250 if the number of sites sampled were to be doubled (see appendix D.0.1).

Univariate linear models showed no correlation between EMF species richness and environmental variables except soil K, see Figure 5.16 (See Figure D.2 for correlations between all environmental variables).

### 5.5.3 Correlations between variables

Exploration of continuous variables showed strong correlations (Spearman correlation = |0.76|) between location and climate variables (see Figure D.1). As would be expected for the climate in the UK, the sites in the south are warmer, whilst those in the west are wetter. Soil density was positively correlated with soil pH (Spearman correlation = 0.72) and negatively correlated with soil C:N ratio (Spearman correlation= -0.74). Soil K and Mg were also highly correlated (Spearman correlation= 0.78). Pollutants nox and nms also showed high correlations of 0.75.

### 5.5.4 EMF community - distance decay

The distance decay of similarity between EMF assemblages was not significant for rare species (see figure 5.18). For higher orders of zeta the coefficient of distance decay is negative and significant but small.This implies that assemblages demonstrate fewer species in common with distance, but the effect is very small. This lack of a

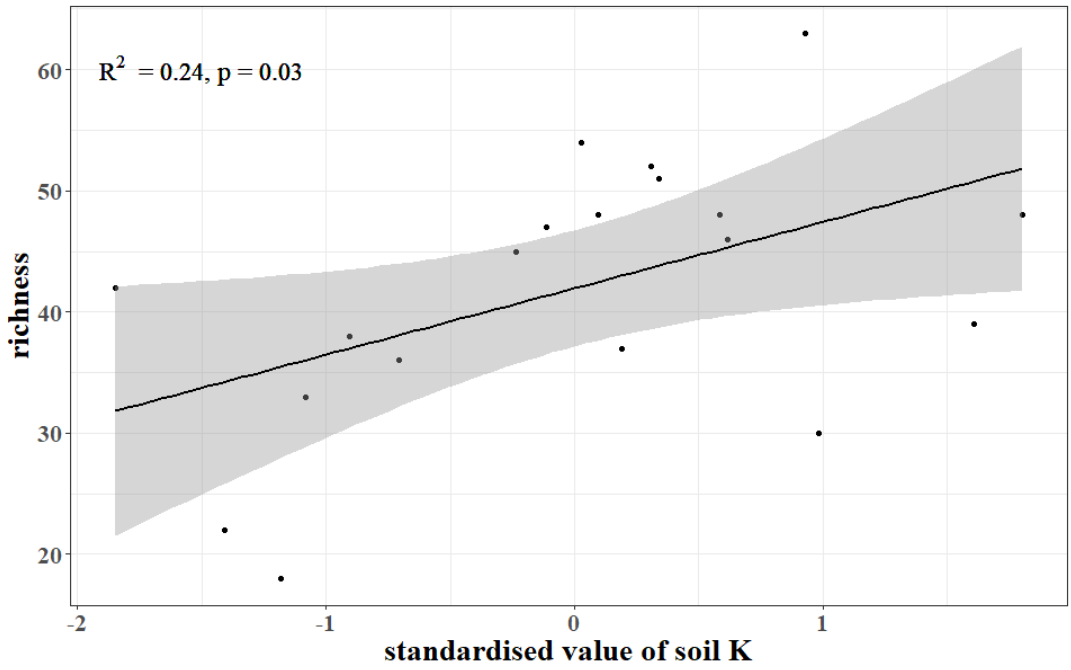


Figure 5.16: Univariate linear model between EMF richness and soil K. explanatory variable is standardised. $R^2$ 0.24, p = 0.03

strong effect of distance on EMF community similarity was also seen in the relative importance of the MSGDM I-spline value of 0 for distance at all orders of zeta.

### 5.5.5 EMF community - drivers

Oxidised nitrogen (nox) was the most important variable for explaining compositional turnover at all orders of zeta. Soil K was important for rare species, but this reduced as species become more common. For $\zeta_3$ onwards elevation and atmospheric pollutants are the most important variables. The I-spline plots in figure 5.20 shows the I-splines generated by the MSGDM for $\zeta_2$ to $\zeta_7$. Only the five most important variables are plotted for clarity, (see table D.4 for all values). Environmental variables explained more of the deviance in the model at higher orders of zeta. The model explained 22% of the deviance at $\zeta_2$ which increased to 44% at $\zeta_7$ (see figure 5.19).

### 5.5.6 Indicator species

Indicator species analysis identified twenty-eight species as significant indicators, (see table 5.2). *Thelephora terrestris*, a common species in this study, was found to be associated with grazed sites, and those with low levels of soil K. *Lactarius chrysorrheus*, also common, was associated with soil pH >3.58. *Tomentella lapida* was more common in plots with moderate levels of soil Mg. No indicators were found for ancient woodland, soil density, soil CN ratio or reduced nitrogen deposition.

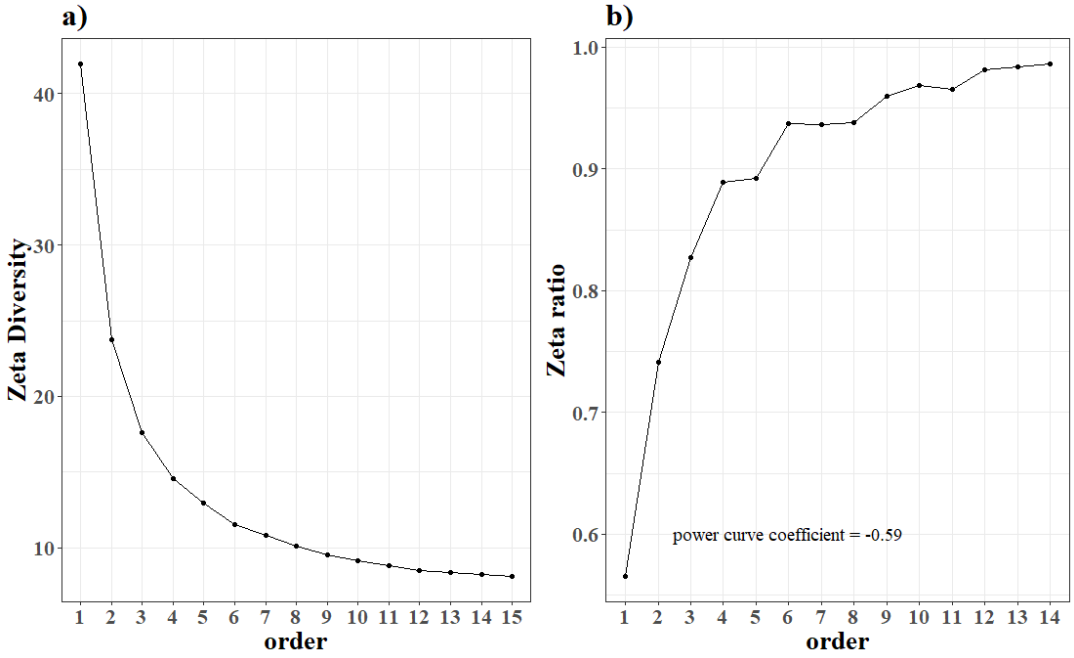


Figure 5.17: a) Zeta diversity decline for the nineteen sites sampled showing an average number of 42 species per site declining to 8 common species shared between at least 15 sites. b) The ratio of subsequent orders of zeta, the retention rate shows a constant increase indicating a power-law relationship for the zeta decline curve. The exponent of the curve was found to be -0.59

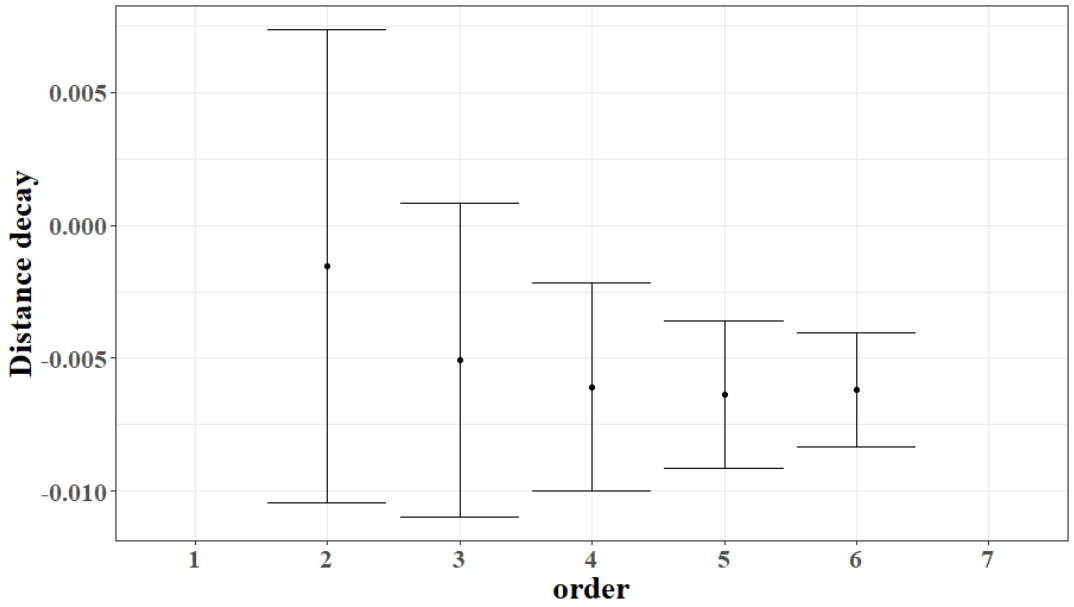


Figure 5.18: Zeta distance decay. Zeta values are normalised (Simpson equivalents). Values are coefficient with 95% confidence intervals of regression of $\zeta_i$ against Euclidean distance. Distance decay is not significant for rare species. For zeta orders of 4 and above distance decay is small but significant

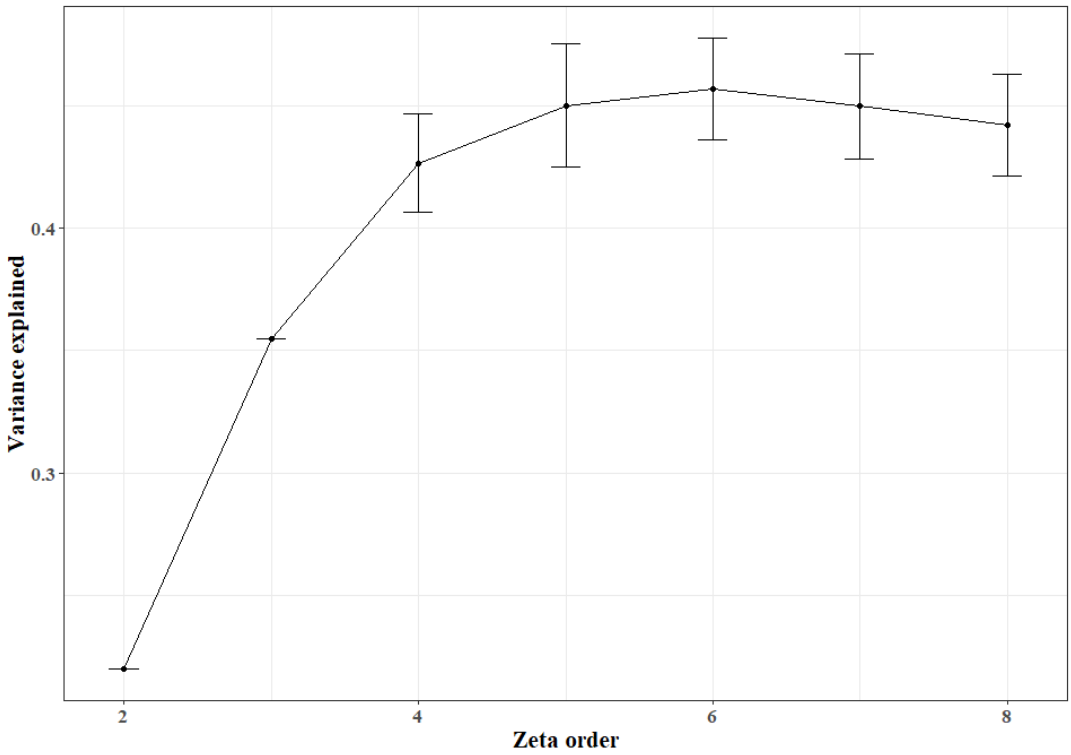


Figure 5.19: Percentage of variance explained by the predictors using MSGDM for modelling zeta diversity of EMF of oak across nineteen British woodlands. The error bars represent the standard deviation of $R^2$ across the 1000 replicates of the model. Since $\zeta_2$ and $\zeta_3$ have less than 1000 combinations no error bars were generated

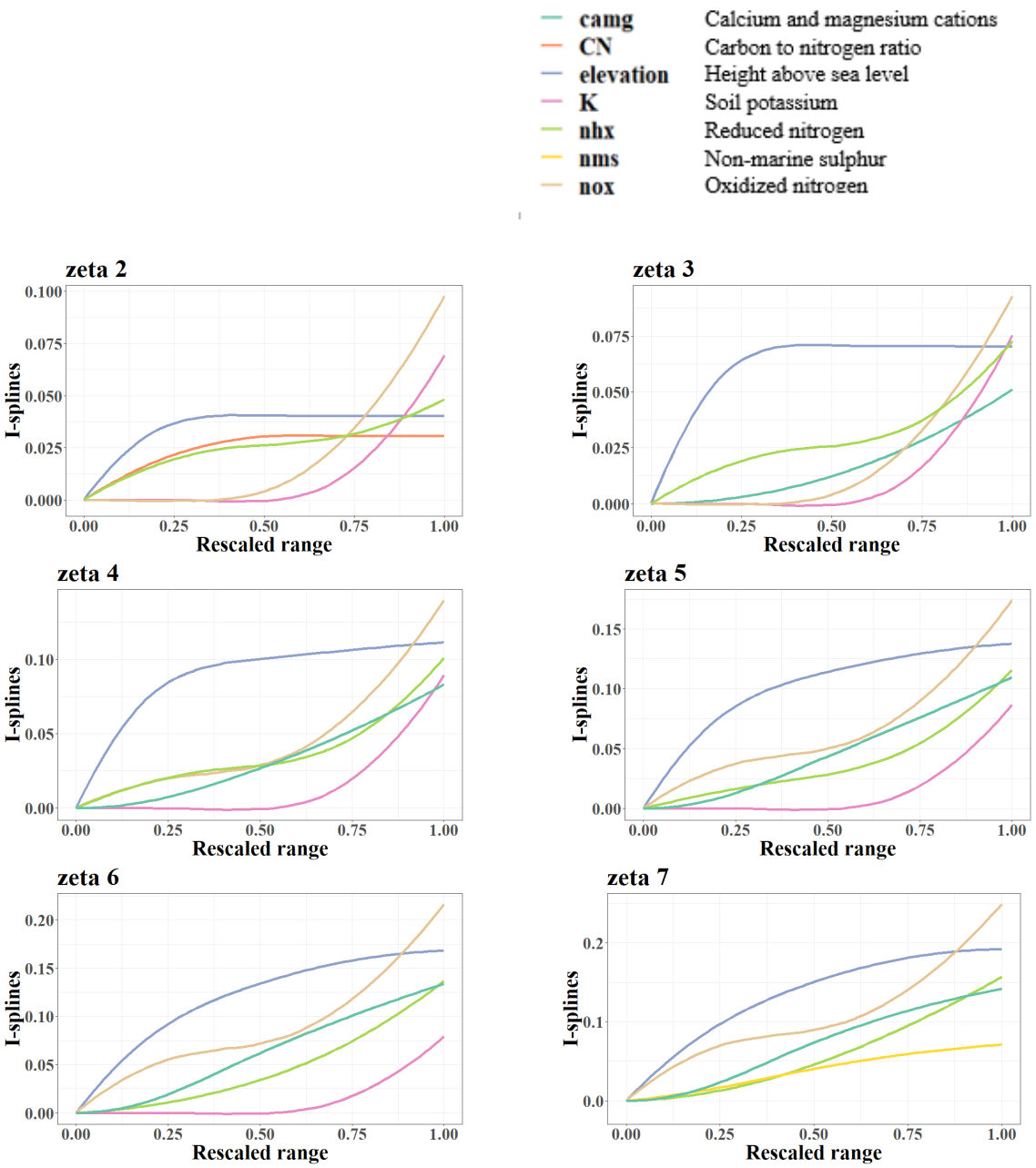


Figure 5.20: I-splines generated by MSGDM for EMF communities of nineteen oak woodlands across Britain for $\zeta_2$ to $\zeta_7$. The horizontal axis is the original variable rescaled between 0 and 1. The vertical axis represents the fitted I-splines. The relative amplitude of each spline represents the relative importance of the predictor variables, whilst the gradient changes of the I-spline indicate where changes in values of the predictor are important to compositional turnover. Only the five most important variables are shown for clarity. Oxidised nitrogen is the most important variable influencing diversity for both common and rare species. Whereas soil K is important at lower orders of zeta only. elevation is important only at higher orders of zeta.

Table 5.2: Results of indicator species analysis for EMF communities in 19 British woodlands. The first column details the environmental condition with the indicative species in the second column. I is the phi coefficient and p is its p value. f is the occurrence for each species within the data

| | **Species** | **I** | **p** | **f** |
|---|---|---|---|---|
| **grazed** | | | | |
| n | *Clavulina coralloides* | 0.69 | 0.04 | 29 |
| y | *Thelephora terrestris* | 0.56 | 0.04 | 54 |
| **tree species** | | | | |
| *Q robur* | *Otidea.onotica* | 0.56 | 0.04 | 9 |
| **soils** | | | | |
| cambisol histosol | *Hydnotrya tulasnei* | 0.95 | 0.00 | 6 |
| histosol luvisol | *Tomentella cinereoumbrina* | 0.84 | 0.04 | 12 |
| | *Cortinarius acutovelatus* | 0.80 | 0.04 | 7 |
| | *Cortinarius gurdus* | 0.80 | 0.05 | 9 |
| histosol luvisol umbrisol | *Humaria hemisphaerica* | 0.79 | 0.05 | 12 |
| **ancient** | none | | | |
| **mixed/single** | | | | |
| mixed | *Russula risigallina* | 0.58 | 0.04 | 8 |
| mixed | *Sebacina epigaea* | 0.58 | 0.04 | 9 |
| **temperature°C** | | | | |
| 13.12<t<15.24 | *Cortinarius anomalus* | 0.88 | 0.00 | 6 |
| | *Lactarius decipiens* | 0.63 | 0.03 | 3 |
| | *Xerocomellus cisalpinus* | 0.59 | 0.04 | 12 |
| **soil pH** | | | | |
| low <3.58 | *Paxillus involutus* | 0.71 | 0.02 | 18 |
| medium+high (>3.58) | *Lactarius chrysorrheus* | 0.63 | 0.05 | 74 |
| **soil density** | none | | | |
| **soil CN ration** | none | | | |
| **K mg/Kg** | | | | |
| low+medium (<618) | *Thelephora.terrestris* | 0.66 | 0.01 | 54 |
| medium (388<K<618) | *Xerocomellus cisalpinus* | 0.63 | 0.04 | 12 |
| medium+high (>388) | *Cortinarius punctatoides* | 0.70 | 0.02 | 28 |
| **Mg mg/Kg** | | | | |
| low (<363) | *Melanogaster ambiguus* | 0.54 | 0.05 | 6 |

*Continued on next page*

Table 5.2 – *Continued from previous page*

| | **Species** | **I** | **p** | **f** |
|---|---|---|---|---|
| medium - high (>363) | *Tomentella lapida* | 0.63 | 0.03 | 41 |
| high (>902) | *Tomentella spinosispora* | 0.69 | 0.01 | 25 |
| | *Amanita rubescens* | 0.57 | 0.03 | 12 |
| | *Elaphomyces asperulus* | 0.50 | 0.05 | 5 |
| **P (mg/Kg)** | | | | |
| low (<89) | *Russula risigallina* | 0.70 | 0.02 | 8 |
| high or low (<89 or >157) | *Humaria hemisphaerica* | 0.76 | 0.01 | 12 |
| **nox (keq ha-1year-1)** | | | | |
| medium (0.365<nox<0.52) | *Russula betularum* | 0.59 | 0.04 | 10 |
| **nhx** | none | | | |
| **nms** | | | | |
| high (>0.225) | *Russula ionochlora* | 0.58 | 0.05 | 13 |
| **camg** | | | | |
| medium - high (>0.09) | *Sebacina incrustans* | 0.58 | 0.04 | 15 |

## 5.6 Discussion

### 5.6.1 EMF Richness

We carried out a below-ground study of EMF communities of oak in nineteen sites across Britain. We identified 125 species, 115 to species level, 53 of these recorded for the first time with oak, to our knowledge. This is a greater number than found in other surveys of oak. Keizer & Arnolds (1994) record 78 species in a sporocarp study, but their work excludes all hypogeous species. In our work sixteen species produced hypogeous fruiting bodies or crusts which would be overlooked in sporocarp studies. Martinová *et al.* (2016) found 76 species sampling 32 trees in a diverse range of urban and woodland habitats. We sampled in such a way to increase species richness. That is, the selection of colonised root tips for subsequent DNA analysis was not entirely random. EMF colonisation is not spatially stochastic, and at sampling distances of less than about 3m, species are likely to be spatially autocorrelated (Pickles *et al.*, 2010, 2012) due to niche partitioning, interspecific competition, dispersal and tree root density (Dickie *et al.*, 2002; Rosling *et al.*, 2003; Baier *et al.*, 2006;

Tedersoo *et al.*, 2008b; Pickles *et al.*, 2012; Mujic *et al.*, 2016). Therefore, random sampling methodologies are likely to underestimate species richness, and this may explain the large number of species found here. Chao, Jackknife and Bootstrap richness estimators suggest that we captured 80 to 90% of species richness. Zeta diversity richness estimators suggest that 250 species could be found if we doubled the number of sites sampled, that is approximately double the number we found here or estimated by asymptotic methods. Our literature review of EMF found with *Quercus robur* and *Q. petreae* suggests that oak could host over 250 EMF species (see table D.2 in the appendix). The papers reviewed cover a range of tree ages from nursery grown saplings in one study to mature trees. Identification methods include molecular analysis of root tips as well as sporocarp surveys. Sporocarp surveys can be unreliable as a definitive means of identifying EMF hosts, however, the surveys included here occurred in pure stands, which should minimise errors. The thirteen papers included in the review cover a range of European countries besides the UK, and hence some of the species may be non-native. However, consulting biological records databases (GBIF, 2022; NBNatlas, 2022) indicated that only 12 species summarised in the table have no occurrence data in the UK. This suggests that a much greater species richness of oak EMF is feasible and therefore that asymptotic estimators may be an under-estimate of the maximum possible EMF species richness.

Various aspects of our methodology would act to reduce species richness. We have not taken account of seasonal variation in EMF communities. The logistics of the study (that is, one person sampling multiple sites) naturally means that sampling time will be spread across several months. However, there are indications that community structure and colonisation rates have a temporal component. Some species have been only found during winter months (Courty *et al.*, 2008; Buée *et al.*, 2005), greater abundance and species richness of EMF taxa has been recorded in summer (Courty *et al.*, 2008; Voříškova *et al.*, 2014). These temporal changes could act to reduce the recorded species richness of the sites. If species have a lower abundance due to sampling month, a limited sampling regime is less likely to find those individuals, and hence their absence is recorded. In this work, we sampled at three locations around each tree, and chose a non-random technique when selecting EM root tips from these samples, which may mitigate these issues somewhat.

We only analysed EMF species found in the upper soil layers. EMF communities have been found to vary across soil horizons (Dickie *et al.*, 2002; Rosling *et al.*, 2003; Baier *et al.*, 2006; Beiler *et al.*, 2012), and a recent meta-analysis suggests that this vertical variability is greater than temporal variability, (Bahram *et al.*, 2015). As with other work (Courty *et al.*, 2008) we found that root tips were more abundant in upper soil layers (data not shown) however, it has been found that whilst different soil horizons share some species, some may be present in only one (Dickie *et al.*, 2002; Courty *et al.*, 2008). This will therefore account for some missing species in

our sampling.

Previous studies find that atmospheric pollutants, elevation, precipitation and temperature all affect EMF richness, (Bahram *et al.*, 2011; Suz *et al.*, 2014, 2017; Rosinger *et al.*, 2018). In contrast, in this study, none of these factors was significant. This could be due to differences in the range of the variables. In this study, the range of site elevation was 350m. Bahram *et al.* (2011) report a negative effect of altitude on EMF richness across elevational gradients of 500m to 2000m. However, although the effect was significant at the landscape scale, it was not always significant at local scales across the same range suggesting that regional and local effects might not always correspond. Soil pH range in this study was pH3.12 - pH5.71. Rosinger *et al.* (2018) demonstrate a unimodal relationship between EMF diversity and pH across a range of approximately pH3 to pH 10, with a peak at around pH6. Tedersoo *et al.* (2012) report a unimodal response to temperature across a range of 0 to 25°C with a peak at around 12°C , whereas the range in this study was only 5°C. We found a positive correlation between EMF richness and soil K. Wang *et al.* (2016) found that K fertilisation increased fine root biomass in mineral soil horizon with significantly greater numbers of root tips in fertilized *Picea abies* plots compared to controls. They found no difference in EMF community structure or richness, however, there was an increase in tree basal area. Most tree species show a positive growth response to K (Tripler *et al.*, 2006) which alleviates negative effects of excess ammonium and helps promote root growth (Sustr *et al.*, 2019) as well as alleviating drought stress (Sardans & Peñuelas, 2015) and may be a limiting nutrient in woodlands (Tripler *et al.*, 2006). These positive effects of K could imply that trees in areas of higher soil K would provide more potential colonisation sites and be able to support a larger EMF abundance, which might lead to greater species richness.

### 5.6.2 Correlations between variables

Soil pH showed a high correlation with soil density (Spearman correlation = 0.72) reflecting the tendency of soils with greater organic matter content to be lighter and more acidic. Soil density was also negatively correlated with soil Mg content (Spearman correlation = -0.75), this relationship has been observed previously (Chaudhari *et al.*, 2013) and may be due to the leeching of magnesium salts from organic material (Staaf, 1980) and the negative correlation between leaf litter decomposition and magnesium content (Ge *et al.*, 2017). Since we sampled soil just below the loose litter, less dense samples may contain high quantities of undecomposed material which may retain unleeched magnesium salts.

Magnesium and potassium showed a positive correlation (Spearman correlation 0.78). This is to be expected as the soils sampled were in general highly organic, particularly because we were sampling the upper soil layers, and would therefore show a high cation exchange capacity such that exchange sites are unlikely to be saturated.

Magnesium was also negatively related to longitude, which is probably related to underlying geology of the sites visited. Longitude and latitude were strongly correlated with precipitation and temperature respectively (Spearman correlation -0.88, -0.76). This is expected as the west coast of the UK tends to be wetter while the south is warmer.

### 5.6.3 EMF communities and their drivers

#### Distance

The power law form of the zeta decline curve indicates that species turnover is predominantly driven by niche differentiation (Hui & McGeoch, 2014). This is in agreement with the results of the distance decay, which was found to be significant but small at orders of zeta of 4 and above. In addition, relative to the explanatory variables assessed here, distance was not important. This suggests that niche processes are more important than dispersal in shaping communities of oak EMF across the UK. This result agrees with other work which has found that EMF communities are not spatially auto-correlated at distances greater than about 3 m (Lilleskov *et al.*, 2004; Pickles *et al.*, 2010, 2012). Bahram *et al.* (2013) conducts a meta-analysis of distance decay across a range of EMF studies from the tropics to Sweden and find that in non-tropical forests median distance decay extent was less than 10 m. Notably, one study in their review showed no distance decay. Kranabetter *et al.* (2018) found that EMF communities over approximately 20km in Vancouver Island, Canada displayed similarity at less than 2.58km.

#### Environmental pollutants

The importance of atmospheric pollutants as drivers of EMF communities is consistent with other studies (Suz *et al.*, 2014; Rosinger *et al.*, 2018; van der Linde *et al.*, 2018). Arnolds (1991) discussed the potential connection between atmospheric pollution and the reduction in EMF sporocarps in forests in the Netherlands. Many studies have demonstrated that above ground sporocarp production, mycelial growth species richness can be reduced and community structure altered as a result of increased nitrogen in soils (Brandrud, 1995; Avis *et al.*, 2003; Nilsson & Wallander, 2003; Avis *et al.*, 2008; Cox *et al.*, 2010; Kjøller *et al.*, 2012; de Witte *et al.*, 2017). Non-marine sulphur was important in shaping communities of more common EMF. Sulphur has the potential to alter EMF communities through inhibition of mycelial growth (Dursun *et al.*, 1996) but can also result in enhanced sporocarp production (Carfrae *et al.*, 2006). The affect of sulphur deposition may depend on other edaphic factors such as soil pH and, as with Nitrogen deposition, may depend on EMF species (Cairney, 1999). Base cation atmospheric deposition was important at all orders of zeta diversity above $\zeta_2$. $Ca_2{}^+$ and $Mg_2{}^+$ have the ability to neutralize acid input

and act as nutrient inputs to soil (Draaijers *et al.*, 1997; Watmough *et al.*, 2014; Fenn *et al.*, 2015). Studies on the effects of these nutrients to EMF communities are limited to the addition of soil amendments rather than atmospheric deposition. Liming (the addition of calcium and magnesium containing soil amendments) has been found to correlate with increases in root growth (Erland & Söderström, 1990; Bakker *et al.*, 2000) and changes in EMF abundances (Bakker *et al.*, 2000; Kjøller & Clemmensen, 2009). In some cases complete community turnover has been observed (Taylor & Finlay, 2003). It has been demonstrated in pot experiments that the addition of CaO to alter pH from 4 to 7 generated a unimodal response in root tip EMF colonisation rate and a change in relative species abundances. Since other studies link soil pH to changes in community (Suz *et al.*, 2014, 2017; Rosinger *et al.*, 2018; Defrenne *et al.*, 2019; van der Linde *et al.*, 2018; Glassman *et al.*, 2017), it seems likely that changes in soil pH due to these pollutants is a factor in changing communities. However, in this study, we found that soil pH was not important, and we saw no correlation between pH and calcium and magnesium cation deposition (camg). This may suggest that these pollutants could also drive community changes by other means, for example, through the ability of calcium to alter soil structure by stabilising soil organic matter (Rowley *et al.*, 2018). Changes in the gradient of the I-spline plots indicates where changes in the predictor values are important to compositional turnover. Changes in potassium and oxidised nitrogen have a greater effect on communities at the upper end of their range. The converse is true for elevation. However, calcium and magnesium cation deposition has the same effect on communities across its range, suggesting that this pollutant can filter communities even at low levels.

### Carbon to nitrogen ratio

In line with other work, carbon to nitrogen ratio was a driver of community change (Jarvis *et al.*, 2013; Suz *et al.*, 2014, 2017; Defrenne *et al.*, 2019), although in this study it was important for only the rare species, and was the least important driver. Carbon to nitrogen ratio was negatively correlated with soil density, that is, the soils with low C:N tend to be mineral or clay soils. We expect communities to be different in these different soil types due to niche effects. That is, variation in resources requires differential enzymatic expression which implies changes in taxonomy (Courty *et al.*, 2016).

### Elevation

Elevation was found to have an important effect on communities. This has been seen in some previous studies (Jarvis *et al.*, 2013; van der Linde *et al.*, 2018) but not all (Suz *et al.*, 2014). A study in northern Iran across larger gradients of 1500m, much larger than those found in this work, linked these community changes to

temperature and precipitation (Bahram *et al.*, 2011). This seems unlikely here where our elevation change is much smaller (45m - 400m), and we saw no strong correlation between altitude, rainfall and temperature. Soil type has been found to influence communities (Suz *et al.*, 2014, 2017; Pena *et al.*, 2017; van der Linde *et al.*, 2018), but we found no significance (p =0.38, Kruskal-Wallis test). However, strong community composition shifts across single host species and smaller altitude changes have been associated with soil moisture and temperature (Jarvis *et al.*, 2015). It is possible that the elevational change in community seen here is, in agreement with Jarvis *et al.* (2015), reflection of fine scale moisture and temperature changes that our coarse scale climatic data does not show.

**Variance explained**

The variance explained by the MSGDM is greater for higher orders of zeta. This suggests that the distribution of common species is more predictable using the drivers explored here (Latombe *et al.*, 2018a). It is possible that we found no relationship between the distribution of the rare species because of their patchy occurrence. For example, more than half the species found occur at 7 trees or fewer. We have referred to these are rare as opposed to common species, but in fact these species are either rare, or incompletely sampled. If the species richness estimated from the species accumulation curve (136 to 154) suggesting reasonably complete sampling (125 found in this study) is valid, we could be more confident that the MSGDM is not useful for predicting drivers of rare species. This implies that drivers not measured here are responsible for changes in rare communities. Alternatively, species richness could be much higher, based on estimated values using the parametric form of the zeta decay and considering our review of EMF species of oak across Europe, see table D.2. In which case, although we can be confident that we have identified some of the drivers of common species, we may need more empirical data in order to fully understand the drivers of less common species.

Indicator species analysis identified species associated with specific environmental conditions (table 5.2). We have included species with low occurrence in this table, however, we do not know if this low occurrence is due to incomplete sampling, or a true representation of the rarity of a species. If a true representation, this species may indeed be an indicator for a given property, but more empirical data is required to confirm this. Of the common species, *Tomentella lapida* was associated with low Mg in soil and *Thelephor terrestris* both with low to intermediate levels of K and grazing. *Lactarius chrysorrheus* was associated all but the lowest pH sites. No indicator species were found for ancient woodland, there was also no correlation between site age and site richness (Pearson correlation coefficient = 0.29), however, most of the sites in this study were classed as ancient and therefore more data from newer woodlands is required to support this result.

## 5.7 Conclusion

In summary, our sampling across a large number of UK woodlands has contributed to the data on distribution and EMF species of oak. We have shown that species richness of EMF of oak is greater than has been found in previous studies, moreover, our review of previous work, combined with an examination of biological records databases and species richness calculations suggests that EMF richness of oak could be as high as 250 species. It is urgent and important that a more accurate estimate of EMF species richness is found in order to provide a benchmark with which we can compare new woodlands. If we do not know the EMF richness of mature or ancient woodlands, we are unable to comment on whether new planting schemes or industrial remediation activities, such as those carried out for the construction of the HS2 rail network, are successful. Our review of EMF of oak is the first step towards providing an estimate, but this needs further empirical data to confirm the results More empirical data with intense, focused, non-random sampling is required to confirm this. Specifically, repeated sampling of EMF throughout the year, across a range of age classes and at different soil depths.

We found that while dispersal had a small effect, environmental filters were the strongest drivers of communities. We found that only soil K was a driver of species richness but that, in line with previous studies, atmospheric pollution is the main driver of community turnover. Using CEH deposition data, we demonstrated that oxidised nitrogen is the most important of these pollutants. We also show that atmospheric cation deposition of Ca and Mg is an important filter. Whilst much previous work considers only drivers of rare species, here we also considered common species and show that, firstly, lack of complete data may mean that models using pairwise distances may not provide a complete picture of the drivers of EMF species, secondly, that drivers of rare species may differ to those of more widespread species. This analysis demonstrates the need to gather further empirical data so that the actual commonness or rarity of species is better understood.

# Chapter 6

# Pilot study into use of translocated soil as a source of ectomycorrhizal inoculum in restoration woodlands

## 6.1 Abstract

Soil translocation refers to the transfer of soil, and particularly the soil biota, during remediative action. Commonly, this approach is used in the restoration of ecosystems that have been damaged or destroyed by commercial activity, such as mining or road and rail building. In the case of forest and woodland restoration, trees depend on ectomycorrhizal fungi (EMF) for nutrients and increased drought and disease protection, therefore, the role of soil translocation as a supply of EMF inoculum to new remediation woodlands is of interest. We wanted to conduct a pilot study in order to trial methods for assessing inoculum potential in a restoration woodland. Here, we used *Quercus petraea* bait trees to explore the EMF community through comparison between four treatments: i) a restoration woodland on translocated soil, ii) bait trees in an adjacent ancient woodland, iii) mature conspecific trees in the same ancient woodland and, iv) pot grown trees from the same stock as the bait trees. We harvested the bait trees after one season and used molecular methods to identify EMF taxa in these four treatments (bait trees in restoration woodland, bait trees in ancient woodland, pot grown trees, mature trees in ancient woodland).

We found that the EMF community on bait trees in the restoration woodland, the ancient woodland and in the pots was similar (Jaccard similarity $> 0.65$), and that the bait trees in the restoration site had a high alpha diversity of EMF taxa (40), greater than that of the bait or mature trees in the ancient woodland (36), or the bait trees in the ancient woodland (34) possibly due to poor growth of trees under the closed canopy of the mature woodland. The communities of EMF on the

bait trees of both treatments, or on the pot trees was not similar to that on the mature oaks (Jaccard similarity 0.27). The pilot study demonstrated that the EMF community on nursery grown trees may have a high species richness, and therefore, it may not be possible to assess the inoculum potential of the translocated soil in this way. The communities found on the bait trees may have been those which were initially present, and we were unable to detect species which may have been collected from the translocated soil. The pilot demonstrated two further points, the study would not have been able to detect dispersion as a source of inoculum and root growth of all bait trees was very limited due to planting conditions.

The pilot study therefore resulted in four findings that will benefit future experimental investigations: 1) Aseptically sprouted seeds grown in sterile medium are required in order to operate as efficient bait trees 2) Bait trees planted in the ancient woodland show restricted growth under the closed canopy and steps would need to be taken to match conditions between the treatments 3) Spore traps would be a beneficial addition to the experiment to detect dispersal 4) Bait trees could be planted in prepared soil in order to maximise lateral root growth rather than restricting roots to a root ball.

## 6.2 Introduction

Soil translocation is carried out as part of mitigation procedures following the loss of ancient woodland as a result of commercial activity, such as road or rail building or mining (Spain *et al.*, 2015). This is typically done by collecting soils from the site of an ancient woodland and moving them to a new receptor site where new woodland is planted. The concept behind this process is that the diversity of the receptor site will be enhanced through the relocation of the seed bank, fungal propagule bank and soil fauna (Box, 2014). Ideally, for ancient woodland mitigation, some translocation of ancient woodland species would occur as part of this process. However, there is very little published literature describing the outcome or long term monitoring of this process in the UK, particularly with regard to mycorrhizal fungi. Some work is available for plant communities. For example, after examining 24 habitat translocations in the UK, Bullock (1998) conclude that none conserved plant or invertebrate community structure. Craig *et al.* (2015) state that *Hyacinthoides non-scripta*, an ancient woodland indicator species, can recover from the effects of soil translocation. In an experiment using forest soil translocation on severely weathered soils in Mexico, Douterlungne *et al.* (2018) show acorn germination and survival is greatest when forest soil and leaf litter have been translocated with their structure maintained. The Woodland Trust reviewed three ancient woodland soil translocations (Ryan, 2013): Crossington Fields, mitigation for the widening of the M2 motorway (Cresswell & Wray, 2005); Biggins Wood, mitigation for the Channel

Tunnel; and Brickhouse Wood mitigation for quarry landfill, all in Kent, England. Whilst there was no data available for Brickhouse Wood, mixed outcomes were reported for the other two schemes. At Biggins wood, after 25 years, five of the 18 ancient woodland indicator species were lost, whilst 70% were retained. However the community was significantly different, which the authors attribute to different soil conditions at the restoration site. Crossington fields was monitored for ten years and some ancient woodland plant indicator species were recorded, however other species were reported as lost. Zubek *et al.* (2019) look at changes in arbuscular mycorrhizal fungi (AMF) in a wetland mitigation project where turfs were translocated. They report that the number of AMF species initially declined, but after 2 years AMF species richness was greater than that at the donor location. No work was found involving changes in the EMF species assemblages after translocation of ancient woodland soils in the UK.

In order to gain more insight into the trajectories for EMF species that we might expect from woodlands developed on translocated soils, we can look to mine rehabilitation. Arbuscular mycorrhizal fungal populations appear to be able to recover from soil translocation processes. In restoration projects after bauxite mining in jarrah forests in South Western Australia, root colonisation of AMF has been found to recover in some cases after five years (Jasper, 2007), whereas ectomycorrhizal fungal populations may take longer to return to levels comparable with undisturbed sites. The species richness of EMF (as measured by sporocarp surveys) was less than half that of undisturbed adjacent woodland after seven years (Gardner & Malajczuk, 1988). However, in the same area, Glen *et al.* (2008) found that disturbed sites reached a similar richness to undisturbed woodland after fifteen years (using molecular methods). The authors note however, that the species composition differs, with some species missing from rehabilitation sites which are abundant in adjacent undisturbed forest. Similarly, in studying lignite mining reclamation sites in Germany, Gebhardt *et al.* (2007) found that the EMF communities differed between reclaimed and reference stands and suggest this may be partly due to soil differences.

The overarching theme of this thesis is woodland health and function from the perspective of mycorrhizal fungi. Therefore, the potential for the use of soil translocation as a means to inoculate new woodlands with mycorrhizal species is of particular interest. But there are several reasons to support the hypothesis that communities on donor and receptor sites may differ.

The EMF community differs between early and later successional habitats (Visser, 1995; Jumpponen *et al.*, 1999; Nara *et al.*, 2003; Twieg *et al.*, 2007) so that different EMF species have been described as early and late successional (Mason *et al.*, 1982, 1983; Deacon *et al.*, 1983; Fleming, 1983, 1984; Last *et al.*, 1984; Dighton *et al.*, 1986). This succession takes place for many reasons. The availability of inoculum (Collier & Bidartondo, 2009), the higher infectivity found in some EMF species

(Ishida *et al.*, 2008) and shifts in inorganic nitrogen availability (LeDuc *et al.*, 2013). Further, trees within woodlands are connected via the hyphae of the EMF which colonise their roots (Simard & Durall, 2004) and young or mature tree roots in existing woodlands can become colonised with EMF, either via access to this common mycorrhizal network (CMN), or through contact with EMF propagules in the soil, but the EMF species able to colonise via these two mechanisms differ. For instance, Fleming (1984) carried out an experiment in which trees were grown in soil patches around which trenches had been dug, separating the trees from the CMN. *Lactarius pubescens*, an EMF commonly found on birch (*Betula pendula*), was a very poor coloniser of these trenched trees, but *Hebeloma* spp and *Inocybe* spp were not. In a similar experiment Simard *et al.* (1997) found that trenched Douglas-fir (*Pseudotsuga menziesii*) trees became colonised by nine EMF species whereas as untrenched seedlings were colonised by seventeen.

When woodland soils are translocated, soil structure and properties are altered, for example with an initial loss of organic matter (Schwenke *et al.*, 2000; Banning *et al.*, 2008; George *et al.*, 2010) such that it more closely resembles soils found in early successional habitats. In addition, colonisation via the CMN is not possible, instead colonisation will take place via the resistant propagule bank in the translocated soil. Further, it has been found that the resistant propagule bank does not always share the same species as those found on tree roots in the same woodlands (Miyamoto & Nara, 2016). For these reasons, we could expect to find a different community of EMF on trees planted in newly translocated soils compared to those either on trees planted in woodlands from which the soil originated, or on mature trees of the same species in similar mature habitats.

The literature review above demonstrates the paucity of consistent monitoring of new woodlands created using soil translocation, and lack of data which monitors the EMF community. To make matters more complex, there is no data which summarises the EMF community of ancient woodlands and how this may differ from that found in newer woodlands (although the EMF species summarised in chapter 5 go some way to tackle that issue for oaks *Quercus petraea, Q. robur*).

We hypothesised that the resistant propagule bank will be retained in the translocated soil and trees planted in the translocated soil will be colonised by early successional EMF taxa that form that propagule bank. Further, the species richness of trees planted at the restoration site will be less than that of trees planted in an established woodland since they lack access to a CMN and cannot be colonised by EMF which preferentially infect roots via live hyphae. Finally, the EMF community of newly planted trees in translocated soils will be different to that of mature trees of the same species in a mature woodland since we expect mature trees to be colonised by later stage fungi and the EMF community of the resistant propagule bank differs from that found on mature trees.

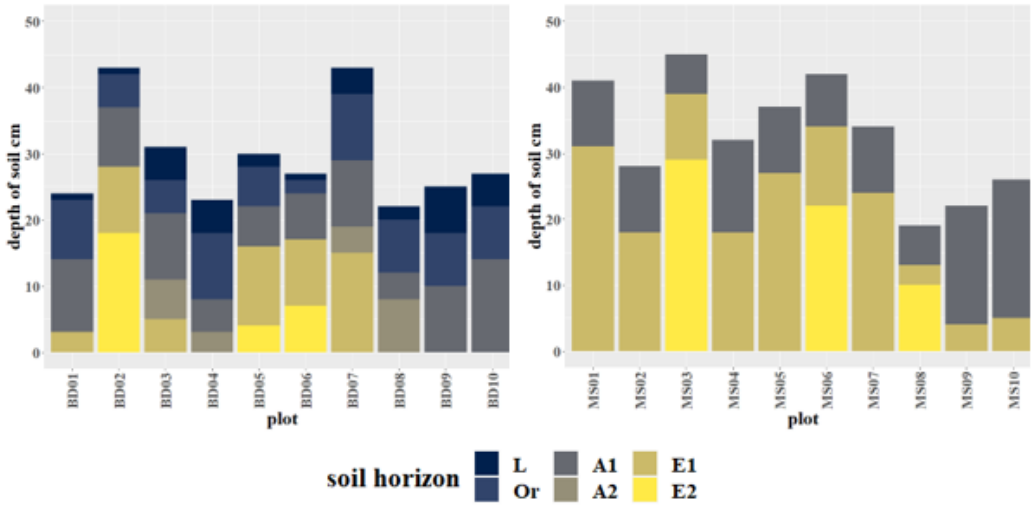


Figure 6.1: This graphic summarises the variation in soils between the sites used in this study. Ten samples were taken in the ancient woodland (BD samples) and ten at the receptor site (MS samples). The bars in the graphic represent the ten soil cores taken in each treatment. The left axis shows the depth for each visually identified soil layer. Each bar depicts a soil core, with the height of each bar showing the depth of the core, and the different coloured stack depict different soil horizons. The ancient woodland soil can be seen to be more complex with a litter layer and a deep organic layer. In some cases, up to four horizons were clearly differentiated in the ancient woodland soil. The soil at the receptor site is less complex without litter or organic material. This is probably in part due to the translocation process which can cause mixing of soil material.

In order to address this lack of data and test our hypothesis we wanted to survey the EMF community in a translocated soil and compare it to that in an adjacent ancient woodland. We therefore conducted a pilot study in order to explore potential experimental methods using bait trees.

For context, we also compare soil properties between the restoration woodland on translocated soil and soils in an adjacent ancient woodland. We do not expect the soils of the ancient woodland and receptor sites to be similar. Recently disturbed soils will have lower levels of organic matter, higher soil pH and less well defined soil horizons (Schwenke *et al.*, 2000; Banning *et al.*, 2008), and we expect to see that in this data. In addition, the donor site woodland and soils were different to those found in the mature woodland used in this experiment, in particular, the organic layer was less defined (Humphries *et al.*, 2019). The results are shown here in order to provide information on the difference between the substrates which the EMF occupy. The graphic in figure 6.1 demonstrates the differences in the soils at the restoration site and the adjacent ancient woodland.

In the ancient woodland, the soil core revealed a well defined organic horizon, and several mineral horizons. As would be expected from a recently disturbed soil, the soils at the restoration site had no organic layer but could be visually separated into a darker upper layer and a lighter lower layer. Photos of two soil cores are


Figure 6.2: The upper photo shows a soil core from one location in the ancient woodland. The litter and organic layers are well defined, and most tree roots would be found in this organic material. The lower core was taken from the restoration site. In most cases, a darker upper layer was obvious, but this layer was less organic than the upper soil in the ancient woodland.

shown in figure 6.2. We are mainly concerned with the upper soil layer since this is the soil experienced by tree roots and any colonising EMF. Even in mature trees, many fine roots occupy the upper organic soil layer, and it is also from that organic soil layer that roots of mature trees were sampled in the ancient woodland. In this chapter we refer to layer 1 which means the topsoil in both treatments. In the ancient woodland this would imply an organic soil, whereas at the restoration site this soil will have a much lower organic content. Similarly, layer 2 refers to the next horizon and so on, but note that layer 1 and layer 2 will have different properties depending on the treatment. In addition, they will occur at different depths, which are detailed in the graphic. The figure below shows soil cores for one location each within the ancient woodland and at the restoration site.

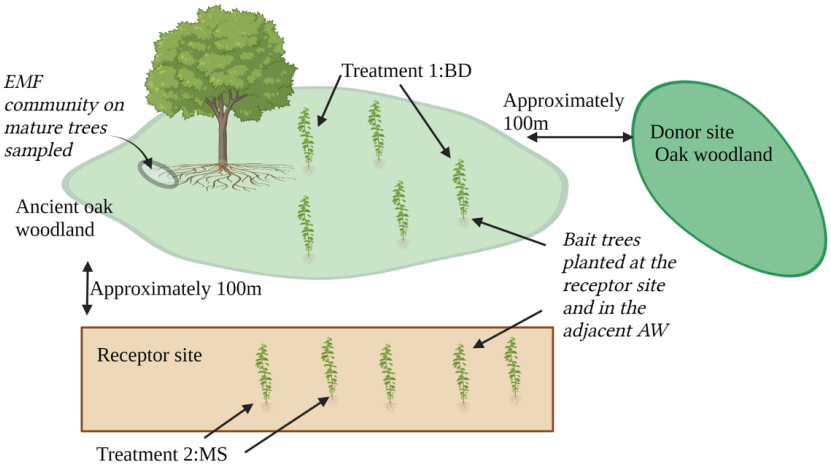


Figure 6.3: Graphic summarising experimental design. It was not possible to sample the donor site prior to translocation, hence ancient oak woodland adjacent to the receptor site is used for comparison. Roots of mature trees were sampled in the ancient wood. 20 'bait' trees were planted in the adjacent wood and 20 in the receptor site. These were then harvested and the EMF colonising their roots determined.

## 6.3 Materials and methods

### 6.3.1 Tree planting and harvest

The donor site was an area of oak (*Quercus petraea, Q. robur*) woodland in England, UK, close to the receptor site. The soil was translocated in 2017, for details refer to Humphries *et al.* (2019). In the summer of 2019 we sampled roots of mature trees in the ancient oak woodland directly adjacent to the receptor site. Forty bait trees of *Quercus petraea* were planted in February 2020, twenty in the ancient woodland (treatment BD) and twenty in the receptor site (treatment MS). The trees were one year old air pruned plug plants that had been nursery grown in peat free compost with the addition of Osmocote fertilizer. No mycorrhizal inoculum had been added, and the seedlings had not been grown in the ground, but they were not physically shielded from outside inoculum sources. Non-random locations, where the undergrowth was less dense, were chosen for trees planted in the mature wood. In order to maximise tree survival, canopy gaps were sought, but since the mature trees were not in leaf at the time the trees were planted, this was not guaranteed. Trees at the restoration site were all planted in a narrow plot which allowed them all to be equidistant from the adjacent ancient woodland. Supports and protection (1.2 Tully plastic tubes) were used for all trees to prevent deer browsing damage and promote elongation growth. Trees were harvested in September 2020. Stems were removed and roots frozen at -20° for 2 weeks until examined. A selection of twenty trees were also planted in pots, (treatment CO). The intention was to use these trees to assess the EMF community on the trees from the nursery. Studies have shown nursery trees of oak (*Quercus petreae, Q. robur*) to have an alpha diversity of EMF

of up to 11 taxa (Leski *et al.*, 2009) while Scots pine (*Pinus sylvestris*) nursery stock has been found to host up to 29 fungal taxa (Rudawska & Leski, 2021). It should be pointed out, however, that this was not a robust control. Ideally, some roots could have been taken from these trees immediately for DNA analysis. However, the plants were extremely small with very limited root systems. Therefore, the plants were potted in order to let the root system, and any colonising fungi, develop. However, due to constraints caused by the first covid lockdown, the plants had to be grown at home. This resulted in them being planted in standard compost rather than autoclaved media. The pots were protected by heavy rubber tops to prevent additional contamination, but we cannot be certain that there were no EMF spores in the potting media.

### 6.3.2 Soil sampling and analysis

A soil auger was used to collect soil at ten locations each within the ancient woodland and the regeneration site. A photographic log was taken for each core as well as depth measurements of soil strata. In preparation for chemical and pH analysis, the soils were subsequently oven dried and 2mm sieved. Approximately 2g of soil was used to measure soil pH (pH: negative log of H+ activity) using a Thermoscientific Orion Star A200 pH probe. Approximately 0.2g of soil was further 0.5mm sieved and infrared absorption analysis was carried out using a LECO elemental analyser (Leco Corporation, St Joseph, USA) to determine soil nitrogen and carbon content ($gKg^{-1}$). Finally, soil nutrients (K, Mg and P, $gKg^{-1}$) were estimated from inductively coupled plasma optical emission spectroscopy of Mehlich 3 extractants.

### 6.3.3 Leaf sampling and analysis

Leaves were removed from trees and oven dried at 70° for 3 days. The dry weight of the leaves was recorded and leaves were subsequently ground. Approximately 0.2g of leaf material was placed in 10 ml of 70% nitric acid and heated for 8 hours at 110°. The digest was filtered and diluted nutrient content assessed by inductively coupled plasma mass spectroscopy (ICP-MS) to give leaf nutrient content (K, P and Mg $\mu gg^{-1}$).

### 6.3.4 Root sampling, preparation and molecular analysis

Roots were removed from the freezer and gently washed. Since the root system was a dense plug, root fragments were chosen by cutting a small area of approximately $2cm^2$ from the root plug. This was placed in a petri dish and examined for ectomycorrhizal morphotypes. All ectomycorrhizal root tips were removed and placed in an Eppendorf tube until 100 root tips had been selected. If the aliquiot did not yield 100 colonised tips, another would be chosen, but with a limit of 5 aliquots

in order to limit processing time and standardise sampling effort. Ectomycorrhizal root tips were sent for molecular analysis, this process has been fully described in chapter 5. Roots were also collected from mature trees within the adjacent ancient woodland as part of the landscape scale survey described in chapter 5. The EMF species found on these mature trees will be included as part of the data exploration of communities at this location.

## 6.4 Data exploration

We collated sets of EMF species found on a) bait trees at the adjacent ancient woodland, b) bait trees at the regeneration woodland c) mature trees in the ancient woodland and d) pot grown trees. A venn diagram was used to summarise shared species and non-shared species. Jaccard similarity was calculated for the species shared between the bait trees, and between the bait trees and the mature oaks. Box plots were used to show differences in the distributions of soil nutrients and soil pH between treatments and at different soil horizons. Significance was tested using t-tests. Soil data were further summarized using principle component analysis (PCA). Box plots were additionally used to explore the differences in leaf weight and nutrient content for bait trees planted either in the ancient woodland or in the restoration site.

## 6.5 Results

We found that the bait trees had 31 species in common; those in the ancient woodland having a richness of 34 and those at the receptor site have a richness of 40. The receptor site bait tree richness was greater than that found on the mature trees in the ancient woodland (36). The community found on the bait trees was very similar (Jacacard similarity 0.72), but differed from the community on the mature trees (Jaccard similarity 0.27). Twenty EMF species were found on the mature trees which did not occur on the bait trees in either treatment. The bait trees in the ancient woodland did not share any additional species with the mature trees that were not already shared with the bait trees at receptor site. However, the pot trees (treatment CO) also showed a high alpha diversity of EMF of 39 species. Although we cannot be certain that no secondary infection occurred in this treatment, the EMF communities of the bait trees and the pot trees was similar (Jaccard similarity $>0.65$). The Jaccard similarities between treatments are summarised in figure 6.5. Figure 6.4 summarises the species shared between treatments and table 6.1 lists taxa found on the trees and mature trees.

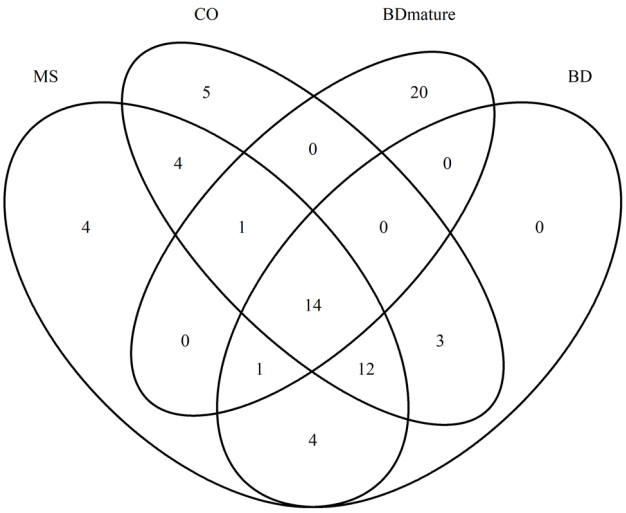


Figure 6.4: Venn diagram shows the species overlap between the bait trees at the receptor site (MS), the bait trees in the adjacent ancient woodland site (BD), the pot trees (CO) and the mature trees in the ancient woodland (BDmature). Fifteen species were common to both the bait trees and the mature oaks. The EMF species found on the different sets of bait trees and the pot trees were very similar (Jaccard similarity $> 0.65$). Nineteen species were common to the trees with twelve shared between all trees. Only eight species occurred on bait trees that were not found on the pot trees. The mature woodland trees demonstrated a different community to either set of bait trees (Jaccard similarity 0.27 between the mature trees and either set of bait trees). The richness found on the mature trees was less than that found on the bait trees at the receptor site.

Table 6.1: Summary of EMF species found on the bait trees at both treatments, on the pot trees and on the roots of mature trees in the ancient woodland. The first column lists the species, the second, third, fourth and fifth columns show the occurrence of the species on bait trees in the mature woodland (BDbait), in the pots (CO), in the restoration woodland (MSbait) or on mature oaks in the ancient woodland (BDmat).

| **Species** | **BDbait** | **CO** | **MSbait** | **BDmat** |
|---|---|---|---|---|
| Amanita fulva | 0 | 1 | 0 | 0 |
| Byssocorticium pulchrum | 0 | 1 | 1 | 0 |
| Cenococcum geophilum | 0 | 0 | 0 | 1 |
| Clavulina | 0 | 1 | 0 | 0 |
| Clavulina amethystina | 0 | 0 | 0 | 1 |
| Clavulina coralloides | 0 | 0 | 0 | 1 |
| Cortinarius acutus | 1 | 1 | 0 | 0 |
| Cortinarius anomalus | 0 | 0 | 0 | 1 |
| Cortinarius punctatoides | 0 | 0 | 0 | 1 |
| Cortinarius2 | 0 | 1 | 0 | 0 |
| Craterellus tubaeformis | 1 | 1 | 1 | 0 |

*Continued on next page*

Table 6.1 – *Continued from previous page*

| **Species** | **BDbait** | **CO** | **MSbait** | BDmat |
|---|---|---|---|---|
| Elaphomyces muricatus | 1 | 1 | 1 | 1 |
| Hebeloma alvarense | 1 | 1 | 1 | 0 |
| Hebeloma pusillum | 1 | 1 | 1 | 0 |
| Hebeloma1 | 1 | 1 | 1 | 0 |
| Hebeloma2 | 1 | 1 | 1 | 0 |
| Hydnotrya tulasnei | 0 | 1 | 0 | 0 |
| Imleria badia | 0 | 0 | 0 | 1 |
| Inocybe petiginosa | 0 | 0 | 0 | 1 |
| Inocybe rufoalba | 1 | 0 | 1 | 0 |
| Laccaria amethystina | 1 | 1 | 1 | 1 |
| Laccaria laccata | 1 | 1 | 1 | 1 |
| Laccaria proxima | 1 | 1 | 1 | 0 |
| Lactarius camphoratus | 0 | 0 | 0 | 1 |
| Lactarius chrysorrheus | 1 | 1 | 1 | 0 |
| Lactarius decipiens | 0 | 0 | 0 | 1 |
| Lactarius quietus | 1 | 1 | 1 | 1 |
| Lactarius subdulcis | 0 | 0 | 0 | 1 |
| Lactarius tabidus | 1 | 1 | 1 | 1 |
| Melanogaster ambiguus | 0 | 0 | 0 | 1 |
| Melanogaster1 | 0 | 0 | 1 | 0 |
| Otidea bufonia | 0 | 0 | 1 | 0 |
| Paxillus involutus | 1 | 1 | 1 | 1 |
| Peziza succosa | 1 | 1 | 1 | 0 |
| Piloderma sphaerosporum | 0 | 0 | 1 | 0 |
| Russula amoenolens | 1 | 1 | 1 | 1 |
| Russula atropurpurea | 0 | 0 | 0 | 1 |
| Russula densifolia | 1 | 1 | 1 | 1 |
| Russula fragilis | 1 | 1 | 1 | 1 |
| Russula ionochlora | 1 | 1 | 0 | 0 |
| Russula nobilis | 0 | 0 | 0 | 1 |
| Russula ochroleuca | 1 | 1 | 1 | 1 |
| Russula peckii | 0 | 0 | 0 | 1 |
| Russula puellaris | 0 | 0 | 0 | 1 |
| Russula1 | 0 | 0 | 1 | 0 |
| Russula2 | 1 | 0 | 1 | 0 |
| Russula3 | 1 | 1 | 0 | 0 |
| Scleroderma areolatum | 0 | 0 | 0 | 1 |
| Scleroderma citrinum | 1 | 1 | 1 | 1 |

*Continued on next page*

Table 6.1 – *Continued from previous page*

| **Species** | **BDbait** | **CO** | **MSbait** | BDmat |
|---|---|---|---|---|
| Scleroderma verrucosum | 0 | 0 | 0 | 1 |
| Sebacina incrustans | 0 | 1 | 1 | 1 |
| Sebacina1 | 0 | 1 | 1 | 0 |
| Sebacina3 | 1 | 0 | 1 | 0 |
| Thelephora albomarginata | 1 | 1 | 1 | 0 |
| Thelephora terrestris | 1 | 1 | 1 | 1 |
| Tomentella botryoides | 0 | 1 | 1 | 0 |
| Tomentella coerulea | 0 | 0 | 0 | 1 |
| Tomentella ellisii | 1 | 1 | 1 | 0 |
| Tomentella papuae | 1 | 1 | 1 | 0 |
| Tomentella punicea | 0 | 0 | 0 | 1 |
| Tomentella stuposa | 1 | 0 | 1 | 1 |
| Tomentella2 | 0 | 1 | 0 | 0 |
| Tomentellopsis echinospora | 1 | 0 | 1 | 0 |
| Tomentellopsis submollis | 1 | 1 | 1 | 0 |
| Tuber anniae | 0 | 1 | 1 | 0 |
| Tuber puberulum | 1 | 1 | 1 | 1 |
| Xerocomellus cisalpinus | 1 | 1 | 1 | 1 |
| Xerocomus ferrugineus | 0 | 0 | 0 | 1 |
| Total alpha diversity | 34 | 39 | 40 | 36 |

The plot of the principle component analysis in figure 6.6 shows the differences between the soils in the two treatments. All measured soil properties make roughly equal contributions to the first principle component, with the contribution of soil pH being negative, due to the the negative correlation between soil organic matter and soil pH. Soil organic matter content was lower at the restoration site (MS) and soil

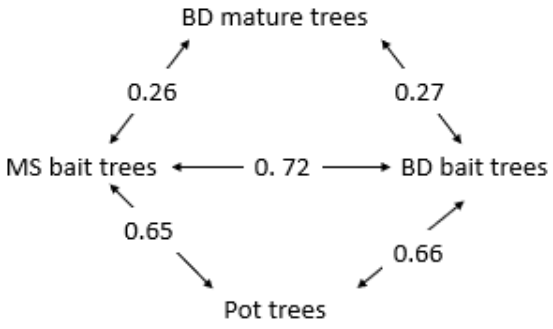


Figure 6.5: The figure summarises the jaccard similarities between the treatments. All trees had very similar communities (treatments MSbait, BDbait and Pot trees, whilst the communities differed from that on tha mature trees.

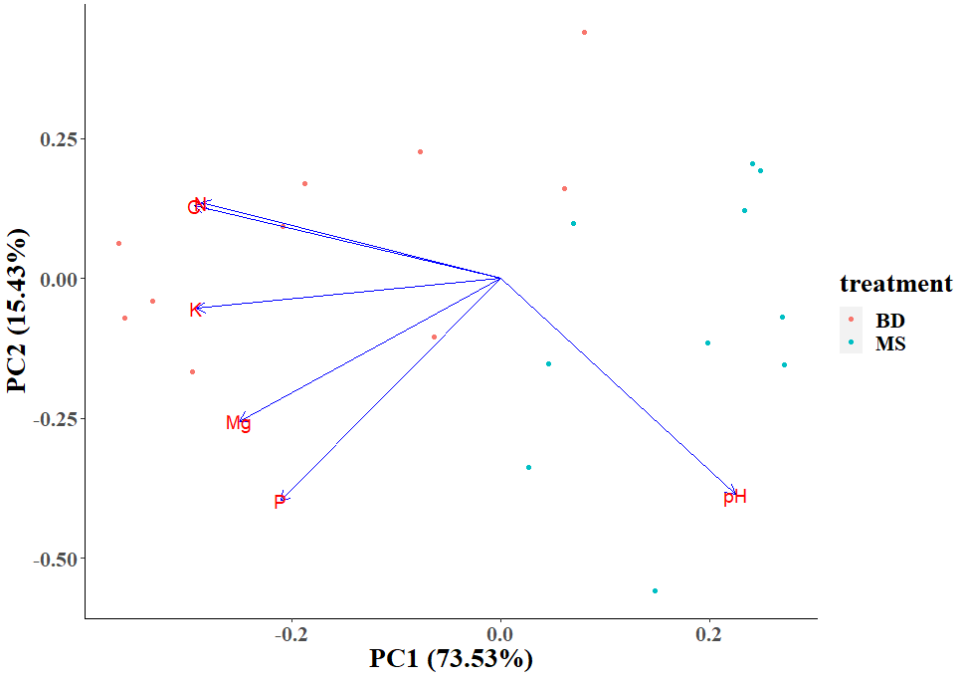


Figure 6.6: PCA-ordination of the soil properties in the two treatments, the ancient woodland (BD) and the restoration site (MS). The first principle component has approximately equal contributions from all soil properties, only soil pH makes a positive contribution. Soil pH and P make large negative contributions to the second principle component. The clustering of the points demonstrates the well defined difference between the soils of the two treatments.

pH higher. The well defined clusters of the points representing the two treatments demonstrates the clear differences in the soils.

The box plots of soil nutrient distribution in figure 6.7 demonstrate the differences in the distribution of soil nutrients between the translocated soil and an adjacent ancient woodland. The box plots show the distribution of elements in the top three soil layers. In the ancient woodland, loose litter was first removed and hence layer 1 is the upper organic soil, which was well defined. At the translocation site, very little litter was present and soil layer 1 was visibly lower in organic matter. This is seen in the chemical analysis. The carbon and nitrogen contents of the upper two soil layers are significantly different between the two treatments (t-test p value 0 and 0.002 for C and N respectively). Values for all soil nutrients are significantly different in the upper two soil layers between the two treatments, apart from P and Mg in layer 2 (t-test p value 0.6 and 0.5 for P and Mg respectively). Soil pH is significantly different between the two treatments (t-test p values = 0, 0.002 respectively for layer 1 and 2 respectively) and higher at the receptor sight with a mean of 5.12 in layer 1 and 5.2 in layer 2, compared to the ancient woodland, 4.08 in layer 1 and 3.8 in layer 2. The mean values for the soil properties are shown in table 6.2.

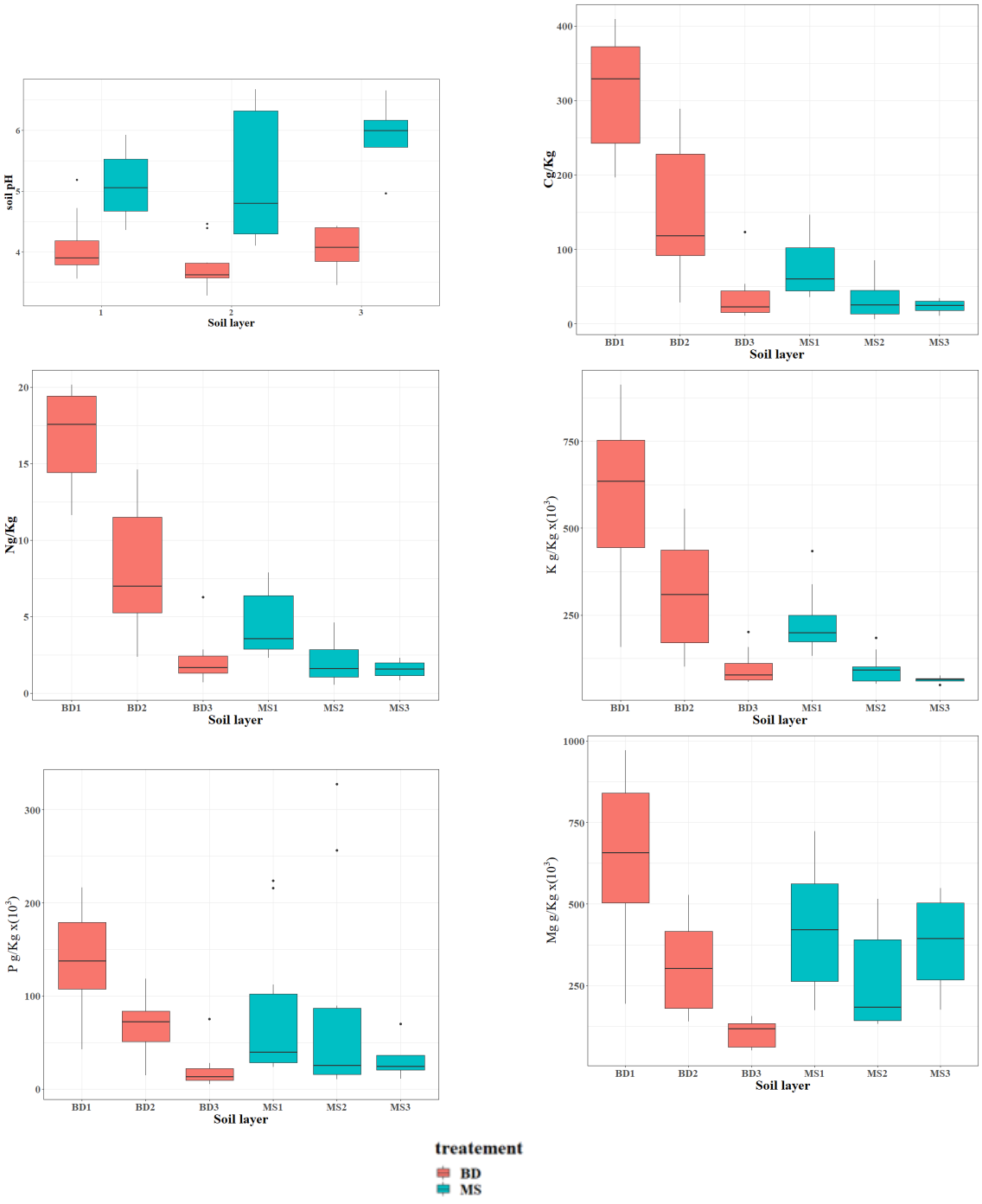


Figure 6.7: Box plots showing distribution of soil elements (as measured by ICP-OES after Mehlich 3 extraction) at the receptor site (MS) and within the adjacent ancient woodland (BD). The layers from 1 to 3 denote the three upper soil layers from each treatment. Within BD, layer 1 will apply to the organic soil layer found below the loose litter. At the receptor site, layer 1 is likewise the upper soil layer below any loose litter, which in general was absent, but the soil was less organic. This is clear from the second plot showing the carbon content of the soils, as determined by infrared absorption analysis. The soil pH was higher at the receptor site, while nitrogen, carbon and potassium were lower.

Table 6.2: Summary of soil properties for three soil layers. MS refers to soils at the translocation site, BD refers to soils collected in an adjacent ancient woodland. The soil layers are labelled 1, 2 and 3. Where layer 1 is the uppermost layer and layer 3 the layer furthest from the soil surface. In the ancient woodland (BD), layer 1 means the organic soil horizon, since this well defined at that at that location. At the receptor site, the relocated soil had fewer horizons and lacked a clear organic upper soil layer.

| Treatment | Soil layer | Soil property | Mean (g/Kg) |
|---|---|---|---|
| MS | 1 | N | 4.48 |
| BD | 1 | N | 16.91 |
| MS | 2 | N | 1.96 |
| BD | 2 | N | 8.03 |
| MS | 1 | C | 74.8 |
| BD | 1 | C | 307 |
| MS | 2 | C | 31.1 |
| BD | 2 | C | 151 |
| MS | 1 | K | 229 |
| BD | 1 | K | 586 |
| MS | 2 | K | 95.4 |
| BD | 2 | K | 308 |
| MS | 1 | P | 80.7 |
| BD | 1 | P | 136 |
| MS | 2 | P | 86.1 |
| BD | 2 | P | 67.2 |
| MS | 1 | Mg | 423 |
| BD | 1 | Mg | 627 |
| MS | 2 | Mg | 263 |
| BD | 2 | Mg | 306 |
| Treatment | Soil layer | property | -log of H+ activity |
| MS | 1 | pH | 5.12 |
| BD | 1 | pH | 4.08 |
| MS | 2 | pH | 5.2 |
| BD | 2 | pH | 3.8 |

The distribution of values for leaf nutrient content is shown in figure 6.8. Whilst the values for Mg and P are similar between treatments, the leaves of bait trees in the ancient woodland contained significantly more K (t-test p value 0.026).

The mean leaf weight for bait trees planted at the restoration site was significantly greater than those planted in the ancient woodland (0.59g, 0.37g, for restoration site and ancient woodland respectively, t-test p value 0.05). Five of the twenty trees planted in the ancient woodland were dead with one missing, whilst two were dead in the restoration site.

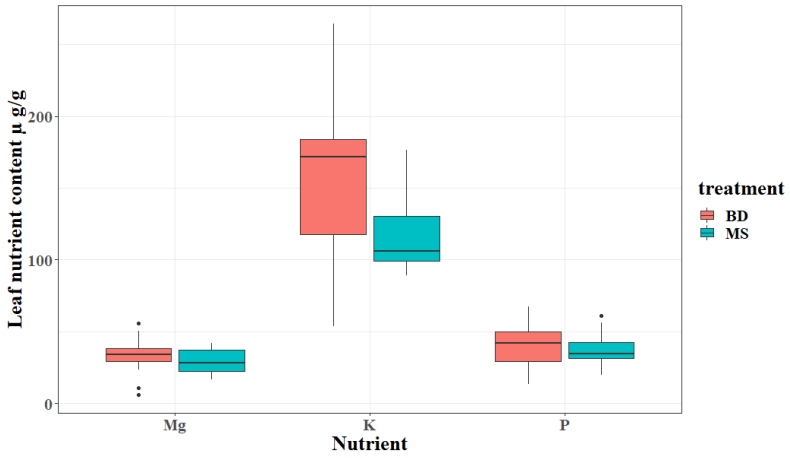


Figure 6.8: The box plots show the distribution of the leaf nutrient content (as measured by ICP-MS after nitric acid digestion) of the leaves in each treatment.The values for Mg and P not significantly different, but leaves of bait trees in the ancient woodland had significantly more K (t-test p = 0.026).

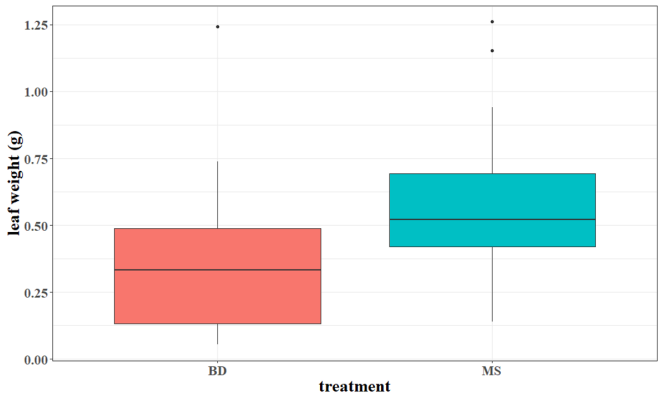


Figure 6.9: The box plots show the distribution of the leaf weights of the leaves in each treatment. The mean leaf weights of the bait trees planted at the restoration site (MS) is higher, and just significant at the level p = 0.05.

## 6.6 Discussion

We conducted a pilot study in order to explore the use of bait trees as a means to assess inoculum potential of translocated soil. We planted bait trees in a translocated soil at a woodland restoration project, within an adjacent ancient woodland and in pots. After one season we harvested these trees and used DNA analysis to ascertain the EMF colonising their roots, and also the EMF colonising roots sampled from mature trees in the ancient woodland. We recorded leaf weights and analysed leaf nutrient contents of the bait trees. In addition, we took soil samples from the restoration site and the ancient woodland. Although we expect soils to be different in these treatments, we believe that it is useful to present this data in order to provide context for the different soil properties experienced by EMF in each treatment. We will then go on to discuss improvements to the methodology such that it may be better used to address our hypotheses.


Figure 6.10: Typical root growth between the treatments. Bait trees in both the restoration site and the mature woodland demonstrate very little root growth. However, the air pruned trees are capable of considerable root growth, as was seen in some planted which we grew in pots in a good potting media. This lack of root growth will limit leaf growth and EMF colonisation rate.

### 6.6.1 Leaf weights and nutrients and root growth

The leaf weights for the trees planted at the restoration site were significantly greater than those planted in the ancient woodland. This was most likely due to poor light conditions or restrictions in precipitation reaching the woodland floor due to the closed canopy in the mature woodland resulting in poor growth. In addition, it was clear from root observations, that root growth was limited for both sets of trees. In most cases the roots did not extend into the surrounding soil. This was related to the planting method and surrounding soil type, rather than the initial status of the small air-pruned trees when they arrived from the nursery. That is, the small trees were planted into compacted soil, and, in the case of those in the mature woodland, tended to receive little water. It was evident that the poor growth was not related to the nursery stock itself, since the pot trees showed large amounts of root growth. Typical root systems are shown in figure 6.10. The stunted root systems will result in reduced leaf growth. This may have some implications for tree planting if we wish to enhance mycorrhizal colonisation. Greater root growth and hence EMF colonisation might occur if bait trees are planted into lightly dug planting holes. We also saw that the trees in the mature woodland had significantly higher potassium levels in their leaves. This could be related to the higher levels of potassium in the soil in that treatment due to the greater amounts of organic matter.

### 6.6.2 Soil properties

Visual examination of the soil cores demonstrated that the ancient woodland had clearly defined horizons, with deep litter and a clear organic horizon. We expect this to influence EMF communities, since different EMF have been shown to access different forms of nitrogen, with some taxa able to access organic nitrogen, whilst others do not (Abuzinadah *et al.*, 1986; Finlay *et al.*, 1992). For instance, *Laccaria laccata* can readily access nitrogen in the form of ammonium, but not when in the form of proteins (Abuzinadah *et al.*, 1986). Similarly, when only protein sources are available, some EMF taxa have been shown to be less successful in transferring nitrogen to their hosts. *Paxillus involutus*, for example, was found to transfer less nitrogen to *Betula pendula* than *Hebelome crustuliniforme* in pot experiments when nitrogen was available in protein form (Abuzinidah *et al.*, 1989b). These functional differences between EMF species will therefore play a part in determining the EMF taxa found in an ancient woodland with highly organic soils, compared to a disturbed soil with lower values of soil carbon and nitrogen.

Principle component analysis, see figure 6.6, shows the clustering of the two treatments according to the soil properties, with higher soil nutrients and lower soil pH explaining most of the variation in the soil data. Table 6.2 shows the higher mean values for soil nutrients and lower pH for samples taken in the ancient woodland, and the distribution of the soil properties is shown in figure 6.7. The higher soil pH is expected due to, for example soil mixing (Borchers *et al.*, 2021), and loss of organic matter (Schwenke *et al.*, 2000; Banning *et al.*, 2008; George *et al.*, 2010). However, it must be borne in mind that the pH of the original donor site is not known, and could have been higher than that in the adjacent ancient woodland sampled here. The box-plots in figure 6.7 also demonstrate the clear soil horizons found in the ancient woodland and the more homogeneous soil found at the restoration site where the soil properties are similar across the layers. They also show the much higher values of carbon and nitrogen at the ancient woodland in the upper soil layers, compared to the restoration site, an indication of the higher organic matter content of the ancient woodland soils.

### 6.6.3 EMF taxa

We found that bait trees were colonised by a high diversity of early successional taxa, such as *Laccaria amethystina, L. laccata, L. proxima, Paxillus involutus* and *Thelephora terrestris*. These taxa have all been shown to have high infectivity in spore germination experiments (Ishida *et al.*, 2008; Nguyen *et al.*, 2012; Miyamoto & Nara, 2016), or occur in early successional habitats (Nara *et al.*, 2003; Collier & Bidartondo, 2009; Olchowik *et al.*, 2021). Likewise, *Tomentella* spp. have been found to be early colonisers after fire, or to colonise successfully from soil samples

(Baar *et al.*, 1999; Buscardo *et al.*, 2010; Miyamoto & Nara, 2016). However, we also found that the pot trees had a high diversity of EMF taxa. This suggests that the bait trees themselves may have introduced a high diversity of EMF taxa to the restoration site, and that we cannot distinguish between taxa already present on the trees, and those collected from the soil. In addition, the bait trees in the mature woodland were not colonised by any species not colonising the trees at the restoration site, suggesting that they did not collect any additional EMF taxa via hyphal contact. All species found at the restoration site, except two, produce above ground fruiting bodies, allowing wind dispersal. This introduces the added difficulty that we cannot eliminate dispersal from the adjacent mature woodland as an inoculum source. In their study of trees invading low land heathlands in the UK, Collier & Bidartondo (2009) found eleven species of EMF colonising trees adjacent to woodland, and therefore it seems unlikely that the high alpha diversity here would be solely the result of dispersion. However, we do not currently have sufficient data to definitively differentiate these two processes. The nursery trees had very immature root systems, and it seems unlikely that they would support high levels of colonisation, however, other work has shown that nursery grown trees may support a high diversity of EMF taxa (Leski *et al.*, 2009; Rudawska *et al.*, 2019; Rudawska & Leski, 2021). Since the pot trees were not grown in sterile media, we cannot eliminate the possibility that the taxa found on the roots was not due to secondary infection, however, the similarity between the communities would seem to suggest otherwise.

We note that the community on the bait trees differed to that on the mature trees. It may be the case that in the single season we allowed for this experiment, colonisation of bait trees was restricted, particularly since the trees demonstrated very little growth. We do not know whether the communities on the trees might change over time to more closely resemble those of the mature wood. We would expect that the EMF initially colonising the trees would be early successional taxa, but we also want to know whether over time, a high diversity of later successional taxa is present and to ensure no net biodiversity loss. Therefore continued regular monitoring is required.

The pilot study therefore demonstrates several useful issues which can be addressed and modified in a full experiment. Firstly, bait trees could be grown aseptically rather than using nursery stock. This would allow us to clearly differentiate between EMF taxa collected in the different treatments. Secondly, bait trees could be planted at different distances from inoculum sources or in adjacent sites where soil was not translocated and used in conjunction with spore traps. This would allow the role of dispersion to be explored in more detail. Thirdly, bait trees in the mature woodland need higher light conditions, preferably matching those in the restoration woodland. To achieve this, they could be planted around a coppiced mature oak.

This would additionally allow more precipitation to reach the trees which would not be beneath the canopy, and hopefully relieve some water stress. The coppiced tree would also act as a source of inoculum allowing colonisation from living hyphae. Finally, soils could be prepared before planting the bait trees in order to maximise root growth rather than causing root restriction. That is, soils could be lightly dug such that trees are planted into softer, loose soil.

## 6.7 Conclusion

We found that bait trees planted in a translocated soil, a mature woodland, and in pots had a similar high alpha diversity of EMF colonising their roots. We therefore conclude that nursery grown trees cannot are not ideal bait trees for this experiment, and that aseptically grown stock is required. We also note that the introduction of additional components to the experiment, such as spore traps, would be useful in order to assess dispersal processes. We found that growth of bait trees in the mature woodland was limited compared to those at the restoration site, and therefore suggest that higher light and moisture may be required, and could be supplied by planting bait trees around a coppiced oak. Finally, steps could be taken to improve root growth, which was extremely restricted, such as lightly turning soil in the planting hole.

An essential factor in ancient woodland mitigation is the retention of ancient woodland taxa, in addition, to ensure no loss of biodiversity, we also wish to retain rare species. In the case of EMF, this is also important to ecosystem processes; different fungi have different functionality and inhabit different ecological niches. For example, some are better at obtaining nitrogen for their hosts from organic sources. Therefore, as woodlands mature, the EMF community changes in order to fit changing soil conditions. If the EMF community in restoration woodlands does not change over time, this may have important negative implications for tree health. We saw here that the EMF communities on mature trees was different to that on bait trees in both treatments. This study seems to imply that in one season, we saw no colonisation of bait trees by later successional taxa. Therefore, we need to then address the next stage in this mitigation process, namely, will the EMF communities in these new woodlands change over time to resemble those in ancient woodlands and include a diverse set of rare and ancient woodland indicator species?

Several areas of research are fundamental to answering this question. Firstly, what are ancient woodland EMF communities? Our work in chapter 5 goes some way to addressing this issue, but more data is needed from newer woodlands in order to identify ancient woodland indicator species. Secondly, what are rare species? Lack of comprehensive biological recording of EMF makes this difficult to ascertain conclusively.

Thirdly, continued monitoring of the EMF communities of restoration sites is essential in order to observe changes in EMF taxa. If it was then observed that community structure was static, perhaps due to lack of dispersal, mitigation process could be explored in order to attempt to introduce new species.

# Chapter 7

# Conclusion

Each chapter of this thesis sought to provide data regarding the role of mycorrhizal fungi in woodland ecosystems. The topics ranged from a theoretical approach to answering the question, 'what are the traits of specialist EMF?' to a detailed analysis of the mycorrhizal type of British woody plants and a landscape scale studies of the drivers of EMF community assemblages. In this conclusion, we will summarise the outcomes of these topics, and discuss in more detail, possible directions for future work.

## 7.1 Traits of specialist and generalist EMF

In chapter two, we sought to answer the question, at least in part, what is a specialist ectomycorrhizal fungus? By this we mean, what traits are particularly associated with specialism as opposed to generalism. Knowledge of which EMF demonstrate either trait can be obtained empirically through repeated biological records which demonstrate the host range of EMF taxa. We wanted to explore the potential functional differences of these two traits. Using the replicator equations, we were able to present contrasting definitions of generalists and specialists when in symbiosis with trees of low or high receptivity. These definitions were generated from the steady state of the replicator equations, which produced two possible outcomes. These can be partially summarised as either:

1) Specialist EMF are fitter than generalists when in association with high receptivity trees.

AND High receptivity trees are fitter than low receptivity trees when in association with generalist EMF.

Or the converse:

2) Generalist EMF are fitter than specialists when in association with high receptivity trees.

AND High receptivity trees are fitter than low receptivity trees when in association with specialists.

The replicator equations do not tell us which of these opposing outcomes is true, to address this, empirical data is required. Even so, they do point out interesting features of mycorrhizal symbiosis. For instance, we may suppose that specialists and their hosts have co-evolved, and that therefore there are fitness benefits to specialism. But are those benefits applied to the fungal symbiont, the host plant or both? If specialists are fitter as a result of this trait, it feels natural to assume that hosts are also fitter when colonised by those specialist EMF. In functional terms, if a specialist EMF is able to extract more carbon from its host, say, then we might assume that, in return, it supplies more nutrients. However, the replicator equations show that this reciprocal relationship is not necessarily going to hold. For example, we might review experiments detailing nutrient exchange between a host plant and multiple EMF taxa. Whilst we might expect to see that a specialist has a greater carbon sink strength than a generalist, the results of the replicator equations tell us that we will not necessarily see any consistent results regarding the nutrients supplied by the different fungal taxa to the host. The trait of specialism and generalism as experienced by hosts is related to the relative benefits to different hosts conferred by a single fungal type. That is, we expect to see that specialists confer greater benefit to non-preferred host plants than they do to their hosts. The mechanism behind this is probably the lower relative carbon cost experienced by the non-host. In other words, the specialist extracts less carbon per unit of nutrient supplied to a non-host than it does to its host.

In order to confirm or refute the definitions supplied by the replicator equations, empirical data is required. This is difficult, as it demands experiments which measure fitness benefits, which are hard to quantify. The first requirement, therefore, is to decide on a suitable proxy for fitness. For slow growing organisms such as trees, seed set may be unrealistic. An alternative might be biomass (Younginger *et al.*, 2017). Similarly, mycelial growth rate might be considered as a proxy for fungal fitness (Pringle & Taylor, 2002). If these were accepted, the experimental design would look something like that in figure 7.1.

Another aspect of this model which requires verification is the tree traits of high and low receptivity. Several pieces of work suggest that this is a real phenomenon (Taudiere *et al.*, 2015; Pither *et al.*, 2018). However, there is the potential that both these results suffer bias due to the data gathering method - which was not specifically designed to answer this question. In Pither *et al.* (2018), for example, records submitted to the UNITE fungal records database were scrutinised, and a tally of the host tree for each fungal record was made. It may be the case that researchers studying the EMF of pine, for instance, generally sampled these in mature forests, where the number of EMF symbionts may be high, and this could give a bias to the data found within UNITE. This would then give the impression that pines are exclusively high receptivity trees. Similarly, *Betula* spp tend to be early successional

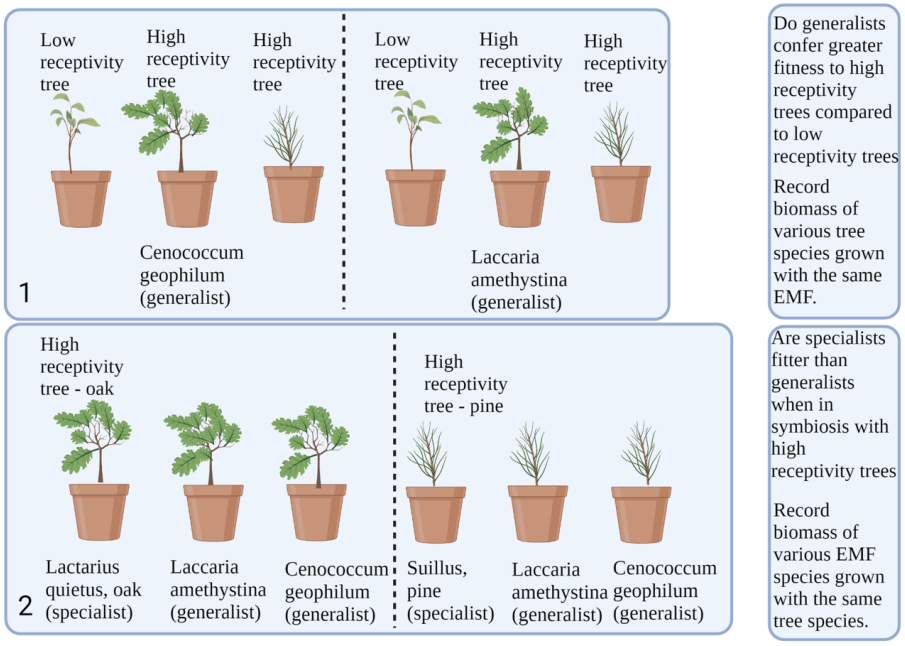


Figure 7.1: Graphic depicting the outline for experimental design required to verify evolutionary game theory models. Box 1 summarises an experiment in which trees with different traits (high and low receptivity) are grown with an EMF with the trait of generalism. The dotted line indicates that several repeats of the experiment would be required, with different generalists. If the tree biomass is used as a proxy for fitness, then the biomass of the different tree species within each repeat would be compared for significant differences. Box 2 summarises the second part to the experiment. Different mycorrhizal taxa, some specialist and some generalist, are grown with a single tree species. The dotted line indicates that repeats should take place with different trees. If mycelial growth is used as a proxy for fitness, then the difference in mycelial mass of each EMF taxa within each repeat would be compared.

trees, if these are usually sampled in early successional habitats, where EMF inoculum is scarce (Collier & Bidartondo, 2009), this may give the impression that this tree has low receptivity. Therefore, in order to exclude the environmental effect, empirical data specifically targeted at answering this question is required, in which putatively low receptivity trees are sampled in mature habitats. Hazel, birch and willows, (*Betula* spp., *Coryllus avellana, Salix* spp) have been suggested as having low receptivity. The species richness of EMF colonising hazel in the Atlantic hazel forests of the north west coast of Scotland would be of interest, as these woodlands are amongst the most ancient in the British Isles. Similarly, birch can often be found with oak (*Quercus petraea*) in mature Scots pine (*Pinus sylvestris*) forests (Lake *et al.*, 2015).

## 7.2 Mycorrhizal types of British woody plants

In chapter three, we conducted an in-depth literature review in order to ascertain the mycorrhizal type of British woody plants. This work was carried out in order to

allow the analysis described in chapter 4. Before carrying out that analysis, we felt it was important to understand the strength of data which assigns mycorrhizal type. Although FungalRoot (Soudzilovskaia *et al.*, 2020), for example, is an up to date, extensive database summarising the literature of mycorrhizal type for nearly fifteen thousand plant species, data is still lacking for many British plants. Rather than use that data without question, we decided to scrutinise all data detailing mycorrhizal type for British woody plants. This focus highlighted the fact that 66% of British woody plants were lacking in data, that is, at most one piece of empirical evidence could be found confirming mycorrhizal type. Databases such as FungalRoot, are not designed to be used uncritically, scrutiny by the user is important (Soudzilovskaia *et al.*, 2022), and therefore we see this work as an important adjunct, as a result of which we are able to highlight taxa for which we must be wary of designations of type, and also suggest areas in which more work is required in order to ensure these designations are robust and can be used unequivocally. If we assumed the mycorrhizal type was conserved within genus, we identified eighteen species for which data was sparse, that is, we found one or no empirical evidence of type. Of these eighteen however, willows (*Salix* spp.,) stand out as having high cover, and are therefore potentially more important in the landscape. Willows are additionally interesting since some are AM type and others are EM type. Hence, data for one species cannot be extrapolated across the genus. We therefore suggest that empirical data across willow species, which looks for both EM and AM colonisation coincidentally, is required.

## 7.3 British landscape scale distribution of mycorrhizal types

In chapter three, we also briefly looked at the distribution of mycorrhizal type across the landscape using the broad habitat codes for British woody plants published in Plantatt (Hill *et al.*, 2004). We saw some expected results, such as bog, fen and heath habitats are dominated by ericoid mycorrhizal type plants. We also saw that woodland habitats contain a large number of AM type woody plants, but these are light demanding understory species, and hence will probably show a reduced occurrence in mature woodlands. In addition to this investigation, it may be interesting to use spatial analysis of mycorrhizal type conducted using species distribution data. Knowledge of the mycorrhizal traits of habitats is important, since we know that these influence ecosystem function. For instance, we saw in chapter four of this work that the proportion of AM type trees in woodlands positively affects understory species richness. But the influence of mycorrhizal type is much broader than this (Wurzburger & Clemmensen, 2018). For instance, the mycorrhizal type of trees is an important predictor of soil organic matter (SOM) dynamics. For

example, Craig *et al.* (2018) found that EMF type tree stands contain more SOM in the top soil, but this pattern does not hold at greater soil depths. This is important for carbon sequestration, as it implies that AM type stands in woodlands may act as more stable carbon pools than EM type stands. Plant occurrence data would therefore allow us to identify areas within the UK which are of particular importance for certain ecosystem services. To continue this work, we would therefore like to use Botanical Society of Britain and Ireland (BSBI) plant occurrence data for all British woody plants. The BSBI data contains the location of every woody plant over seven time periods from 1930 to 2020, and hence further allows exploration of the changes to ecosystem services offered by different habitats over time.

## 7.4 Mycorrhizal mediation hypothesis

Chapter four was a response to the first Covid lockdown, which occurred as roots and soils were being processed in the lab from our large landscape survey, described in chapter 5. Since we were not initially sure when the laboratories would be accessible, this chapter was planned using an existing data-set, hence allowing progress on the PhD during lockdown. In this work, we sought to answer the question, does the proportion of AMF type trees influence herbaceous plant species richness in broadleaved woodlands in Britain? We found a positive effect, which supports the mycorrhizal mediation hypothesis (Veresoglou *et al.*, 2017), and we published our findings in the New Phytologist (Guy *et al.*, 2022). We included soil pH, soil organic matter and year of survey as effects in this model, and whilst soil pH had the largest effect size, the relative number of AM type trees in 103 broadleaved woodlands across Britain had a significant effect on understory richness. This result has important implications for woodland planning and management. The analysis in chapter four was targeted at variables which we knew to be precise at plot level, but it would be interesting to extend this modelling to include other effects which are known to influence plant diversity. This is of particular interest, since no other work currently considers the effect of mycorrhizal mediation, in conjunction with other factors, on woodland plant richness. Knowledge regarding the most important factors influencing woodland richness is vital, since it allows the implementation of effective management strategies. For instance, we know soil pH is important, but there is little we can do to change this. However, if we found woodland area to be more important than the proportion of AM type trees, then there is an argument for increasing the size of a site, as opposed to planting more AM type trees within existing woodlands. Several studies show woodland area to be a significant factor influencing woodland plant richness (Peterken & Game, 1984; Dzwonko & Loster, 1988, 2008; Brudvig & Damschen, 2011). Surrounding land use could also be considered as an explanatory variable, in order to incorporate effects related to connectivity

and eutrophication from farmland. The Bunce survey data is extremely precise, and therefore climate data would be more difficult to incorporate without sacrificing this precision somewhat. In addition, local landscape effects, such as slope or aspect, might be important. For example, O'Brien (2000) points out that inclusion of topographic relief increases the explanatory power of models over using climatic gradients alone. Topographic variables are available within the Bunce dataset, and the work of O'Brien (2000) is a good argument for their inclusion. Habitat diversity is also an important factor for woodland plant richness (Dzwonko & Loster, 1988; Dumortier *et al.*, 2002). The importance of habitat diversity is seen in British woodlands where increasing homogeneity due to lack of management has lead to reduced species richness (Keith *et al.*, 2009). However, habitat diversity is difficult to quantify without using a circular argument which incorporates the response variable. But clearly, a woodland which includes several habitat types will have the potential for a richer understory. For instance, a site may include a mixture of plots composed of ash/field maple (*Fraxinus excelsior, Acer campestre*), oak, (*Quercus robur*) and alder (*Alnus glutinosa*). These will have different understory plant assemblages due, in part, to the different soil types on which they occur. For instance, ash/field maple stands will occur on base rich soils, whereas oak/birch stands usually occur on more acid soil types, whereas alder woodlands occur in nutrient rich riparian zones. So a woodland which incorporates a selection of these habitats should be more species rich due to the inclusion of several different plant assemblages. A value which describes these vegetation types is the National Vegetation Classification (NVC) (Hall *et al.*, 2004). These NVC codes may give a way to incorporate habitat diversity as an effect, by using a count of the number of different NVC codes per woodland. Whilst the NVC code itself may be correlated with richness, this does not apply to the count of codes. For example, a woodland could include multiple species poor plots, such as NVC codes W13, W14, W15 or W16, or a small number of species rich plots, such as W12. Similarly, Báldi (2008) used CORINE land cover codes to count the number of habitat types in Hungarian nature reserves and hence explore the relationship between reserve richness, area and habitat heterogeneity. Understory richness has also been shown to correlate positively with woodland management (Schmidt, 2005; Boch *et al.*, 2013), although this effect does not necessarily extend to non-plant taxa Paillet *et al.* (2010). Woodland management can be incorporated as an effect through a count of certain features which appear in the Bunce survey data set, such as signs of brash piles, timber stacks, and coppiced stools.

We also noted in the discussion of chapter four, that we could not ascertain whether the understory richness was driven by inoculum potential or AMF richness, and therefore, it would be useful to address this question. Hence, we suggest that an important development of this work, in order to examine the possible effect of AMF richness on understory richness, would be collect data on the AMF richness

in a subset of the plots of the Bunce survey and explore the use of this value as an explanatory variable.

## 7.5 Ectomycorrhizal communities of oak in the UK

Chapter five describes the outcome of a large landscape scale survey of the EMF community of oak. This was the largest part of the PhD research, requiring four months of sampling across nineteen woodlands, nine months laboratory time processing roots, followed by an additional four months preparing soils, carrying out Mehlich 3 extraction, LECO analysis and pH measurements on over 300 soil samples. In this section of the work, we wanted to both gather biological records of the EMF of oak, and explore the drivers of community assemblages. The first is important as it builds on fundamental data of EMF taxa and allows more accurate assessment of, for instance, which are rare species, which are oak specialists and what is the expected species richness of oaks. Without information of this sort, we cannot assess below ground woodland health, because we are unable to make judgements as to whether the EMF community is 'healthy' that is, does it contain a set of functionally diverse EMF. Similarly, we cannot provide answers regarding conservation value, without knowing whether a woodland hosts rare or specific taxa. For both these tasks, we need more information regarding the EMF communities of mature, healthy forests. To that end, we identified 115 EMF to species level, with 53 being recorded with oak for the first time. The survey confirms that *Lactarius quietus* tends to associate with oaks and that species such as *Lactarius amethystina, L. tabidus, Russula ochroleuca* and *R. fragilis* are common on oaks across a range of environmental and climatic gradients. Comparison with other work tells us that these species are also generalists and associate with many other tree types. What is more difficult to assess are the rare species. In a single survey such as this, species may appear rare only because sampling effort was insufficient. Repeated sampling is an option to address this issue, but costly and time consuming. Therefore, it would be useful to extend this section of the work to an extensive in-depth review of the literature in order to ascertain, for instance, whether other surveys consistently find certain species to be rare. We conducted a comprehensive review of the literature for EMF of oak, a starting point would be to compare the occurrence of species within these studies. Secondly, to extend this review to other host trees. This would allow, both an analysis of rare and common species, but also add to information regarding host specific taxa. Further, where available, environmental data could be included in such a summary, such as soil pH, rainfall and average temperature. This would then be the start of a trait data base for EMF. This could utilise, and build upon, large meta-analysis and sampling projects such as those conducted by Rosinger *et al.*

(2018) and van der Linde *et al.* (2009).

An important question for woodland conservation in general is, do indicator species of EMF exist for ancient woodlands, and if so, which species are indicators? We know that EMF communities change over time (Visser, 1995; Jumpponen *et al.*, 1999; Nara *et al.*, 2003; Twieg *et al.*, 2007), so that, by definition, ancient woodland taxa will be these later successional species. However, when we talk about ancient woodland indicators, we mean, is there a subset of these later successional species that almost always or only occur in very old forests. There is some work to suggests that this is not the case. Spake *et al.* (2016) found that EMF communities in seven, 180 year old woodlands in the UK were indistinguishable from those in woodlands over 1000 years old. Similarly, Twieg *et al.* (2007) found that 65 year old Douglas-fir stands were similar to 100 year old stands in British Columbia, Canada. In a meta-analysis, Spake *et al.* (2015) suggest that EMF may approach values found in undisturbed woodlands after 90 years. However, it is worth noting that the empirical data on which these observations are based is not large, and if we are dealing with rare taxa, greater sampling effort may be required for their detection. When examining 41 forest fragments in Belgium Boeraeve *et al.* (2018) find that forest age affects EMF assemblages on hazel *Corylus avellana*. In light of the large number of ancient woodland that are either being lost or disturbed in the UK, recently estimated to be over 1000 (WoodlandTrust, 2020), if we are to reduce biodiversity loss, and potential losses of EMF species, it is of vital importance that we understand the EMF communities of ancient woodland. Therefore additional empirical data covering a larger number of sites known to be ancient, as well as across a chronosequence, would be useful in order to establish the presence of ancient woodland taxa.

As part of our analysis in chapter five, we considered the species richness of EMF on oaks. Whilst we found that several metrics estimated richness to be between 136 and 154, zeta diversity calculations estimated the potential richness of oaks to be as high as 250. This much larger estimate may not be surprising when we consider the distribution of oaks, compared to, for example, *Pseudotsuga menziesii*. Douglas-fir, which has a latitudinal distribution of around 15 degrees, hosts around 250 EMF species (Kranabetter *et al.*, 2018). Oaks are found ranging from Norway to Greece, around 16 degrees of latitude. In addition, our literature review of the EMF found to associate with oak across Europe found 250 species. It would be interesting to empirically confirm the scale of this potential species richness. That is, do oaks within the UK host 250 species, or does this number occur at the continental scale. This would require further sampling of oak woodlands both with in the UK and continental Europe.

Our model results for this chapter indicated, in agreement with other studies, that atmospheric pollution is the main driver of change in EMF communities. We

also found that deposition of atmospheric cations of Ca and Mg were important filters, and that drivers may differ between rare and common species. When reviewing the drivers of EMF communities for this chapter, we noticed that, whilst some work found factors identified as possible drivers of change in EMF communities, others did not. The answer to this may partly be an issue of scale. Perhaps in local studies variable range is low, and an effect will not be seen. Large scale meta-analysis, such as that carried out by Rosinger *et al.* (2018) are therefore useful. However, there are are still some discrepancies in large scale studies. For instance, while Rosinger *et al.* (2018) find that mean annual precipitation does not significantly affect EMF communities but mean annual temperature does, in a European study of oaks, Suz *et al.* (2014) find that total precipitation is significant whilst mean temperature is not. There are a range of mathematical tools available to explore community data, in our literature review of the drivers of EMF communities authors utilise Mantel tests, non-metric multidimensional scaling, canonical correspondence analysis, permanova, distance based redundancy analysis and generalised dissimilarity models. There are subtle differences between these techniques. For example, some use distance matrices whilst others use raw data, some will be better suited for detecting unimodal relationships often seen in ecological data, whist others are non-parametric (Paliy & Shankar, 2016). In addition, distance metrics calculate dissimilarities between combinations of two sites, and hence between combinations of rare species and do not take account of species shared between multiple sites (Hui & McGeoch, 2014; Hui *et al.*, 2018). All species will exhibit a distribution across their abundance (McGill *et al.*, 2007), with a high abundance of a few common taxa, and a low abundance of many rare taxa. Rare species may have limited ecological niche or poor dispersal, alternatively, they may appear to be rare due to lack of sampling effort or because they are difficult to detect (Magurran & Henderson, 2011). Taxa could be rare at local or landscape scales (Rosinger *et al.*, 2018). If they are rare at landscape scales, then differential detection of species across sites could give the impression of similarity or dissimilarity, that is in fact, an artifact of sampling. This raises the question of whether the rare species detected could influence the outcome of the data exploration. We suggest, therefore, that an interesting extension to this work would be a mathematical exploration of different model types together with different dummy datasets which mimic the range of potential sampling outcomes. For example, do a range of modelling methods give the same results, and are these results altered if a different selection of rare species, with different environmental niches, is used. Further, Bray-curtis dissimilarity metrics based on PCR derived species abundances are sometimes used when modelling EMF communities (Pickles *et al.*, 2020), however, the correlation between PCR and actual abundance has been questioned, (Amend *et al.*, 2010; Yu *et al.*, 2012; Nguyen *et al.*, 2015; Edgar, 2017). It would also therefore be interesting to compare outputs from models when using

presence-absence data or species abundance data.

## 7.6 Soil translocation for EMF inoculation in woodland restoration

Finally, in chapter 6, we conducted a pilot study which we hoped would allow us to design a full experiment to address whether soil translocation is a useful process for inoculating saplings in restoration woodlands. We found that nursery grown stock may host a high initial EMF diversity, and therefore are not suitable as bait trees for this experiment. We also could not definitely exclude dispersal as a mechanism. Therefore, we suggested that an experiment in which aseptically grown bait trees, in conjunction with spore traps, are planted in translocated and non-translocated soil, at different distances from the mature woodland would be useful. Comparing EMF communities found on saplings and in spore traps from translocated or non-translocated soil would allow an additional confirmation of dispersal processes. If the communities are similar in both treatments, then the use of translocated soils offers no benefits in terms of inoculum supply. We noted that whilst pot grown trees developed extensive root systems, those planted out did not, which would limit EMF colonisation. We therefore felt that the full experiment would benefit if bait saplings within the mature woodland were not planted under a closed canopy and could perhaps be planted around a coppiced 'mother' tree. A potential experiment is depicted in figure 7.2 and may have additional uses; if it was found that the trajectory of EMF assemblages was not approaching that of mature woodlands, as has been observed elsewhere (Glen *et al.*, 2008), the potential for these bait trees as inoculum sources could be explored. That is, the bait seedlings could be transplanted into the restoration site. Although mature trees are sometimes moved to supply inoculum, this process tends to remove most of the fine roots which EMF occupy. In addition, the trees are pollarded to facilitate the removal, hence removing carbon supply and likely resulting in the senescence of the symbionts. Therefore, the use of smaller saplings, which would be easier to transplant, could be a useful alternative. We also saw that the saplings demonstrated poor root growth into the surrounding soil. It might be interesting to plant some saplings in such as way as to maximise root growth, that is, to prepare the soil before planting. The colonisation rate and alpha diversity of these saplings could be compared with saplings planted in unprepared soil. If the colonisation rate or alpha diversity is higher, this could imply that a small subset of saplings planted in this way might be a useful inoculum resource, in that they could harbour EMF until such as times as the remaining saplings were more mature with larger root systems. In this experiment, the restoration site was adjacent to an ancient woodland, and therefore it is more likely that over time, species can disperse to the restoration site. It would also therefore be useful to

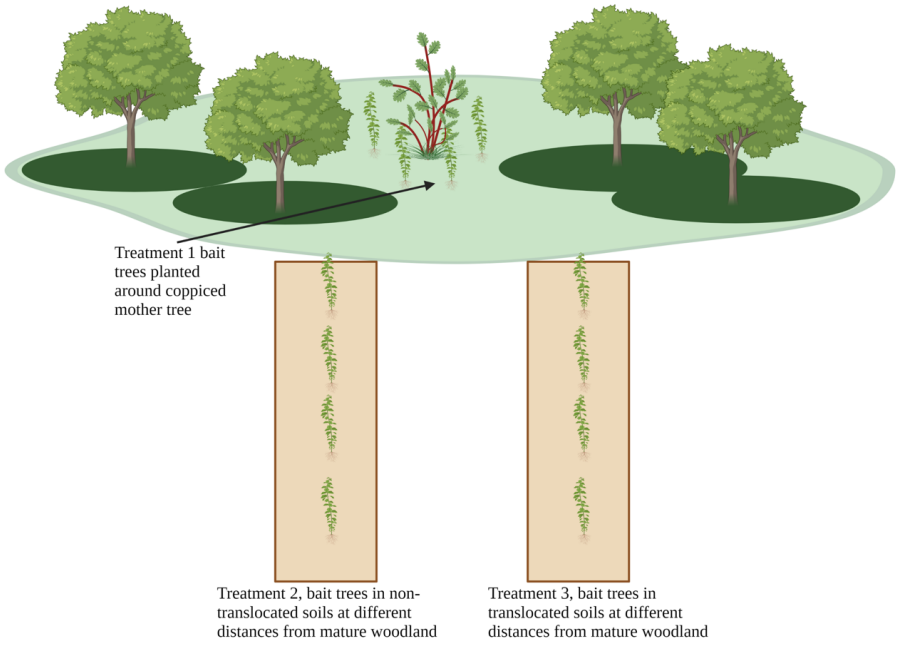


Figure 7.2: Graphic depicting the outline for extension of work in translocated soil. In treatment 1, bait trees are planted in the mature woodland, but more care is taken to ensure high light conditions, perhaps by coppicing. The EMF community on these would be assessed to ascertain whether it contained additional species that were not supported by the stunted trees in our initial experiment. In treatment 3 bait trees would be planted in both translocated and non-translocated soil to compare dispersal. If the non translocated soil contained the same species, we can assume that the EMF community is due entirely to dispersal.

monitor sites which are at different distances from mature woodland, and here, spore traps may be a useful way to assess dispersal over different scales.

## 7.7 Summary

In summary, in this work we have proposed a partial description of functional traits of specialist EMF, we have provided an in depth discussion and database of the mycorrhizal type of British woody plants and highlighted areas where data is sparse, we have confirmed the mycorrhizal mediation hypothesis in British broadleaved woodlands and compared its effect size to other important variables, we have identified drivers of EMF communities of oak, demonstrated that these appear vary between common and rare species, and that the richness of these communities may be as high as 250 species. Finally, we have explored an experiment which would allow the efficacy of translocated soils as a potential EMF inoculum supply to be assessed. We have also proposed several areas for future research which would develop the work carried out here - these are summarised in table 7.1 along with key findings from this thesis.

Table 7.1: Summary of results achieved in this work, and directions proposed for future development.

| **Summary of outcomes detailed in this thesis** | **Future directions** |
|---|---|
| Description of traits of specialist EMF | Pot experiments to quantify fitness of different tree species with a single EMF guild and different EMF guilds with the same tree species |
| | Sampling of putatively low receptivity trees in mature woodlands |
| Detailed review of mycorrhizal type of British woody plants | Sampling of *Salix* spp |
| | Spatial models of mycorrhizal type of habitats across the UK using BSBI data |
| Confirmation and extension of the mycorrhizal mediation hypothesis in British woodlands | Empirical exploration of the relationship between AMF richness and herb richness |
| | Repeat modeling of influence of AM tree type using increased number of explanatory variables |
| Gathered important biological records for EMF of oak | Extend literature review to analysis of occurrence of EMF taxa in order to reveal potential rare species |
| Demonstrate that atmospheric pollution is strong driver of EMF communities, but that drivers mat differ between rare and common species | Modeling using constructed dummy datasets to test for consistency between different modelling method, different occurrence and distributions of rare species and presence absence only data as opposed to abundance data |
| Data analysis suggests EMF richness of oaks could be as high as 250 species | Additional sampling of oak in order to confirm species richness |
| | Increased sampling in chronosequence of woodlands in order to confirm or deny presence of ancient woodland taxa |
| Nursery grown trees may contain a high diversity of EMF taxa and are not suitable as bait trees | Use aseptically grown bait trees in mature woodlands under higher light conditions and in restoration woodlands in conjunction with spore traps to assess inoculum potential |

# Appendix A

# Appendix Chapter 2

## A.1 Review of Ectomycorrhizal fungi found with *Betula pendula*

Table A.1: Review of Ectomycorrhizal fungi found with *Betula pendula*. A,(Ingleby *et al.*, 1990) B, (Cuvelier, 1991),C,(Jonsson *et al.*, 2001), D, (Staudenrausch *et al.*, 2005), E, (Tedersoo *et al.*, 2008b), F,(Collier & Bidartondo, 2009), G,(Rudawska *et al.*, 2019) , H,(Bierza *et al.*, 2020), I,(Sarsekova *et al.*, 2020) J,(Deemy, 2022)

| **Taxon name** | **A** | **B** | **C** | **D** | **E** | **F** | **G** | **H** | **I** | **J** |
|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | G | H | I | J |
| Amanita muscari | | | 1 | 1 | | | | | | 1 |
| Amanita rubescens | | | | | | 1 | | | | |
| Amanita strobiliformis | | | | | | | | | | 1 |
| Amphinema byssoides | | | | | 1 | | | | | |
| Byssocorticium atrovirens | | | | | 1 | | | | | |
| Cantharellus cibarius | | | | | | | | | | |
| Cenococcum geophilum | | | 1 | 1 | 1 | 1 | | | | 1 |
| Cortinarius albobiolaceus | | | | 1 | | | | | | |
| Cortinarius armillatus | | | | | | | | | | 1 |
| Cortinarius atrocoeruleus | | | | 1 | | | | | | |
| Cortinarius bolaris | | | | | 1 | | | | | |
| Cortinarius casimiri | | | | | 1 | | | | | |
| Cortinarius flexipes | | | | | 1 | | | | | |
| Cortinarius hemitrichus | | | | | 1 | | | | | |
| Cortinarius olivaceifuscus | | | | | 1 | | | | | |
| Cortinarius subsertipes | | | | | 1 | | | | | |
| Cortinarius umbrinolens | | | | | 1 | | | | | |
| Dermocybe phoenicea | | | | | | | | | | 1 |
| Geopora cervina | | | | | | | 1 | | | |

*Continued on next page*

Table A.1 – *Continued from previous page*

| **Taxon name** | **A** | **B** | **C** | **D** | **E** | **F** | **G** | **H** | **I** | **J** |
|---|---|---|---|---|---|---|---|---|---|---|
| Hebeloma cavipes | | | | | | 1 | | | | |
| Hebeloma crustuliniforme | | | 1 | | | | | | | |
| Hebeloma edurum | | | | 1 | | | | | | |
| Hebeloma fusiporum | | | | | | | 1 | | | |
| Hebeloma incartum | | | | 1 | | | | | | |
| Hebeloma laucosarx | | | | | 1 | | | | | |
| Hebeloma mesophaeum | 1 | | | | | | 1 | | | |
| Hebeloma velutipes | | | | | 1 | | | | | |
| Hydnotrya tulasnei | | | | | 1 | | | | | |
| Inocybe curvipes | | | | | | | 1 | | | |
| Inocybe lacera | 1 | | | | | | 1 | | | |
| Inocybe petiginosa | 1 | | | | | | | | | |
| Laccaria amethystina | | 1 | | | 1 | | | | | |
| Laccaria bicolor | | | 1 | | | | | | | |
| Laccaria laccata | | | | | 1 | | | | | |
| Laccaria proxima | 1 | | | | | | 1 | | | |
| Laccaria tortilis | | | | | | | | | | |
| Lactarius camphoratus | | | | | 1 | | | | | |
| Lactarius fulvissimus | | | | 1 | | | | | | |
| Lactarius glyciosmus | 1 | | | | | | | | | |
| Lactarius hepaticus | | | | | | 1 | | | | |
| Lactarius pubescens | 1 | | | | | | 1 | | | |
| Lactarius rufus | 1 | | 1 | | | 1 | | | | |
| Lactarius tabidus | | | | | 1 | | | | | |
| Lactarius torminosus | | | | | | | | | 1 | |
| Lactarius uvidus | | | | | 1 | | | | | |
| Leccinum holopus | | | | | | 1 | | | | |
| Leccinum scabrum | | | | | | | | | 1 | |
| Melinomyces bicolor | | | | | | | 1 | | | |
| Paxillus involutus | | | 1 | | 1 | 1 | | | 1 | |
| Peziza badia | | | | | 1 | | | | | |
| Peziza michelli | | | | | | | 1 | | | |
| Peziza ostracoderma | | | | | | | 1 | | | |
| Piloderma byssinim | | | | | 1 | | | | | |
| Piloderma fallax | | | | | 1 | | | | | |
| Russula aquosa | | | | | 1 | | | | | |
| Russula betularum | | | | | 1 | | | | | |
| Russula decolorans | | | | | 1 | | | | | |

*Continued on next page*

Table A.1 – *Continued from previous page*

| **Taxon name** | **A** | **B** | **C** | **D** | **E** | **F** | **G** | **H** | **I** | **J** |
|---|---|---|---|---|---|---|---|---|---|---|
| Russula emetica | | | | | | 1 | | | | |
| Russula grate | | | | | | | 1 | | | |
| Russula nauseosa | | | | | 1 | | | | | |
| Russula ochroleuca | | 1 | | 1 | | | | | | |
| Russula paludosa | | | | | 1 | | | | | |
| Russula sphagnophila | | | | | 1 | | | | | |
| Russula undulata | | | | | | | | | 1 | |
| Russula velenovskyi | | | | 1 | 1 | | | | | |
| Russula vesca | | | | | | | | | 1 | |
| Sebacina epigaea | | | | | 1 | | | | | |
| Sphaerosporella brunnea | | | | | | | 1 | | | |
| Thelephora terrestris | 1 | | | 1 | 1 | 1 | | | | |
| Tomentell elliisii | | | | | 1 | | | | | |
| Tomentell lapida | | | | | 1 | | | | | |
| Tomentella badia | | | | | 1 | | | | | |
| Tomentella bryophila | | | | | 1 | | | | | |
| Tomentella coerulea | | | | | 1 | | | | | |
| Tomentella stuposa | | | | | 1 | | | | | |
| Tomentella subclavigera | | | | | 1 | | | | | |
| Tomentella sublilacina | | | | | 1 | | | | | |
| Tomentella terrestris | | | | | 1 | | | | | |
| Tomentellopsis cinerascens | | | | | | | | 1 | | |
| Tomentellopsis echinospora | | | | | | | | 1 | | |
| Tricholoma muricatum | | | | 1 | | | | | | |
| Tuber maculatum | | | | | | | 1 | | | |
| Tylospora asterophora | | | | | 1 | | | | | |
| Tylospora fibrillosa | | | | | 1 | | | | | |
| Xerocomus badius | | | 1 | | | | | | | |
| Xerocomus subtomentosus | | | 1 | | | | | | | |

## A.2 Replicator Dynamics for specialist and generalist ectomycorrhizal fungi and low and high receptivity trees

We have described two guilds of ectomycorrhizal fungi, specialist and generalists and two tree types, high and low receptivity. The terms used are explained below, and then the replicator equations are stated. The notations used are summarised below.

$f_{gen}$ = fitness of generalist emf
$f_{spec}$ = fitness of specialist
$f_{lo}$ = fitness of low receptivity tree
$f_{hi}$ = fitness of high receptivity tree
$\phi_x$ = fitness of emf population
$\phi_y$ = fitness of tree population
$x$ = proportion of generalist emf
$y$ = proportion of low receptivity trees.

The fitness terms for the fungi and trees, $f_{gen}, f_{spec}, f_{lo}, f_{hi}$ are time invariant, whereas the terms for the population fitness, $\phi_x, \phi_y$, as well as the different proportions of population represented by the different guild members,$x, y$, can change with time. Writing the replicator equations for the rate of change of $x$ and $y$ gives

$$\frac{dx}{dt} = x(f_{gen} - \phi_x) \tag{A.1}$$
$$\frac{dy}{dt} = y(f_{lo} - \phi_y) \tag{A.2}$$

The total fitness of the fungi and trees is then the sum of the fitness for the sub-populations adopting different strategies:
$\phi_x = xf_{gen} + (1-x)f_{spec}$ and $\phi_y = yf_{lo} + (1-y)f_{hi}$. Substituting these into equations 2.1 and 2.2 gives

$$\frac{dx}{dt} = x(f_{gen} - xf_{gen} - (1-x)f_{spec}) = xf_{gen} - x^2 f_{gen} - x(1-x)f_{spec} = x(1-x)(f_{gen} - f_{spec}) \tag{A.3}$$

$$\frac{dy}{dt} = y(f_{lo} - yf_{lo} - (1-y)f_{hi}) = yf_{lo} - y^2 f_{lo} - y(1-y)f_{hi} = y(1-1)(f_{lo} - f_{hi}) \tag{A.4}$$

The expected fitness of a fungal symbiont when exhibiting behaviour A, $f_A$ in-

teracting with host trees with behaviours C or D is dependent on the number of times that symbiont encounters those trees. The fitness of the emf will then have four components depending on whether the interaction takes place between type A emf and type C tree, type B emf and type D tree, and so on. The matrix below is a concise method for denoting the set of fitnesses for the emf and the trees, a, b, c, d are the different emf fitnesses when interacting with different host trees and e, f, g, h are the tree fitness when interacting with different emf.

Table A.2: Summary of terms for fitness of emf and trees. a,b,c,d are the fitness of the emf when in association with type C or D trees; e,f,g,h are the fitness for the trees when is association with type A or B emf.

| | Low receptivity | High receptivity | expected fitness of emf |
|---|---|---|---|
| type Generalist | a, e | b,g | $f_{gen} = ay+b(1-y)$ |
| type Specialist | c,f | d, h | $f_{spec} = cy + d(1 - y)$ |
| expected fitness of trees | $f_{lo} = ex+f(1-x)$ | $f_{hi} = gx+h(1-x)$ | |

If a proportion, $y$, of the tree population has behaviour C, and therefore $(1 - y)$ behaviour D, the fitness to symbionts with behaviour A will be

$$f_{gen} = ay + b(1 - y) \tag{A.5}$$

$$\tag{A.6}$$

Similarly

$$f_{spec} = cy + d(1 - y) \tag{A.7}$$

$$f_{lo} = ex + f(1 - x) \tag{A.8}$$

$$f_{hi} = gx + h(1 - x) \tag{A.9}$$

Substituting equations 2.6 to 2.9 into 2.3 and 2.4 and simplifying we get

$$\frac{dx}{dt} = x(1 - x)[(a - c)y + (b - d)(1 - y)] \tag{A.10}$$

$$\frac{dy}{dt} = y(1 - y)[x(e - g) + (f - h)(1 - x)] \tag{A.11}$$

In order to simplify the analysis Markesjö (2015) suggests that instead of considering the fitness to each group of the population, consider the difference in fitness.

Let $(a-c)=p$, $(b-d)=q$, $(e-g)=r$, $(f-h)=s$. Although Markesjö (2015) suggest this in order to simplify the analysis, this does make sense in terms of the ecology. It means that rather than looking at the fitness of type A fungi when associating with type C tree, and separately that of type B fungi when associating with the same tree species, instead, we consider the difference in fitness for the same tree species when associating with either types of emf. This simplifies the equations to give:

$$\frac{dx}{dt} = x(1-x)[py + q(1-y)] \tag{A.12}$$

$$\frac{dy}{dt} = y(1-y)[rx + s(1-x)] \tag{A.13}$$

We want to examine the critical points of the system, when $\frac{dx}{dt}=0$ and $\frac{dy}{dt}=0$. In a a mature woodland, this corresponds to the solutions where $x$ and $y$ are not 0 or 1. Although there are solutions where $x$ and $y$ are 0 or 1, in woodlands, these values do not occur. Rather, there is always some proportion of generalist and specialist fungi, and early and late successional trees. This is represented by the critical points given by:

$$[py + q(1-y)] = 0 \tag{A.14}$$

$$[rx + s(1-x)] = 0 \tag{A.15}$$

This gives the critical points $x_c$, $y_c$

$$x_c = \frac{s}{s-r} \tag{A.16}$$

$$y_c = \frac{q}{q-p} \tag{A.17}$$

To examine the mathematical behaviour of the critical points, we need to solve the replicator equations and examine the behaviour of the solutions close to the critical points. The replicator equations form a nonlinear set of ordinary differential equations which we cannot solve directly. The standard approach is to linearize using a Taylor expansion. The linearized Taylor expansion about a point $a, b$ of a function with two variables is given by:

$$f(x,y) = f(a,b) + \frac{\partial f}{\partial x}(x-a) + \frac{\partial f}{\partial y}(x-b) \tag{A.18}$$

This is linearized by leaving out higher order terms, which is valid if we want

to examine the behaviour of the functions very close to the critical point since the higher order terms will be vanishingly small. If $\frac{dx}{dt} = f(x, y)$ and $\frac{dy}{dt} = g(x, y)$ then the linearized Taylor expansion of equations 2.11 and 2.12 will have the form:

$$\frac{dx}{dt} = f(a, b) + \frac{\partial f}{\partial x}(x - a) + \frac{\partial f}{\partial y}(x - b) \tag{A.19}$$

$$\frac{dy}{dt} = g(a, b) + \frac{\partial g}{\partial_x}(x - a) + \frac{\partial g}{\partial y}(x - b) \tag{A.20}$$

Since we are considering a critical point, $f(a, b) = g(a, b) = 0$. Leaving

$$\begin{pmatrix} \frac{dx}{dt} \\ \frac{dy}{dt} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial g}{\partial x} \\ \frac{\partial f}{\partial y} & \frac{\partial g}{\partial y} \end{pmatrix} \begin{pmatrix} (x - a) \\ (y - b) \end{pmatrix} \tag{A.21}$$

Using vector notation for simplicity

$$\frac{d\boldsymbol{x}}{dt} = \boldsymbol{J}(\boldsymbol{x} - \boldsymbol{a}) \tag{A.22}$$

If we let $\boldsymbol{y} = (\boldsymbol{x} - \boldsymbol{a})$, then $\frac{dy}{dt} = \frac{dx}{dt}$ and the vector equation simplifies to

$$\frac{d\boldsymbol{y}}{dt} = \boldsymbol{J}\boldsymbol{y} \tag{A.23}$$

Since J is the Jacobian evaluated at the critical points,it will be a constant and the system of nonlinear equations in reduced to a pair of linear ordinary differential equations. The solutions to these equations are of the form $y_i = C_i e^{\lambda_i t}$. We find the eigen values in the standard way, that is, if solutions have the form $y_i = C_i e^{\lambda_i t}$, then $\frac{dy_i}{dt} = \lambda_i C_i e^{\lambda_i t}$ , substituting this into equation 2.22 and rearranging gives:

$$(\boldsymbol{J}\boldsymbol{y} - \boldsymbol{\lambda}\boldsymbol{y}\boldsymbol{I}) = \boldsymbol{0} \tag{A.24}$$

$$(\boldsymbol{J} - \boldsymbol{\lambda}\boldsymbol{I}) = \boldsymbol{0} \tag{A.25}$$

We evaluate J at the critical points and solve 2.24 to find the eigen values. This allows us to explore the behaviour of the function close to the critical points. We need an expression for each partial derivative in order to evaluate the Jacobian. Firstly, notice that if we write $f(x, y)$ as

$$f(x, y) = x(1 - x)\psi(y) = x\psi(y) - x^2\psi(y) \tag{A.26}$$

Where

$$\psi(y) = (p - q)y + q \tag{A.27}$$

Substituting $y_c$ from equation 2.16 into equation 2.24 gives

$$\psi(y) = (p - q)\frac{q}{q - p} + q = 0 \tag{A.28}$$

Therefore $\frac{\partial f}{\partial x} = 0$ and similarly $\frac{\partial g}{\partial y} = 0$, the Jacobian evaluated at the critical points given by equations 2.14 and 2.15 is therefore

$$\begin{pmatrix} 0 & \frac{\partial g}{\partial x} \\ \frac{\partial f}{\partial y} & 0 \end{pmatrix} \tag{A.29}$$

Substituting this in equation 2.24 gives

$$\begin{pmatrix} 0 - \lambda & \frac{\partial g}{\partial x} \\ \frac{\partial f}{\partial x} & 0 - \lambda \end{pmatrix} = 0 \tag{A.30}$$

So

$$\lambda^2 = \frac{\partial f}{\partial y}\frac{\partial g}{\partial x} \tag{A.31}$$

With the partial derivatives evaluated at the critical point given by equations 2.14 and 2.15. The partial derivatives $\frac{\partial f}{\partial y}$ and $\frac{\partial g}{\partial x}$ are given by:

$$\frac{\partial f}{\partial y} = (p - q)x - (p - q)x^2 = (p - q)x[1 - x] \tag{A.32}$$

$$= (r - s)y - (r - s)y^2 = (r - s)y(1 - y) \tag{A.33}$$

Evaluating these at the critical points gives

$$\frac{\partial f}{\partial y} = \frac{(p - q)rs}{(r - s)(s - r)} \tag{A.34}$$

$$\frac{\partial g}{\partial x} = \frac{(r - s)pq}{(q - p)(p - q)} \tag{A.35}$$

Then

$$\frac{\partial f}{\partial y}\frac{\partial g}{\partial x} = \frac{pqrs}{(s-r)(q-p)} \tag{A.36}$$

Giving that

$$\lambda = \pm\sqrt{\frac{pqrs}{(s-r)(q-p)}} \tag{A.37}$$

We know that the critical points must be in the interval [0,1] because they represent some proportion of type A fungi and type C trees, so $\frac{s}{(s-r)}$ and $\frac{q}{(q-p)}$ are positive since these are the same values as given by equations 2.14 and 2.15.The stability of the critical points is therefore determined by the sign of $pr$. In order for the solutions to be stable, the real part of the eigen values must be negative. Therefore, the only stable solution here occurs when the the discriminant is negative giving complex roots. Therefore either $p > 0$ and $r < 0$ or $p < 0$ and $r > 0$.

Going back to our original game theory matrix, this means that, since we know that this is a steady state, either

$$a > c \text{ and } g > e \tag{A.38}$$

or the converse.

$$c > a \text{ and } e > g \tag{A.39}$$

These statements can be rephrased using equations 2.14 and 2.15. Instead of rearranging to give the critical points, equations 2.14 and 2.15 could be rearranged to give the proportion of generalists to specialists:

$$\frac{x}{1-x} = \frac{-s}{r} = \frac{h-f}{e-g} \tag{A.40}$$

$$\frac{y}{1-y} = \frac{-q}{p} = \frac{d-b}{a-c} \tag{A.41}$$

Then, since this proportion must be positive

$$a > c \implies g > e \implies f > h \tag{A.42}$$

$$\text{and } a > c \implies d > b \tag{A.43}$$

or

$$c > a \implies e > g \implies h > f \tag{A.44}$$

$$\text{and } c > a \implies b > d \tag{A.45}$$

The statements are represented pictorially in figure A.1.

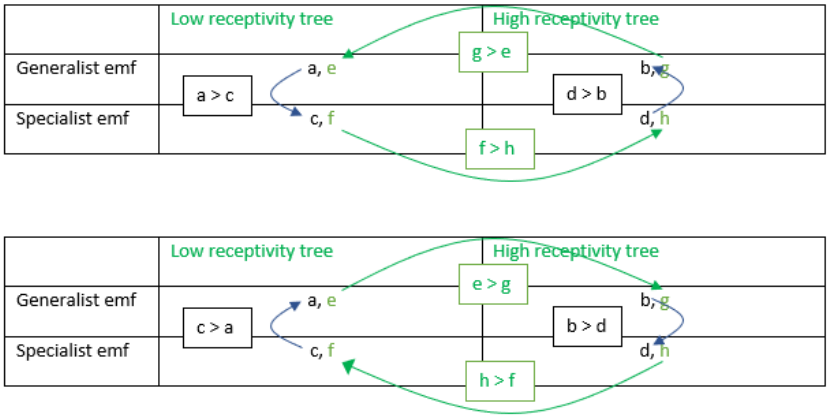


Figure A.1: Diagram showing the fitness relationships between EMF and their hosts. Since we do not know which relationship is true, both are shown: a) represents statement A.43 and b) A.45. a,b,c,d represent the fitness of EMF when associating with low or high receptivity trees. e,f,g,h, represents the fitness of high or low receptivity trees when associated with specialist or generalist EMF. For instance, a is the fitness of generalist EMF in association with a low receptivity tree. h is the fitness of a high receptivity tree in association with a specialist EMF. The arrows describe the direction of the relation ship, green arrows apply to trees and black to EMF. For example, the green arrows in the upper figure show that a high receptivity tree is fitter than a low receptivity tree when associated with a generalist. The replicator equations allow either of the opposing scenarios depicted to be true

# Appendix B

# Appendix Chapter 3

## B.1 Discussion of allocation of mycorrhizal type to UK woody plants

This section contains a detailed summary of all literature found for each the specific taxa of interest in this work, woody plants which occur in Plantatt (Hill *et al.*, 2004). In addition, for context, literature for other members of the family of genus is also discussed and cited.

**Adoxaceae**

*Sambucus nigra, S. racemosa* AM

Several members of the genus are AM type trees, with some reports of non-mycorrhizal plants. Akhmetzhanova *et al.* (2012) report three out of five species as AM type, but also mention no AM colonisation in some cases. Malloch & Malloch (1982) find two thirds of *S. pubens* surveyed from disturbed soil to be arbuscular mycorrhizal type (based on the presence or arbuscules) and the remaining third to be non-mycorrhizal. Similarly, Brundrett & Kendrick (1987) find *S. pubens* to be colonised by AMF in the summer months, but that these had senesced later in the year. A study in deciduous forests in Hungary finds *S. nigra* to be AM type (Kovács & Bagi, 2001). These results suggest that *Sambus* may be facultatively mycorrhizal.

*Viburnum lantana, V. opulus* AM

Sixteen members of this genus are reported in FungalRoot, all show AM type, except for one report of a non-mycorrhizal plant and one of an EM association. These latter two papers were not available for scrutiny but are unusual. Akhmetzhanova (2012) report AM type for four *Viburnum* spp., including the two native British species. Other work looking for AM colonisation using microscopic techniques also report AM type for three other members of this genus (Cooke & Lefor, 1998) Maremmani *et al.* (2003), who looked at both EM and AM colonisation, find only AMF in *V. tinus*.

**Aizoaceae**

*Carpobrotus edulis* NM

Only two studies were found of this plant, in Australia and South Africa, both would indicate that the plant is not mycorrhizal in those habitats (Logan *et al.*, 1989; Allsopp & Stock, 1993), although more work is needed to be certain of this allocation.

**Amaranthaceae**

*Atriplex portulacoides* AM

Several field studies find no mycorrhizal colonisation (Carvalho *et al.*, 2001; Agwa & Abdel-Fattah, 2002; Sonjak *et al.*, 2009; Karaarslan & Uyanöz, 2011). Of five species listed in Akhmetzhanova (2012), 4 show no colonisation. Fungalroot has 63 entries for this genus, about half are listed as non-mycorrhizal, including *A. portulacoides*, but others are recorded as AM, suggesting that under certain conditions AMF do colonise these plants. *Atriplex nummularia* collected in the field in South Australia have been found to have colonisation rates which varied greatly between plants collected from the same location, (Asghari *et al.*, 2005), and even low levels of colonisation have been found to result in positive growth responses (Asghari *et al.*, 2005; Plenchette & Duponnois, 2005). This suggests that these plants may be FM.

*Suaeda vera* AM

As with the other member of this family discussed above, colonisation levels seem to vary for plants in this genus, with both high and low colonisation reported (Sengupta & Chaudhuri, 1990; Wang *et al.*, 2004; Chaudhry *et al.*, 2005; Sonjak *et al.*, 2009; Chaudhry *et al.*, 2009). Half the entries in FungalRoot for this genus show non-mycorrhizal type. Agwa & Abdel-Fattah (2002) find no colonisation in *S. vera* sampled from the Mediterranean coast of Egypt. However, since colonisation levels appear to fluctuate in this genus, this one study may be insufficient to allocate non-mycorrhizal status.

**Aquifoliaceae**

*Ilex aquifolium* AM

*I. opaca* was found to be an AM type on mine reclamation sites (Rothwell & Vogel, 1985), although the authors do not specify the criteria for classification. Andrade *et al.* (2000) find intracellular coils and arbuscules in *I. paraguariensis*, (Cooke & Lefor, 1998) report coils, arbuscules and vesicles in *I. verticillata*, although one plant had a low colonisation rate. A study in China reports *I. triflora* as AM but *I. memecylifolia* as non-mycorrhizal (Weimin *et al.*, 1994), but the author does not specify selection criteria. Akhmetzhanova (2012) report AM type for an additional two species. Newman *et al.* (1994) looked for hyphal links and mycorrhizal infection between *I. aquifolium* grown with *Dactylis glomerata*, but commented that the evidence for hyphal links was weak, as was the evidence for AM colonisation in the holly. FungalRoot shows over 30 entries for this genus which consistently report

AM type.

**Araliaceae**

*Hedera helix* AM

Maremmani *et al.* (2003) looked for both AMF and EMF colonisation and report only AM. Davison *et al.* (2015) carry out a worldwide study of AM plants and used molecular techniques to identify AM colonisation in three ivy species, including *H. helix*. However, some authors also report that the plant is non-mycorrhizal (Kowalczyk & Błaszkowski, 2013). Songachan *et al.* (2011) find AMF using microscopic techniques and show images of arbuscules and vesicles, although the colonisation rate was lower than for other plant species measured.

**Asparagaceae**

*Ruscus aculeatus* AM

Three modern papers using a combination of microscopic and molecular methods report AM type (Maremmani *et al.*, 2003; Akhmetzhanova *et al.*, 2012; Davison *et al.*, 2015).

**Berberidaceae**

*Berberis vulgaris* AM

Bagyalakshmi *et al.* (2010) report no mycorrhizal colonisation for *B tinctoria* in southern India whilst two reports of Argentian species, *B buxifolia, B. darwinii* and *B. ruscifolia*, find AM colonisation (Fontenla *et al.*, 1998; Fracchia *et al.*, 2009). Godoy *et al.* (1994) report AMF colonisation for three Chilean species: *B linearifolia, B montana* and *B serrato-dentata*. Akhmetzhanova (2012) list seven additional species as AM, including *B vulgaris*. *B vulgaris* was also found to be AM in Hungarian woodland and grassland habitats,(Kovács & Bagi, 2001; Kovács & Szigetvári, 2002).

*Mahonia aquifolium* AM

We found very little work looking at the mycorrhizal type of this plant. Akhmetzhanova (2012) find *M. japonica* and *M. aquifolium* to be AM type while (Bagyalakshmi *et al.*, 2010) report *M. leschenaultia* to be non-mycorrhizal.

**Betulaceae**

*Alnus glutinosa* Dual

Although empirical data tends to be skewed towards reports of EM type, alders are known to form both arbuscular and ectomycorrhizas (Maremmani *et al.*, 2003; Becerra *et al.*, 2007; Tedersoo *et al.*, 2009; Põlme *et al.*, 2013, 2016; Boeraeve *et al.*, 2019). It may be the case that the proportion of each mycorrhizal type depends on edaphic conditions and the age of the plant (Becerra *et al.*, 2007; Teste *et al.*, 2019).

*Betula pendula, B. pubescens, B. nana* EM

There are some reports that suggest that birch could be dual. (Bainard *et al.*, 2011) found B. lutea and B. papyrifera to have an AM colonisation rate of between 5 and 10% and an EMF colonisation rate of about 15 – 35% depending on the species

and the location, urban or rural, although other authors have suggested this may be an error (Brundrett & Tedersoo, 2020). Other authors also report low rates AM colonisation, for example Malloch and Malloch (1982) find evidence for AMF in 2 out of 30 samples of *B. papyrifera* but EMF in 27 out of 30, Berliner & Torrey (1989b) report AMF as infrequent in *B. papyrifera* and *B. populifolia*, and Heklau *et al.* (2021) report 3% of OTUs found on *B. pendula* to be Glomeromycota, but these were young trees planted on former agricultural soils. Some other research also indicates AMF colonisation without indicating the abundance, for example Thormann *et al.* (1999) report AMF on *B. pumila*. Akhmetzanova (2012) list 9 of 67 records for *Betula* spp as AM, 8 of the trees originating from the same site, which raises the question of whether, if AM colonisation is correct, is it habitat dependent. Other work suggests that AMF colonisation could be the exception. In studies using microscopic techniques to look for both AMF and EMF several authors report only EMF colonisation for *B. alleghaniensis, B. papyrifera., B. nana, B. glandulosa* and *B. pendula* (Frankland & Harrison, 1985; Brundrett *et al.*, 1990; Treu *et al.*, 1995; Michelsen *et al.*, 1996; Cripps & Eddington, 2005; Collier & Bidartondo, 2009). In a study of stress on *B. pubescens* Ruotsalainen *et al.* (2009) describe 31 EM morphotypes, the authors were not looking for AM colonisation. Seedling survival of *B pubescens* has also been shown to be increased by EMF colonisation (Óskarsson, 2010). Although there is some evidence that birch may in some cases host AMF, we do not know whether AMF offer growth benefits, moreover, insufficient evidence was found to suggest that any of the UK species are dual, current evidence would suggest that these trees are almost exclusively EM type (Tedersoo *et al.*, 2008b; Hrynkiewicz *et al.*, 2015; Rudawska *et al.*, 2019).

*Carpinus betulus* EM

Several studies demonstrate EMF association for hornbeam (Selosse *et al.*, 2002; Lang *et al.*, 2011; Rudawska *et al.*, 2019). No work was found suggesting AM colonisation.

*Corylus avellana* and *C. maxima* EM

*C. avellana* is a well-known EM type tree used for truffle growing and much work has focused on its mycorrhizal type in this regard (Etayo *et al.*, 1999; Mello *et al.*, 1999; Wedén *et al.*, 2009). In these papers, the authors were not looking for AMF and we therefore cannot preclude their presence based on that research. Hazel has been shown to associate with AMF when inoculated in greenhouse experiments (Mirabelli *et al.*, 2009). Higher values for shoot weight were found for inoculated compared, but these experiments do not tell us about the natural associations of mature woodland plants. Evidence for EMF in natural growing woodland hazel comes from Selosse's study into Sebinaceae Selosse *et al.* (2002) and Boeraeve *et al.* (2018) study of forest fragments in Belgium. These two authors were not looking for AMF and therefore we cannot be certain that AMF colonisation does not occur,

but there is not a strong reason to consider it likely. *C. avellana* is allocated as EM type, but further work within British woodlands looking for both AMF and EMF colonisation would be useful. There is no data for *C. maxima*, and it is therefore assigned the same type. This also needs to be confirmed by further research.

**Buxaceae**

*Buxus sempervirens* U

We could find no work relating to this genus. In a study of the effects of mycorrhizal symbiosis on drought tolerance, Augé (2001) list *B. japonica* and *B microphylla* as AM type citing a paper by Newman and Davies, which we were unable to access. Akhmetzhanova (2012) show *B. colchia* as AM and *B sempervirens* as EM. All citations in FungalRoot for this species are over 50 years old.

**Caprifoliaceae**

*Lonicera periclymenum, L. nitida* AM

There is convincing evidence of AM type for *L. implexa* and *L. etrusca* from two papers, (Maremmani *et al.*, 2003; Çakan & Karataş, 2006). Other authors demonstrate that AMF colonisation of *L. confusa* and*L. japonica* results in positive growth response and alleviated stress (Shi *et al.*, 2013; Jiang *et al.*, 2016). Akhmetzhanova (2012) report fifteen other species as AM. We found no work on the two species commonly found in British woodlands. AM type was allocated based on other members of the genus.

**Celastraceae**

*Euonymus europaeus* AM

Gómez-Bellot *et al.* (2015) look at the use of *E. japonica* in water treatment. In this work the plants were inoculated using AMF and colonisation confirmed microscopically. AMF inoculation was also found to alleviate salt stress in *E. maackii*. A study in deciduous woodlands reports hyphal coils in *E. europaeus* (Kovács & Bagi, 2001). Akhmetzhanova (2012) report AM type for six members of the genus, including *E. europaeus*.

**Cornaceae**

*Cornus sericea, C. sanguinea* AM

Abundant literature finds members of this genus to be AM type both in lab (Sylvia, 1986) and field studies (Malloch & Malloch, 1982; Rothwell & Vogel, 1985; Brundrett & Kendrick, 1987; Berliner & Torrey, 1989b; Morrison & Nicholl, 1993; Cooke & Lefor, 1998). Akhmetzhanova (2012) cites seven species as AM type, including both British species. Only 1 study specific to *C sericea* was found (Weishampel & Bedford, 2006), and none for *C sanguinea*.

**Cupressaceae**

*Chamaecyparis lawsoniana, Thuja plicata* AM

Most literature shows Cupressaceae to be AM type. In a study of southern Indian gymnosperms, Nagaraj *et al.* (2015) found that six genera in this family were

AM type. Lee *et al.* (1981) conducted a large morphological study looking for EMF in Korean forests; no ectomycorrhizas were found in the six Cupressaceae surveyed. In a large sporocarp study, Matsuda (1994) found that in general, only a handful of sporocarps were found in stands containing predominantly *Chamaecyparis obtusa* and *Cryptomeria japonica*. In a large study of *Chamaecyparis lawsoniana* in its natural range, all trees sampled were found to have AM type and only spores of *Glomus macrocarpus* and *G. fasiculatus* were retrieved from soil samples (Zobel & Hawk, 1980). *C. lawsoniana* has been found to be AM in field experiments in Pakistan (Yaseen *et al.*, 2016) and Poland (Blaszkowski, 1994). *Thuja* spp. Have also been found to have AM type (Brundrett *et al.*, 1990; Bainard *et al.*, 2011). Few field studies were found for *T. plicata*, however, positive growth responses to AMF have been demonstrated (Kough *et al.*, 1985) and one study in old growth forests find they host a large variety of AMF, (Gorzelak *et al.*, 2017). The only work found which implies that EMF colonize Cupressaceae comes from (Toju & Sato, 2018). DNA analysis of roots of *Chamaecyparis obtusa* yielded some reads of*Rhizopogon* spp.

*Juniperus communis*

Of all the Cupressaceae in this study, junipers are the only ones which are occasionally referred to as being dual. In a botanical account of *J. communis* EM are reported as occasional (Thomas *et al.*, 2007), citing Reinsvold & Reeves (1986). Reinsvold's work was focused on *J. osteosperma* and one plant of five in the study was reported as having ectomycorrhizas with both mantle and Hartig net. Most plants in that study had a 78% AMF colonisation rate. Belomesyatseva (2002) is also cited by Thomas as an indication of EMF associations with juniper. (Belomesyatseva, 2002) was interested in all fungi found in association with juniper and isolated fungi from soils, roots and leaves. Microscopy was used to identify taxa and several EMF species were reported (*Suillus luteus, Xerocomus badius, Amanita gemmata*), however, the authors do not explain the root sampling protocol in detail, and hence it is not clear whether root sampling was accurate to the intended tree species. Reports of EMF colonisation in juniper are thought to be an error by some researchers in the field, caused by either thickening of cortical cell walls seen in this genus (Brundrett *et al.*, 1990) being mistaken for the Hartig net or root contamination from intermingled roots of EM type trees under which junipers are often found (Brundrett & Tedersoo, 2020). Several field studies find AMF colonisation for *J communis*, Kovacic *et al.* (1984); Kovács & Szigetvári (2002); He *et al.* (2019); Skinkis *et al.* (2021). Akhmetzhanova (2012) report AM type for 69 out of 73 entries for this genus.

**Ericaceae**

*Arctostaphylos alpinus, A. uva-ursi* Ar

*Andromeda polifolia, Calluna* spp, *Empetrum* spp., *Erica* spp., *Gaultheria shal-*

*lon, Phyllodoce caerula; Rhododendron* spp., *Vaccinium* spp.,Er

This group is in general under-researched (Vohník, 2020; Albornoz *et al.*, 2021), and therefore still an evolving field. Work in Abernathy Forest, Scotland demonstrates that heathland shrubs such as *Calluna vulgaris* and *Vaccinium* spp., can host a high diversity of fungal symbionts (Bougoure *et al.*, 2007). Many authors describe ericoid mycorrhizas in the British ericaceous species (Treu *et al.*, 1995; Allen *et al.*, 2003; Bougoure *et al.*, 2007; Krpata *et al.*, 2007; Mühlmann & Peintner, 2008; Liston & Harrington, 2012; Vohník, 2020; van Geel *et al.*, 2020) and other members of the genera (Malloch & Malloch, 1982; Godoy *et al.*, 1994; Cripps & Eddington, 2005; Bagyalakshmi *et al.*, 2010).

**Fabaceae**

*Colutea arborescens* U. No work found

*Robinia pseudoacacia* AM

Some reports of EM associations can be found for this species (Kovács *et al.*, 2003; Tian *et al.*, 2003). These are laboratory experiments in which *R. pseudoacacia* has been inoculated with EMF, but these, and other authors question whether improved plant growth is due to ectomycorrhiza formation or plant growth stimulation by EMF, and also ask whether functional ectomycorrhizas are formed when colonisation takes place (Bratek *et al.*, 1996; Kovács *et al.*, 2003). Moreover, being a nitrogen fixing leguminous plant, AM type would be more likely, (Brundrett & Tedersoo, 2018). In field experiments this tree is found to be an AM type (Kovács & Bagi, 2001; Bainard *et al.*, 2011; He *et al.*, 2016, 2019).

*Laburnum anagyroides* U

Oba *et al.* (2001) show that L. alpinum can be inoculated with AMF, no other work found for this species or genus

*Genista anglica, G. tinctoria* AM

Sánchez-Castro *et al.* (2012) find AM in *G. cinerea*, Lansac *et al.* (1995) used microscopic methods to look for both AMF and EMF, in Mediterranean shrubs and find only AM colonisation in *G. hirsute*. They do not specify their criteria. Akhmetzhanova (2012) report only AM in *G. tinctoria* . Inoculation studies demonstrate that *G. tinctoria* and *G. germania* can be colonised by *Glomus mosseae* (Oba *et al.*, 2001).

*Cytisus scoparius* AM

Other member of this genus have been found to be AM in research using microscopy to look for both AM and EM colonisation Kovács & Szigetvári (2002); Akhmetzhanova *et al.* (2012). Crush (1975) report vesicles and arbuscules in *C. scoparius* and Oba *et al.* (2001) show that *Cytisus albidus* can be inoculated with AMF.

*Ulex eurpaeus, Ulex gallii, Ulex minor* AM

Inoculation studies find that *U. europeaus* will be colonised by *Glomus mosseae*

(Oba *et al.*, 2001). Field studies in India (Santhoshkumar *et al.*, 2018) and the Mediterranean (Maremmani *et al.*, 2003) find AMF in this species. No studies were found for the other British gorse.

*Lupinus arboreus* NM

In an inoculation experiment Oba (2001) found that no *Lupinus* spp. tested became mycorrhizal. In field experiments, other members of the genus have been found to be non-mycorrhizal (Kovacic *et al.*, 1984; Treu *et al.*, 1995; Štajerová *et al.*, 2009) although Akhmetzhanova (2012) report AM colonisation.

**Elaeagnaceae**

*Hippophae rhamnoides* AM

Akhmetzhanova (2012) have only one listing and find it non-mycorrhizal. However, other work finds AMF colonisation (Zhang *et al.*, 2010; He *et al.*, 2016). Furthermore, Ming & Hui (1999) demonstrate positive growth responses to AMF inoculation in pot experiments.

**Fagaceae**

*Fagus sylvatica, Castanea sativa* EM

Fagaceae are well known as EM type (Tedersoo & Brundrett, 2017). There is plenty of literature confirming this for Fagus sylvatica (Buée *et al.*, 2005; Lang *et al.*, 2011; Kubisch *et al.*, 2015) and *Castanea sativa* (Peintner *et al.*, 2007; Baptista *et al.*, 2010). Although the latter study is a sporocarp study, it is conducted in a monodominant *C. sativa* orchard.

*Quercus petraea, Q. robur, Q. cerris, Q, ilex* EM

Several authors report colonisation by both AMF and EMF in oaks. (Dickie *et al.*, 2002) find that *Q. rubra* seedlings grown near AM type trees show a higher rate of AMF colonisation than those grown near EM types. However, the authors point out that no growth benefits due to the AM colonisation was seen. AMF colonisation has also been found in a variety of oak species (Rothwell *et al.*, 1983; Watson *et al.*, 1990; Querejeta *et al.*, 2009; Toju *et al.*, 2013). These papers point to the link between AMF colonisation and soil moisture conditions, as has been discussed in detail elsewhere (Teste *et al.*, 2019). In Bainard's (2011) study of urban and rural trees which looked for both AMF and EMF, *Q. palustris* and *Q. rubra* were reported to have AM colonisation. Egerton-Warburton & Allen (2001) conducted a study of AM and EM colonisation of *Q. agrifolia* along a chronosequence as well as in inoculated seedlings. Seedlings were colonised by both AMF and EMF increased seedling survival was seen for both types of mycorrhizal inoculation. Plants inoculated with AMF had the highest foliar N, and those with EMF the highest foliar P. The authors also observed that for field sampled trees, the colonisation of AMF reduced with time, while EMF colonisation increased. Most work on *Q. cerris* concerns inoculation with truffle species, The only field work from mature woodlands trees was a morphotype study from mature trees in Romania which found a wide

variety of ectomycorrhizal root tips (Fodor *et al.*, 2011). No other field work was found. *Quercus ilex* is a non-native Mediterranean tree which has been shown to form EM in its native range (Maremmani *et al.*, 2003; De Román & De Miguel, 2005; Richard *et al.*, 2005). The EMF community for the two native oaks, *Q. petraea, Q. robur* has been found to be very similar (Leski *et al.*, 2009; Suz *et al.*, 2014). Work on these species is mainly concerned with EMF colonisation (Bakker *et al.*, 2000; Urban *et al.*, 2008; Bzdyk *et al.*, 2019) with few authors looking for both AMF and EMF (Maremmani *et al.*, 2003). We cannot deduce absolutely that *Q. robur* and *Q. petraea* are purely EM type in all environmental conditions based on available studies, and studies would suggest that some AMF colonisation occurs and may have growth benefits for seedlings, although it would seem to be at a lower level in mature trees.

**Grossulariaceae**

*Ribes rubrum, R. uva-crispa* AM

No work was found for these two species. Kovacic *et al.* (1984) report AM type for *R. cereum* based on the presence of vesicles. Fontenla *et al.* (1998) report arbuscules in *R. magellanicum* and Weishampel & Bedford (2006) record AM type for *R. hirtellum* based on the presence of vesicles and arbuscules while *R. valdivianum* is reported as vesicular arbuscular in coniferous woodlands in Chile (Godoy *et al.*, 1994). Akhmetzhanova (2012) report EM in one study and and two non-mycorrhizal plants of *R. alpinum* and *R. aureum*, however 22 of 24 studies on *Ribes* spp. are recorded as AM.

**Hypericaceae**

*Hypericum androsemum, H. calycinum* AM

Members of this genus have been found to be AM (Muthukumar & Udaiyan, 2000; Meers *et al.*, 2010) although Eriksen *et al.* (2002) find some plants of *H. maculatum* to be uncolonized therefore more studies are required to confirm FM status, however, of sixteen studies in Akhmetzhanova (2012) only one finds no colonization.

**Juglandaceae**

*Juglans regia* AM

Positive effects on growth of *J. regia* after inoculation with AMF has been demonstrated (Dolcet-Sanjuan *et al.*, 1996). Similar glasshouse experiments show a positive effect on *J. nigra* when infected with AMF (Ponder Jr., 1984; Dixon, 1988; Behrooz *et al.*, 2019), and also that AMF hyphae transport the allelopathic chemical juglone (Achatz & Rillig, 2014). Although other members of Juglandaceae may be EM type (Bonito *et al.*, 2011; Ge *et al.*, 2017; Tedersoo & Brundrett, 2017), this does not appear to be the case for *J. regia*. Evidence for the AMF association of walnut trees in the field comes from studies of Ontario trees (Brundrett *et al.*, 1990; Bainard *et al.*, 2011) which show *J. nigra* to be exclusively AM.

**Lauraceae**

*Laurus nobilis* AM

We found very little work for this species, although records in FungalRoot (Soudzilovskaia *et al.*, 2020) show Lauraceae tend to be AM type. However, of eleven members of this family studied in subtropical China, Weimin *et al.* (1994) report that only four demonstrate evidence of AMF colonisation, they do not specify their criteria. Brundrett (2009) note that 16 members of this family are reported as non-mycorrhizal and Cooke & Lefor (1998) find low levels of colonisation in *Lindera benzoin*, a laurel native to Eastern North America. Maremmani *et al.* (2003) report L. nobilis to be AM type in its native range in the Mediterranean basin.

**Myricaceae**

*Myrica gale* NM

This plant produces cluster roots as a mechanism for nutrient uptake. Although some AM colonisation has been observed (Rose, 1980), the contribution to nutritional status of the plant is thought to be nominal (Crocker & Schwintzer, 1993, 1994). Berliner & Torrey (1989a) found that plants inoculated with either Frankia or Glomus intraradices or both were only colonised by Frankia. It is therefore likely that this plant is non-mycorrhizal, depending on cluster roots and root nodules for nutrition.

**Malvaceae**

*Tilia cordata, T. platyphllos* EM

In field experiments *Tilia* spp. are found to be EM type (Rothwell & Vogel, 1985; Brundrett & Kendrick, 1987; Brundrett *et al.*, 1990; Selosse *et al.*, 2002; Timonen & Kauppinen, 2008). Fruit body studies of urban avenues in Hungary demonstrate that *T. cordata, T. platyphllos* and *T. tomentosa* host a large variety of EMF (Csizmár *et al.*, 2021). Fini *et al.* (2011) find both AM and EM on roots of inoculated *T. cordata* in a greenhouse experiment, but they report no effect on leaf growth for AMF inoculation, compared to increased leaf growth following EMF inoculation. *T. cordata* and *T. platyphyllos* are reported as EM (Timonen & Kauppinen, 2008; Lang *et al.*, 2011; Rudawska *et al.*, 2019). *Lavatera arborea* AM

Both mycorrhizal and non-mycorrhizal plants are reported for this genus (Koske & Halvorson, 1989; Allsopp & Stock, 1993; Nobis *et al.*, 2015). No work was found for *L. arborea*.

**Oleaceae**

*Fraxinus excelsior* AM

Glasshouse experiments on *Fraxinus* spp., show a positive response to AMF inoculation (Ponder Jr., 1984; Pirazzi *et al.*, 1999). In field experiments ash is found to be exclusively AM type (Rothwell & Vogel, 1985; Mayr & Godoy, 1989; Brundrett *et al.*, 1990; Bainard *et al.*, 2011; Lang *et al.*, 2011; Kubisch *et al.*, 2015)

*Ligustrum ovalifolium, L. vulgare* AM

There are reports of AM type for *L. lucidum* (Kovács & Bagi, 2001) and *L. vul-*

*gare* (Maremmani *et al.*, 2003). Although of five plants sampled by Akhmetzhanova (2012) two are reported as non-mycorrhizal, we have not considered this sufficient evidence of FM status.

*Syringa vulgaris* AM

No field work found. Nine out of eleven samples for this genus are reported as AM by Akhmetzhanova (2012), including *S. vulgaris*.

**Onagraceae**

*Fuchsia magellanica* AM

We find only one inoculation study of *F. excorticata* which demonstrated that the plant could become colonised by a variety of AMF (Johnson, 1977). Akhmetzhanova (2012) only show one entry for *F. gracilis*, also as AM.

**Pinaceae**

*Abies* spp., *Larix* spp., *Picea* spp., *Pinus* spp., *Pseudotsuga menziesii, Tsuga heterophylla* EM

A large body of work finds members of this family to be EM type (Horton *et al.*, 1998, 1999; Eberhardt *et al.*, 2000; Ishida *et al.*, 2007; Pickles *et al.*, 2010; Rudawska *et al.*, 2016; Rasmussen *et al.*, 2017; Suz *et al.*, 2017; Gehring *et al.*, 2020). Massicotte *et al.* (1999) find only EM in a detailed morphological microscopic analysis of five trees species including *Pseudotsuga menziesii*. Studies on volcanic mountains in Japan find EM colonisation in Larix kaempferi, (Yang *et al.*, 1998; Tsuyuzaki *et al.*, 2005). The latter study also reports low levels of AMF. Leski *et al.* (2008) use molecular methods to study naturally regenerating *Larix decidua* and find them to be EM type. Palfner *et al.* (2005) studied a chronosequence in *Picea sitchensis* and found only EM colonisation, however, this was a morphological study using a low power microscope so that AM infection would not have been seen. There are a few reports of AM colonisation in some Pinaceae. Horton *et al.* (1998) study two sites after wildfire, one which was previously occupied by *Pinus muricata* and one which was not. Arbuscules and vesicles were found in seedlings in the first five month of regrowth. The proportion of seedlings with EMF compared to AMF colonisation is much greater at a site which previously held *P. muricata* compared to a scrub site which did not. The richness of EMF species is also greater at the burnt forest site. This suggests that whilst this species may be able to form AM, the natural state for a mature plant within a woodland setting would be EM type. Cázares & Smith (1995) examined the potential for *Pseudotsuga Menziesii* and *Tsuga Heterophylla* to form AM. Soils were collected from Douglas fir plantations into which Douglas fir and western hemlock were grown with *Rhododendron macrophyllum* and *Gaultheria shallon*. Nearly half the Douglas fir and a quarter of the western hemlock were colonised by AMF. This study suggests that these two species readily form AM under certain conditions. For example, AMF inoculant may have persisted in the soil samples where EMF did not, and in the absence of EMF inoculant, AM colonisation

could occur. It has been shown that *Pseudotsuga menzeisii* can be colonised by AMF as a seedling and in pot experiments (Smith *et al.*, 1998; Dučić *et al.*, 2009; Salomón *et al.*, 2018). While these papers point to the potential for members of Pinaceae seedlings to form AM in early successional settings or as seedlings, mature *P. menzeisii* in the field have been shown to host a high richness of EMF (Horton *et al.*, 1999; Benucci *et al.*, 2016; Defrenne *et al.*, 2019)

**Platanaceae**

*Platanus x hispanica* AM

Very little literature was available for the Plane tree, which is surprising given its importance in the landscape as a street tree. All the work found involved glasshouse experiments on the parent trees *P. acerifolia* or *P. occidentalis* in which seedlings were inoculated with AMF and a positive effect on growth was seen (Pope, 1980; Schultz *et al.*, 1981; Kormanik *et al.*, 1982; Pope *et al.*, 1983; Tisserant *et al.*, 1996). No work was found which examined the parent trees in their native habitat or which looked at the mycorrhizal type of *Platanus x hispanica* as a street tree. Given the positive response to AM inoculation in greenhouse experiments we assigned plane as AM type.

**Ranunculaceae**

*Clematis vitalba* AM

Several pieces of work looking for both EMF and AMF colonisation find only AMF in this genus (Brundrett & Abbott, 1991; Fracchia *et al.*, 2009), while Maremmani *et al.* (2003) find *C. vitalba* to be AM type in the field in Italy. Akhmetzhanova (2012) show six genera of clematis as AM type, including *C. vitalba*.

**Rhamnaceae**

*Rhamnus cathartica* AM

There are various reports on the mycorrhizal type for this genus. Some authors find no AM structures (Weimin *et al.*, 1994; Kovács & Bagi, 2001; Akhmetzhanova *et al.*, 2012). Çakan & Karataş (2006) report observing a Hartig net in roots of *R. hirtella*, although it has been suggested that this is an error (Soudzilovskaia *et al.*, 2020). Low colonisation rates have been noted in *R. lycioides* (Caravaca *et al.*, 2003). *R. wightii* was found to be AM type in tropical montane forests in Southern India (Bagyalakshmi *et al.*, 2010). Akhmetzhanova *et al.* (2012) list four species, including *R. cathartica*, as AM type.

*Frangula alnus* AM

We were unable to find any modern published work on this plant, despite its importance as an invasive species in North America.Godwin (1943) conduct a species account of *F. alnus* in the UK, and although the work is a broad account, they do describe finding frequent vesicles. Repas *et al.* (1999) describe a high AMF colonisation rate, but this comment was taken from an abstract only, we were unable to access the full paper.

**Rosaceae**

*Acaena novae-zelandiae* AM

Members of this genus have been found to be AM (Laursen *et al.*, 1997; Vázquez-Santos *et al.*, 2019) including *A. novae-zelandiae* (Meers *et al.*, 2010).

*Cotoneaster* spp. AM

We found only one piece of field work which reports AMF in *C. pannosus* (Dandan & Zhiwei, 2007) apart from Akhmetzhanova *et al.* (2012) which shows list 15 out of 16 entries for other members of this genus as AM. FungalRoot (Soudzilovskaia *et al.*, 2020) has two entries for recent work in China, but we were unable to view these.

*Crataegus monogyna* AM

*C. monogyna* has been reported as being colonised by both EMF and AMF by (Kovács & Bagi, 2001) in a study of woodland plants, although the authors do not state that a Hartig net was required if EM was recorded. The same authors reported only AM in a later study of grassland plants (Kovács & Szigetvári, 2002). The difference in these two reports could be related to sources of inoculum, the former study took place in mixed broad-leaved forests and the latter on grassland. Possibly suggesting that the plant may be colonised by EMF if there is a supply of inoculum.Blaszkowski (1994) found roots of *C. monogyna* to have an AMF colonisation rate of around 11% while Maremmani *et al.* (2003) report finding only EMF in this species. Other members of the genus have been reported as AM type (Lee *et al.*, 1981; Mirzaei *et al.*, 2015). It has been suggest that the allocation of EM type is an error for this plant (Tedersoo & Brundrett, 2017; Brundrett & Tedersoo, 2019), which would seem sensible in light of the fact that other members of this family appear to be exclusively AM type. However, work by Boeraeve *et al.* (2018) identified six EMF species associated with hawthorn in forest fragments in Belgium. In that work, roots were carefully traced back to host trees, avoiding errors in host identity, and molecular methods used to identify mycorrhizal species, avoiding any errors in microscopic identification, although molecular identification establish the functionality of the mycorrhiza. A more recent detailed analysis (Boeraeve *et al.*, 2021) supports the findings of Kovács & Bagi (2001) by demonstrating evidence of low EMF colonisation in plants sampled from a forest edge but not in plants sampled in grasslands settings, suggesting that Hawthorn may support EMF in woodland settings. Hawthorn was allocated AM type in line with other members of the genus, even though there is now some evidence that EMF do colonise this tree, it would appear to be in low numbers, and the functionality of the association needs further exploration. No work was found looking at *C. laevigata*.

*Dryas octopetala* EM

Despite being a member of the Rosaceae, studies in Austria, Norway, Sweden, USA and the west of Ireland indicate that this plant may be EM type (Read &

Haslewandter, 1981; Treu *et al.*, 1995; Cripps & Eddington, 2005; Harrington & Mitchell, 2002; Ryberg *et al.*, 2009; Bjorbækmo *et al.*, 2010).

*Malus* spp. AM

Being an important crop, most mycorrhizal studies on apples are confined to pot studies, (Miller *et al.*, 1985), although some work samples orchard trees (Sharma *et al.*, 2005). The positive effects of AM colonisation on root and shoot growth and increased disease resistance is well known (Matsubara *et al.*, 1996; Mehta & Bharat, 2013; Berdeni *et al.*, 2018). (Maremmani *et al.*, 2003) reports AMF colonisation for *M. domestica* in the field.

*Prunus* spp. AM

Experiments demonstrate AM colonisation leads to positive effects on growth of seedlings of *P. avium, P. cerasifera , P. domestica* and *P. persica* (Fortuna *et al.*, 1992; Berta *et al.*, 1995; Pirazzi *et al.*, 1999; Calvet *et al.*, 2004; Wu *et al.*, 2011; Razouk & Kajji, 2015). Some work can also be found demonstrating that *Prunus* spp. are AM type in natural settings,(Malloch & Malloch, 1982; Berliner & Torrey, 1989b; Maremmani *et al.*, 2003; Bainard *et al.*, 2011; Akhmetzhanova *et al.*, 2012). For the British species, AM type is reported for *P. avium* (Kirti *et al.*, 2016) and *P. padus* (Kovács & Bagi, 2001); in this study, dual colonisation is reported for *P spinosa*. Reports of EMF colonisation are exceptional for Rosaceae, it is though in general that these are in error and due to root morphologies that can give the appearance of ectomycorrhizal roots, (Tedersoo & Brundrett, 2017; Brundrett & Tedersoo, 2020). It also interesting that a positive effect of EMF inoculation on some *Prunus* spp. has been demonstrated (Grange *et al.*, 1997; El-bashiti *et al.*, 2017), but as these authors point out, this does indicate EM or dual type, but is most likely an effect of indole-3-acetic acid, a root growth stimulating phytohormone released by EMF. It may be worth noting the lack of data for *Prunus laurocerasus*, an important invasive plant in Britain (Marrs *et al.*, 2013).

*Potentilla fruticosa* AM

Many reports find this genus to be AM (Read & Haslewandter, 1981; Rothwell & Vogel, 1985; Berliner & Torrey, 1989b; Eriksen *et al.*, 2002; Cázares *et al.*, 2005; Davison *et al.*, 2015; Nobis *et al.*, 2015) although no work was found for *P. fruticosa*.

*Pyrus communis, P cordata* AM

AM is reported for other members of this genus (Cooke & Lefor, 1998; Kamareh *et al.*, 2011; Yoshimura *et al.*, 2013). and *Glomus* sp has been shown to promote growth in *P. communis* (Rapparini *et al.*, 1996).

*Rosa* spp. AM

*R. acicularis* has been reported as both colonised and uncolonized by AMF (Malloch & Malloch, 1982; Johnson-Green *et al.*, 1995). Greenhouse experiments have demonstrated that AMF increase drought tolerance in *R. hybrida* (Davies *et al.*, 1996). Other members of the genus are reported as AM in field samples (Berch

*et al.*, 1988; Maremmani *et al.*, 2003; Koul *et al.*, 2012). The only report for a British species is for AM type in *R. canina* (Blaszkowski, 1994).

*Rubus* spp. AM

Other members of the genre have been found to be AM (Kovacic *et al.*, 1984; Cornwell *et al.*, 2001; Weishampel & Bedford, 2006; Põlme *et al.*, 2016). Thormann *et al.* (1999) reports vesicles but not arbuscles for *R. chamaemorus*. Work British species find AM type for in *R. idaeus* and *R. fruticosus* (Berliner & Torrey, 1989b; Newman *et al.*, 1994).

*Sorbus* spp. AM There are four diploid Sorbus species in the UK, *S. aria, S aucuparia, S. domestica*, and *S. torminalis*. Hybridisation and apomixis results in over 50 endemic microspecies. Seventy percent of the citations in FungalRoot (Soudzilovskaia *et al.*, 2020) assign AM type to this genus, although Akhmetzhanova *et al.* (2012) report *S. torminalis* as EM type. However, other work suggests this species to be AM (Malloch & Malloch, 1982; Moradi *et al.*, 2016; Bzdyk *et al.*, 2016). (Cázares *et al.*, 2005) report EM on the subalpine species, *S. sitchensis* at a lower rate than AMF colonisation. *S aucuparia*, has been seen to respond positively to AMF inoculation (Morrison & Nicholl, 1993) and to only form AM when inoculated with both EMF and AMF (Kilpeläinen *et al.*, 2019).

**Salicaceae**

*Populus* spp. Dual

Poplars are well known dual mycorrhizal plants (Lodge, 1989; Brundrett *et al.*, 1990; Teste *et al.*, 2019). Not all reports demonstrate dual colonisation, as authors may focus on the effect of EM colonisation (Jakucs, 2002; Jabeen *et al.*, 2012; Danielsen & Polle, 2014) while others consider AMF (Beauchamp *et al.*, 2006; Danielsen & Polle, 2014). Neville *et al.* (2002) report on both AM and EM colonisation rates at different soil depths for P tremuloides. Tyburska *et al.* (2014) show dual colonisation of *P. nigra* and *P. alba*

*Salix* spp. AM, EM

Willows in the UK tend to show either AMF or EMF colonisation. Willows grow in a wide variety of habitats from coastal dunes, (*Salix repens*) and montane acid grassland (*S. myrsinites*) to fen or standing water (*S. cinerea, S. purpurea, S. viminalis*). Tree species occupying flood zones are often found to be dual with damp soil conditions correlating with greater AM colonisation (Lodge, 1989; Teste *et al.*, 2019). EM type willows are found in flooded habitats, and it may be the case that EM species richness is reduced (Hashimoto & Higuchi, 2003; Sumorok & Kiedrzyńska, 2007). Many authors examine willows for either AM or EM colonisation, so that dual status may occur, but is not easy to assign. Of authors who look for both Dhillion (1994) report AM and EM colonisation only in the non-UK species in *S. glauca* and *S. nigricans*. Sumorok & Kiedrzyńska (2007) report low levels of AM colonisation in young roots of *S. cinerea* and *S. viminalis*, but comment that

arbuscules were not found. Akhmetzhanova *et al.* (2012) also find AM in *S. viminalis* from one site, but EM in this species at four other locations. EMF are found in *S. repens* (van der Heijden *et al.*, 1999), but the authors were not looking for AMF colonisation. Positive growth responses have been demonstrated for low levels of AMF colonisation in *S. repens* (van der Heijden, 2001). One other study finds both AMF and EMF in roots of this plant using DNA analysis (Botnen *et al.*, 2015) while Kovács & Szigetvári (2002) comment that as well as ectomycorrhizas, hyphal coils and other endogenous structures were found. Similarly, *S. atrocinera* has been seen to demonstrate AMF species specific growth responses (Oliveira *et al.*, 2001, 2006). Data is sparse for many willow species, such as *S. lapponum*. The assignment of EM type to this species was only found in one paper, (Milne *et al.*, 2006), but it is a convincing study of the willow in its natural habitat in which cuttings were planted in upland plots dominated either by grass and herbaceous plants or by *Vaccinium myrtillus*, the authors report EMF colonisation was found for all the willows from either setting. Due to lack of data, we have allocated most willows as EM type, except *S. repens*, but caution that these allocations are made on extremely limited data often where studies were usually focussed on looking for one type of colonisation, on a genus which appears to host both AM and EM fungi.

**Sapindaceae**

*Acer campestre, A. pseudoplatanus, A, platanoides* AM

There is little evidence that this genus contains EM type trees. In a study on sandy grassland plains in Hungary, (Kovács & Szigetvári, 2002) report EMF on *Acer negundo*, as well as vesicles and arbuscules, but other authors do not find this dual colonisation (Bainard *et al.*, 2011; Veselkin & Prokina, 2016). Field experiments in which roots are examined for both EM and AM show only AMF colonisation for many members of this genus (Lee *et al.*, 1981; Berliner & Torrey, 1989b; Bainard *et al.*, 2011; Veselkin & Prokina, 2016). No field work was found for the two British species, except for a study on urbanisation on AM colonisation of *A. pseudoplatanus* (Rusterholz *et al.*, 2020) but glasshouse studies demonstrate the positive benefits of AMF inoculation on growth for the two British species (Pirazzi *et al.*, 1999; Fini *et al.*, 2011) as well as *A. platanoides* (Verkade, 1991).

*Aesculus hippocastanum* AM

Several studies demonstrate AM type (Bainard *et al.*, 2011; Tyburska *et al.*, 2013; Karliński *et al.*, 2014)

**Scrophulariaceae**

*Buddleja davidii* AM

Buddleja is cited as an example of why entries in mycorrhizal type databases must be carefully scrutinised.Dickie *et al.* (2007) elucidate how a single entry of no colonisation for this plant in Harley & Harley (1987) was then used several times as evidence of a non-mycorrhizal status. As Dickie *et al.* (2002) explains, if this plant

had been investigated, as Harley & Harley (1987) suggest, records of AM colonisation would have been found for several other members of the genus. Dickie *et al.* (2007) themselves then explored *B. davidii* in New Zealand and Surrey, England, and record vesicles and arbuscules at both locations. Dickie *et al.* (2007) conclude that the record in Harley & Harley (1987) is either an error or an exceptional specimen of low colonisation.

**Taxaceae**

*Taxus baccata* AM

There is little current work for this tree. Of 21 records in FungalRoot (Soudzilovskaia *et al.*, 2020), only two are less than forty years old and only one of these was readily available for scrutiny (Wubet *et al.*, 2003). *T. canadensis* and *T. baccata* have been found to be exclusively AM type in field experiments (Berliner & Torrey, 1989b; Wubet *et al.*, 2003) and inoculation with AMF has been found to increase shoot and root growth (Sainz *et al.*, 2000).

**Thymelaeaceae**

*Daphne laureola, D. mezereum* AM

There is no recent work on *D. laureola*. Citations in all databases were traced back to two pieces of work from the 1960's which are no longer easily accessible (Steltz, 1968; Boullard, 1966). More recent work on other daphne species is reported in FungalRoot (Soudzilovskaia *et al.*, 2020), but many of these papers were not found for inspection. Read & Haslewandter (1981) state that *D. striata* examined in alpine communities was found to have EM root tips. Akhmetzhanova *et al.* (2012) report AM colonisation for *D. glomerata* and *D. mezereum* while Maremmani *et al.* (2003) report AM type for *D. gnidium*. Phylogenetic evidence for EM type in Thymelaeaceae is considered to be scant (Tedersoo & Brundrett, 2017).

**Ulmaceae**

*Ulmus minor* AM

Elms are thought to be unable to form EM associations due to their root structure (Brundrett *et al.*, 1990; Tedersoo & Brundrett, 2017). Glasshouse experiments demonstrate that AMF inoculum reduces stress in *Ulmus* spp., (Cartmill *et al.*, 2012; Rewald *et al.*, 2015). Field experiments to confirm AM type in other members of the genus,(Brundrett *et al.*, 1990; Song *et al.*, 2019). Kovács & Bagi (2001) find AM in *U. minor*.

## B.2 Summary table of mycorrhizal type of British woody plants

Table B.1: Mycorrhizal type of UK woody plants. The first columns gives the species name. The second column is the assigned mycorrhizal type and column three gives the number of field studies found on which the allocation is made. The fourth column, C, is the confidence score. That is, a count of the number of records found in the number of entries in FungalRoot (Akhmetzhanova *et al.*, 2012) since 1990 which agree with our assignment. The final column gives the list of references used in addition to Fungalroot which are specific to that species. For further references which may be available for the genus or family see the detailed discussion in the previous appendix

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Acaena novae-zelandiae | AM | 1 | 0 | Meers et al., 2010 |
| Acer campestre | AM | 1 | 33 | Helgason et al., 2014 |
| Acer platanoides | AM | 1 | 33 | Bainard et al., 2011 |
| Acer pseudoplatanus | AM | 2 | 33 | Pirazzi et al., 1999; Helgason et al., 2014 |
| Aesculus hippocastanum | AM | 2 | 4 | Bainard et al., 2011;Karli?ski et al., 2014 |
| Alnus glutinosa | Dual | 5 | | Rose, 1980; Rothwell and Vogel, 1983;Pritsch et al., 1997; Maremmani et al., 2003;Tedersoo et al., 2009(only looking at EM) |
| Alnus incana | Dual | 4 | | Rose, 1980; Berliner and Torrey, 1989a; Cornwall et al., 2001 Tedersoo et al., 2009 |
| Andromeda polifolia | Er | 4 | 11 | Väre et al, 1997; Thormann et al., 1999; Selosse et al., 2007; van Geel, 2020 |
| Arctostaphylos alpinus | Ar | 1 | 3 | Treu et al., 1995 |
| Arctostaphylos uva-ursi | Ar | 5 | 3 | Treu et al., 1995; Cripps and Eddington, 2005; Krpata et al., 2007;Muhlmann and Peintner, 2008; Liston and Harrington, 2012 |

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Table B.1 – *Continued from previous page*

| Species | Type | NF | C | References |
|---|---|---|---|---|
| Atriplex portulacoides | AM | 4 | 42 | Carvalho et al., 2001; Agwa et al., 2002; Sonjak et al., 2009; Karaarslan,and Uyanöz,2011 |
| Berberis vulgaris | AM | 2 | 31 | Kovÿcs and Bagi2001; Kovÿcs and Szigetvÿri 2002) |
| Betula nana | EM | 4 | 109 | Miller, 1982; Treu et al., 1995; Väre, et al., 1997; Cripps et al., 2008 |
| Betula pendula | EM | 4 | 109 | Mason et al., 1982; (Frankland and Harrison, 1985); Tedersoo et al., 2008; Collier and Bidartondo, 2009; Hrynkiewicz et al., 2015; (Rudawska et al., 2019) |
| Betula pubescens | EM | 2 | 109 | Mason et al., 1985;Ruotsalainen et al., 2009;?skarsson, 2010 |
| Buddleja davidii | AM | 2 | 6 | Lucia et al., 2003; Dickie et al., 2007 |
| Buxus sempervirens | U | 0 | 2 | |
| Calluna vulgaris | Er | 6 | 8 | Haslewanter and Read, 1980; Väre et al., 1997; Johansson, 2000; Diaz et al., 2006; Bougoure et al., 2007; van Geel et al., 2020 |
| Carpinus betulus | EM | 3 | 8 | Rudawska et al., 2019; Selosse et al., 2002; Lang et al., 2011 |
| Carpobrotus edulis | NM | 2 | 2 | Logan et al., 1989; Allsopp abd Stock, 1993 |
| Castanea sativa | EM | 2 | 15 | Peintner et al., 2007; Baptista et al., 2010 (sporocarp) |

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Table B.1 – *Continued from previous page*

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Chamaecyparis lawsoniana | AM | 3 | 15 | Zobel and Hawk, 1980; Blaszkowski et al., 1994; Yaseen et al., 2016 |
| Clematis vitalba | AM | 1 | 29 | Maremmani et al., 2003; (Fracchia et al., 2009) |
| Colutea arborescens | U | 0 | 0 | |
| Cornus sanguinea | AM | 0 | 17 | |
| Cornus sericea | AM | 1 | 17 | Weishampel et al., 2006 |
| Corylus avellana | EM | 3 | 42 | Etayo et al., 1999; (Mello et al., 1999) ;Selosse et al., 2002; (Wedn et al., 2009); Boeraeve et al., 2018 |
| Cotoneaster bullatus | AM | 0 | 20 | |
| Cotoneaster cambricus | AM | 0 | 20 | |
| Cotoneaster horizontalis | AM | 0 | 20 | |
| Cotoneaster integrifolius | AM | 0 | 20 | |
| Cotoneaster microphyllus agg. | AM | 0 | 20 | |
| Cotoneaster simonsii | AM | 0 | 20 | |
| Crataegus laevigata | AM | 0 | 17 | |
| Crataegus monogyna | AM | 6 | 17 | Blaszkowski, 1994;Kovacs and Szigetvÿri, 2002; Kovacs and Bagi , 2001;Boeraeve et al 2021;Maremmani et al., 2003, Boeraeve et al., 2018 |
| Cytisus scoparius | AM | 1 | 4 | Crush, 1975, |
| Daphne laureola | AM | 0 | 15 | |
| Daphne mezereum | AM | 0 | 15 | |
| Dryas octopetala | EM | 6 | 30 | Read and Haslewandter, 1981; Miller, 1982; Treu et al., 1995; Cripps et al., 2005; Harrington and Mitchell., 2005; Bjorb?kmo et al., 2010 |

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Table B.1 – *Continued from previous page*

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Empetrum nigrum | Er | 3 | 17 | Treu et al., 1995; Väre et al., 1997; van Geel et al., 2020 |
| Erica ciliaris | Er | 1 | 22 | Selosset al., 2007 |
| Erica cinerea | Er | 3 | 22 | Haslewanter and Read, 1980; Selosse et al., 2007;van Geel et al., 2018 |
| Erica tetralix | Er | 4 | 22 | Kovÿcs and Bagi, 2001;Kowal et al., 2016; van Geel et al., 2018; Kiheri et al., 2020 |
| Erica vagans | Er | 1 | 22 | Selosse et al., 2007 |
| Euonymus europaeus | AM | 1 | 15 | Kovacs and Bagi, 2001; |
| Fagus sylvatica | EM | 3 | 38 | Buee et al., 2005; Lang et al., 2011; Kubisch et al, 2015 |
| Frangula alnus | AM | 1 | 7 | Godwin, 1943; |
| Fraxinus excelsior | AM | 6 | 29 | Rothwell and Vogel, 1985; Mayr and Godoy, 1989; Brundrett et al., 1990; Bainard et al., 2011; Lang et al., 2011; Kubisch et al., 2016 |
| Fuchsia magellanica | AM | 0 | 1 | (Johnson, 1977) |
| Gaultheria shallon | Er | 2 | 13 | Xiao and Berch, (1995);1996; Allen et al., 2003 |
| Genista anglica | AM | 0 | 4 | |
| Genista pilosa | AM | 0 | 4 | |
| Genista tinctoria | AM | 0 | 4 | |
| Hedera helix | AM | 4 | 15 | (Newman et al., 1994); Maremmani et al., 2003; Songachan et al., 2011; Davison et al., 2015; Kowalczyk and Blaszkowski, 2013; |
| Hippophae rhamnoides | AM | 2 | 1 | Zhang et al., 2010; He et al., 2016 |

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Table B.1 – *Continued from previous page*

| Species | Type | NF | C | References |
|---|---|---|---|---|
| Hypericum androsaemum | AM | 1 | 28 | Davison et al., 2015 |
| Hypericum calycinum | AM | 0 | 28 | |
| Ilex aquifolium | AM | 0 | 18 | (Newman et al., 1994) |
| Juglans regia | AM | 2 | 16 | Brundrett et al., 1990; Bainard et al., 2011 |
| Juniperus communis | AM | 4 | 77 | Kovacic et al., 1984; Kovács and Szigetvári, 2002; He et al., 2019; Skinkis et al., 2021 |
| Laburnum anagyroides | U | 0 | 0 | |
| Larix decidua | EM | 1 | 52 | Leski and Rudawska, 2008; |
| Larix kaempferi | EM | 2 | 52 | Yang et al., 1998; Tsuyuzaki et al., 2005 |
| Laurus nobilis | AM | 1 | 5 | Maremmani et al., 2003; |
| Lavatera arborea | AM | 0 | 1 | |
| Leycesteria formosa | U | 0 | 0 | |
| Ligustrum ovalifolium | AM | 0 | 8 | |
| Ligustrum vulgare | AM | 1 | 8 | Maremmani et al., 2003; |
| Loiseleuria procumbens | Er | 3 | 1 | Haselwandter and Read 1980; Treu et al., 1995; Selosse et al., 2007 |
| Lonicera periclymenum | AM | 0 | 33 | |
| Lonicera xylosteum | AM | 0 | 33 | |
| Lupinus arboreus | NM | 0 | 2 | |
| Mahonia aquifolium | AM | 0 | 2 | |
| Malus domestica | AM | 3 | 15 | Miller et al., 1985; Maremmani et al., 2003; Sharma et al., 2005; (Mehta and Bharat, 2013) |
| Malus sylvestris | AM | 0 | 15 | |
| Mespilus germanica | AM | 0 | 0 | |
| Myrica gale | NM | 3 | 10 | Rose, 1980; Berliner and Torrey, 1989b; (Crocker and Schwintzer, 1994) |
| Phyllodoce caerulea | Er | 1 | 4 | Väre et al., 1997 |

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Table B.1 – *Continued from previous page*

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Picea abies | EM | 4 | 96 | Baier et al., 2006; Tedersoo et al., 2008; Schirkonyer et al., 2013;Wang et al., 2017; |
| Picea sitchensis | EM | 2 | 96 | Flynn et al., 1998; Palfner et al., 2005; |
| Pinus contorta | EM | 4 | 293 | Byrd et al., 2000; Cullings et al., 2001: 2005; Warzburger et al., 2004 |
| Pinus nigra | EM | 1 | 293 | (Karkouri et al., 2005); Trocha et al., 2012 |
| Pinus sylvestris | EM | 7 | 293 | Termorshuizen, 1991; Jonsson et al., 1999; Pickles et al., 2010; Rudawska et al., 2011; Jarvis et al., 2013;Suz et al., 2011,2017; |
| Populus alba | Dual | 3 | | Kovács and Bagi, 2002 ; Jakucs, 2002; Tyburska et al., 2013 |
| Populus alba x tremula (P. x canescens) | Dual | 1 | | Kovács and Bagi, 2001 |
| Populus nigra | Dual | 1 | | Tyburska et al., 2013 |
| Populus tremula | Dual | 2 | | Krpata et al., 2008, Bahram et al., 2011 |
| Potentilla fruticosa | AM | 0 | 76 | |
| Prunus avium | AM | 1 | 91 | Kirti et al., 2016 |
| Prunus cerasifera | AM | 0 | 91 | |
| Prunus cerasus | AM | 0 | 91 | |
| Prunus domestica | AM | 0 | 91 | (Razouk and Kajji, 2015) |
| Prunus laurocerasus | AM | 0 | 91 | |
| Prunus lusitanica | AM | 0 | 91 | |
| Prunus padus | AM | 1 | 91 | Kovÿcs and Bagi, 2001 |
| Prunus spinosa | AM | 1 | 91 | Kovÿcs and Bagi, 2001 |

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Table B.1 – *Continued from previous page*

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Pseudotsuga menziesii | EM | 4 | 16 | Horton et al., 1999; Massicotte et al., 1999; Benucci et al., 2016; Defrenne et al., 2019 |
| Pyrus communis | AM | 0 | 10 | |
| Pyrus cordata | AM | 0 | 10 | |
| Quercus cerris | EM | 1 | 64 | Fodor et al., 2011 |
| Quercus ilex | EM | 3 | 64 | Maremmani et al., 2003; De Romÿn and De Miguel, 2005; Richard et al., 2011 |
| Quercus petraea | EM | 5 | 64 | Courty et al., 2008; Urban et al., 2008, Suz et al., 2014; Barsoum et la., 2021; Guy et al., 2022 |
| Quercus robur | EM | 13 | 64 | (Tyler, 1992 sporocarp survey); Keizer and Arnolds, 1994; Kovács and Bagi, 2001; Maremmani et al., 2003; Mosca et al., 2007;Courty et al., 2008; Trocha et al., 2012; Suz et al., 2014; Martinova et al., 2016;Rasmussen et al., 2017; Bzdyk et al., 2019; Olchowik et al., 2019; Barsoum et al., 2021; Guy et al., 2022 |
| Rhamnus cathartica | AM | 1 | 7 | Kovacs and Bagi, 2001 |
| Rhododendron ponticum | Er | 1 | 15 | Vohník et al., 2011 |
| Ribes alpinum | AM | 0 | 26 | |
| Ribes nigrum | AM | 0 | 26 | |
| Ribes rubrum | AM | 0 | 26 | |
| Ribes spicatum | AM | 0 | 26 | |
| Ribes uva-crispa | AM | 0 | 26 | |

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Table B.1 – *Continued from previous page*

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Robinia pseudoacacia | AM | 4 | 9 | Kovÿcs and Bagi, 2001; Bainard et al., 2011;He et al., 2016,2019 |
| Rosa agrestis | AM | 0 | 49 | |
| Rosa arvensis | AM | 0 | 49 | |
| Rosa caesia | AM | 0 | 49 | |
| Rosa canina agg. | AM | 1 | 49 | Blaszkowski, 1994 |
| Rosa micrantha | AM | 0 | 49 | |
| Rosa mollis agg. | AM | 0 | 49 | |
| Rosa obtusifolia | AM | 0 | 49 | |
| Rosa pimpinellifolia | AM | 0 | 49 | |
| Rosa rubiginosa agg. | AM | 0 | 49 | |
| Rosa rugosa | AM | 0 | 49 | |
| Rosa sherardii | AM | 0 | 49 | |
| Rosa stylosa | AM | 0 | 49 | |
| Rosa tomentosa | AM | 0 | 49 | |
| Rubus caesius | AM | 0 | 78 | |
| Rubus fruticosus agg. | AM | 1 | 78 | Newman et al., 1994 |
| Rubus idaeus | AM | 1 | 78 | Berliner and Torrey, 1989 |
| Rubus spectabilis | AM | 0 | 78 | |
| Ruscus aculeatus | AM | 2 | 7 | Maremmani et al., 2003; Davison et al., 2012 |
| Salix alba | EM | 4 | 9 | Par di and Baar, 2006; Sumorok and Kiedrzy?ska, 2007; Tedersoo et al., 2013; Hrynkiewicz et al.,2015 |
| Salix arbuscula | U | 0 | 0 | |
| Salix aurita | EM | 2 | 2 | Sumorok and Kiedrzyska, 2007; Tedersoo et al., 2013 |
| Salix caprea | EM | 2 | 36 | Tedersoo et al., 2013; Hrynkiewicz et al.,2015 |
| Salix cinerea | EM | 2 | 8 | Sumorok and Kiedrzyska, 2007(dual); Tedersoo et al., 2013 |

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Table B.1 – *Continued from previous page*

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Salix fragilis | EM | 2 | 9 | Sumorok and Kiedrzyska, 2007; Tedersoo et al., 2013 |
| Salix herbacea | EM | 3 | 5 | Haselwandter and Read, 1980; Dhillon, 1994; Väre et al., 1997; Mühlmann and Peintner, 2008 |
| Salix lanata | EM | 1 | 1 | Dhillion, 1994 |
| Salix lapponum | EM | 1 | 0 | Milne et al., 2006 |
| Salix myrsinifolia | U | 0 | 0 | |
| Salix myrsinites | EM | 1 | 0 | Dhillion, 1994 |
| Salix pentandra | EM | 2 | 7 | Sumorok,and Kiedrzyska, 2007; Tedersoo et al., 2013 |
| Salix phylicifolia | EM | 2 | 11 | Dhillion, 1994; Tedersoo et al., 2013 |
| Salix purpurea | AM | 1 | 0 | Sumorok,and Kiedrzyska, 2007 |
| Salix repens | Dual | 3 | 0 | van der Heijden et al., 1999; Kovács and Szigetvári, 2002 ; Botnen et al., 2015 |
| Salix reticulata | EM | 2 | 1 | Dhillion et al. 1994; Treu et al., 1995;Väre et al., 1997 |
| Salix triandra | EM | 2 | 2 | Sumorok and Kiedrzyska, 2007; Tedersoo et al., 2013 |
| Salix viminalis | EM | 1 | 0 | Sumorok and Kiedrzyska, 2007 |
| Sambucus nigra | AM | 1 | 14 | Kovacs and Bagi, 2001; |
| Sambucus racemosa | AM | 0 | 14 | |
| Sorbus anglica | AM | 0 | 26 | |
| Sorbus aria agg. | AM | 0 | 26 | |
| Sorbus arranensis | AM | 0 | 26 | |
| Sorbus aucuparia | AM | 0 | 26 | |
| Sorbus bristoliensis | AM | 0 | 26 | |
| Sorbus devoniensis | AM | 0 | 26 | |

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Table B.1 – *Continued from previous page*

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Sorbus domestica | AM | 0 | 26 | |
| Sorbus eminens | AM | 0 | 26 | |
| Sorbus hibernica | AM | 0 | 26 | |
| Sorbus intermedia | AM | 0 | 26 | |
| Sorbus lancastriensis | AM | 0 | 26 | |
| Sorbus leptophylla | AM | 0 | 26 | |
| Sorbus leyana | AM | 0 | 26 | |
| Sorbus minima | AM | 0 | 26 | |
| Sorbus porrigentiformis | AM | 0 | 26 | |
| Sorbus pseudofennica | AM | 0 | 26 | |
| Sorbus rupicola | AM | 0 | 26 | |
| Sorbus subcuneata | AM | 0 | 26 | |
| Sorbus torminalis | AM | 3 | 26 | Malloch and Malloch, 1982; Moradi et al., 2015, Bzdyk et al., 2016 |
| Sorbus vexans | AM | 0 | 26 | |
| Suaeda vera | AM | 1 | 23 | Agwa and Abdel-Fattah 2002 |
| Symphoricarpos albus | AM | 2 | 1 | Kovacic et al., 1984; Berch et al., 1988 |
| Syringa vulgaris | AM | 0 | 10 | |
| Taxus baccata | AM | 1 | 2 | Wubet et al., 2003; |
| Thuja plicata | AM | 1 | 17 | Gorzelak et al., 2017; |
| Tilia cordata | EM | 2 | 32 | Timonen and Kauppinen, 2008; Lang et al., 2011; (Rudawska et al., 2019) |
| Tilia cordata x platyphyllos (T. x europaea) | EM | 0 | 32 | |
| Tilia platyphyllos | EM | 1 | 32 | Lang et al., 2011 |
| Tsuga heterophylla | EM | 2 | 22 | Kropp and Trappe 1982, Wurzburger et al., 2004 |
| Ulex europaeus | AM | 2 | 3 | Maremmani et al., 2003; Santhoshkumar et al., 2018 |
| Ulex gallii | AM | 0 | 3 | |
| Ulex minor | AM | 0 | 3 | |
| Ulmus glabra | AM | 0 | 11 | |

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Table B.1 – *Continued from previous page*

| **Species** | **Type** | **NF** | **C** | **References** |
|---|---|---|---|---|
| Ulmus minor | AM | 0 | 13 | |
| Ulmus plotii | AM | 0 | 11 | |
| Ulmus procera | AM | 0 | 11 | |
| Vaccinium myrtillus | Er | 4 | 98 | Haslewandter and Read, 1980; Treu et al., 1995; Väre et al., 1997; van Geel et al., 2020 |
| Vaccinium uliginosum | Er | 4 | 98 | Haslewandter and Read, 1980; Treu et al., 1995;Väre et al., 1997; van Geel et al., 2020 |
| Vaccinium vitis-idaea | Er | 3 | 98 | Treu et al., 1995;Väre et al., 1997; van Geel et al., 2020 |
| Viburnum lantana | AM | 0 | 29 | |
| Viburnum opulus | AM | 0 | 29 | |

# Appendix C

# Appendix Chapter 4

## C.1 Distribution of mycorrhizal types in woodlands

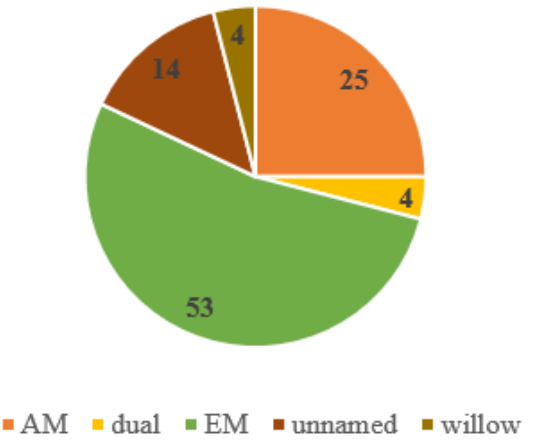


Figure C.1: Distribution of the mycorrhizal type of broadleaved tree species in woodlands in Great Britain based on data from the National Forest Inventory (NFI) for 2011 (National Forest Inventory, 2012). (AM, arbuscular mycorrhizal. EM, ectomycorrhizal, dual, thought to host both arbuscular and ectomycorrhizal fungi. Unnamed, these trees were not identified in the NFI and hence mycorrhizal type could not be allocated). EM trees specified in the NFI are oak (Quercus robur, Q. petraea), beech, (Fagus sylvatica), birch (Betula pendula, B. pubescens), sweet chestnut (Castanea sativa, and hazel (Corylus avellana). Birch is sometimes referred to as a dual host, but we found little evidence for this in British woodlands. AM trees are sycamore (Acer pseudoplatanus), hawthorn (Crataegus monogyna), and ash (Fraxinus excelsior). Dual mycorrhizal trees are alder (Alnus glutinosa). Willows (Salix spp.) are shown separately as they can be either EM or AM type. Note that even if all unnamed species were AM type hosts (e.g., rowan (Sorbus spp.) or holly (Ilex aquifolium)), the proportion of EM type hosts in British woodlands is still greater.

## C.2 Correlation plot

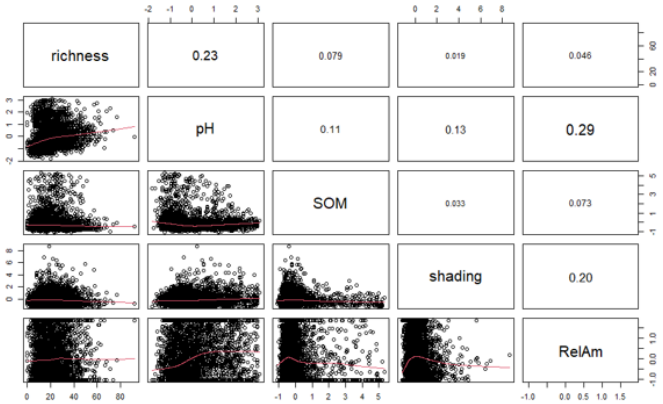


Figure C.2: Correlation plot for all pooled data across both years of the Bunce survey, after, sites with correlated variables were removed, with smoothed regression lines. Upper panel shows Spearman correlation coefficient. (Richness, understory herb richness; pH, soil pH; SOM, soil organic matter; shading; shading, calculated as the sum over the DBH classes multiplied by the number of stems in that class; RelAm, relative abundance of AM type trees and shrubs)

## C.3 Species richness response to soil pH

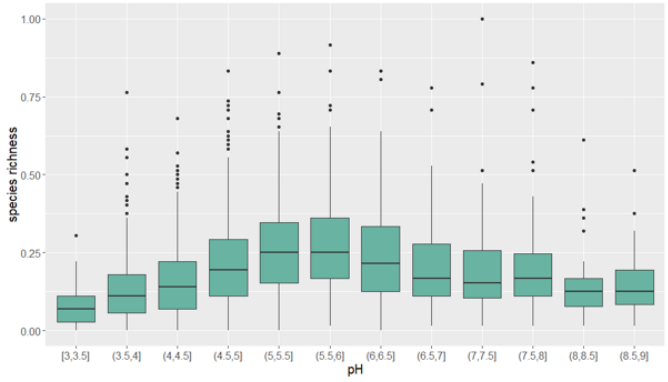


Figure C.3: Response of understory plant species richness in woodlands of the Bunce dataset to soil pH. The soil pH has been grouped into bin widths of 0.5. The peak richness can be seen at around pH 5.5 to pH 6. Horizontal lines on the box-plots indicate the median, the 1st and 3rd quartiles. Whiskers denote 1.5x the inter quartile range (IQR) and points denote values outside the IQR. Square and round brackets denote the half open interval $(a, b] = a < x \leq b$.

## C.4 Spline correlogram

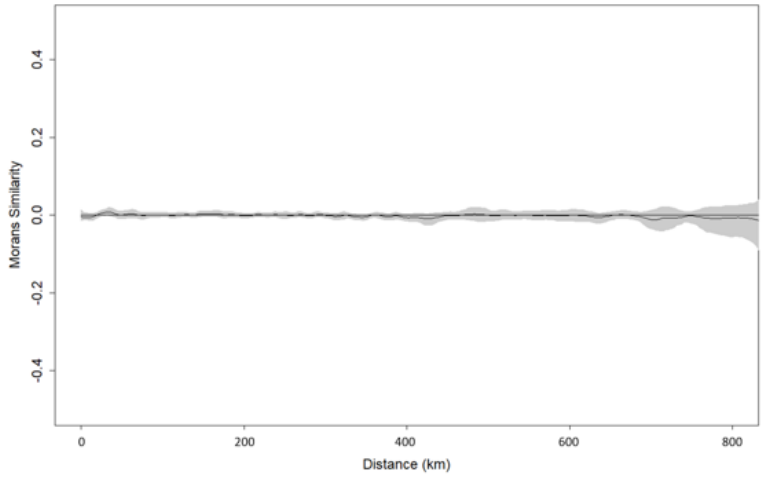


Figure C.4: Spline correlogram with 95% confidence intervals of the Pearson residuals of the mixed effects negative binomial model. There is no evidence of significant spatial autocorrelation, which suggests that i) the mixed effects model takes account of any within site spatial autocorrelation, and ii) between site autocorrelation is negligible.

## C.5 Details of model output

| variable | effect size | std error | z value | Pr(>\|z\|) | | AIC | ΔAIC | conditional $R^2$ | marginal $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| **ph** | 0.31 | 0.03 | 11.13 | < 2e-16 | *** | 22262.07 | 0.00 | 0.49 | 0.11 |
| **RelAm** | 0.05 | 0.01 | 4.76 | 1.97e-06 | *** | | | | |
| **SOM** | -0.01 | 0.01 | -1.42 | 0.156 | | | | | |
| **yr** | -0.16 | 0.02 | -9.74 | < 2e-16 | *** | | | | |
| **ph:yr** | -0.10 | 0.02 | -6.40 | 1.58e-10 | *** | | | | |
| | | | | | | | | | |
| **ph** | 0.31 | 0.03 | 11.11 | < 2e-16 | *** | 22262.09 | 0.02 | 0.49 | 0.11 |
| **RelAm** | 0.05 | 0.01 | 4.77 | 1.87e-06 | *** | | | | |
| **yr** | -0.16 | 0.02 | -9.80 | < 2e-16 | *** | | | | |
| **ph:yr** | -0.10 | 0.02 | -6.34 | 2.28e-10 | *** | | | | |
| | | | | | | | | | |
| **ph** | 0.31 | 0.03 | 10.56 | < 2e-16 | *** | 22262.78 | 0.71 | 0.49 | 0.11 |
| **RelAm** | 0.07 | 0.03 | 2.80 | 0.00504 | ** | | | | |
| **SOM** | -0.01 | 0.01 | -1.43 | 0.1528 | | | | | |
| **yr** | -0.16 | 0.02 | -9.72 | < 2e-16 | *** | | | | |
| **ph:yr** | -0.10 | 0.02 | -5.90 | 3.64e-09 | *** | | | | |
| RelAm:yr | -0.02 | 0.02 | -1.14 | 0.25533 | | | | | |
| | | | | | | | | | |
| **ph** | 0.31 | 0.03 | 10.55 | < 2e-16 | *** | 2262.82 | 0.75 | 0.49 | 0.11 |
| **RelAm** | 0.07 | 0.03 | 2.80 | 0.00519 | ** | | | | |
| **yr** | -0.16 | 0.02 | -9.79 | < 2e-16 | *** | | | | |
| **ph:yr** | -0.10 | 0.02 | -5.85 | 4.98e-09 | *** | | | | |
| RelAm:yr | -0.02 | 0.02 | -1.12 | 0.26131 | | | | | |
| | | | | | | | | | |
| **ph** | 0.31 | 0.03 | 10.52 | < 2e-16 | *** | 22263.42 | 1.35 | 0.49 | 0.11 |
| **RelAm** | 0.08 | 0.03 | 2.95 | 0.00322 | ** | | | | |
| **yr** | -0.16 | 0.02 | -9.42 | < 2e-16 | *** | | | | |
| **shading** | 0.00 | 0.01 | 0.18 | 0.85808 | | | | | |
| **ph:yr** | -0.10 | 0.02 | -5.83 | 5.55e-09 | *** | | | | |
| **RelAm:shading** | -0.02 | 0.01 | -1.77 | 0.07723 | . | | | | |
| **RelAm:yr** | -0.02 | 0.02 | -1.44 | 0.14917 | | | | | |
| | | | | | | | | | |
| **ph** | 0.32 | 0.03 | 11.09 | < 2e-16 | *** | 22263.51 | 1.44 | 0.49 | 0.11 |
| **RelAm** | 0.04 | 0.01 | 4.28 | 1.90e-05 | *** | | | | |
| **yr** | -0.16 | 0.02 | -9.44 | < 2e-16 | *** | | | | |
| **shading** | 0.00 | 0.01 | 0.17 | 0.866 | | | | | |
| **ph:yr** | -0.10 | 0.02 | -6.37 | 1.95e-10 | *** | | | | |

Figure C.5: Effect sizes, standard errors, significance, AIC values, ΔAIC, and conditional and marginal R2 for the six lowest AIC models (all models with $\Delta AIC < 2$). The same set of variables (pH, RelAm, year, and the interaction between year and pH), highlighted in bold, are the only significant predictors of understory species richness in all models in this set. Asterisks indicate significance level. (pH; soil pH; RelAm, the relative abundance of AM trees and shrubs; SOM, soil organic matter content; yr, year; shading, calculated as the sum over the DBH classes multiplied by the number of stems in that class)

## C.6 Sensitivity analysis

| variable | effect size | std error | z value | Pr(>\|z\|) | | AIC | conditional $R^2$ | marginal $R^2$ |
|---|---|---|---|---|---|---|---|---|
| *Crataegus*: AM. *Ilex*: unknown | | | | | | | | |
| **ph** | 0.31 | 0.03 | 11.02 | < 2e-16 | *** | 22246.01 | 0.50 | 0.12 |
| **RelAm** | 0.06 | 0.01 | 6.23 | 4.76e-10 | *** | | | |
| **SOM** | -0.01 | 0.01 | -1.44 | 0.15 | | | | |
| **yr** | -0.15 | 0.02 | -9.59 | < 2e-16 | *** | | | |
| **ph:yr** | -0.10 | 0.02 | -6.43 | 1.32e-10 | *** | | | |
| | | | | | | | | |
| *Crataegus*: EM. *Ilex*: AM | | | | | | | | |
| **ph** | 0.32 | 0.03 | 11.18 | < 2e-16 | *** | 22261.46 | 0.49 | 0.11 |
| **RelAm** | 0.05 | 0.01 | 4.82 | 1.43e-06 | *** | | | |
| **SOM** | -0.01 | 0.01 | -1.46 | 0.144 | | | | |
| **yr** | -0.16 | 0.02 | -9.76 | < 2e-16 | *** | | | |
| **ph:yr** | -0.10 | 0.02 | -6.43 | 1.29e-10 | *** | | | |
| | | | | | | | | |
| *Crataegus*: EM. *Ilex*: unknown | | | | | | | | |
| **ph** | 0.31 | 0.03 | 11.09 | < 2e-16 | *** | 22244.68 | 0.50 | 0.12 |
| **RelAm** | 0.06 | 0.01 | 6.33 | 2.42e-10 | *** | | | |
| **SOM** | -0.01 | 0.01 | -1.49 | 0.135 | | | | |
| **yr** | -0.15 | 0.02 | -9.63 | < 2e-16 | *** | | | |
| **ph:yr** | -0.10 | 0.02 | -6.47 | 1.00e-10 | *** | | | |

Figure C.6: Sensitivity analysis. Allocation of mycorrhizal type to *Crataegus monogyna* and *Ilex aquifolium* was questionable. Although it is likely that *C. monogyna* is AM type in line with other members of the Rosaceae family, there was some suggestion in the literature that this plant might associate with EMF in woodland settings. *I. aquifolium* is likely to be AM type in line with other *Ilex* spp., however, in our literature search, we found no work looking at this specific species. Therefore, we carried out sensitivity analysis by changing the mycorrhizal type of these two plants. In the main model both *C. monogyna* and *I. aquifolium* are allocated as AM type. The model was repeated with three different permutations: *C. mongyna* AM, *I. aquifolium* unknown; *C. monogyna* EM, *I. aquifolium* AM; *C. monogyna* EM, *I. aquifolium* unknown. In each case, the same full global model was created and the 'dredge' function was used to extract the model with the lowest AIC. The table shows effect sizes for the lowest AIC model when the mycorrhizal status of *C. monogyna* and *I. aquifolium* were changed. The results are not sensitive to changes in the mycorrhizal type of these plants; the same set of variables appear in the lowest AIC model in every permutation. Asterisks indicate significance level. (pH; soil pH; RelAm, the relative abundance of AM trees and shrubs; SOM, soil organic matter content; yr, year; shading, calculated as the sum over the DBH classes multiplied by the number of stems in that class)

# Appendix D

# Appendix Chapter 5

## D.1 Species found and accession numbers

Table D.1: Ectomycorrhizal fungi identified in Nineteen oak woodlands across Britain, listed in alphabetical order with occurrences in data and accession number.

| **Taxon name** | **Occurrences in data** | **Accession** |
|---|---|---|
| Amanita fulva | 7 | UDB001477 |
| Amanita gemmata | 3 | KY596001 |
| Amanita griseoverrucosa | 2 | KM052536 |
| Amanita rubescens | 12 | UDB025060 |
| Byssocorticium pulchrum | 1 | UDB0754273 |
| Cenococcum geophilum | 85 | LC095145 |
| Clavulina | 1 | UDB025066 |
| Clavulina amethystina | 8 | MT859115 |
| Clavulina coralloides | 29 | KX449469 |
| Cortinarius acutovelatus | 7 | FJ039609 |
| Cortinarius acutus | 1 | UDB017978 |
| Cortinarius anomalus | 6 | KY595995 |
| Cortinarius anthracinus | 2 | MT934878 |
| Cortinarius caesiostramineus | 1 | KJ421179 |
| Cortinarius comptulus | 2 | MT934983 |
| Cortinarius danicus | 9 | MT934996 |
| Cortinarius decipiens | 5 | KY640617 |
| Cortinarius diasemospermus | 17 | KY640619 |
| Cortinarius fragrantissimus | 10 | KU041739 |
| Cortinarius gurdus | 9 | MT935107 |
| Cortinarius megacystidiosus | 1 | MT935218 |

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Table D.1 – *Continued from previous page*

| **Taxon name** | **Occurrences in data** | **Accession** |
|---|---|---|
| Cortinarius obtusus | 15 | KY287718 |
| Cortinarius parhonestus | 4 | MT935284 |
| Cortinarius punctatoides | 28 | MT935358 |
| Cortinarius stillatitius | 4 | MN992364 |
| Cortinarius2 | 1 | UDB024917 |
| Cortinarius3 | 1 | UDB034857 |
| Craterellus tubaeformis | 3 | UDB036582 |
| Elaphomyces asperulus | 5 | MG597453 |
| Elaphomyces cyanosporus | 3 | MG820046 |
| Elaphomyces granulatus | 16 | KR029768 |
| Elaphomyces muricatus | 51 | UDB028086 |
| Hebeloma aestivale | 3 | KT218454 |
| Hebeloma alvarense | 1 | UDB019711 |
| Hebeloma pusillum | 1 | UDB036800 |
| Hebeloma2 | 1 | UDB017969 |
| Humaria hemisphaerica | 12 | JX907812 |
| Humaria1 | 11 | EU024887 |
| Hydnotrya tulasnei | 6 | MT859130 |
| Hygrophorus arbustivus | 4 | JF908066 |
| Hymenogaster griseus | 1 | JQ723996 |
| Imleria badia | 49 | MN970521 |
| Inocybe asterospora | 10 | MN540272 |
| Inocybe cincinnata | 6 | UDB035846 |
| Inocybe geophylla | 1 | KX449458 |
| Inocybe napipes | 10 | AM087253 |
| Inocybe petiginosa | 4 | MN947362 |
| Inocybe stellatospora | 2 | AM882747 |
| Inocybe tabacina | 3 | HQ586865 |
| Inocybe3 | 3 | HF675507 |
| Inosperma maculatum | 3 | MN959783 |
| Laccaria amethystina | 84 | MT859121 |
| Laccaria laccata | 20 | UDB037039 |
| Laccaria proxima | 1 | UDB037815 |
| Lactarius camphoratus | 61 | MT859123 |
| Lactarius chrysorrheus | 74 | KX449473 |
| Lactarius decipiens | 3 | KT165316 |
| Lactarius fulvissimus | 2 | KT165245 |

*Continued on next page*

Table D.1 – *Continued from previous page*

| **Taxon name** | **Occurrences in data** | **Accession** |
|---|---|---|
| Lactarius quietus | 92 | MW027925 |
| Lactarius serifluus | 2 | UDB039266 |
| Lactarius subdulcis | 27 | MN959786 |
| Lactarius tabidus | 87 | LK932113 |
| Lactifluus vellereus | 21 | UDB039234 |
| Leotia lubrica | 5 | MK253753 |
| Melanogaster ambiguus | 6 | AJ555512 |
| Melanogaster1 | 1 | UDB0778706 |
| Otidea alutacea | 1 | KY498600 |
| Otidea bufonia | 3 | JN942767 |
| Otidea onotica | 9 | MN627807 |
| Paxillus involutus | 18 | MG597401 |
| Peziza succosa | 3 | UDB0780252 |
| Pseudotomentella umbrina | 11 | MH270630 |
| Russula amoenolens | 64 | MN663161 |
| Russula atropurpurea | 54 | KX449425 |
| Russula betularum | 10 | KX579810 |
| Russula brunneoviolacea | 14 | MG687327 |
| Russula chloroides | 25 | MN265650 |
| Russula cuprea | 2 | KU886592 |
| Russula cyanoxantha | 1 | KR364093 |
| Russula densifolia | 28 | MG687332 |
| Russula foetens | 8 | MG687323 |
| Russula fragilis | 86 | KY681458 |
| Russula graveolens | 19 | UDB002538 |
| Russula heterophylla | 3 | UDB000909 |
| Russula ionochlora | 13 | UDB022526 |
| Russula laeta | 6 | MG679812 |
| Russula nobilis | 9 | UDB031193 |
| Russula ochroleuca | 87 | MT859128 |
| Russula odorata | 12 | UDB000916 |
| Russula peckii | 57 | MK131580 |
| Russula puellaris | 15 | MH248054 |
| Russula risigallina | 8 | UDB0799028 |
| Russula1 | 1 | UDB032615 |
| Russula2 | 1 | UDB013176 |
| Scleroderma areolatum | 62 | MN684210 |

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Table D.1 – *Continued from previous page*

| **Taxon name** | **Occurrences in data** | **Accession** |
|---|---|---|
| Scleroderma citrinum | 56 | KY694393 |
| Scleroderma verrucosum | 49 | KM247623 |
| Sebacina dimitica | 8 | UDB0754284 |
| Sebacina epigaea | 9 | JQ665514 |
| Sebacina incrustans | 15 | UDB014117 |
| Thelephora albomarginata | 3 | UDB016649 |
| Thelephora terrestris | 54 | U83486 |
| Russula | 17 | UDB000255 |
| Tomentella bryophila | 42 | UDB000254 |
| Tomentella cinereoumbrina | 12 | UDB011602 |
| Tomentella coerulea | 22 | MN947340 |
| Tomentella ellisii | 3 | UDB016490 |
| Tomentella fuscocinerea | 9 | UDB003300 |
| Tomentella galzinii | 18 | UDB003321 |
| Tomentella lapida | 41 | MN947361 |
| Tomentella lilacinogrisea | 1 | UDB020322 |
| Tomentella papuae | 3 | UDB018442 |
| Tomentella punicea | 37 | UDB000271 |
| Tomentella spinosispora | 25 | UDB037875 |
| Tomentella stuposa | 30 | UDB028233 |
| Tomentella2 | 1 | UDB018677 |
| Tomentellopsis echinospora | 1 | UDB008250 |
| Tomentellopsis submollis | 16 | KY693726 |
| Tuber anniae | 3 | UDB028385 |
| Tuber borchii | 2 | EU784422 |
| Tuber maculatum | 1 | MT554444 |
| Tuber puberulum | 17 | AJ969625 |
| Tylopilus felleus | 2 | MG597437 |
| Xerocomellus cisalpinus | 12 | HM356015 |
| Xerocomus ferrugineus | 16 | MT955158 |

## D.2 Review of EMF species of Oak

Table D.2: Summary of ectomycorrhizal fungal species reported for *Q.robur* and *Q. petraea*. A,(Tyler, 1992) B, (Keizer & Arnolds, 1994),C,(Mosca *et al.*, 2007), D, (Courty *et al.*, 2008), E, (Leski *et al.*, 2009), F,(Trocha *et al.*, 2012), G,(Schirkonyer *et al.*, 2013) , H,(Suz *et al.*, 2014), I,(Martinová *et al.*, 2016) J,(Olchowik *et al.*, 2019), K,(Bzdyk *et al.*, 2019), L, (Barsoum *et al.*, 2021), M, this work

| **Taxon name** | **A** | **B** | **C** | **D** | **E** | **F** | **G** | **H** | **I** | **J** | **K** | **L** | **M** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Alnicola macrospora | | | | | | | | | 1 | | | | |
| Amanita citrina | | 1 | | | | | | | | 1 | 1 | | |
| Amanita fulva | 1 | 1 | | | | | | | | | | | 1 |
| Amanita gemmata | | | | | | | | | | | | | 1 |
| Amanita griseoverrucosa | | | | | | | | | | | | | 1 |
| Amanita muscaria | | 1 | | | | | | | | | | | |
| Amanita pantherina | | | | 1 | | | | | | | | | |
| Amanita rubescens | | 1 | | | | | | 1 | | | | 1 | 1 |
| Amanita spissa | | 1 | | | | | | | 1 | | | | |
| Amanita virosa | 1 | | | | | | | | | | | | |
| Amphinema byssoides | | | | | 1 | | | | | | | | |
| Boletus aestivalis | | | | 1 | | | | | | | | | |
| Boletus badius | 1 | 1 | | | | | | | 1 | | 1 | 1 | |
| Boletus chrysenteron | | 1 | | 1 | | | | | | | | | |
| Boletus cisalpinus | | | | | | | | | 1 | | | 1 | |
| Boletus edulis | | 1 | | 1 | | 1 | | | | | | | |
| Boletus erythropus | | | | | | | | | 1 | | | | |
| Boletus porosporus | | 1 | | | | | | | | 1 | | 1 | |
| Boletus pruinatus | | | | | | | | 1 | | | 1 | 1 | |
| Boletus reticulatus | | | | | | | | 1 | | | | | |
| Boletus rubellus | | 1 | | | | | | | 1 | | | 1 | |
| Boletus subtomentosus | 1 | | | 1 | | | | 1 | | | 1 | | |
| Byssocorticium atrovirens | | | 1 | 1 | | | 1 | | | | | | |
| Byssocorticium pulchrum | | | | | | | | | | | | | 1 |
| Cantharellus cibarius | 1 | 1 | | | | | | | | | | | |
| Cenococcum geophilum | | | | 1 | 1 | 1 | 1 | | 1 | 1 | | 1 | 1 |
| Chalciporus piperatus | | 1 | | | | | | | | | | 1 | |
| Clavulina amethystina | | | | | | | | | | | | 1 | 1 |
| Clavulina cinerea | | | 1 | | | | | | | | | | |
| Clavulina coralloides | | 1 | | | | | | 1 | | | | | 1 |
| Clavulina cristata | | | 1 | | | | | | | | | | |
| Clitopilus prunulus | | 1 | | | | | | | | | | | |
| Cortinarius acutovelatus | | | | | | | | | | | | | 1 |
| Cortinarius acutus | | | | | | | | | | | | | 1 |

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Table D.2 – *Continued from previous page*

| Taxon name | A | B | C | D | E | F | G | H | I | J | K | L | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cortinarius anomalus | | 1 | | 1 | | | | 1 | | | | | 1 |
| Cortinarius anthracinus | | | | 1 | | | | | | | | | 1 |
| Cortinarius caesiostramineus | | | | | | | | | | | | | 1 |
| Cortinarius casimiri | | | | | | 1 | 1 | 1 | | | | | |
| Cortinarius comptulus | | | | | | | | | | | | | 1 |
| Cortinarius danicus | | | | | | | | | | | | | 1 |
| Cortinarius decipens | | | | | | | | | | | | | 1 |
| Cortinarius diasemospermus | | | | | | | | | | | | | 1 |
| Cortinarius erythrinus | | 1 | | | | | | | | | | | |
| Cortinarius flexipes | | 1 | | | | | | | | | | | |
| Cortinarius fragrantissimus | | | | | | | | | | | | | 1 |
| Cortinarius fulvoconicus | | | | | | | | | 1 | | | | |
| Cortinarius gurdus | | | | | | | | | | | | | 1 |
| Cortinarius helobius | | | | | | | | | 1 | | | | |
| Cortinarius helodes | | 1 | | | | | | | | | | | |
| Cortinarius helveolus | | 1 | | | | | | | | | | | |
| Cortinarius hinnuleus | | 1 | | | | | | | | | | | |
| Cortinarius laetissimus | | | | | | | | | 1 | | | | |
| Cortinarius lanatus | | 1 | | | | | | | | | | | |
| Cortinarius megacystidiosus | | | | | | | | | | | | | 1 |
| Cortinarius obtusus | | 1 | | | | | | | | | | | 1 |
| Cortinarius paleaceus | | 1 | | | | | | | | | | | |
| Cortinarius parhonestus | | | | | | | | | | | | | 1 |
| Cortinarius privignus | | 1 | | | | | | | | | | | |
| Cortinarius punctatoides | | | | | | | | | | | | | 1 |
| Cortinarius saniosus | | 1 | | | | | | | | | | | |
| Cortinarius semisanguineus | | | | 1 | | | | | | | | | |
| Cortinarius stillatitius | | | | | | | | | | | | | 1 |
| Cortinarius striaepilus | | 1 | | | | | | | | | | | |
| Cortinarius subpuellaris | | | | | | | | | | | | 1 | |
| Cortinarius subsertipes | | 1 | | | | | 1 | | | | | | |
| Cortinarius umbrinolens | | 1 | | | | | | | | | | | |
| Cortinarius violilamellatus | | 1 | | | | | | | | | | | |
| Craterellus tubaeformis | | | | | | | | | | | | | 1 |
| Elaphomyces muricatus | | | | | | 1 | | | 1 | | | 1 | 1 |
| Elaphomyces asperulus | | | | | | | | | | | | | 1 |
| Elaphomyces. cyanosporus | | | | | | | | | | | | | 1 |
| Elaphomyces granulatus | | | | | | | | | | | | | 1 |

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Table D.2 – *Continued from previous page*

| **Taxon name** | **A** | **B** | **C** | **D** | **E** | **F** | **G** | **H** | **I** | **J** | **K** | **L** | **M** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Entoloma araneosum | | | | | | | | | | | | 1 | |
| Entoloma nitidum | | | | 1 | | | | | | | | | |
| Entoloma sinuatum | | | | | | | | | 1 | | | | |
| Entoloma undatum | | | | | | | | | 1 | | | | |
| Fagirhiza cystidiophora | | | | | | | 1 | | | | | | |
| Fagirhiza tubulosa | | | | | | | 1 | | | | | | |
| Genea hispidula | | | | | | | 1 | 1 | | | | 1 | |
| Geopora cervina | | | | | | | | | 1 | | | | |
| Hebeloma aestivale | | | | | | | | | 1 | | | | 1 |
| Hebeloma alvarense | | | | | | | | | | | | | 1 |
| Hebeloma cavipes | | | | | | | | | 1 | | | | |
| Hebeloma helodes | | | | | 1 | | | | | | | | |
| Hebeloma longicaudum | | 1 | | | | | | | | | | | |
| Hebeloma mesophaeum | | 1 | | | | | | | 1 | | | | |
| Hebeloma pallidoluctuosum | | 1 | | | | | | | 1 | | | | |
| Hebeloma pseudofragilipes | | | | | | | | | | | | 1 | |
| Hebeloma sacchariolens | | | | 1 | 1 | | | | | | | | |
| Hebeloma pusillum | | | | | | | | | | | | | 1 |
| Helvella maculata | | | | | | | | | 1 | | | | |
| Humaria hemisphaerica | | | 1 | | | 1 | | | | 1 | | | 1 |
| Hyaloscypha bicolor | | | | | | | | | | 1 | | | |
| Hydnotrya tulasnei | | | | | | | | 1 | 1 | | 1 | 1 | 1 |
| Hygrophorus arbustivus | | | | | | | | | | | | | 1 |
| Hymenogaster citrinus | | | | | | | | | 1 | | | | |
| Hymenogaster griseus | | | | | | | | | | | | | 1 |
| Hymenogaster niveus | | | | | | | | | 1 | | | | |
| Hymenogaster olivaceus | | | | | | | | | 1 | | | | |
| Hymenogaster populetorum | | | | | | | | | 1 | | | | |
| Hymenogaster pusillus | | | | | | | | | 1 | | | | |
| Hymenogaster tener | | | | | | | | | 1 | | | | |
| Hymenogaster vulgaris | | | | | | | | | 1 | | | | |
| Ilyonectria radicicola | | | | | | | | | | | 1 | | |
| Imleria badia | | | | | | | | | | | | 1 | 1 |
| Inocybe albomarginata | | 1 | | | | | | | | | | | |
| Inocybe assimilata | | 1 | | | | | | | 1 | | 1 | | |
| Inocybe asterospora | | | 1 | | | | | | 1 | | | 1 | 1 |
| Inocybe calamistrata | | | 1 | | | | | | | | | | |
| Inocybe calida | | | | | 1 | | | | | | | | |

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Table D.2 – *Continued from previous page*

| Taxon name | A | B | C | D | E | F | G | H | I | J | K | L | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Inocybe cincinnata | | | | | | | | | | | | | 1 |
| Inocybe curvipes | | | | | 1 | | | | | | | | |
| Inocybe geophylla | | | | | | | | | 1 | | | | 1 |
| Inocybe grammopodia | | | | | | | | | 1 | | | | |
| Inocybe griseolilacina | | 1 | | | | | | | | | | | |
| Inocybe lacera | | 1 | | | | | | | 1 | | | | |
| Inocybe lanuginella | | 1 | | | | | | | | | | | |
| Inocybe lanuginosa | | 1 | | | | | | | | 1 | | | |
| Inocybe maculata | | 1 | 1 | | | | | | 1 | | | | |
| Inocybe mixtilis | | 1 | | | | | | | | | | | |
| Inocybe napipes | | 1 | | | | | | | | | | | 1 |
| Inocybe petiginosa | | 1 | | | | | | | | | | | 1 |
| Inocybe phaeocomis | | | | | | | | | 1 | | | | |
| Inocybe phaeoleuca | | | | | | | | | 1 | | | | |
| Inocybe putilla | | | | | | | | | 1 | | | | |
| Inocybe stellatospora | | | | | | | | | | | | | 1 |
| Inocybe tabacina | | | | | | | | | 1 | | | | 1 |
| Inocybe tigrina | | | | | | | | | 1 | | | | |
| Inosperma maculatum | | | | | | | | | | | | | 1 |
| Laccaria amethystina | | 1 | | 1 | | | 1 | 1 | | | | 1 | 1 |
| Laccaria anglica | | | | | | | | | | | | 1 | |
| Laccaria bicolor | | 1 | | | | | | | 1 | | | 1 | |
| Laccaria laccata | | 1 | | | | | | 1 | 1 | | | | 1 |
| Laccaria proxima | | 1 | | | 1 | | | | | | | | 1 |
| Laccaria tortilis | | 1 | | | 1 | | | | | | | | |
| Lactarius camphoratus | | 1 | | | | | | 1 | | | | 1 | 1 |
| Lactarius chrysorrheus | | 1 | | 1 | | | | 1 | | | 1 | | 1 |
| Lactarius decipiens | | | | | | | | | | | | | 1 |
| Lactarius fulvissimus | | | | | | | | | | | | | 1 |
| Lactarius necator | | | 1 | | | | | | | | | | |
| Lactarius quietus | 1 | 1 | 1 | 1 | | 1 | 1 | 1 | 1 | | 1 | 1 | 1 |
| Lactarius serifluus | | 1 | | | | | | | | | | 1 | 1 |
| Lactarius subdulcis | | | | | | | 1 | | | | | 1 | 1 |
| Lactarius subumbonatus | | | | | | | | 1 | | | | | |
| Lactarius tabidus | | | | | | 1 | 1 | | | | | 1 | 1 |
| Lactarius theiogalus | | 1 | | | | | | | | | | | |
| Lactarius vellereus | 1 | | | | | | | | | | | | |
| Lactifluus vellereus | | | | | | | | | | | | | 1 |

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Table D.2 – *Continued from previous page*

| Taxon name | A | B | C | D | E | F | G | H | I | J | K | L | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Leccinum crocipodium | | | | 1 | | | | | | | | | |
| Leotia lubrica | | 1 | | | | | | | | | | | 1 |
| Lyophyllum loricatum | | | | | | | | | 1 | | | | |
| Melanogaster ambiguus | | | | | | | | | 1 | | | | 1 |
| Melanogaster variegatus | | | | | | | 1 | | | | | | |
| Meliniomyces bicolor | | | | | | | | 1 | | | | | |
| Naucoria bohemica | | 1 | | | | | | | | | | | |
| Otidea alutacea | | | | | | | | | | | | | 1 |
| Otidea bufonia | | 1 | | | | | | | | | | | 1 |
| Otidea onotica | | | | | | | | | | | | | 1 |
| Pachyphlodes nemoralis | | | | | | | | | | 1 | 1 | 1 | |
| Pachyphloeus citrinus | | | | | | | | | 1 | | | | |
| Pachyphloeus conglomeratus | | | | | | | | | 1 | | | | |
| Paxillus involutus | | 1 | 1 | | 1 | 1 | 1 | | | | 1 | 1 | 1 |
| Peziza michelii | | | 1 | | | | | | | | | | |
| Peziza ostracoderma | | | | | 1 | | | | | | | | |
| Peziza succosa | | | 1 | | | | | | | | | | 1 |
| Piloderma croceum | | | | 1 | | | | | | | | | |
| Pseudoboletus parasiticus | | | | | | | | | 1 | | | | |
| Pseudocraterellus sinuosus | | 1 | | | | | | | | | | | |
| Pseudocraterellus undulatus | | | | | | | | 1 | | | | | |
| Pseudotomentella umbrina | | | | | | | | | | | | | 1 |
| Rhizopogon luteolus | | | | | | | | | 1 | | | | |
| Rhizoscyphus ericae | | | | | 1 | | | | | | | | |
| Rhodocybe truncata | | 1 | | | | | | | | | | | |
| Russula albonigra | | | | | | | | | 1 | | | | |
| Russula amoenipes | | | | | | | | 1 | 1 | | | | |
| Russula amoenolens | | 1 | | | | | | | 1 | 1 | | 1 | 1 |
| Russula atropurpurea | | 1 | | | | | | | 1 | | | | 1 |
| Russula betularum | | | | | | | | | | | | | 1 |
| Russula bicolor | | | | | | | | | | | | 1 | |
| Russula bresadolae | | | | | | | | | | | | 1 | |
| Russula brunneoviolacea | | | | | | | | 1 | | | | | 1 |
| Russula chloroides | | | | | | | | | | | | | 1 |
| Russula cuprea | | | | | | | | | | | | | 1 |
| Russula cyanoxantha | | 1 | | 1 | | | | | 1 | | | | 1 |
| Russula densifolia | | | | | | | | 1 | | | | | 1 |
| Russula emetica | | 1 | | | | | | | | | | 1 | |

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Table D.2 – *Continued from previous page*

| Taxon name | A | B | C | D | E | F | G | H | I | J | K | L | M |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Russula foetens | | | | | | | | | | | | | 1 |
| Russula fragilis | 1 | 1 | | | | 1 | | | | | | | 1 |
| Russula graveolens | | 1 | | | | | | | | | | 1 | 1 |
| Russula grisea | | | | | | | | | 1 | | | | |
| Russula heterophylla | | | 1 | | | | | | | | | 1 | 1 |
| Russula insignis | | | | | | | | | 1 | | | | |
| Russula ionochlora | | 1 | | | | | | | 1 | | | | 1 |
| Russula krombholzii | | | | 1 | | | | | | | | | |
| Russula laeta | | | | | | | | | | | | | 1 |
| Russula laurocerasi | | 1 | | 1 | | | | | | | | | |
| Russula lepida | | | | | | | | | | | 1 | | |
| Russula nigricans | | 1 | 1 | 1 | | | | 1 | 1 | 1 | | | |
| Russula nobilis | | | | | | | | | | | | | 1 |
| Russula ochroleuca | | 1 | | 1 | | 1 | 1 | | 1 | 1 | 1 | 1 | 1 |
| Russula odorata | | 1 | | | | | | | | | | 1 | 1 |
| Russula parazurea | | 1 | | | | | | 1 | 1 | | | | |
| Russula peckii | | | | | | | | | | | | 1 | 1 |
| Russula pectinatoides | | 1 | | | | | | | | | | | |
| Russula praetervisa | | | | | | | | | 1 | | | | |
| Russula puellaris | | | | 1 | | | | | | | | 1 | 1 |
| Russula risigallina | | | | 1 | | | | | | | | | 1 |
| Russula rosea | | | | 1 | | | | 1 | | | | | |
| Russula rutila | | | | | | | | | | | | 1 | |
| Russula sororia | 1 | | | | | | | | | | | | |
| Russula velenovskyi | | 1 | | | | | | | | | | | |
| Russula vesca | | 1 | | | | | | | 1 | | | | |
| Russula violeipes | | | | | | | | | 1 | | | | |
| Scleroderma areolatum | | 1 | | | 1 | | | | 1 | | | 1 | 1 |
| Scleroderma bovista | | | | | | | | | 1 | | | | |
| Scleroderma citrinum | 1 | 1 | | | | 1 | | 1 | 1 | 1 | 1 | | 1 |
| Scleroderma verrucosum | 1 | | | | 1 | | | | 1 | | | | 1 |
| Sebacina dimitica | | | | | | | | | | | | | 1 |
| Sebacina epigaea | | | | | | | | | | | | | 1 |
| Sebacina incrustans | | | 1 | | | | | | 1 | | | | 1 |
| Suillus grevillei | | | | | | | | | 1 | | | | |
| Thelephora albomarginata | | | | | | | | | | | | | 1 |
| Thelephora terrestris | | 1 | | 1 | | | 1 | | | 1 | 1 | | 1 |
| Tomentella atramentaria | | | | 1 | | | | | | | | | |

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Table D.2 – *Continued from previous page*

| **Taxon name** | **A** | **B** | **C** | **D** | **E** | **F** | **G** | **H** | **I** | **J** | **K** | **L** | **M** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tomentella badia | | | 1 | | | | | | 1 | | | | |
| Tomentella botryoides | | | | 1 | | | | 1 | | | | 1 | 1 |
| Tomentella bryophila | | | | 1 | | | | | | | | | 1 |
| Tomentella cinereoumbrina | | | | | | | | | | | | | 1 |
| Tomentella coerulea | | | | | | | | | | | | | 1 |
| Tomentella ellisii | | | 1 | 1 | | | | | 1 | | | | 1 |
| Tomentella fuscocinerea | | | | 1 | | | | | | | | | 1 |
| Tomentella galzinii | | | 1 | | | | | | | | | | 1 |
| Tomentella lapida | | | | | | | | | | | | | 1 |
| Tomentella lateritia | | | 1 | | | | | | 1 | | | | |
| Tomentella lilacinogrisea | | | | 1 | | | | | | | | | 1 |
| Tomentella papuae | | | | | | | | | | | | | 1 |
| Tomentella punicea | | | | | | | | | | | | | 1 |
| Tomentella spinosispora | | | | | | | | | | | | | 1 |
| Tomentella stuposa | | | | 1 | | | | | | | | 1 | 1 |
| Tomentella sublilacina | | | 1 | 1 | | | | 1 | | | 1 | 1 | |
| Tomentella subtestacea | | | 1 | | | | | | 1 | | | | |
| Tomentella terrestris | | | | | | | | 1 | | | | | |
| Tomentellopsis echinospora | | | | | | | | | | | | | 1 |
| Tomentellopsis submollis | | | | | | 1 | | | | | | | 1 |
| Tricholoma columbetta | | | | 1 | | | | | | | | | |
| Tricholoma saponaceum | | 1 | | | | | | | | | | | |
| Tricholoma sulphureum | | 1 | | | | | | | | | | | |
| Tuber anniae | | | | | | | | | | | | | 1 |
| Tuber borchii | | | | | | | | | 1 | | | | 1 |
| Tuber foetidum | | | | | | | | | 1 | | | | |
| Tuber puberulum | | | | 1 | | | | | | | | | 1 |
| Tuber rapaeodorum | | | 1 | | | | | | 1 | | | | |
| Tuber rufum | | | 1 | | | | | | 1 | | | | |
| Tuber maculatum | | | | | | | | | | | | | 1 |
| Tylopilus felleus | 1 | | | 1 | | | 1 | | | | | 1 | 1 |
| Tylospora asterophora | | | | | | | | | 1 | 1 | | | |
| Xerocomellus cisalpinus | | | | | | | | | | | | | 1 |
| Xerocomus ferrugineus | | | | | | | | | | | | | 1 |

## D.3 Correlation plot

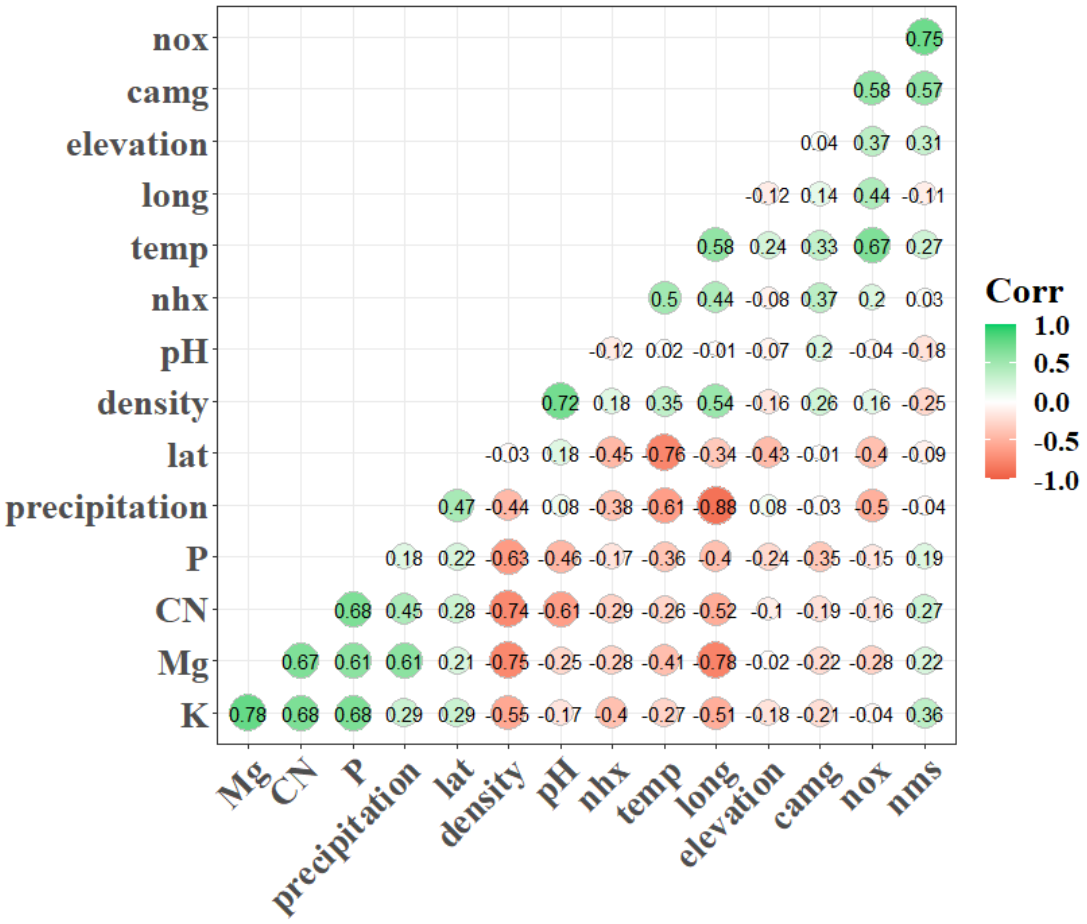


Figure D.1: Spearman correlations between continuous explanatory variables.

## D.4 Estimating species richness using zeta decay

Hui & McGeoch (2014) give the calculation of estimated species richness from the index in the power law relationship of zeta decay as follows.

If $d$ is the index of the power law decay curve $\zeta_i = ci^{-d}$

Then calculate $z = \frac{ln(2-2^{-d})}{ln2}$ And the number of species $S_n$ is given by $\frac{S_n}{S_{n+1}} = (\frac{n}{n+1})^z$

By extrapolating from the known number of species found after $n$ surveys, the number of species at $n+1$ surveys can be calculated. For instance, we found 125 species after 19 surveys, giving $S_{20} = 125(\frac{19}{20})^z$

## D.5 Univariate scatter plots for richness with environmental variables

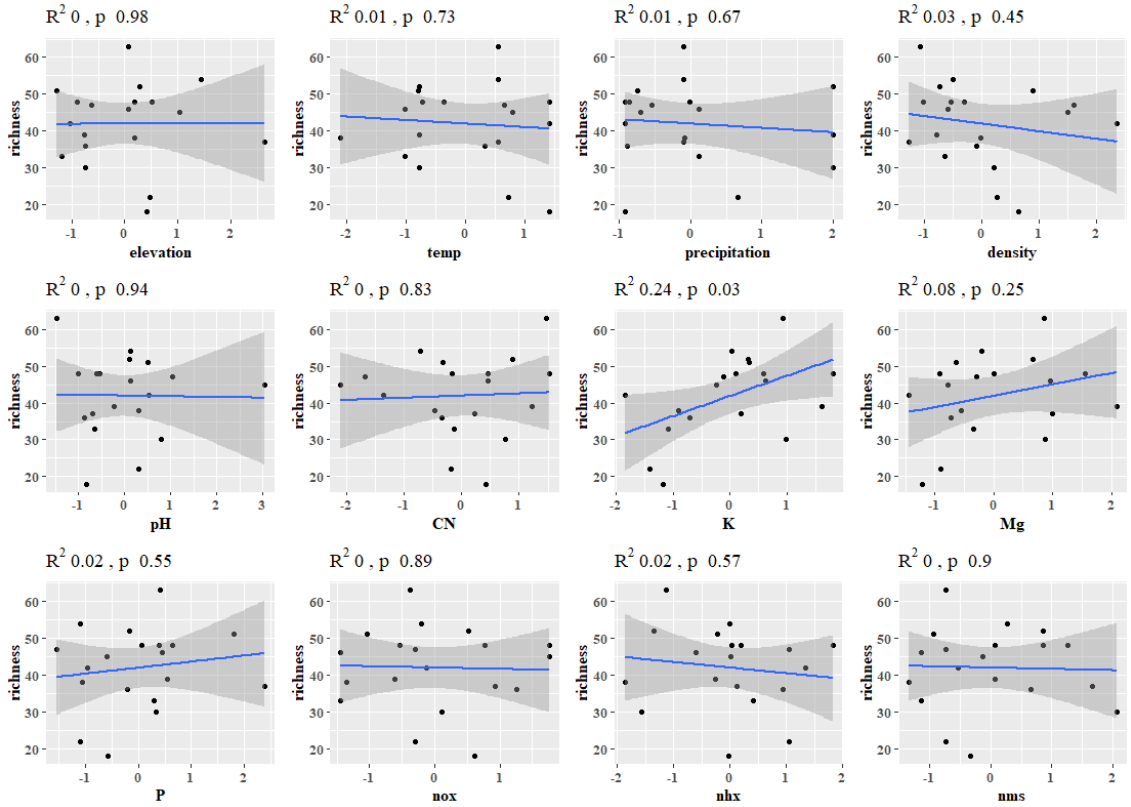


Figure D.2: Univariate linear relationships between EMF richness and environmental variables. Only soil potassium shows a significant linear relationship to EMF richness

## D.6 $R^2$ and p values of environmental variables on NMDS ordination

Table D.3: $R^2$ and p values of fit of environmental vectors to NMDS ordination. Soil K and precipitation are significant at the 0.1 and 0.05 levels respectively.

| Variable | $R^2$ | p |
|---|---|---|
| elevation | 0.09 | 0.47 |
| temp | 0.00 | 0.98 |
| precipitation | 0.35 | 0.04 |
| density | 0.01 | 0.91 |
| pH | 0.13 | 0.33 |
| CN | 0.06 | 0.61 |
| K | 0.28 | 0.08 |
| Mg | 0.20 | 0.17 |
| P | 0.01 | 0.93 |
| nox | 0.21 | 0.15 |
| nhx | 0.06 | 0.60 |
| nms | 0.10 | 0.43 |
| camg | 0.12 | 0.34 |

## D.7 Maximum Ispline values from MSGDM for EMF communities of oak

Table D.4: Maximum value of the Isplines calculated using MSGDM for EMF communities of oak in nineteen woodlands across Britain. The value indicates the relative importance of the predictor variable

| $\zeta_2$ | VI | $\zeta_3$ | VI | $\zeta_4$ | VI | $\zeta_5$ | VI | $\zeta_6$ | VI | $\zeta_7$ | VI | $\zeta_8$ | VI |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| nox | 0.10 | nox | 0.09 | nox | 0.14 | nox | 0.17 | nox | 0.22 | nox | 0.25 | nox | 0.27 |
| K | 0.07 | K | 0.08 | elevation | 0.11 | elevation | 0.14 | elevation | 0.17 | elevation | 0.19 | elevation | 0.21 |
| nhx | 0.05 | nhx | 0.07 | nhx | 0.10 | nhx | 0.12 | nhx | 0.14 | nhx | 0.16 | nhx | 0.18 |
| elevation | 0.04 | elevation | 0.07 | K | 0.09 | camg | 0.11 | camg | 0.13 | camg | 0.14 | camg | 0.16 |
| CN | 0.03 | camg | 0.05 | camg | 0.08 | K | 0.09 | K | 0.08 | nms | 0.07 | nms | 0.09 |
| precip'n | 0.03 | CN | 0.04 | CN | 0.04 | nms | 0.05 | nms | 0.06 | K | 0.07 | K | 0.06 |
| camg | 0.02 | precip'n | 0.03 | precip'n | 0.04 | precip'n | 0.04 | precip'n | 0.05 | precip'n | 0.05 | CN | 0.05 |
| nms | 0.01 | nms | 0.02 | nms | 0.04 | CN | 0.04 | CN | 0.04 | CN | 0.04 | P | 0.05 |
| density | 0.00 | temp | 0.01 | temp | 0.01 | pH | 0.03 | pH | 0.03 | pH | 0.04 | precip'n | 0.04 |
| temp | 0.00 | density | 0.00 | pH | 0.01 | temp | 0.01 | temp | 0.02 | P | 0.03 | pH | 0.03 |
| pH | 0.00 | pH | 0.00 | density | 0.01 | P | 0.01 | P | 0.02 | temp | 0.02 | Mg | 0.02 |
| Mg | 0.00 | Mg | 0.00 | P | 0.00 | density | 0.00 | Mg | 0.01 | Mg | 0.01 | temp | 0.01 |
| P | 0.00 | P | 0.00 | Mg | 0.00 | Mg | 0.00 | density | 0.00 | density | 0.00 | density | 0.00 |
| distance | 0.00 | distance | 0.00 | distance | 0.00 | distance | 0.00 | distance | 0.00 | distance | 0.00 | distance | 0.00 |

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