THE SPILLOVER EFFECT HYPOTHESIS: USING MYCORRHIZAL ASSOCIATIONS OF TEMPERATE HARDWOOD FORESTS AS STUDY MODELS FOR COMMUNITY-WIDE PLANT-SOIL FEEDBACK EFFECTS

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Andrew Charles Eagar

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Dissertation written by

Andrew Charles Eagar

B.S., Tennessee Tech University, 2015

Ph.D., Kent State University, 2022

Approved by

Christopher B. Blackwood, Ph.D. , Chair, Doctoral Dissertation Committee

Kurt A. Smemo, Ph.D. , Members, Doctoral Dissertation Committee

Andrea L. Case, Ph.D.

David M. Ward, Ph.D.

David M. Singer, Ph.D.

Accepted by

Laura G. Leff, Ph.D. , Chair, Department of Biological Sciences

Mandy J. Munro-Stasiuk, Ph.D. , Dean, College of Arts and Sciences

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CHAPTER I

INTRODUCTION

Mycorrhizas are symbiotic relationships between plant roots and fungi in which the host plant exchanges photosynthetically-derived carbon for soil nutrients obtained by their fungal partners (Smith & Read 2008). They are one of the oldest known symbioses, originating with the emergence of land plants in the Ordovician period 488 Ma (Wang & Qui 2006). It is estimated that at least 90% of all vascular plants engage in some form of mycorrhizal symbiosis, with the majority (79%) of these plants associating with arbuscular mycorrhizal fungi (Brundrett 2009). The remaining 11% of mycorrhizal associations are limited to specific groups of plants and include orchid mycorrhizas (8%), ectomycorrhizas (2%), and ericoid mycorrhizas (1%) (Smith & Read 2008, Brundrett 2009). Orchid mycorrhizas are exclusive to the plant family *Orchidaceae*, while ericoid mycorrhizas are found in members of the plant family *Ericaceae* and ectomycorrhizas are found within certain families of trees and shrubs (Smith & Read 2008, Brundrett 2009). In addition to playing key roles in nutrient uptake, mycorrhizas also aid in soil moisture retention (Augé *et al.* 2001) and defense of host plants (Pozo & Azcón-Aguilar 2007, Teste *et al.* 2017). Due to their widespread and beneficial nature, mycorrhizas are recognized as an integral component of plant-soil interactions of considerable research interest.

Despite their shared role of facilitating soil nutrient uptake, there are distinct differences among mycorrhizal types in how they function. Arbuscular mycorrhizas primarily obtain mineralized phosphorus (P) from soil and form unique structures (arbuscules) within the roots of

host plants (Smith & Read 2008, Smith & Smith 2011). In contrast, many ectomycorrhizas obtain organic nitrogen (N) by decomposing plant litter and soil organic matter and form structures that cover the outer surface of roots (Smith & Read 2008, Wurzburger & Hendrick 2009). Arbuscular mycorrhizal fungi are unable to break down plant litter to assimilate organic N and are reliant on saprotrophic fungi to release mineral forms of N through decomposition (Smith & Smith 2011, Whiteside *et al.* 2012). Ectomycorrhizal fungi, on the other hand, directly compete with saprotrophic fungi for organic forms of nutrients derived from plant litter (Gadgil & Gadgil 1971, Averill *et al.* 2014) and most are capable of producing extracellular enzymes that decompose litter and soil organic matter (Read & Perez-Moreno 2003, Pellitier & Zak 2018). Additionally, ectomycorrhizal plants often have more recalcitrant litter with higher lignin concentrations and C:N ratios that decompose slower than arbuscular mycorrhizal plant litter (Wurzburger & Hendrick 2009, Keller & Phillips 2019). The slower decomposition of this recalcitrant litter contributes to greater amounts of soil carbon in ecosystems where ectomycorrhizal plants are prevalent (Soudzilovskaia *et al*. 2015, Averill & Hawkes 2016) and slows the rate of nutrient cycling in these systems (Cornelissen *et al.* 2001, Lin *et al.* 2017). These contrasts in nutrient acquisition strategies indicate that mycorrhizas facilitate different interactions between plants and their soil environment based on the specific type of mycorrhizal association formed.

Plant-soil interactions and feedback effects between plants and soil

Plant-soil interactions refer to the many ways that plants connect aboveground processes, such as primary production, to belowground systems that include mycorrhizas, bacterial and fungal soil communities, and the abiotic soil environment (Wardle *et al.* 2004). Because plants are sedentary organisms, they influence their local soil environment over time in a specific type

of interaction known as plant-soil feedback (Ehrenfeld *et al.* 2005, van der Putten *et al.* 2013). Feedback between plants and soil occurs when a plant affects the soil, which in turn affects the plant, resulting in either a weakening of this interaction through attenuated fitness (i.e., negative feedback) or a strengthening of this interaction through amplified fitness (i.e., positive feedback) (Ehrenfeld *et al.* 2005, van der Putten *et al.* 2013).

Plant-soil relationships are complicated, involving pathways that operate through abiotic (e.g., water availability or temperature), biogeochemical (e.g., nutrients and organic matter), and biotic (e.g., mesofauna and microbiota) soil compartments (Wardle *et al.* 2004, Ehrenfeld *et al.* 2005). Some plant species experience stronger negative or positive feedback than others, through either heightened sensitivity to feedback drivers or by exerting greater influences on the mechanisms responsible for feedback pathways (Binkley & Giardina 1998, Stump & Comita 2018). The latter presents the possibility for plant species that induce strong negative or positive feedback on shared soil resources or microbiota to affect other plant species that would otherwise experience weaker feedback, resulting in the strong negative or positive feedback effects from one plant species spilling over onto other plant species.

Plant-soil feedback directions and their effects on plant populations and communities

Negative feedback between plants and soil is common (Kulmatiski *et al.* 2008) and is observed when plants alter their soil environment in ways that reduce the growth of their progeny and other conspecific plants (Bever 1994, Ehrenfeld *et al.* 2005). This reduction in growth subsequently dampens the effect these plants have on their soil environment, resulting in a negative feedback loop (Ehrenfeld *et al.* 2005, van der Putten *et al.* 2013). Strong negative feedback within a species can even lead to increased rates of mortality (Packer & Clay 2000) and is a key mechanism regulating plant population size (Hovatter *et al.* 2013) and community

diversity (Teste *et al.* 2017). Negative plant-soil feedback is primarily generated through plant-microbe interactions, with host-specific pathogens building up in soil over time (Mills & Bever 1998, Bever *et al.* 2015), but can also result from the depletion of specific soil resources required for growth (Bever 1994, Ehrenfeld *et al.* 2005, van der Putten *et al.* 2013). Because of this, negative plant-soil feedback is typically studied as a species-specific process where the cumulative effects of multiple species on plant-pathogen interactions and their consequences are not typically considered (Kulmatiski *et al.* 2008, van der Putten *et al.* 2013). This is exemplified by the experimental design of many plant-soil feedback experiments, in which differences in plant growth and survival in soils previously conditioned by growth of conspecific and heterospecific individuals are compared (Pernilla Brinkman *et al.* 2010).

While negative plant-soil feedback can be detrimental to an individual plant species, it is often viewed as a beneficial effect at the community and ecosystem scale. Negative feedback experienced by a dominant plant species can weaken its competitive ability (Mordecai 2013a), preventing it from competitively excluding other plant species and allowing for their persistence (Connell 1971, van der Putten *et al.* 1993). The effect of this weakened competition through negative feedback can promote coexistence and ultimately lead to increased plant diversity within a community by preventing dominant plant species from taking over (Mills & Bever 1998, Mordecai 2013b). Plant diversity is closely associated with primary productivity, with more diverse communities having higher primary production than less diverse ones (Tilman *et al.* 1996, Tilman *et al.* 1997, Schnitzer *et al.* 2011, Zhang *et al.* 2017). Additionally, plant diversity is a core component of ecosystem stability and resilience (Elton 1958, Tilman 1996, Peterson *et al.*1998). These connections between plant diversity and ecosystem function suggest

that negative plant-soil feedback contributes to more productive, stable, and resilient ecosystems by promoting diverse plant communities (Schnitzer *et al.* 2011, Thakur *et al.* 2021).

Positive plant-soil feedback is rare among plants compared to negative feedback (Kulmatiski *et al.* 2008) and results from plants interacting with soil in ways that increase growth, survival, and the strength of these interactions (Ehrenfeld *et al.* 2005, Teste *et al.* 2017). This type of feedback is primarily generated in two ways; like negative feedback, interactions between plants and soil microorganisms contribute to positive plant-soil feedback (Ehrenfeld *et al.* 2005, Mangan *et al.* 2010, van der Putten *et al.* 2013). In positive feedback, however, the buildup of beneficial or mutualistic microorganisms overrides the negative effects attributed to microbial pathogens (Mangan *et al.* 2010). Positive feedback can also be achieved through plants gaining access to specific soil resources that further increase their access to these resources (Wardle *et al.* 1999, Teste *et al.* 2017). For example, hydraulic lift is a phenomenon where a plant moves water from deep inside the soil horizon into the upper layers of the soil through its roots, making water available to smaller conspecific individuals and other plants that lack deeper root systems (Richards & Caldwell 1987, Meinzer *et al.* 2001). Access to this water increases plant growth in arid environments and drought conditions, resulting in deeper root systems capable of inducing additional hydraulic lift (Ehrenfeld *et al.* 2005, Comas *et al.* 2010). Both ways of generating positive feedback can co-occur among plants and are not mutually exclusive. Some microbial mutualists, such as ectomycorrhizal fungi, provide access to organic sources of nutrients for their host plants that other plants are unable to obtain, resulting in both instances of positive feedback as plant and mycorrhizal fungal populations grow larger (Wurzburger & Hendrick 2009, Mangan *et al.* 2010).

Unlike negative feedback, positive plant-soil feedback can create conditions that favor a single plant species and result in low diversity communities (Connell & Lowman 1989, Teste *et al.* 2017), which are less productive (Paquette & Messier 2011, Kulmatiski *et al.* 2012) and of higher risk to disease (Lau *et al.* 2008, Rottstock *et al.* 2014) and species invasion (Hector *et al.* 2001, Kennedy *et al.* 2002). Given the species-specific nature of plant-soil feedback effects, feedback types are not mutually exclusive across a community and may occur at varying strengths among community members (LaManna *et al.* 2016, Bennett *et al.* 2017). Researchers are beginning to explore the potential for one plant species to facilitate feedback among other plant species (e.g., Kuťáková *et al.* 2018), which occurs through shared interactions with generalist pathogens and mutualists in the soil (Mangan *et al.* 2010, Mordecai 2013b). However, more work is needed in this area to broaden our understanding of how negative and positive plant-soil feedback operates at the community level (Forero *et al.* 2019).

Influences of mycorrhizas on plant-soil feedback

Mycorrhizas facilitate above and belowground interactions between plants and soil, and research has shown these associations influence the strength and direction of plant-soil feedback (Connell & Lowman 1989, Wurzburger & Hendrick 2009, Bennett *et al.* 2017). There is both observational (Connell & Lowman 1989, Terborgh 2012, Eagar *et al.* 2020) and experimental (Wurzburger & Hendrick 2009, Bennett *et al.* 2017) evidence of this phenomenon across multiple types of ecosystems, though the drivers are complicated and involve direct and indirect interactions between plants, their mycorrhizal fungi, and other soil microorganisms (Phillips *et al.* 2013, Averill *et al.* 2019). Furthermore, plants, mycorrhizal fungi, and plant pathogens all exist on a gradient of host specificity which affects the strength of these interactions. The host preference of some mycorrhizal fungi and pathogens are more general than others (Klironomos

2000, Bever 2002, Augspurger & Wilkinson 2007), while some plants are less selective about, or less susceptible to, the mycorrhizal fungi and pathogens they host (Augspurger & Wilkinson 2007, van der Linde *et al.* 2018, Teste *et al.* 2020). This presents an avenue for the drivers of plant-soil feedback to affect multiple plant species within the same community; if one plant induces the buildup of mycorrhizal fungi that benefit it, other heterospecific plants may also benefit. Conversely, if one dominant plant species causes the growth of generalist pathogens, other nearby plant species may be negatively affected.

As mutualists, mycorrhizal fungi directly induce positive feedback among their host plants by providing access to key soil resources that increase plant growth and reproduction, thereby facilitating greater host availability among the population (Smith & Read 2008, Mangan *et al.* 2010). However, the growth of plants also encourages the buildup of plant pathogens in the soil, generating a trade-off between positive feedback from mycorrhizas and negative feedback from pathogens (van der Putten 2013). Mycorrhizal fungi also provide defensive benefits to their host plants, which directly affect plant-pathogen interactions (Smith & Read 2008). Both arbuscular (Pozo *et al.* 2002) and ectomycorrhizal fungi (Kanekar *et al.* 2018) confer these benefits, but it is unclear if one type of association provides more protection than the other. Furthermore, both arbuscular and ectomycorrhizal fungi interact with the saprotrophic fungi that are responsible for soil carbon and nutrient cycling (Phillips *et al.* 2013, Netherway *et al.* 2021), albeit in drastically different ways. Arbuscular mycorrhizal fungi are dependent on saprotrophs to release mineral nutrients through the decomposition of senesced plant tissue (Smith & Smith 2011, Whiteside *et al.* 2012), while ectomycorrhizal fungi directly compete with saprotrophs for access to organic nutrients from leaf and root litter (Gadgil & Gadgil 1971, Averill *et al.* 2014). Some saprotrophs can act as facultative pathogens (Olson *et al.* 2012, Smith *et al.* 2017),

suggesting that plants with arbuscular mycorrhizas may be at higher risk to pathogen-driven negative feedback compared to plants with ectomycorrhizas.

Mycorrhizal associations also indirectly influence plant-soil feedback through traits associated with litter chemistry that create differences in the nutrient availability of soil (Cornelissen *et al.* 2001, Phillips *et al.* 2013). The higher lignin and C:N ratios associated with litter from ericoid and ectomycorrhizal plants induces lower soil mineral nutrient availability while providing these mycorrhizas access to an exclusive pool of organic nutrients, thereby facilitating positive feedback (Wurzburger & Hendrick 2009, Phillips *et al.* 2013). Conversely, labile litter associated with arbuscular mycorrhizas induces greater soil mineral nutrient availability, which can increase plant pathogen activity and facilitate negative feedback (LaManna *et al.* 2016; Segnitz *et al.* 2020). The net outcome of plant-soil feedback on an individual plant and its surrounding community is therefore driven by the relative contribution of these direct and indirect drivers of microbial community composition and soil nutrient availability (Ehrenfeld *et al.* 2005, Kotanen *et al.* 2007, van der Putten 2013).

In evidence of this, recent work by Bennett *et al*. (2017) has shown that arbuscular mycorrhizal tree species largely experience negative plant-soil feedback and ectomycorrhizal tree species largely experience positive feedback. Beyond the species level, the mycorrhizal associations found within plant communities also appear to influence community-wide patterns of feedback, with plant communities primarily composed of arbuscular mycorrhizal plants experiencing negative feedback and those composed of ectomycorrhizal plants experiencing positive feedback (Connell & Lowman 1989, Johnson *et al.* 2018, Eagar *et al.* 2020). Given this, there is a pressing need to study plant communities where multiple mycorrhizal types are present

to understand the relative importance of feedback drivers and their consequences on community and ecosystem level processes.

Temperate hardwood forests as model systems for studying mycorrhizal influences on plant-soil feedback

Due to their unique species composition, the temperate hardwood forests of the northern hemisphere are ideal systems for testing hypotheses concerning mycorrhizally-driven plant-soil feedback effects (Phillips *et al.* 2013, Netherway *et al.* 2021). Tree mycorrhizal associations are largely species-specific, with an individual tree species primarily associating with either arbuscular or ectomycorrhizal fungi (Brundrett 2009, Maherali *et al.* 2016). Despite ectomycorrhizas making up only two percent of all species-based mycorrhizal associations (Brundrett 2009), arbuscular and ectomycorrhizal trees are equally abundant in temperate hardwood forests (Phillips *et al.* 2013). Here, the capabilities of different mycorrhizas to affect soil nutrient cycling, carbon storage, and microbial community dynamics through direct and indirect pathways have been recognized under an integrated, trait-based framework known as the mycorrhizal-associated nutrient economy (Phillips *et al.* 2013). Arbuscular mycorrhizal temperate hardwood tree communities are linked to faster rates of soil nutrient cycling, greater availability of soil mineral nutrients, and lower amounts of soil carbon due to their labile litter and reliance on saprotrophic fungi for decomposition (Phillips *et al.* 2013, Keller & Phillips 2019, Averill *et al.* 2019). Contrastingly, ectomycorrhizal temperate hardwood tree communities are linked to slower rates of soil nutrient cycling, lower soil mineral nutrient availability, and greater amounts of soil carbon due to their recalcitrant leaf litter and competitive suppression of saprotrophic fungi (Phillips *et al.* 2013, Keller & Phillips 2019, Averill *et al.* 2019).

Under this framework, we are able to make predictions and answer questions based on localized forest community composition and explore how areas composed of arbuscular, ectomycorrhizal, and combinations of both mycorrhizal tree types differ. Global change factors, such as anthropogenic nitrogen deposition and climate warming, are predicted to have substantial impacts in temperate hardwood forests in the forms of increased mortality, smaller stand sizes, and younger ages (McDowell *et al.* 2020). Additionally, trees from southern regions are predicted to expand northward, with the species composition of these forests changing in ways that increase the dominance of arbuscular mycorrhizal trees (Jo *et al.* 2019, Steidinger *et al.* 2019). These compositional changes will also affect soil processes and plant-soil interactions, so studies incorporating gradients of mycorrhizal dominance in different temperate hardwood forests from various geographic areas are essential to understand the consequences of global change.

Aims and objectives of this work

The primary goal of my work, presented here, was three-fold. First, I investigated the potential for temperate hardwood forest mycorrhizal associations to influence the soil fungal communities responsible for plant-soil feedback in forested communities. Second, I sought to expand the concept of plant-soil feedback from intraspecific interactions between trees and their offspring to entire communities of mixed species composition using mycorrhizal associations in what I term the "spillover effect" hypothesis. Third, I tested for signs of these spillover effects along natural mycorrhizal and environmental gradients. Working within the mycorrhizal-associated nutrient economy (MANE) framework, I hypothesize that plant-soil feedback effects generated from dominant community member mycorrhizal associations should be "spilling over" onto less dominant community members, thus influencing the strength and direction of plant-soil

feedback experienced by them. For example, if a tree species predicted to experience positive feedback (Bennett *et al.* 2017) was surrounded by numerous or large (i.e., dominant) members of a different species predicted to generate negative feedback, that negative feedback should override any positive feedback experienced by the first species.

This chapter presented a general description of the drivers and mechanisms contributing to plant-soil feedback as it relates to the mycorrhizal associations of temperate hardwood forest trees and their associated microbial communities. Through these connections, I outline my spillover effect hypothesis and present temperate hardwood forests as model systems for studying these effects.

My second chapter, titled *Arbuscular mycorrhizal tree communities have greater soil fungal diversity and relative abundances of saprotrophs and pathogens compared to ectomycorrhizal tree communities*, explores patterns in fungal community composition under the mycorrhizal associated nutrient economy framework through amplicon sequencing. By documenting that tree communities associated with arbuscular mycorrhizal fungi have a greater portion of their soil microbial community represented by pathogens, I demonstrate the potential for stronger negative plant-soil feedback in these communities. Additionally, by revealing trade-offs between the relative abundances of ectomycorrhizal fungi and fungal saprotrophs and pathogens, I provide support for the competitive suppression hypothesis known as the Gadgil effect. The observation that dominant community mycorrhizal associations affect soil microbial community composition in predictable ways also provides support for my spillover hypothesis. This chapter is published in *Applied and Environmental Microbiology*.

Chapter III, *Spillover effects from dominant mycorrhizal associations on fungal communities are more prominent surrounding arbuscular mycorrhizal trees and vary in strength*,

builds upon the results in Chapter II by looking for similar patterns in fungal community composition in a different geographic region – the Adirondack mountains in New York state, USA. Compared to south-central Indiana, forests in the Adirondacks are less diverse, cooler, wetter, and of higher elevation. Here, I take a more in-depth sampling approach to test for potential geographic differences in the strength of mycorrhizal-linked fungal communities at both the regional and topographic scale. I utilize plots specifically established to test for differences in fungal community composition as it relates to tree community mycorrhizal associations along an environmental gradient of temperature and precipitation, between north vs. south-facing slopes, and between individual, large trees vs. the surrounding tree community to directly test my spillover hypothesis. This manuscript will be submitted for publication in an appropriate journal and has a companion paper discussing the biogeochemistry and soil properties of these sites.

My fourth chapter, titled *Dominant community mycorrhizal types influence local spatial structure between adult and juvenile temperate forest tree communities*, presents evidence that positive and negative plant-soil feedback effects operate across entire forest communities and that tree species expected to experience either negative or positive feedback instead experience the same type of feedback as their surrounding community members. This chapter further supports my spillover hypothesis by demonstrating that the patterns seen among soil fungal communities and tree mycorrhizal associations have *in situ* consequences for tree community assembly. To accomplish this, I used a series of spatial point pattern analyses in a third study system: Jennings Woods in Northeast Ohio. This chapter is published in *Functional Ecology*.

My final chapter (Chapter V: *Overview, chapter synthesis, and future directions*) presents a synthesis of the chapters presented before it, placing my body of work in the context of current

research on these interactions and in these systems. I discuss the similarities and differences found between chapters II and III and how they relate to my fourth chapter, as well as the potential consequences of my spillover hypothesis on global change outcomes and evolutionary processes in temperate hardwood forests.

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CHAPTER II

ARBUSCULAR MYCORRHIZAL TREE COMMUNITIES HAVE GREATER SOIL FUNGAL DIVERSITY AND RELATIVE ABUNDANCES OF SAPROTROPHS AND PATHOGENS COMPARED TO ECTOMYCORRHIZAL TREE COMMUNITIES

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ABSTRACT

Trees associating with different mycorrhizas often differ in their effects on litter decomposition, nutrient cycling, soil organic matter (SOM) dynamics, and plant-soil interactions. For example, due to differences between arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) tree leaf and root traits, ECM-associated soil has slower rates of C and N cycling and lower N availability

compared to AM-associated soil. These observations suggest many groups of non-mycorrhizal fungi should be affected by the mycorrhizal associations of dominant trees through controls on nutrient availability. To test this overarching hypothesis, we explored the influence of predominant forest mycorrhizal type and mineral N availability on soil fungal communities using next-generation amplicon sequencing. Soils from four temperate hardwood forests in Southern Indiana, USA, were studied; three forests formed a natural gradient of mycorrhizal dominance (100% AM tree basal area – 100% ECM basal area), while the fourth forest contained a factorial experiment testing long-term N addition in both dominant mycorrhizal types. We found that overall fungal diversity, as well as the diversity and relative abundance of plant pathogenic and saprotrophic fungi, increased with greater AM tree dominance. Additionally, tree community mycorrhizal associations explained more variation in fungal community composition than abiotic variables, including soil depth, SOM content, nitrification rate, and mineral N availability. Our findings suggest that tree mycorrhizal associations may be good predictors of the diversity, composition, and functional potential of soil fungal communities in temperate hardwood forests. These observations help explain differing biogeochemistry and community dynamics found in forest stands dominated by differing mycorrhizal types.

Importance

Our work explores how differing mycorrhizal associations of temperate hardwood trees (i.e., arbuscular (AM) vs ectomycorrhizal (ECM) associations) affect soil fungal communities by altering the diversity and relative abundance of saprotrophic and plant pathogenic fungi along natural gradients of mycorrhizal dominance. Because temperate hardwood forests are predicted to become more AM-dominant with climate change, studies examining soil communities along mycorrhizal gradients are necessary to understand how these global changes may alter future soil

fungal communities and their functional potential. Ours, along with other recent studies, identify possible global trends in the frequency of specific fungal functional groups responsible for nutrient cycling and plant-soil interactions as they relate to mycorrhizal associations.

INTRODUCTION

Mycorrhizal fungi are well-known for their effects on plant-soil interactions, particularly through enhancing plant nutrient uptake from the soil. However, the type of mycorrhizal association of a plant may explain a much broader array of processes affecting soil biogeochemistry and plant community dynamics (Tedersoo *et al*. 2020b). In temperate forests, the decomposition of labile leaf litter from arbuscular mycorrhizal (AM) trees by saprotrophic fungi induces greater soil mineral nutrient availability (Phillips *et al*. 2013, Lin *et al*. 2017) and greater amounts of N-rich mineral-associated organic matter (Cotrufo *et al.* 2013, Craig *et al*. 2018) compared to lignin-rich, high C:N leaf litter from ectomycorrhizal (ECM) trees (Wurzburger & Hendrick 2009, Keller & Phillips 2019). The direction of plant-soil feedback is also structured by mycorrhizal type, with ECM trees experiencing positive feedback and AM trees experiencing negative feedback (Bennett *et al*. 2017; Eagar *et al.* 2020; Liang *et al*. 2020). These differences imply that effects of the mycorrhizal type of dominant plants extends beyond mycorrhizal fungi alone to include saprotrophic and pathogenic fungi. As tree species' ranges shift due to global change factors, temperate forests are expected to become more AM-dominant (Jo *et al*. 2019, Steidinger *et al*. 2019) and may therefore experience changes in these broad processes. Thus, there is a pressing need to study concomitant changes between mycorrhizal dominance and soil fungal communities if we are to understand the full impact that shifts in mycorrhizal dominance will have in temperate forests.

Soil fungal communities are likely influenced by mycorrhizal associations through both direct interactions between free-living and mycorrhizal fungi, and through differences in leaf and root litter quality between AM and ECM trees. AM fungi have limited saprotrophic capabilities and primarily scavenge for mineral nutrients released from the decomposition of plant tissue by saprotrophic fungi (Smith & Smith 2011, Whiteside *et al.* 2012). Conversely, many ECM fungi have saprotrophic capabilities and produce extracellular enzymes that decompose plant tissue to acquire organic forms of nutrients (Read & Perez-Moreno 2003, Lindahl & Tunlid 2014). Direct competition between ECM and saprotrophic fungi therefore has the potential to reduce saprotroph relative abundances and diversity, in addition to rates of litter decomposition (Gadgil & Gadgil 1971, Averill *et al.* 2014, Averill & Hawkes 2016). ECM fungi also likely provide a greater defensive benefit to host trees compared to AM fungi by covering the outer surface of roots with a protective sheath, weakening the effects of plant pathogens on ECM trees (Teste *et al*. 2017, Chen *et al.* 2019).

Similarly, differences in leaf litter quality between AM and ECM tree species may indirectly affect fungal community composition. The breakdown of N-rich, labile AM leaf litter results in increased mineral N availability and changes SOM content relative to ECM soil (Phillips *et al.* 2013, Lin *et al.* 2017, Keller & Phillips 2019). Higher available soil resources such as N can affect fungal diversity (Cline *et al.* 2018, Bai *et al*. 2019) and biomass (Smolander *et al.* 1994, Frey *et al.* 2004), leading to notable increases in fungal species richness (Castaño *et al.* 2019). Furthermore, a positive relationship has been observed between soil resource availability and plant disease severity, particularly for AM trees (LaManna *et al.* 2016; Segnitz *et al.* 2020), suggesting that labile AM leaf litter with increased N content may also lead to increased plant pathogen presence or diversity. When considered together, the direct and indirect interactions

between mycorrhizas and soil fungi should lead to lower fungal diversity and decreased saprotroph and plant pathogen relative abundances in ECM soil (compared to AM soil), as recently observed in one study of Baltic temperate and boreal forests (Bahram *et al.* 2020).

As described above, N availability is a major factor driving the hypothesized effects of dominant mycorrhizal type on soil fungal communities. Increasing the supply of N in an ectomycorrhizal system should facilitate saprotrophic activity on otherwise N-poor litter by alleviating competitive interactions between ECM and saprotrophic fungi (as well as necrotrophic fungal pathogens that live saprotrophically between hosts). While soil N availability is strongly influenced by leaf litter chemistry and microbial activity, anthropogenic N deposition is now an important source of available soil N, which may disrupt systems such as ECM symbioses that are adapted to low soil resource conditions. Nitrogen deposition has been associated with increasing abundance of AM tree species (Jo *et al.* 2019), and also alters soil organic matter (SOM) content in different ways depending on dominant tree species (Waldrop *et al.* 2004, Janssens *et al.* 2010). Importantly, increased anthropogenic N deposition has been shown to alter soil fungal community composition (Entwistle *et al.* 2013, Freedman *et al.* 2015), leading to increased saprotroph diversity and decreased ECM fungal diversity in forest soil (Kjøller *et al*. 2012, van Strien *et al.* 2018). Furthermore, increases in soil N availability may increase plant pathogen diversity (LaManna *et al.* 2016, Castaño *et al.* 2019). Thus, the effects of anthropogenic N deposition on fungal community composition may be particularly strong in ECM-dominated systems where elevated N can alleviate competitive interactions, reducing ECM fungal activity on leaf litter while increasing saprotrophic fungal activity. AM tree-associated fungal communities, on the other hand, may see little response to N deposition as a result of their already faster mineral N cycling and greater mineral N availability.

In this study, we explored how the taxonomic and functional composition of soil fungal communities differ in relation to AM or ECM tree species dominance and change in response to experimental mineral N addition in temperate hardwood forests. Our study employed two sampling designs to test our overarching hypothesis: one is a natural gradient consisting of plots ranging from 100% AM trees to 100% ECM trees across three temperate forests. The other sampling design is a complete factorial experiment in which forest plots of AM- or ECM-tree dominance have been subjected to a long-term mineral N addition experiment. Based on the above-mentioned influences on communities of free-living soil fungi within differing mycorrhizal systems, we tested the following two predictions: Soil associated with forest stands dominated by AM trees will have **P1**) greater fungal taxonomic diversity, and **P2**) higher relative abundances of plant pathogenic and saprotrophic fungi when compared to soil associated with ECM trees. We also tested a third prediction specific to N deposition, **P3**) that elevating available N will increase the relative abundances of plant pathogenic and saprotrophic fungi, and that this effect will be stronger in ECM-dominant forest stands.

MATERIALS AND METHODS

Natural mycorrhizal gradients

Five soil cores (0-5cm depth, 5cm diameter) were collected in August 2014 from 48 experimental plots in three mixed deciduous forests in southern Indiana, USA. Within each forest, study plots represent a gradient of mycorrhizal dominance ranging from 0% AM basal area (ECM trees dominant) to 100% AM basal area (AM trees dominant). The mycorrhizal dominance of each plot was calculated by summing the basal areas of all tree species of a particular mycorrhizal type and dividing by the total basal area of the plot.

The three sites included in the gradient represent a range of forest conditions in the region. Soil types at Griffy Woods (GW; 15 study plots; 39°11'N, 86°30'W) and Morgan-Monroe State Forest (MMSF; 15 study plots; 39°19'N, 86°25'W) are loamy-skeletal, mixed, active, mesic Typic Dystrudepts and Hapludults in the Brownstown–Gilwood complex, while the third site at Lilly-Dickey Woods (LDW; 18 study plots; 39°14'N, 86°13W) has loamy-skeletal, mixed, active, mesic Typic Dystrudepts, Ultic Hapludalfs, and Typic Hapludults in the Berks-Trevlac-Wellston complex. All three sites are broadleaf hardwood forests with similar tree communities that vary in the number of dominant (i.e., abundant) species that are part of Indiana University's Research and Teaching Preserve. At Griffy Woods, the dominant AM trees are sugar maple (*Acer saccharum*), yellow poplar (*Liriodendron tulipifera*) and black cherry (*Prunus serotina*) whereas dominant ECM trees are Northern red oak (*Quercus rubra*), white oak (*Q. alba*), and American beech (*Fagus grandifolia*). Canopy trees at Griffy Woods are ~90 years-old and the forest has little understory due to high deer densities and the presence of invasive plant species (Midgley *et al*. 2015). Morgan-Monroe State Forest is the same age as Griffy Woods and has similar overstory tree species, as well as dominant AM trees such as sassafras (*Sassafras albidum*), and ECM trees such black oak (*Q. velutina*), shagbark hickory (*Carya ovata*) and pignut hickory (*C. glabra*) (Schmid *et al*. 2000). Here, deer densities are much lower than Griffy Woods resulting in a dense understory. Lilly-Dickey Woods is the oldest site, resembling an old-growth forest with many trees exceeding 150 years-old due to forest succession following agricultural abandonment. It contains many of the same tree species as the other sites, but the dominant ECM species is chestnut oak (*Q. montana*). This site is also free of invasive species (Johnson *et al*. 2018). Trees were assigned a mycorrhizal type based on information from Brundrett (2009) and Maherali *et al*. (2016).

Mycorrhizal type × nitrogen fertilization experiment

Moores Creek (MC) is also part of the IU Research and Teaching Preserve and is located in southern Indiana a few kilometers away from the other study sites (39°05′ N, 86°28′ W). It contains a similar tree species composition to GW, LDW, and MMSF and has loamy, mixed, semiactive, mesic Typic Dystrudepts and Hapludults in the Brownstown–Gilwood complex. Here, sixteen 20 x 20-m^2 paired plots were located across eight forest stands. Four stands with eight plots were dominated by AM tree species, while the other four stands with eight plots were dominated by ECM species (dominance indicates >85% of the basal area of the stand). One plot in each pair was treated with $(NH_4)_2SO_4$ and $NaNO_3$ granular fertilizer monthly (May to October) beginning in 2011 for a total of 50 kg N ha^{-1} y^{-1}. The mass ratio of N from ammonium and nitrate was equivalent for each monthly fertilizer application (Midgley & Phillips 2016, Mushinski *et al.* 2019). Five soil cores 5cm in diameter from each plot were sampled to a depth of 15 cm and separated by approximate horizon (O = 0–5 cm; A = 5–15 cm) in August 2017 before being pooled for DNA extraction and analysis.

DNA sequencing and taxonomic assignments

All soil samples were passed through a 2-mm sieve for homogenization and processed to remove fine roots and other non-soil particulates. Once homogenized, a subsample of soil was stored at −80 °C for DNA extraction, which was carried out within a month of sampling, while the remaining soil was used to measure abiotic soil properties (*Abiotic Soil Property Measurements*, below). For samples from the mycorrhizal gradient sites, DNA was extracted from soil samples using a PowerSoil DNA isolation kit (MOBIO Laboratories, Inc, Carlsbad, CA, USA) following the manufacturer's guidelines. Polymerase chain reaction (PCR) amplification of the ITS1 region of fungi (White *et al.* 1990) was achieved using barcode-labeled

primers ITS1F (5'-CTT GGT CAT TTA GAG GAA GTA A) and ITS2 (5' GCT GCG TTC TTC ATC ATC GAT GC) following methods from Buée *et al.* (2009) using a Bio-Rad C1000 Touch Thermal Cycler (Bio-Rad Laboratories, Hercules, CA, USA). Briefly, 2 µl of dilute DNA template was amplified in four, 25 µl PCR reactions. Cycle numbers varied between 28 – 35 cycles for each sample to achieve similar band intensities on an agarose gel, with negative controls included to verify lack of contamination. One hundred µl of amplified PCR product was purified using an Agencourt AMPure XP magnetic bead cleanup kit (Beckman Coulter Life Sciences, Indianapolis, IN, USA) following the manufacturer's instructions. Purified PCR products from all 48 samples were then combined in equimolar concentration (values obtained via fluorometric assay using an AccuClear Ultra High Sensitivity dsDNA Quantitation Kit from Biotium (Biotium, Inc., Fremont, CA, USA) and a BioTek Synergy 2 Microplate Reader (BioTek Instruments, Winooski, VT, USA) following Biotium's supplied protocol) and submitted for single-lane, paired-end 2x 300 bp MiSeq Illumina sequencing at the Ohio State University's Molecular and Cellular Imaging Center (Wooster, OH, USA). Resulting sequence data (approximately 2 million reads) were analyzed with the bioinformatics platform Qiime (Caporaso *et al*. 2010) by clustering sequences into operational taxonomic units (OTUs) based on a 97% sequence similarity threshold using the UCLUST algorithm (Edgar 2010). Chimeric sequences were removed and OTUs representing < 10 total sequences across all samples were discarded prior to analysis. Taxonomic information was assigned to representative OTU sequences using the UNITE database ver. 7.2 (UNITE Community 2017) and a Naive Bayesian classifier with a confidence threshold of > 80%. Community composition data was rarified to 2788 sequences for each of the 48 sampled plots.

For samples from the nitrogen fertilizer experiment, DNA was extracted using a DNEasy PowerSoil DNA isolation kit (Qiagen, Hilden, Germany) following the manufacturer's guidelines. PCR amplification and sequencing were performed by the DOE Joint Genome Institute (Walnut Creek, CA, USA). PCR amplification of the ITS2 region (White *et al.* 1990) was achieved using the primers ITS9F (5'- GAA CGC AGC RAA IIG YGA) and ITS4R (5'- TCC TCC GCT TAT TGA TAT GC) following protocol from Ihrmark *et al*. (2012) prior to single-lane, paired-end 2x 300 bp MiSeq Illumina sequencing. Resulting amplicon reads were quality controlled, clustered, aligned, and assigned taxonomy using iTagger V2.2 (Tremblay *et al.* 2015; https://bitbucket.org/berkeleylab/jgi_itagger). Samples were rarified to 473,143 sequences per sample.

For all samples, the functional role (e.g., primary saprotroph, ectomycorrhizal, etc.) of each taxon was assigned using the FUNguild database from Nguyen *et al*. (2016). Taxa with multiple or unknown functional assignments were checked against a thorough literature review and corrections were made when applicable, with plant pathogens being further categorized as biotrophic or necrotrophic plant pathogens. Animal and fungal pathogens were excluded from our functional analyses, as they were low abundance and unrelated to our hypotheses. Taxa with multiple assignments that remained unresolved were grouped into a "various" category, while those with no known function were placed into an "unknown" category. Taxa in both of these categories were excluded from our functional group analyses, but were retained during the taxonomic level analyses. Due to the specific nature of our hypotheses, we limited our analyses on functional groups to these groups of interest: primary saprotrophs (non-wood degrading saprotrophs), biotrophic plant pathogens, necrotrophic plant pathogens, and ectomycorrhizal fungi. Arbuscular mycorrhizal fungi were excluded from our analyses due to their overall low

relative abundances, as shown previously by Tedersoo *et al.* (2015) regardless of primer choice. Sequence data for GW, LDW, and MMSF has been deposited in the Sequence Read Archive (project ID PRJNA679581), while sequence data for MC has been deposited in the Joint Genome Institute Genome Portal (project ID 1182214).

Abiotic soil property measurements

Abiotic soil properties (moisture, pH, organic matter, soil organic matter content, total C & N, nitrification, and N mineralization) were measured for the mycorrhizal gradient samples. Methods used to measure soil properties are described briefly here, with additional details provided in Midgley and Phillips (2016). Soil moisture was measured gravimetrically, and SOM content was measured by ashing soils in a muffle furnace at 450 °C for 16 h. Soil pH was measured using an Orion pH meter (ThermoFisher Scientific, Waltham, MA, USA) in a 1:2 solution of air-dried soil and 0.01 M $CaCl_2$. Total soil C and N were measured by drying a 10-g aliquot of sieved soil at 60 °C for 48 h and using a mortar and pestle to pulverize the sample before analysis on a Costech ECS 4010 elemental analyser (Costech Analytical Technologies Inc.). Nitrification and N mineralization rates were determined by quantifying changes in 2 M KCl-extractable pools of NH_4^+-N + NO_3^--N on 4.5g of soil after a 21-d incubation period at 23 °C using a Lachat QuikChem 8000 Flow Injection Analyzer (Lachat Instruments, Loveland, CO, USA).

Statistical analysis

All analyses were performed in R v. 3.3.0 (R Development Core Team 2017). Sequence data from three samples from our mycorrhizal gradient were discarded before analysis due to low numbers of reads. OTUs that did not receive a taxonomy assignment or those that were only

assigned to “Fungi” were removed prior to analysis. OTU abundance data were rarified and Hellinger-transformed before analysis using the vegan package (Oksanen *et al*. 2007). We performed redundancy analysis (RDA) to examine how fungal community composition changed in response to our mycorrhizal dominance gradient. RDAs were performed for each different taxonomic rank (phyla through OTUs), as well as for functional group composition. Significance of predictor variables was assessed using 999 random permutations of sample identity. Percent AM basal area (0% - 100%) and location (GW, LDW, or MMSF) were supplied as predictor variables. The goodness() command in vegan was used to obtain R^2 values for changes in fungal family relative abundances related to the mycorrhizal gradient. Additionally, these same community data were analyzed by stepwise, forward selection RDAs using the vegan ordiR2step command to determine their response to abiotic predictor variables, selecting only those that were both significant ($P < 0.05$) and resulted in an increase in adjusted R^2 value (Blanchet *et al.* 2008). Thus, soil moisture, soil organic matter, soil pH, and nitrification rate were tested as abiotic predictor variables. Other abiotic variables were eliminated before the analysis using a variance inflation factor cutoff of < 10 to detect confounded predictor variables (Borcard *et al*. 2018) through the vegan command vif.cca(). The adjusted R^2 values from the RDAs with mycorrhizal percent and the stepwise RDAs were used to assess the fit of significant models (Peres-Neto *et al.* 2006).

Our first prediction, that AM soil will have greater fungal taxonomic diversity compared to ECM soil (**P1**), was tested using the full community as well as separately for each functional group of interest. For each plot, OTU data was used to calculate the first three Hill numbers (Chao *et al*. 2014), representing a gradient of emphasis on evenness: ${}^0D$ or richness, ${}^1D$ or the exponentiated Shannon-Wiener diversity index, and ${}^2D$ or the inverse Simpson index. To test for

an effect of mycorrhizal dominance on these diversity measures, we performed mixed-effects linear modeling using the nlme package (Pinheiro *et al.* 2017) after testing for normality. Forest site (GW, LDW, and MMSF) was used as a random factor while percent AM basal area (0% - 100%) was tested as the predictor. In order to test our second prediction that AM soil has higher relative abundances of pathogenic and saprotrophic fungal taxa compared to ECM soil (**P2**), we again used linear modeling. For each functional group of interest (biotrophs, necrotrophs, and primary saprotrophs), relative abundances were used as the response variable, percent AM basal area of the plots as the predictor variable, and location was used as a random effect. R^2 values were used to assess the fit of each linear model for each taxonomic and functional group of interest and were obtained using the MuMIn package (Bartoń 2009).

In addition to testing **P1** and **P2**, samples from the nitrogen fertilization experiment were used to test our third prediction that chronic inorganic N addition will increase the relative abundances of non-mycorrhizal soil fungi and have a larger impact on fungal communities associated with ECM-dominant forests (**P3**). First, RDAs were performed as described above for each taxonomic rank (phylum through genus), as well as for functional group composition. Dominant tree mycorrhizal type (AM or ECM), sampling depth (0 – 5 or 5 – 15cm), and N treatment were included (with interactions) as predictor variables. Next, linear modeling was used to evaluate the responses of biotroph, necrotroph, and primary saprotroph relative abundances, as well as the first three Hill numbers, to the same predictor variables.

RESULTS

Fungal community response to the gradient in mycorrhizal types

For samples from the mycorrhizal gradient sites, 3,626,080 sequences representing 11,729 OTUs were assigned to 1347 unique fungal taxa. All Hill numbers, ${}^{0}D$ or OTU richness (R^2 = 23.2%), ${}^{1}D$ (R^2 = 21.6%), and ${}^{2}D$ (R^2 = 16.2%), displayed a significant, positive trend with increasing AM-tree dominance (d.f. = 41; $P < 0.005$; Figure 1a-c), in agreement with our first prediction (fungal diversity is greater in AM soil). Examining the changes in diversity for each functional group revealed that biotrophic plant pathogen (R^2 = 13.3%), necrotrophic plant pathogen (R^2 = 15.6%), and primary saprotroph (R^2 = 32.2%) OTU richness significantly increased with AM-tree dominance ($P < 0.02$; Figure 2a-c), while ${}^{1}D$ and ${}^{2}D$ were not significantly affected. Meanwhile, ectomycorrhizal fungal OTU richness showed the opposite trend, significantly decreasing with increasing AM-tree dominance ($P < 0.001$; R^2 = 24.7%; Figure 2d), while ${}^{1}D$ and ${}^{2}D$ were not significantly correlated.

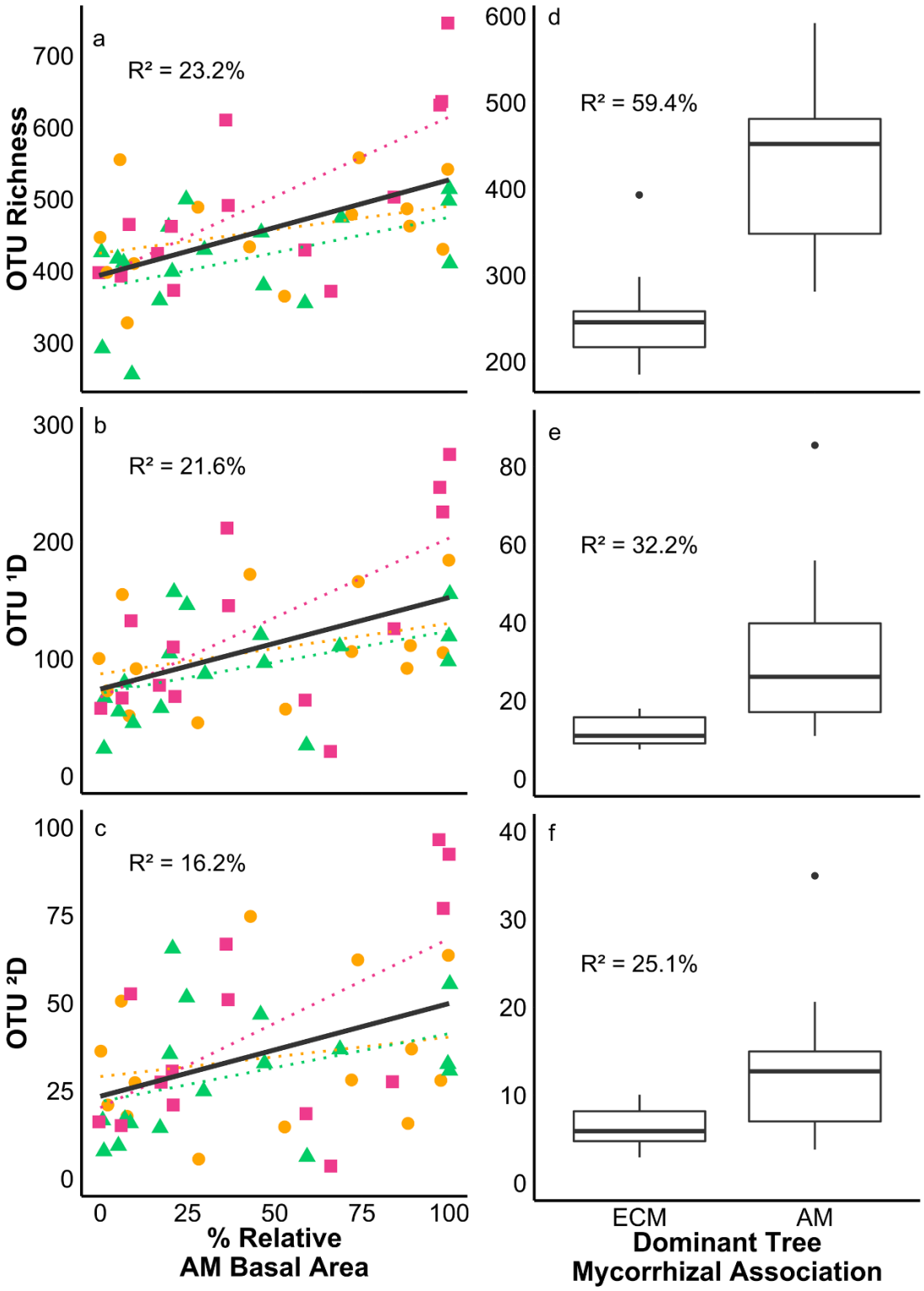
a
R² = 23.2%
OTU Richness
700
600
500
400
300
b
R² = 21.6%
OTU ¹D
300
200
100
0
c
R² = 16.2%
OTU ²D
100
75
50
25
0
0
25
50
75
100
% Relative
AM Basal Area
d
R² = 59.4%
600
500
400
300
200
e
R² = 32.2%
80
60
40
20
0
f
R² = 25.1%
40
30
20
10
0
ECM
AM
Dominant Tree
Mycorrhizal Association

Figure 1. Overall fungal OTU richness (^0D), ^1D, and ^2D from: a-c) sites forming natural gradients of mycorrhizal dominance (circles = Griffy Woods, triangles = Lilly-Dickey Woods, squares = Morgan-Monroe State Forest) and d-f) plots with > 85% relative basal area of ECM or AM trees from Moores Creek. Colored regression lines correspond to each individual site, while the black regression line and reported R^2 value correspond to the entire linear model conducted with site as a random effect.

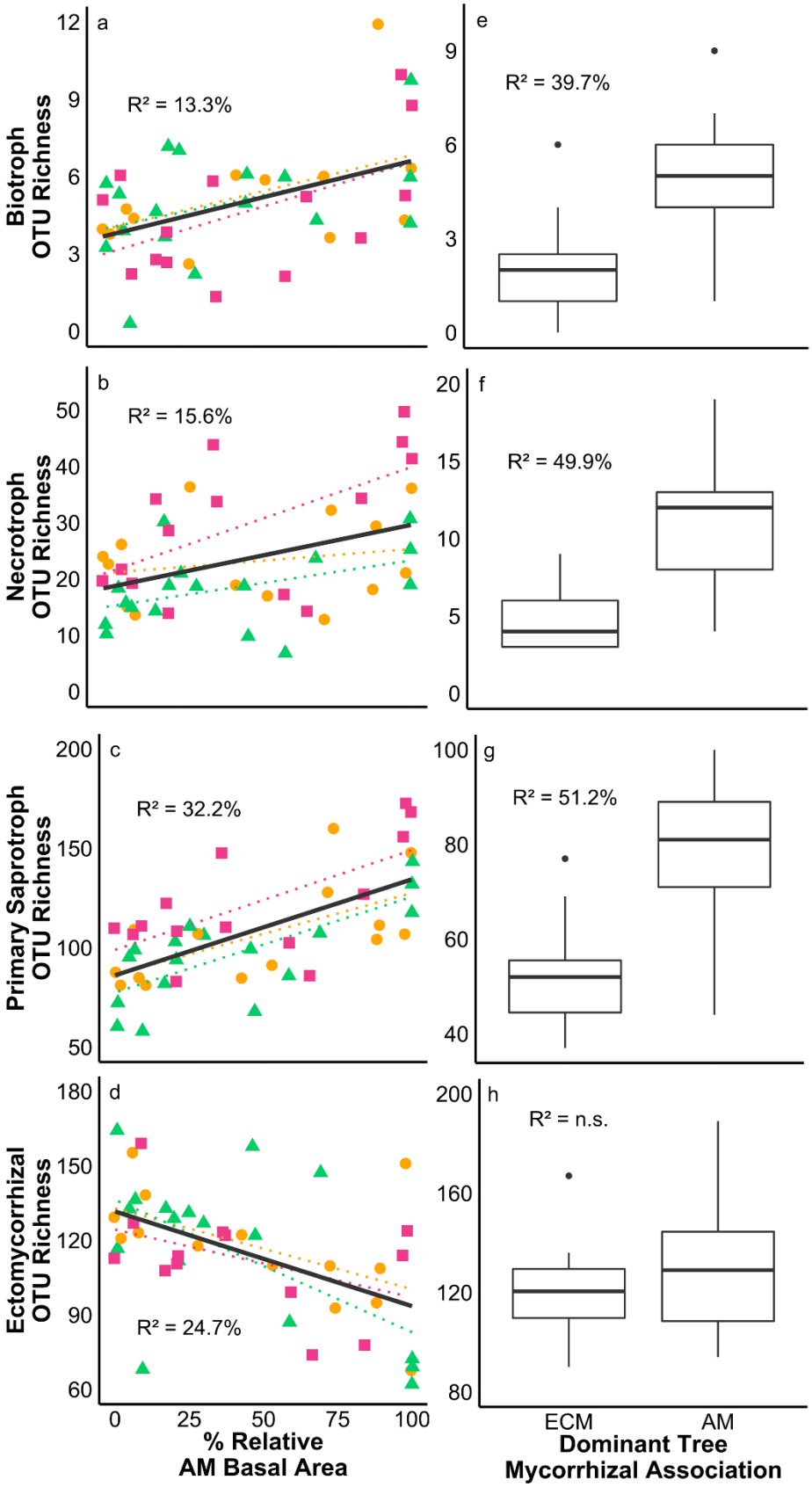
a
R² = 13.3%
Biotroph OTU Richness
e
R² = 39.7%
b
R² = 15.6%
Necrotroph OTU Richness
f
R² = 49.9%
c
R² = 32.2%
Primary Saprotroph OTU Richness
g
R² = 51.2%
d
R² = 24.7%
Ectomycorrhizal OTU Richness
h
R² = n.s.
% Relative AM Basal Area
ECM
AM
Dominant Tree Mycorrhizal Association

Figure 2. OTU richness (^0D), ^1D, and ^2D for biotrophic pathogens, necrotrophic pathogens, primary saprotrophs, and ectomycorrhizal fungi from: a-d) sites forming natural gradients of mycorrhizal dominance (circles = Griffy Woods, triangles = Lilly-Dickey Woods, squares = Morgan-Monroe State Forest) and e-h) plots with > 85% relative basal area of ECM or AM trees from Moores Creek. Colored regression lines correspond to each individual site, while the black regression line and reported R^2 value correspond to the entire linear model conducted with site as a random effect.

Redundancy analyses revealed that both AM-tree dominance and site location affected fungal community composition at every taxonomic rank, explaining from 4.7% of the variation at the OTU rank up to 43.3% at the rank of phyla ($P < 0.05$; Table 1). When analyzed separately, AM-tree dominance explained approximately twice as much variance as site at all taxonomic ranks except species and OTU (Table 1). Results from the stepwise forward selection RDAs with abiotic data as explanatory variables indicated that, for genera through phyla, nitrification was the only significant variable selected, whereas SOM and nitrification were both selected at the species and OTU ranks (Table 1). Significant abiotic variables ($P < 0.05$) explained a similar amount of variation in fungal community composition as did AM-tree dominance at every taxonomic rank. Nitrification rate was positively correlated with increasing AM-tree dominance ($P < 0.001$; $R^2 = 50.0\%$).

Table 1. Adjusted R^2 values from the RDAs conducted on fungal community composition in the samples representing a gradient of mycorrhizal types expressed as percent of variance explained.

Explanatory Variables	**Phylum**	**Class**	**Order**	**Family**	**Genus**	**Species**	**OTU**	**Functional Group**
AM Percent + Site	43.3	30.0	18.7	16.8	13.9	8.5	4.7	33.3
AM Percent	27.1	19.5	11.6	11.5	9.2	4.5	2.6	26.6
Site	15.3	9.8	6.6	5.1	4.6	4.1	2.1	6.5
Soil Properties	26.5a	22.1a	12.3a	11.9a	10.2a	7.1b	3.8b	-

Sites include Griffy Woods, Lilly-Dickey Woods, and Morgan-Monroe State Forest. A value displayed in the table indicates that the explanatory variable was significant ($\alpha = 0.05$).

a. Nitrification identified as significant during the stepwise, forward selection RDA.
b. b. SOM + nitrification identified as significant during the stepwise, forward selection RDA.

Linear modeling of relative abundances of separate functional groups was used to test our second prediction (relative abundances of fungal plant pathogens and saprotrophs are greater in AM-tree dominant soil compared to ECM-tree dominant soil). Fungal biotrophic plant pathogen (R^2 = 11.5%), necrotrophic plant pathogen (R^2 = 14.9%), and primary saprotroph (R^2 = 28.3%) relative abundances all significantly increased with increasing AM-tree dominance, while ectomycorrhizal fungal (R^2 = 39.6%) relative abundances decreased ($P < 0.05$; Figure 3a-d). According to the RDA, AM-tree dominance and site location explained 33.3% of the variation in fungal functional group frequency (Table 1). No abiotic variables were selected as significant explanatory factors for fungal functional groups. Note that these functional group abundances were obtained from the lowest taxonomic level identified wherever possible, often genus or species. Table 2 displays relative abundances of fungal families with >1% average relative abundance in AM-tree or ECM-tree dominant soils along with the major functional groups assigned to various taxa found within each family. Ten out of 15 families containing plant biotrophic, plant necrotrophic, and saprotrophic members increased in relative abundance in AM-tree dominant soil. Notable exceptions include the Atheliaceae, Cortinariaceae, Thelephoraceae, and Tricholomataceae (all Basidiomycota), which decreased in relative abundance in AM-tree dominant soil, but which also contain ectomycorrhizal taxa in addition to their saprotrophic members. Similarly, four families dominated by ectomycorrhizal members (Russulaceae, Amanitaceae, Clavulinaceae, and Boletaceae) decreased in relative abundance in AM-tree dominant soil, with the Russulaceae (Basidiomycota) demonstrating the largest change (a decrease) in relative abundance of 55.5%. On the other hand, the ectomycorrhizal families Inocybaceae (Basidiomycota), Sebacinaceae (Basidiomycota), and Tuberaceae (Ascomycota),

increased in relative abundance in AM-tree dominant soil (although their variance explained was <3%).

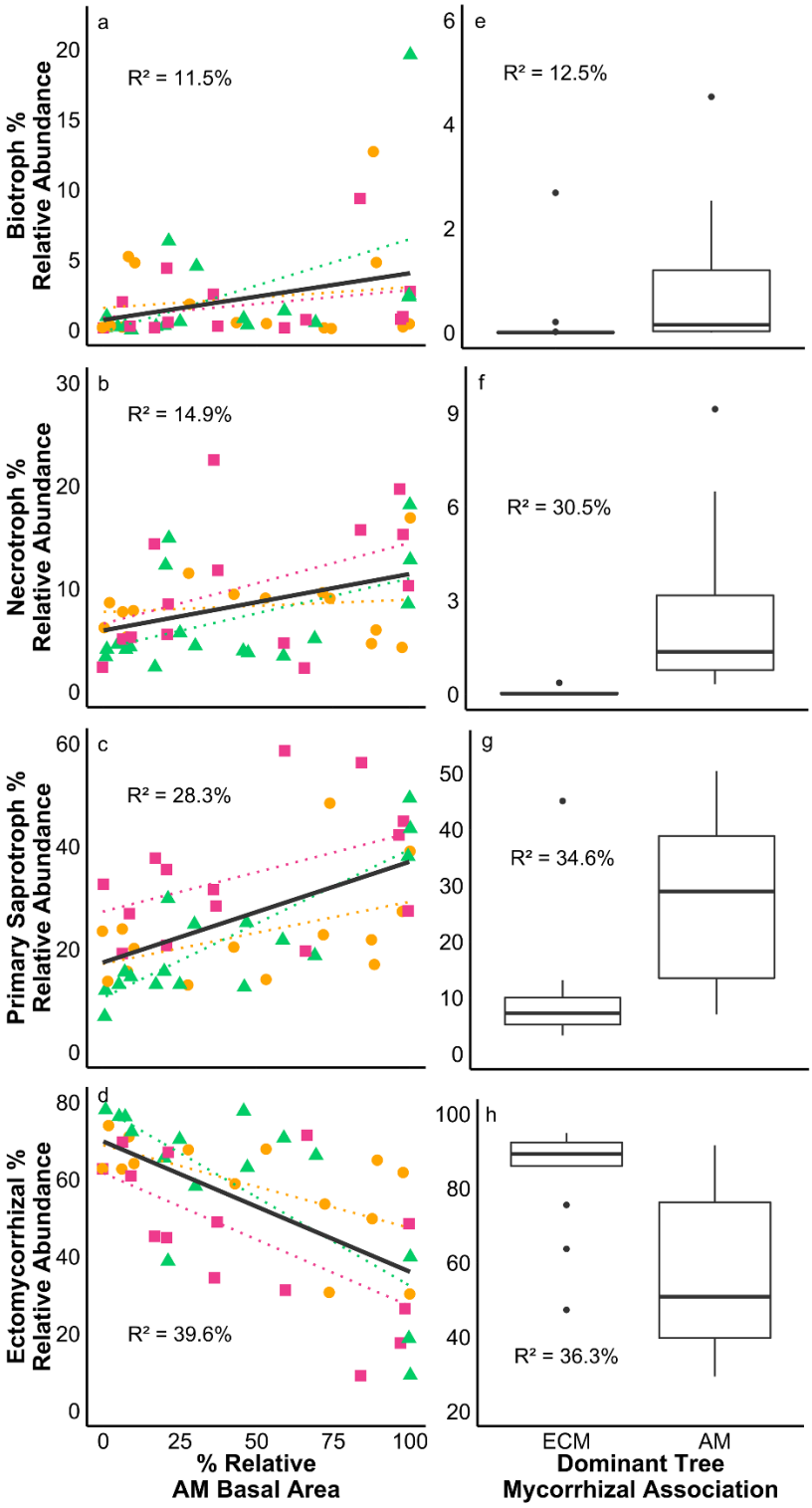

Figure 3. Percent relative abundances of biotrophic pathogens, necrotrophic pathogens, primary saprotrophs, and ectomycorrhizal fungi from: a-d) sites forming natural gradients of mycorrhizal dominance (circles = Griffy Woods, triangles = Lilly-Dickey Woods, squares = Morgan-Monroe State Forest) and e-h) plots with > 85% relative basal area of ECM or AM trees from Moores Creek. Colored regression lines correspond to each individual site, while the black regression line and reported R^2 value correspond to the entire linear model conducted with site as a random effect.

Table 2. Fungal families with an average relative abundance > 1% from the mycorrhizal gradient across Griffy Woods, Lilly-Dickey Woods, and Morgan-Monroe State Forest.

Phylum	Family	Functional Role	R^2	AM-tree dominant soil	Intermediate soil	ECM-tree dominant soil
Ascomycota	Tuberaceae	Ectomycorrhizal	1.1	1.6 ± 3.51	0.69 ± 0.75	1.08 ± 1.39
	Nectriaceae	Necrotroph or Primary Saprotroph	32.75	1.42 ± 0.78	0.5 ± 0.32	0.52 ± 1.05
	Mycosphaerellaceae	Necrotroph or Various	21.34	2.57 ± 2.14	1.78 ± 2.3	1.05 ± 1.55
	Helotiaceae	Necrotroph, Primary or Wood Saprotroph, Ectomycorrhizal, Ericoid Mycorrhizal, Endophyte, or Various	12.41	3.91 ± 4.34	2.01 ± 0.97	1.92 ± 1.29
	Herpotrichiellaceae	Necrotroph, Primary or Wood Saprotroph, Endophyte, or Various	3.2	1.31 ± 0.72	0.63 ± 0.31	1.09 ± 0.73
	Helotiales (inc. sed.)	Necrotroph, Primary Saprotroph, Ectomycorrhizal, Endophyte, Various, or Unknown	20.04	2.34 ± 1.75	1.82 ± 1.4	1.04 ± 0.96
	Dermateaceae	Necrotroph, Primary Saprotroph, Unknown, or Various	2.41	0.59 ± 0.39	1.9 ± 3.77	1.09 ± 1.51
	Hyaloscyphaceae	Primary or Wood Saprotroph, Endophyte, Fungal Parasite, or Various	2.08	1.55 ± 1.67	0.8 ± 0.55	0.89 ± 0.75
	Clavicipitaceae	Primary Saprotroph or Fungal Parasite	30.02	1.24 ± 0.95	0.53 ± 0.29	0.48 ± 0.3
Basidiomycota	Hygrophoraceae	Biotroph, Primary Saprotroph, Ectomycorrhizal, or Various	15.86	5.17 ± 6.96	1.22 ± 1.34	1.74 ± 2.5
	Russulaceae	Ectomycorrhizal	22.26	17.5 ± 14.8	31.5 ± 14.5	31.5 ± 13.7
	Inocybaceae	Ectomycorrhizal	0.24	3.6 ± 4.61	3.16 ± 2.93	2.2 ± 2.49
	Amanitaceae	Ectomycorrhizal	12.53	0.15 ± 0.19	0.76 ± 1.13	1.29 ± 2.24
	Sebacinaceae	Ectomycorrhizal or Various	2.77	5.64 ± 6.34	5.7 ± 4.25	3.11 ± 3.65
	Clavulinaceae	Ectomycorrhizal or Various	1.81	0.68 ± 0.65	0.6 ± 0.88	1.79 ± 2.99
	Boletaceae	Ectomycorrhizal or Various	3.26	0.73 ± 0.87	0.53 ± 0.54	1.59 ± 3.37
	Trimorphomycetaceae	Fungal Parasite or Various	11.96	1.11 ± 0.77	0.67 ± 0.56	0.65 ± 0.35

	Atheliaceae	Necrotroph, Primary Saprotroph, Ectomycorrhizal, or Various	18.07	1.16 ± 0.94	4.63 ± 5.3	10.5 ± 13.9
	Cortinariaceae	Primary Saprotroph or Ectomycorrhizal	8.43	0.49 ± 0.37	6.26 ± 13.9	5.92 ± 11.8
	Clavariaceae	Primary Saprotroph or Various	37.31	2.5 ± 2.39	1.07 ± 0.68	0.64 ± 1.14
	Tricholomataceae	Primary Saprotroph, Ectomycorrhizal, or Various	4.22	0.49 ± 0.45	0.52 ± 0.76	3.04 ± 7.6
	Thelephoraceae	Primary Saprotroph, Ectomycorrhizal, or Various	6.04	4.09 ± 3.5	5.69 ± 4.71	6.04 ± 3.58
Zygomycota	Mortierellaceae	Primary Saprotroph	21.69	17.9 ± 11.1	13.2 ± 12.1	7.45 ± 7.5

Functional role includes all taxa present in each family. Biotroph and Necrotroph designations are specific to plant pathogens and do not include animal or fungal pathogens. The Various designation was used for taxa within a family who were assigned multiple functional roles that remained unresolved after a thorough literature search. Average relative abundances and standard deviations were obtained from plots with > 65% relative basal area of one mycorrhizal type (AM or ECM dominant) and from plots with < 60% relative basal area of both mycorrhizal types (Intermediate). Adjusted R^2 values reported are from the redundancy analysis performed at the family rank. Relative abundance values are displayed as percentages and include standard deviations.

Dominant mycorrhizal type × nitrogen amendment factorial experiment

For samples from the nitrogen amendment experiment, 54,116,487 sequences representing 2180 unique OTUs were assigned to 492 different taxa. Redundancy analysis indicated that dominant mycorrhizal type significantly affected fungal community composition, explaining from 9.7% of the variation at the OTU rank, up to 42.7% of the variation at the rank of phyla (d.f. = 29; $P < 0.05$; Table 3). Additionally, depth was a significant factor for intermediate taxonomic ranks, but explained only 2-3% of variation in community composition (Table 3). Nitrogen treatment and all interaction terms were not significant for any taxonomic rank (Table 3).

Table 3. Adjusted R^2 values from the RDAs conducted on the fungal community data from the mycorrhizal type × N fertilization experiment at Moores Creek.

Explanatory Variables	**Phylum**	**Class**	**Order**	**Family**	**Genus**	**OTU**	**Functional Group**
Mycorrhizal Type	42.7	29.6	18.3	22.6	16.4	9.7	32.0
Depth	-	3.3	2.2	2.1	2.2	-	-
N Treatment	-	-	-	-	-	-	-
All Interactions	-	-	-	-	-	-	-

A value displayed in the table indicates that the explanatory variable was significant ($\alpha = 0.05$).

OTU richness was significantly higher in AM-tree dominant soil ($P = 0.0001$; $R^2 = 59.4\%$; Figure 1d) and significantly higher at a sampling depth of 0 – 5 cm ($P = 0.0001$; $R^2 = 18.9\%$). Additionally, there was no significant effect of N addition treatment or any significant interactions between dominant mycorrhizal type, depth, or treatment on OTU richness. Likewise, ${}^1D$ ($R^2 = 32.2\%$) and ${}^2D$ ($R^2 = 25.1\%$) were higher in AM-tree dominant soil ($P < 0.008$; Figure 1e-f), while depth, N addition treatment, and all interactions were not significant. Plant biotroph ($R^2 = 39.7\%$), plant necrotroph ($R^2 = 49.9\%$), and primary saprotroph ($R^2 = 51.2\%$) OTU richness were all significantly higher in AM-tree dominant soil $P = 0.003$; Figure 2e-g), while only primary saprotroph ${}^1D$ ($R^2 = 68.5\%$) and ${}^2D$ ($R^2 = 55.1\%$) were significantly higher in AM-tree dominant soil ($P < 0.05$). Additionally, plant necrotroph and primary saprotroph OTU richness were significantly higher at a depth of 0 – 5 cm than the 5 – 15 cm depth. A significant interaction between dominant mycorrhizal type and sampling depth for plant necrotroph OTU richness was also identified ($P = 0.01$; $R^2 = 76.6\%$), with AM-tree dominant soil having greater plant necrotroph OTU richness at a depth of 0 – 5 cm compared to the 5 – 15 cm depth and ECM-tree dominant soil showing no differences between depths. Ectomycorrhizal fungal OTU richness was significantly higher only at a depth of 0 – 5 cm ($P = 0.003$; $R^2 = 33.1\%$), while ectomycorrhizal fungal ${}^1D$ and ${}^2D$ were not significantly affected by dominant mycorrhizal type, depth, N treatment, or any interactions.

Dominant mycorrhizal type explained 32% of the variation in relative abundance between functional groups, but depth was not significant (Table 3). Nitrogen treatment and interaction terms were also not significant for functional groups (Table 3). Similar to the results from our mycorrhizal gradient analyses, significant changes in fungal functional group composition at MC were the result of reduced ectomycorrhizal fungal ($R^2 = 36.3\%$) relative

abundance and increased plant biotroph (R^2 = 12.5%), plant necrotroph (R^2 = 30.5%), and primary saprotroph (R^2 = 34.6%) relative abundances in AM-tree dominant soil ($P < 0.05$; Figure 3e-h). Differences in the relative abundance of fungal families from MC with >1% average relative abundance in AM-tree or ECM-tree dominated soil are reported in Table 4. Generally, families with biotrophic plant pathogen, necrotrophic plant pathogen, and saprotrophic members again increased in relative abundance in AM-tree dominant soil while families containing ectomycorrhizal members decreased in relative abundance. The Elaphomycetaceae, a family in Ascomycota containing ectomycorrhizal taxa, and the Marasmiaceae, a family in Basidiomycota containing various saprotrophic and ectomycorrhizal taxa, however, both increased in relative abundance in AM-tree dominant soil. Additionally, 58% of fungal families with >1% average relative abundance overlapped between the MC and mycorrhizal gradient datasets, with 12 out of 14 of these shared families demonstrating similar responses to dominant tree mycorrhizal type. The two exceptions were both ectomycorrhizal families in Basidiomycota: the Boletaceae increased in relative abundance in AM-tree dominant soil at MC but decreased in the mycorrhizal gradient sites, while the trends for Sebacinaceae were the opposite.

Table 4. Fungal families with an average relative abundance > 1% from AM-tree and ECM-tree dominant plots at Moores Creek.

Phylum	Family	Functional Role	R^2	AM-tree dominant soil	ECM-tree dominant soil
Ascomycota	Elaphomycetaceae	Ectomycorrhizal	0.05	3.12 ± 9.5	0.95 ± 1.45
	Herpotrichiellaceae	Primary Saprotroph, Endophyte, or Various	31.27	2.46 ± 2.29	0.49 ± 0.41
Basidiomycota	Hygrophoraceae	Biotroph or Ectomycorrhizal	30.59	10.9 ± 15.9	0.22 ± 0.75
	Russulaceae	Ectomycorrhizal	21.25	19.4 ± 18.9	35.8 ± 18.5
	Amanitaceae	Ectomycorrhizal	25.40	0.77 ± 1.48	8.99 ± 15.9
	Boletaceae	Ectomycorrhizal	15.19	6.05 ± 8.48	0.6 ± 1.14
	Cortinariaceae	Ectomycorrhizal	23.43	2.25 ± 7.95	5.35 ± 5.27
	Hydnangiaceae	Ectomycorrhizal	10.73	0.03 ± 0.08	1.93 ± 5.08
	Sebacinaceae	Ectomycorrhizal	5.14	2.51 ± 5.8	3 ± 3.04
	Hydnaceae	Ectomycorrhizal or Various	16.68	0.05 ± 0.08	7.29 ± 12.9
	Clavulinaceae	Ectomycorrhizal or Various	2.22	2.29 ± 5.4	6.37 ± 14.2
	Ceratobasidiaceae	Necrotroph, Ectomycorrhizal, or Various	52.45	2.02 ± 3.04	0 ± 0
	Tricholomataceae	Necrotroph, Primary Saprotroph, or Ectomycorrhizal	25.13	0.3 ± 0.44	9.91 ± 17.4
	Strophariaceae	Primary or Wood Saprotroph, or Ectomycorrhizal	38.23	3.41 ± 4.33	0.17 ± 0.61
	Clavariaceae	Primary Saprotroph	50.06	5.38 ± 4.29	0.83 ± 2.01
	Agaricaceae	Primary Saprotroph	44.48	1.83 ± 2.27	0.12 ± 0.14
	Geminibasidiaceae	Primary Saprotroph	25.00	1.48 ± 2.13	0.09 ± 0.16
	Entolomataceae	Primary Saprotroph or Ectomycorrhizal	77.12	2.32 ± 1.76	0.03 ± 0.07
	Marasmiaceae	Primary Saprotroph or Ectomycorrhizal	0.31	0.66 ± 1.26	2.15 ± 8.01
	Thelephoraceae	Primary Saprotroph or Ectomycorrhizal	0.41	2.19 ± 2.32	2.36 ± 2.46
	Atheliaceae	Primary Saprotroph, Ectomycorrhizal, or Various	30.24	0.19 ± 0.49	3.65 ± 6.22
	Inocybaceae	Wood Saprotroph or Ectomycorrhizal	18.09	4.19 ± 5.3	0.66 ± 1.11
Mucoromycota	Umbelopsidaceae	Primary Saprotroph	4.65	5.22 ± 8.15	5.12 ± 1.93
Zygomycota	Mortierellaceae	Primary Saprotroph	59.69	14.3 ± 12	1.33 ± 2.72

Functional role includes all taxa present in each family. Biotroph and Necrotroph designations are specific to plant pathogens and do not include animal or fungal pathogens. The Various designation was used for taxa within a family who were assigned multiple functional roles that remained unresolved after a thorough literature search. Average relative abundances and standard deviations were obtained from plots with > 85% relative basal area of one mycorrhizal type (AM or ECM dominant). Adjusted R^2 values reported are from the redundancy analysis performed at the family rank. Relative abundance values are displayed as percentages and include standard deviations.

DISCUSSION

Dominance of different mycorrhizal tree types affects fungal functional group relative abundances and overall fungal species diversity

In this study, we found that AM and ECM tree communities affect soil fungal communities in distinct ways, consistent with our overarching hypothesis, which may have important consequences for forest community dynamics and ecosystem processes. Within all four forests, areas with increased AM tree dominance were associated with increased fungal diversity and increased relative abundances of biotrophic plant pathogens, necrotrophic plant pathogens, and primary saprotrophs (Figs. 1 – 3). Additionally, percent AM tree basal area consistently explained as much or more variation in fungal community composition as soil properties, such as SOM content and nitrification rate, sampling depth, and mineral N availability (Table 1). Mycorrhizal type is increasingly viewed as a key trait with cascading effects that go well beyond nutrient acquisition, potentially affecting global patterns in soil biogeochemistry and plant-soil feedbacks (Lin *et al*. 2017, Jiang *et al*. 2020, Tedersoo *et al*. 2020b). Such broad effects imply that tree mycorrhizal types must consistently influence non-mycorrhizal fungi, as demonstrated here across four forest stands. Indeed, our findings are similar to Bahram *et al.* (2020), who demonstrated comparable patterns in relative abundance of plant pathogens and saprotrophs in Baltic temperate forests based on mycorrhizal dominance, and support the ideas offered by Netherway *et al*. (2021) regarding differences between plant pathogen and saprotroph abundance between AM- and ECM-dominant systems.

Plant-soil feedbacks tend to be more negative for AM trees than ECM trees (Bennett *et al*. 2017, Segnitz *et al*. 2020), including at Lilly-Dickey Woods (Johnson *et al*. 2018), and this pattern has recently been associated with greater accumulation of potentially pathogenic fungi on

AM tree roots vs. ECM tree roots (Chen *et al*. 2019, Liang *et al*. 2020). Our data on bulk soil fungal communities suggests that this effect on biotrophic and necrotrophic plant pathogen abundances may create a "mycorrhizal spillover" effect that influences the fungal functional groups responsible for plant-soil feedback encountered by other trees within the community (Eagar *et al*. 2020). Due to the increased diversity of plant biotrophs and necrotrophs in AM-tree dominated stands, both heterospecific and conspecific plants may experience a greater likelihood of encountering a pathogenic fungal strain capable of causing an infection. Increased relative abundances of fungal biotrophic and necrotrophic plant pathogens also suggests that infectious populations encountered may be a larger fraction of the community, increasing the likelihood of plant disease (Liu and He 2019). Hence, these patterns should result in more negative plant-soil feedback in AM-dominated stands, helping to explain how juvenile tree recruitment, regardless of the juvenile species mycorrhizal type, can be strongly influenced by the mycorrhizal type of surrounding dominant trees (Johnson *et al*. 2018, Chen *et al*. 2019, Eagar *et al*. 2020).

Plant pathogen relative abundances may be greater in AM-dominant soil because of the greater association of pathogens with AM roots as noted above, but other factors are likely to drive increased primary saprotroph relative abundance and diversity, as well as contribute to specialized necrotrophic plant pathogens that are facultatively saprotrophic (Netherway *et al.* 2021). ECM-dominant tree communities are known to induce slower rates of nutrient and SOM cycling compared to AM-dominant tree communities (Talbot & Finzi 2008, Phillips *et al.* 2013, Craig *et al*. 2018, Tatsumi *et al*. 2020), which may be explained by the lower primary saprotroph relative abundances observed in our study. AM leaf litter also tends to be more labile than ECM leaf litter due to increased nutrient and polyphenol contents (Lin *et al.* 2017, Averill *et al*. 2019, Keller & Phillips 2019), creating more favorable conditions for fungal plant pathogens and

saprotrophs that rely on plant litter for carbon and energy (Cline *et al*. 2018, Bai *et al*. 2019). Increased labile carbon and energy availability may also drive enhanced saprotrophic fungal diversity (Feinstein and Blackwood 2012, Bai *et al*. 2019), which may be tied to plant diversity through controls on available types of leaf litter (i.e., labile vs. recalcitrant). Furthermore, reduced saprotroph relative abundance (and necrotrophic plant pathogen relative abundance) in ECM-dominant tree communities may also be a consequence of competitive interactions with ECM fungi (McGuire *et al*. 2010, Averill and Hawkes 2016). Although ECM fungi obtain most of their carbon from their host tree, they compete with free-living fungi for nitrogen and other resources, including access to leaf litter.

While dominant mycorrhizal types have emerged as a convenient framework by which to classify forests, shifts in fungal community composition have also been attributed to many other factors, such as soil organic matter (Tedersoo *et al*. 2020a) or the species identity of dominant trees (Prescott and Grayston, 2013), which may be confounded with mycorrhizal associations in these systems. Trees that do not conform to trait predictions under the MANE framework, such as AM trees with recalcitrant leaf litter (e.g., *Platanus occidentalis*) or ECM trees with labile leaf litter (e.g., *Carya ovata*; personal observations) may induce weaker effects on soil carbon and nutrient cycling and could potentially drive opposite patterns in local fungal community composition to those observed in our study. Likewise, tree species that are dual mycorrhizal, such as members of *Alnus, Populus,* and *Salix* (Teste *et al.* 2019), may also drive different relationships between soil microbial communities and soil nutrient dynamics. Dual mycorrhizal relationships and their effects on soil in comparison to AM or ECM associations are currently an underexplored area warranting further research (Teste *et al.* 2019). Finally, variation among broad controls on decomposition caused by geographic factors, such as temperature and

precipitation, may override mycorrhizal-associated patterns in nutrient cycling and fungal community composition. It is therefore critical to continue testing the hypotheses presented here in forests of varying tree species composition and geographical range before drawing ultimate conclusions about the role mycorrhizas play in structuring soil community dynamics.

Mineral N addition and soil depth do not influence fungal communities as much as forest mycorrhizal dominance.

Soil sampling depth has been shown to affect the community composition of root-associated fungi (Clemmensen *et al*. 2015), with depth interacting with tree mycorrhizal dominance to influence the relative abundances of saprotrophic and mycorrhizal fungi (Carteron *et al.* 2020). While sampling depth explained some variation in OTU richness of our various functional groups, we found this depth x mycorrhizal type interaction to only be significant for plant necrotroph OTU richness. This appears to suggest that plant necrotroph diversity is primarily associated with the more organic horizons of AM soil, but further work is needed to fully explain the drivers behind this result. Additionally, sampling depth did not significantly affect fungal relative abundances, either as a main effect or as an interaction with dominant mycorrhizal type. Dominant mycorrhizal type consistently explained more than twice as much variation in plant biotroph, plant necrotroph, and primary saprotroph OTU richness compared to sampling depth, demonstrating the strong influence different mycorrhizal associations have on soil fungal communities.

Contrary to our third prediction, mineral N addition did not increase the relative abundances of plant pathogenic and saprotrophic soil fungi in our study. Neither the relative abundance of fungal taxa and functional groups, nor fungal OTU richness, were affected by the six years of inorganic N addition at Moores Creek. Only plant necrotroph OTU evenness

appeared to be weakly influenced by a mycorrhizal dominance x mineral N treatment interaction ($P = 0.07$), with N treatment slightly increasing necrotroph OTU evenness in ECM soil while having no effect in AM soil. While some studies on the effects of simulated mineral N deposition on temperate hardwood forest soils have demonstrated changes to overall fungal community composition (e.g., Pregitzer *et al.* 2008, Edwards *et al.* 2011, Morrison *et al.* 2016), other studies have shown that fungi may instead alter the expression of extracellular enzyme genes when community composition remains unchanged (Entwistle *et al.* 2013, Freedman *et al.* 2015, Hesse *et al.* 2015, Zak *et al.* 2019). Additionally, in relation to dominant mycorrhizal associations, extracellular enzyme production has been documented to shift from C-degrading to N-degrading enzymes with increasing ECM dominance (Cheeke *et al*. 2020). These variable responses of soil fungi to changes in mineral N availability suggest that our fungal communities may have altered their activity instead of composition, as seen in ECM-dominant plots from Midgley and Phillips (2016). Alternatively, larger amounts of N than those applied at Moores Creek can induce changes in fungal community composition, as observed at Harvard Forest (Morrison *et al.* 2016, 2018). It is also possible our plots may be limited by resources other than N or co-limited by multiple nutrients (DeForest *et al.* 2012, Rosling *et al.* 2016). For example, DeForest *et al.* (2012) documented microbial community composition changes in response to P addition in unglaciated forest soils in southern Ohio, but not in glaciated northern Ohio soils.

While mineral N addition can elicit varying responses in soil fungal communities, the form or quality of N added can also affects fungal community composition and function. For example, Cline *et al.* (2018) found that saprotrophic and ECM fungal species richness responded negatively to organic N addition, indicating that inorganic vs. organic N availability is an important consideration when studying fungal community responses to N addition. Similarly,

Beidler *et al.* (2020) found that high-quality substrates, represented by fungal tissue with low melanin and high N content, decomposed much more rapidly than low-quality substrates. They also demonstrated variable responses in fungal community composition to substrate quality depending on dominant mycorrhizal associations, with low substrate quality, AM-associated communities having overall higher relative abundances of pathogens and saprotrophs (Beidler *et al.* 2020). Both of these studies suggest that the addition of bioavailable, mineral N may bypass important metabolic barriers that would otherwise alter the representation of specific fungi in soil communities of varying mycorrhizal dominance. It would therefore be worthwhile to examine whether fungal enzyme activity or gene expression changes on the basis of inorganic vs. organic N addition in forests of different dominant mycorrhizal types.

Conclusions

Our study and those from Bahram *et al.* (2020) and Netherway *et al.* (2021) suggest that there are widespread patterns in the distribution of fungal functional groups based on tree mycorrhizal types present in forest ecosystems. Additional research in other forests will be required to confirm that these patterns in functional groups are ubiquitous, or if these patterns are instead driven by other factors such as specific dominant tree species, specific fungal taxa, or geography. The effect of mycorrhizal dominance on the diversity and relative abundance of saprotrophic and plant pathogenic fungi is closely related to important differences in nutrient and SOM cycling (Phillips *et al.* 2013, Frey 2019) and plant-soil feedback (Bennett *et al*. 2017, Eagar *et al.* 2020). Future work should address the relative importance of these mechanisms as drivers of carbon storage and community dynamics in ecosystems of varying mycorrhizal composition, while also examining how widespread these phenomena are globally. With temperate forests expected to become more AM-tree dominant under global change factors (Jo *et*

al. 2019, Steidinger *et al*. 2019), understanding these patterns of co-occurrence between tree mycorrhizal associations and soil microbial communities is vital if we are to understand the full effects of global change on temperate forests.

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CHAPTER III

SPILLOVER EFFECTS FROM DOMINANT MYCORRHIZAL ASSOCIATIONS ON FUNGAL COMMUNITIES ARE MORE PROMINENT SURROUNDING ARBUSCULAR MYCORRHIZAL TREES AND VARY IN STRENGTH

This work has been submitted as

Eagar, A.C., Smemo, K.A., Phillips, R.P. and Blackwood, C.B. Arbuscular Mycorrhizal Tree Communities Have Greater Soil Fungal Diversity and Relative Abundances of Saprotrophs and Pathogens than Ectomycorrhizal Tree Communities. *Submitted to Soil Biology & Biochemistry*.

Author Contributions: ACE, CBB, RPP, and KAS designed the field study, while ACE, CBB, and KAS designed the sampling approach. ACE collected the molecular data and KAS collected the environmental and soil data. ACE performed the bioinformatics and statistical analyses. ACE and CBB wrote the manuscript with input from all authors.

ABSTRACT

Tree community mycorrhizal associations have been proposed as predictors of soil biogeochemistry and nutrient cycling in forests where multiple mycorrhizal types are present, which may also influence microbial community composition and function. Importantly, mycorrhizal associations may facilitate negative plant-soil feedback between arbuscular mycorrhizal (AM) trees and positive plant-soil feedback between ectomycorrhizal (ECM) trees

in temperate forest ecosystems. These effects are thought to be driven by species-specific plant-microbe interactions, but recent work has demonstrated that plant-soil feedback outcomes may be further influenced by surrounding tree communities. Currently, it is unclear the extent to which dominant, community-level mycorrhizal associations override the expected feedback experienced by an individual tree through a phenomenon known as the mycorrhizal "spillover" effect. By sampling individual AM and ECM trees across a gradient of community mycorrhizal types, we found support for the hypothesis that dominant mycorrhizal associations influence the fungal communities encountered by individual trees. Additionally, we observed the strongest effects from dominant mycorrhizal associations in our warmest, driest site and weakest effects in our coolest, wettest site. Pathogenic fungi were especially sensitive to individual tree vs surrounding tree community mycorrhizal types, with their richness and relative abundance increasing with AM dominance around individual AM trees but not ECM trees. These results were consistent, yet varied in intensity among fungal habitats, being generally strongest in soil and weakest in leaf litter samples, with root fungi intermediately affected. Our work supports using mycorrhizal associations as a framework for studying plant-microbe interactions and plant-soil feedback effects in forests of mixed mycorrhizal types, revealing important details about interactions that shape forest dynamics in a changing world.

INTRODUCTION

Plant mycorrhizal associations are considered a potential predictor of various terrestrial ecosystem processes, such as nutrient cycling rates and soil carbon (C) dynamics (Cornelissen *et al.* 2001, Read & Perez-Moreno 2003, Phillips *et al.* 2013, Lin *et al.* 2017). Because different types of mycorrhizal associations vary in their nutrient acquisition strategies and are specific to a given plant species (Smith & Read 2008, Brundrett 2009), frameworks that generalize these

associations as a driver of plant-soil interactions have been proposed (e.g., Phillips *et al.* 2013, Averill & Hawkes 2016, Bennett *et al.* 2017). Under the mycorrhizal-associated nutrient economy (MANE) hypothesis, arbuscular mycorrhizal (AM) trees are generally thought to have labile leaf litter and trait profiles associated with rapid mineral nutrient acquisition and turnover, leading to soil with increased mineral nutrient availability (Phillip *et al.* 2013, Lin *et al.* 2017, Averill *et al.* 2019). Conversely, ectomycorrhizal (ECM) trees are thought to have more recalcitrant leaf litter and trait profiles associated with nutrient conservation, thereby reducing soil mineral nutrient availability (Phillip *et al.* 2013, Lin *et al.* 2017, Averill *et al.* 2019). Given these hypothesized biogeochemical differences between forest stands dominated by AM and ECM trees, the MANE framework has recently been extended to make predictions about microbial community composition and tree dynamics as a function of tree mycorrhizal type (e.g., Eagar *et al.* 2020, Bahram *et al.* 2020, Eagar *et al.* 2022, Netherway *et al.* 2021).

Traditionally, plant-soil feedback has been thought of as a species-specific phenomenon (e.g., Pernilla Brinkman *et al.* 2010), with the majority of plant species experiencing varying degrees of negative feedback caused by soil-borne pathogens (Kulmatiski *et al.* 2008, Bever *et al.* 2015). Positive feedback between plants and soil is rarer (Kulmatiski *et al.* 2008) and occurs through the promotion of plant-mutualist interactions (Mangan *et al.* 2010) or due to access to unique pools of resources (Teste *et al.* 2017). The majority of plant-soil feedback research, however, has been conducted with grassland species or in grassland ecosystems (Kulmatiski *et al.* 2008, Forero *et al.* 2019). Recently, tree mycorrhizal associations have been implicated as potential drivers of plant-soil feedback effects in both experimental (Bennett *et al.* 2017, Liang *et al.* 2020) and observational (Johnson *et al.* 2017, Eagar *et al.* 2020) studies. These studies suggest that the prevailing mycorrhizal association within a temperate tree community can

influence the strength and direction of feedback experienced by individual trees through controls on soil nutrient cycling and the broader microbial community (i.e., spillover effects; Eagar *et al.* 2020, Eagar *et al.* 2022). In evidence of this, Bahram *et al.* (2020) and Eagar *et al.* (2022) both provided support for spillover effects by documenting predicted increases in fungal pathogen and saprotroph relative abundance with increasing AM tree basal area.

Forest communities dominated by AM trees also tend to reflect patterns consistent with negative plant-soil feedback, whereas ECM-dominant communities demonstrate patterns of positive feedback – regardless of individual species identity or mycorrhizal association (Johnson *et al.* 2017, Eagar *et al.* 2020). Specifically, these community-wide feedback patterns are attributed to the disparate effects of AM and ECM trees on soil nutrient availability, fungal pathogen abundance (LaManna *et al.* 2016, Castaño *et al.* 2019), and competitive interactions between saprotrophic and ectomycorrhizal fungi (Gadgil & Gadgil 1971, Averill *et al.* 2014). Considering that temperate forests are predicted to become more AM-dominant due to tree species' range shifts under global change (Jo *et al.* 2019; Steidinger *et al.* 2019), these forests may shift to more pathogen-dominant systems if their microbial communities change predictably according to mycorrhizal dominance. However, the mycorrhizal spillover effects on microbial communities also must be placed in the context of variation in abiotic conditions and the various fungal habitats present in terrestrial ecosystems.

Soil, roots, and leaves represent unique environments that serve as habitats for distinct microbiomes (Turner *et al.* 2013) where microorganisms compete for different resources (Hassani *et al*. 2018). For example, fungal communities are known to shift in composition in response to leaf litter versus root sources of carbon (Fu *et al.* 2017). Interactions between soil, roots, and leaf litter are integral to the MANE framework (Phillips *et al.* 2013), but it is

reasonable to expect that fungal communities associated with these compartments will respond to changes in mycorrhizal dominance to different degrees. For example, root-associated fungal communities may be better explained by shifts in mycorrhizal dominance compared to soil-associated fungal communities due to roots being the site of mycorrhiza formation. To our knowledge, no study to date has examined distribution patterns of fungal communities and their function in these compartments simultaneously in the context of dominant mycorrhizal associations. Additionally, the functional groups of fungi most affected by mycorrhizal dominance can make up the majority of fungal relative abundances in a community (Bahram *et al.* 2020, Eagar *et al.* 2022), but it is unclear which taxonomic groups, if any, are more responsive to dominant mycorrhizal spillover effects.

Similar to plants, fungal distribution patterns are frequently controlled by climatic factors, such as mean annual precipitation and temperature (Tedersoo *et al.* 2014). However, several studies have documented that dominant tree community mycorrhizal associations can explain more variation in fungal community composition than soil characteristics, such as moisture, soil organic matter (SOM) content, or pH (Bahram *et al.* 2020; Eagar *et al.* 2022). Additionally, while the effect of small-scale climate variation due to topography has been extensively studied for aboveground vegetation, much less has been explored regarding microbial communities (Geml 2019). It is therefore possible that the effects of climate on fungal community composition, driven by both regional and topographic differences in temperature and precipitation, will completely mask or affect the strength of dominant mycorrhizal influences. Thus, studying how climatic and mycorrhizal gradients interact to influence fungal community composition is critical to our understanding of global change outcomes.

Our work presented here had three goals. First, we explored how changes in moisture and temperature along an environmental gradient and between slope aspects interact with tree mycorrhizal associations to change the strength or direction of mycorrhizal spillover effects on fungal community composition in several areas of the Adirondack Mountains, USA. If mycorrhizal associations have a stronger effect on fungal communities than specific tree species, climatic factors, or edaphic conditions, we should find patterns consistent with previous studies among fungal functional groups and taxa. Second, we tested the relative influence of the mycorrhizal type of single, large individual trees ("focal trees") compared to the influence of the surrounding tree community on fungal communities. Thus, in the case of mismatches between mycorrhizal type dominating the overall tree community and focal tree mycorrhizal type, we directly test the spillover hypothesis. Third, we sampled soil, roots, and senesced leaves to see how these fungal communities change differently in response to mycorrhizal dominance.

MATERIALS AND METHODS

Study site and design

This study utilizes experimental plots established across three forests at the northern end of a temperate ecosystem in the Adirondack (ADK) Park of upstate New York, USA (detailed in Smemo *et al. in prep*). The region includes mostly mixed northern hardwood and conifer forest ecosystems and exhibits distinct climatic gradients illustrated by the increase in average annual precipitation and decrease in average annual temperature from the southeast to the northwest (Smemo *et al. in prep*; Appendix A: Figure 13). Soils in our study sites are primarily spodosols (haplorthods) with some less developed inceptisols (dystrochrepts) in the southeastern sites. Overall species richness is low in the ADK region and AM species in our study plots are primarily *Acer saccharum* (sugar maple), *Acer rubrum* (red maple), and *Fraxinus americana*

(white ash). Deciduous ECM species are dominated by *Fagus grandifolia* (American beech), *Betula alleghaniensis* (yellow birch), and *Quercus rubra* (red oak; southeast only). Coniferous ECM species present include *Pinus strobus* (eastern white pine), *Tsuga canadensis* (eastern hemlock), and *Picea rubens* (red spruce).

Twenty-four 15 m radius plots were established in each of three locations: Lake George Wild Forest (43.661, -73.545), Huntington Wildlife Forest (43.987, -74.245), and Shingle Shanty Preserve (43.894, -74.732). Within each site, 12 plots were established on north-facing slopes and 12 on south-facing slopes. Plots were located so that six plots on each aspect included a mature AM focal tree as the plot center, and six included a mature ECM focal tree. Surrounding trees within each plot were also identified and those with a diameter at breast height > 2cm were measured for calculation of basal area (BA; Appendix A). Species mycorrhizal associations were made based on a thorough review of existing literature (Brundrett 2009, Maherali *et al.* 2016, Soudzilovskaia *et al.* 2020). Overall, surrounding tree community composition ranged from 22.3% ECM BA (77.7% AM BA) to 96.3% ECM BA (3.7% AM BA). This study design resulted in n = 72 plots distributed equally across the gradient and balanced among focal tree mycorrhizal type and slope aspect. Further details regarding our field sites can be found in Smemo *et al.* (*in prep*).

Field sampling

All samples were collected between June 24th and June 27th, 2017. In close proximity to the focal tree (within 3 m) in each of our 72 plots, we sampled soil to a depth of 15 cm using a 2.5 cm metal soil probe in 3 separate locations, combining to create one composite sample. All PVC cores were cleaned with 70% EtOH and allowed to dry between samples. At each core location we also collected composite leaf litter samples using gloves sterilized with 70% EtOH.

All samples were transported to the lab in coolers on ice and kept at 4° C until processing. All composite soil samples were passed through a 2 mm mesh sieve to separate roots from soil. Roots were not washed in order to retain any soil or other particulates directly associated with root tissue. All sample types were then stored at -80° C.

Plot and soil variables measured around each focal tree included: rarefied tree species richness and evenness (Hill's ${}^{0}D$ and ${}^{2}D$, the inverse Simpson index, respectively; Chao *et al.* 2014), forest floor mass (dry g/m^2), fine root biomass (dry kg/m^3), total C & N (μg/dry g soil), percent C & N, soil C:N ratio, pH, soil respiration (μmol CO_2/m^2/s), NH_4^+ and NO_3^- concentrations (μg/dry g soil), and net nitrification and N mineralization rates (μg/dry g soil per day). Specific methods pertaining to each variable measured can be found in Appendix A and are reported in Smemo *et al.* (*in prep*).

DNA extraction and ITS region amplification

DNA from soil samples was extracted using Qiagen DNeasy PowerSoil kits (Qiagen, Hilden, Germany) following the manufacturer's instructions. DNA from root and leaf samples was obtained via standard CTAB extraction with β-mercaptoethanol in which equivalent amounts of tissue for each sample type was pulverized by genogrinding with sterilized grinding beads following the protocol detailed in Wu *et al.* (2011). Polymerase chain reaction (PCR) amplification was performed targeting the internal transcribed spacer (ITS) 1 and 2 regions. We used a 100 μM mixture of ITS3ngs1-3 and ITS3ngs4-5 as forward primers paired with the ITS4ngsUni reverse primer (Tedersoo and Lindahl, 2016), with an annealing temp of 55° C. The cycle number (between 28 – 35 cycles) and genomic DNA dilution factor (1:20 or 1:100) varied among samples and sample types to achieve uniform band intensity on an agarose gel. For each reaction, a control blank was included to account for contamination (Tedersoo *et al.* 2021).

Approximately 90 ul of amplified PCR product per sample was pooled and purified using Agencourt AMPure XP magnetic beads (Agencourt Bioscience Corporation, Beverly, MA). All purified fungal amplicons were barcoded through PCR using Nextera® XT DNA Library Preparation Kits (Illumina, California, USA), purified again with Agencourt AMPure XP magnetic beads, diluted to an equal concentration, and pooled following standard Illumina protocol. Pooled, barcoded samples were then submitted for 2x300 bp MiSeq Illumina sequencing at the Ohio State University's Molecular and Cellular Imaging Center (Wooster, OH, USA).

Bioinformatics

Sequences were demultiplexed by the sequencing facility and all other bioinformatics were conducted in QIIME 2 ver. 2019.7 (Bolyen et al. 2019). Primer sequences were removed using cutadapt (Martin 2011). Forward and reverse sequence reads were quality filtered, paired ends were joined, chimeric sequences were removed, and joined sequences were grouped into amplicon sequence variants (ASVs) using DADA2 (Callahan *et al*. 2016). ASVs were then assigned taxonomy using the Unite database ver. 18.11.2018 (UNITE community 2019) using a naive Bayesian classifier (Bokulich *et al*. 2018). Once taxonomy was assigned, functional group (i.e., "guild") classifications were made using FUNGuild ver. 1.1 (Nguyen *et al*. 2016). Unresolved guild assignments (i.e., those with multiple functional roles or unknown classifications) were corrected, when possible, through an extensive literature search. Fungal taxa that remained unresolved were classified as "various" (multiple functional assignments) or "unknown" (where information is not available) and were excluded from the analysis of specific functional groups of interest. Biotrophic and necrotrophic taxa were combined for analyses into a

single group – plant pathogens – based on previous findings of similar trends related to mycorrhizal dominance between both groups (Eagar *et al.* 2022).

Data analysis

All analyses were conducted in R 4.1.1 (R Core Team 2021). Sequence data were rarefied to 1327 sequences per sample prior to analysis using the *vegan* package (Oksanen *et al.* 2013). To examine the fungal community composition of each substrate type, rarefied data were Hellinger transformed and redundancy analyses (Borcard *et al.* 2011) were conducted at three levels: ASV, Family, and Guild. Site, plot aspect, focal tree mycorrhizal type (FTMT), and plot % ECM BA were used as explanatory variables. All three-way interactions, in addition to pairwise interactions and individual terms, were tested. To partition explainable variation (Adjusted R^2 values) of each modeled variable on fungal community composition consistent with our study goals (Peres-Neto *et al.* 2006), we used a series of condition() statements in *vegan's* rda() function. The goodness() command was used to assess the amount of variance explained in each fungal group by the redundancy analysis models (Oksanen *et al.* 2013). To determine the effect of tree species identity that is unrelated to tree species' mycorrhizal association, a second redundancy analysis with focal tree species (FTS) included as the main effect and FTMT included as a conditional term was used. Forward selection of soil variables (e.g., soil pH, % soil C, etc.) was also conducted through *vegan's* ordir2step() function (Oksanen *et al.* 2013) to assess their effects on fungal community composition.

Linear mixed effect models were used to evaluate location-based and mycorrhizal-based effects on fungal ASV richness (Hill's ${}^{0}D$; Chao *et al.* 2014) and the relative abundances of saprotrophic fungi, ectomycorrhizal fungi, and fungal plant pathogens. Relative abundance values were analyzed with logistic regression using a binomial error distribution. We tested two

separate models and a third, combined model using AIC scores for model comparison (Burnham & Anderson 2004) with the R packages *lme4* (Bates *et al.* 2014) and *lmerTest* (Kuznetsova *et al.* 2017). Adjusted R^2 values were obtained with the R package *MuMIn* (Bartoń *et al.* 2009). Model 1 was a location-based model testing the effects of site location (capturing our climate gradient), aspect, and a site x aspect interaction. Model 2 was a mycorrhizal-based model that included plot % ECM BA, FTMT, and a % ECM BA x FTMT interaction. The combined model (model 3) included all terms and possible two- and three-way interactions from both model 1 and model 2 to test for interactions between location-based and mycorrhizal-based effects. In all three models, the species identity of plot focal trees was included as a random effect.

Fungal families acting as potential drivers of the observed trends in functional group relative abundances were identified via comparison to the redundancy analyses described above. Families with an adjusted R^2 value > 10% in the model inclusive of all three sites (Tables 1 – 3) and an adjusted R^2 value > 15% in the model for each individual site (Appendices B – D: Tables 6 – 8) are reported. Similar to our community composition analyses, variation among explanatory variables was partitioned. We did this by subtracting the variation associated with models missing or inclusive of specific terms from the total variation explained by the complete model. For example, to obtain variation attributable to interaction terms and overlap between variables, the variation explained by four models containing singular terms (site, aspect, % ECM BA, and FTMT) was subtracted from the variation explained by the entire model containing individual terms, two-way interactions, and three-way interactions.

RESULTS

Fungal richness

For overall fungal ASV richness, the model including both geographic and mycorrhizal terms (model 3) was consistently selected through AIC comparison (Appendix A: Table 8). Overall, the amount of variation in ASV richness explained by the combined mycorrhizal + geographic model was similar for soil, root, and leaf fungal communities (45 – 60%), although the variance explained by each modeled term differed substantially depending on sample type (Figure 4a). When compared to one another, root samples demonstrated the lowest fungal ASV richness among all three sample types while soil and leaf litter sample fungal ASV richness were comparable (Figure 5). However, there were no significant terms identified in model 3 for root fungal ASV richness (all $P > 0.1$; Appendix A: Table 8). Aspect and an aspect x % ECM BA interaction were significant terms for both soil and leaf litter fungal ASV richness ($P \leq 0.06$), while focal tree mycorrhizal type was also a significant term for soil fungal ASV richness ($P = 0.03$; Appendix A: Table 8).

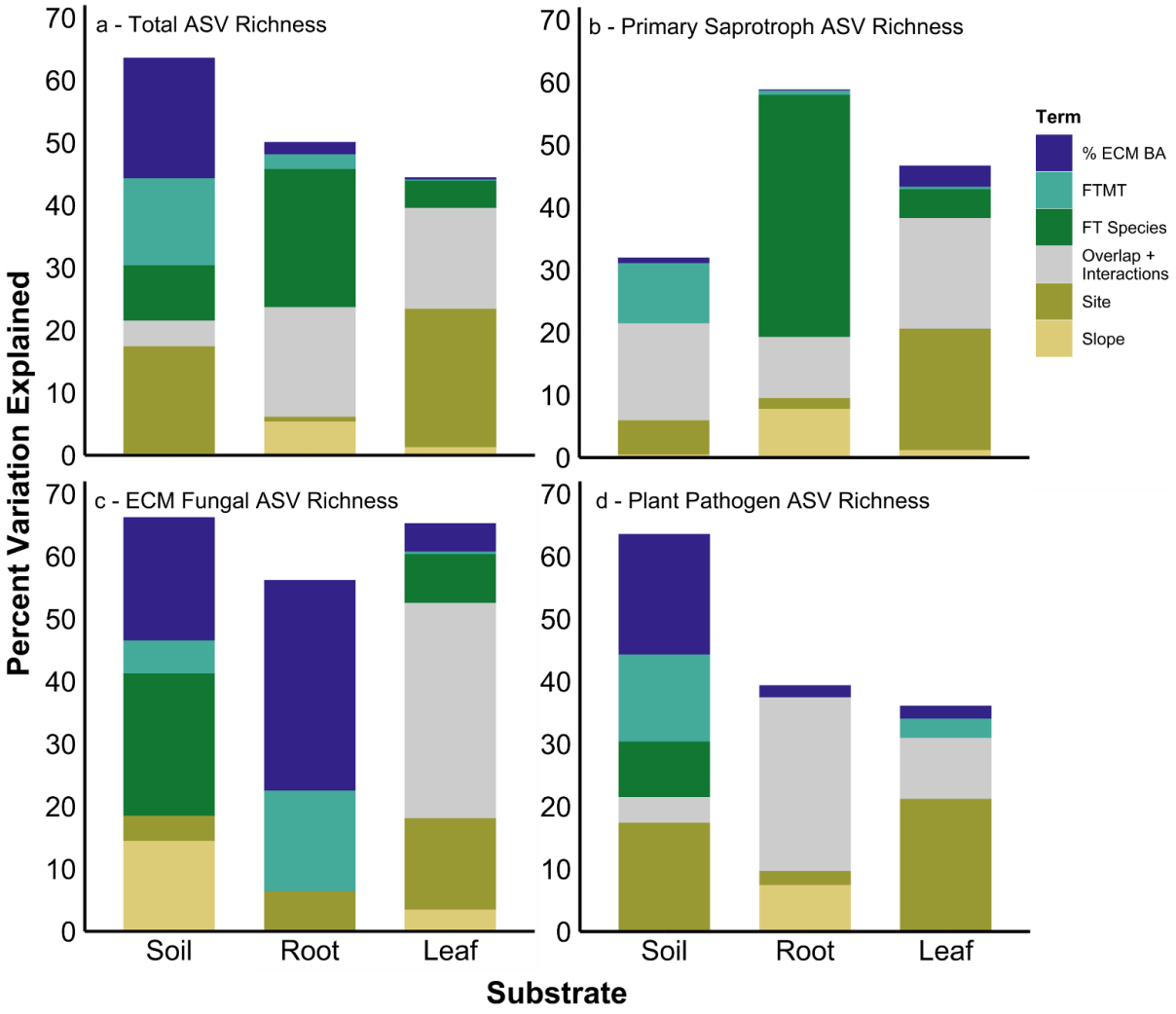

Figure 4. Variance partitioning (Adj. R^2) of a) overall fungal diversity and b – d) specific functional groups of fungi. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type; FT Species = plot focal tree species.

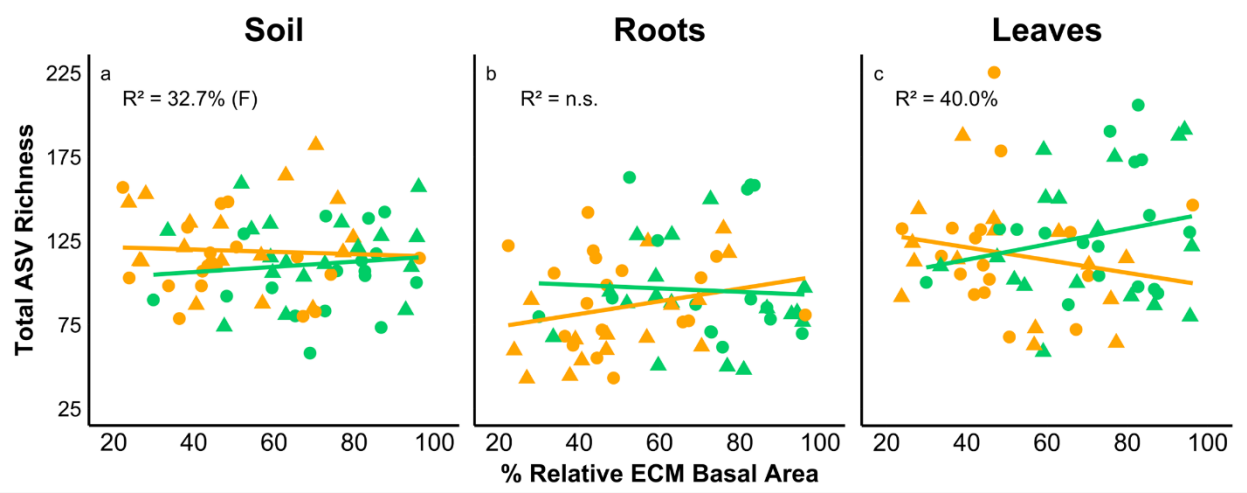

Figure 5. Total ASV richness reported for soil, root, and leaf litter samples. Colors correspond to plot focal tree mycorrhizal type (gold = AM focal trees, green = ECM focal trees), shapes correspond to slope aspect (circles = northern-facing slopes, triangles = southern-facing slopes), and R^2 values correspond to the most parsimonious model selected through AIC comparison (combined model 3 in all cases). Trend lines are displayed for visualization purposes and do not indicate significance. (F), (G), and (X) after an R^2 value denote significant model terms focal tree mycorrhizal type, % ECM BA (gradient), and the interaction between the two, respectively. Supporting data for significant model terms can be found in Appendix A: Table 8.

Among the functional groups of interest (primary saprotrophs, ectomycorrhizal fungi, and plant pathogens), the drivers of ASV richness also varied in magnitude among sample types (Figure 4b – d). Primary saprotroph ASV richness (Figure 4b) in soil was the least well-explained among all functional group + sample type combinations. In roots, focal tree species explained two-thirds of the total variation in saprotroph richness. Notably, saprotroph richness did not decrease with increasing % ECM BA as seen in previous studies and leaf-associated saprotroph richness increased with increasing % ECM BA in plots with ECM focal trees (Figure 6a – c). Ectomycorrhizal fungal ASV richness demonstrated the largest amount of explainable variation among the studied functional groups, with % ECM BA explaining a large portion of this variation in all three sample types (Figure 7c). In soil and root samples, ectomycorrhizal fungal ASV richness increased with increasing % ECM BA surrounding both AM and ECM focal trees, while also being higher in plots with ECM focal trees (Figure 6d & e). The variation in plant pathogen ASV richness in soil was best explained by mycorrhizal factors, but in roots and leaves site or interactions were more important (Figure 7d). Additionally, plant pathogen richness was the lowest of the three groups by a wide margin and trends with respect to tree mycorrhizal types were opposite of the trends in ECM fungal richness (Figure 6g – i). Supporting data (P-values, AIC scores) can be found in Appendix B Table 13 (soil samples), Appendix C Table 21 (root samples), and Appendix D Table 29 (leaf litter samples).

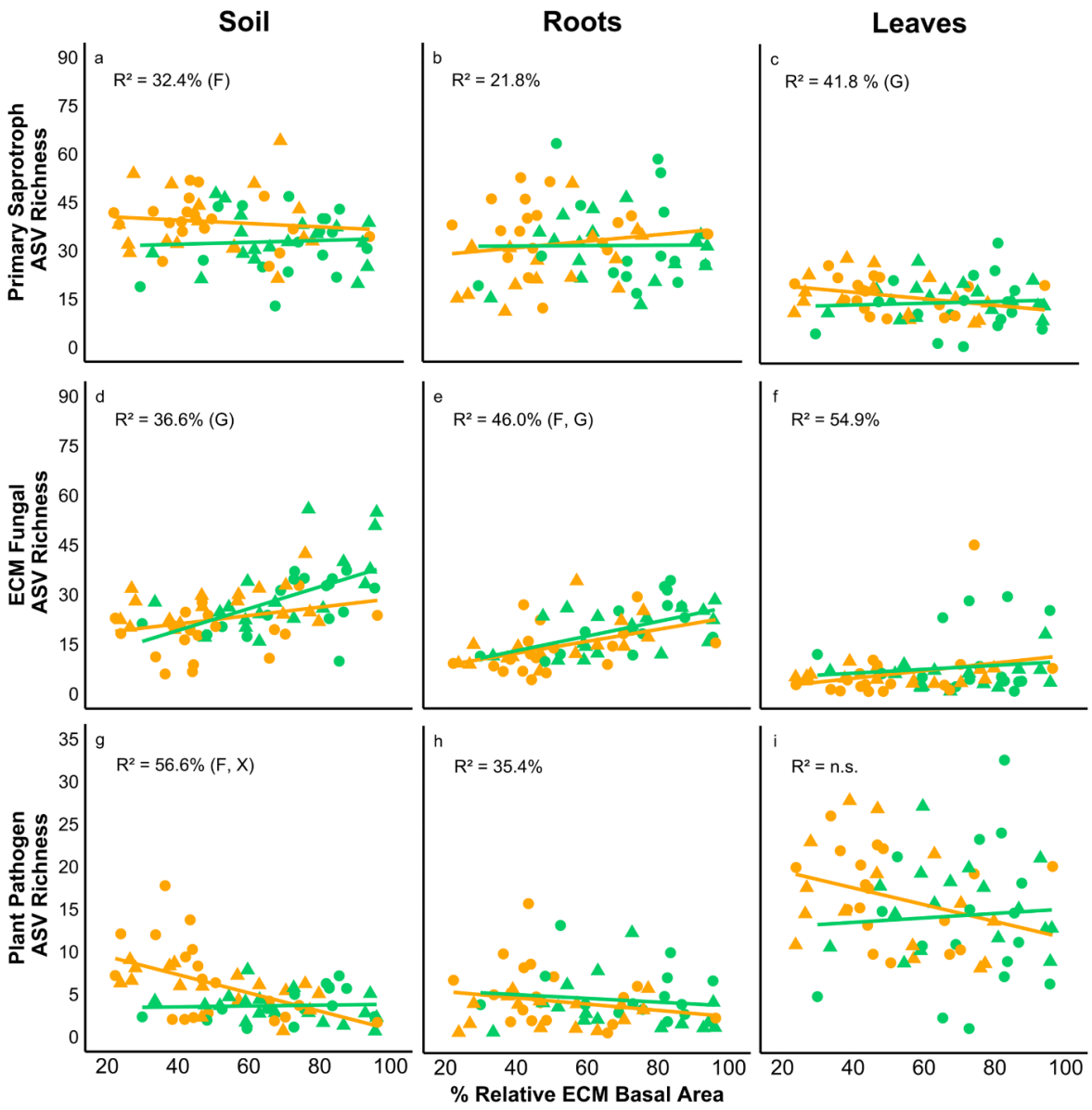

Figure 6. Fungal functional group ASV richness reported for soil, root, and leaf litter samples. Colors correspond to plot focal tree mycorrhizal type (gold = AM focal trees, green = ECM focal trees), shapes correspond to slope aspect (circles = northern-facing slopes, triangles = southern-facing slopes), and R^2 values correspond to the most parsimonious model selected through AIC comparison (combined model 3 in all cases). Trend lines are displayed for visualization purposes and do not indicate significance. (F), (G), and (X) after an R^2 value denote

significant model terms focal tree mycorrhizal type, % ECM BA (gradient), and the interaction between the two, respectively. Supporting data for significant model terms can be found in Appendices B – D.

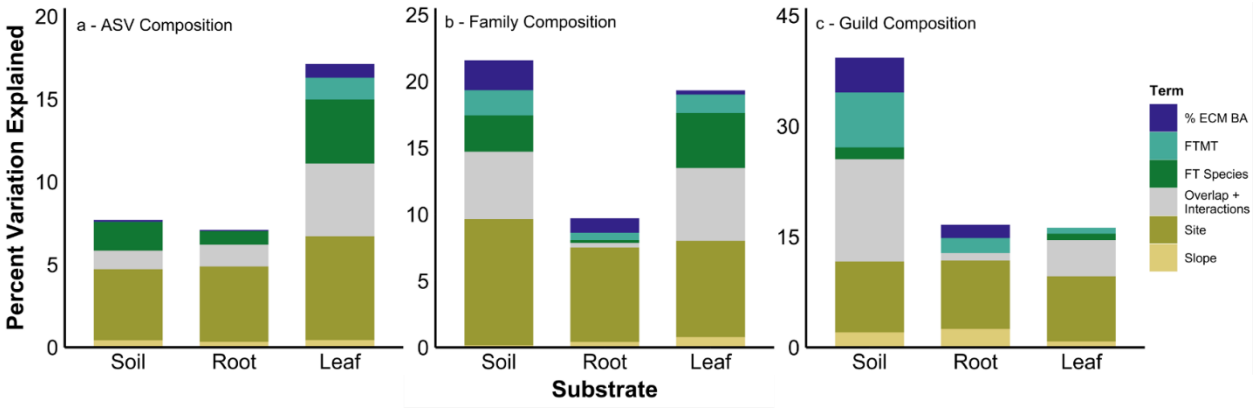

Figure 7. Variance partitioning (Adj. R^2) of fungal community composition. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type; FT Species = plot focal tree species.

Fungal community composition

After rarefaction, sequences were grouped into 9864 unique ASVs and assigned to 1449 different taxonomic groups. Site was consistently identified as a driver of community composition for all sample types (P = 0.001; Figure 7), while the remaining terms and two-way interactions varied in significance depending on taxonomic level/guild and sample type (Appendix A: Table 9). In soil and root samples, mycorrhizal effects (both % ECM BA and focal tree mycorrhizal type) explained a significant portion of community variation at the Family level, but was not significant at the ASV level (Figure 7a & b). However, mycorrhizal effects in soil and root habitats were strongest for guild composition (Figure 7c). The reverse was true in senesced leaves, where mycorrhizal effects were strongest at the ASV level. Variation explained in the composition of fungal guilds was greatest in soil-associated communities (40%), where mycorrhizal effects explained as much variation as geographic effects (Figure 7c). Focal tree species identity was also consistently significant (in all cases except guild composition in senesced leaves), and was particularly important for ASV and Family composition (Figure 7a – c, Appendix A: Table 9). When sites were analyzed separately, however, the importance of focal tree species identity varied substantially across sample types and sites, with some site and sample combinations demonstrating no effect of focal tree species on fungal community composition and others demonstrating large effects (Appendices B – D).

Soil physiochemical properties identified as significant drivers of fungal community composition by the RDA with forward selection consistently explained less variation than the RDA that included the mycorrhizal and geographic terms (Appendix A: Table 10; Figure 7a – c). The soil properties selected varied between ASV, Family, and Guild analyses, and between sample types. Soil pH and C:N ratio were selected the most often out of all variables (Appendix

A: Table 10). Additionally, results of the forward selection process differed among sites, with few terms being identified as significant drivers of local fungal community composition (Appendices B – D).

Fungal functional group relative abundances

Similar to fungal ASV richness, our combined model 3, including both geographic and tree community terms, consistently resulted in the lowest AIC score for all functional groups and sample types (Appendices B – D). For each sample type we report general relative abundance changes for fungal functional groups, as well as the families likely responsible for these trends in the main text. Site was identified as a significant variable in all analyses ($P < 0.001$), and detailed results for analysis of each site separately are shown in Appendices B – D. Across our climate gradient, we observed the strongest patterns between mycorrhizal spillover effects and fungal community relative abundances at our drier, warmer site (Lake George Wild Forest) and the weakest patterns at our cooler, wetter site (Shingle Shanty Preserve) (Appendices B – D).

Primary saprotroph relative abundances were similar in each sample type and demonstrated no notable trends with % ECM BA (Figure 8a – c). However, the families Geoglossaceae (Ascomycota), Hypocreales (Ascomycota), Clavariaceae (Basidiomycota), and saprotrophic members of Entolomataceae (Basidiomycota) demonstrated shifts in relative abundance dependent on aspect or mycorrhizal factors (Tables 5 – 7).

In soil and root samples, the relative abundance of ectomycorrhizal fungi was positively correlated with % ECM BA, and was also greater surrounding ECM focal trees. The Russulaceae (Basidiomycota) were associated with this trend in both soil and roots. Several other ectomycorrhizal families were also consistent with this pattern in soil (Amanitaceae, Boletaceae,

Cortinariaceae; Table 5) and roots (Gloniaceae, Sebacinaceae, Suillaceae; Table 6). South-facing slopes also had generally higher ectomycorrhizal fungal relative abundances (Figure 8d & e), with the Boletaceae (Basidiomycota) associated with this pattern. In contrast, there were no prominent trends in leaf-associated ectomycorrhizal fungal relative abundances correlated with % ECM BA or focal tree mycorrhizal type (Figure 8f). Also as expected, the AM fungal family Glomeraceae declined in relative abundance due to both % ECM BA and surrounding ECM focal trees, although this group was very low in abundance as is typical in broad fungal surveys.

In all three habitat types, plant pathogen relative abundance displayed a negative correlation with increasing % ECM BA, but only surrounding AM focal trees (Figure 8g – i). Plant pathogen relative abundance was uniformly low surrounding ECM focal trees. In soil and root samples, the Herpotrichiellaceae (Ascomycota) and Hygrophoraceae (Basidiomycota) were identified as potential drivers of these patterns, although both families are known to contain some taxa that are not plant pathogens (Tables 5 & 6). In leaf samples, three different families were associated with these patterns: the Dothideaceae, Cryphonectriaceae, and Teratosphaeriaceae (Ascomycota; Table 7).

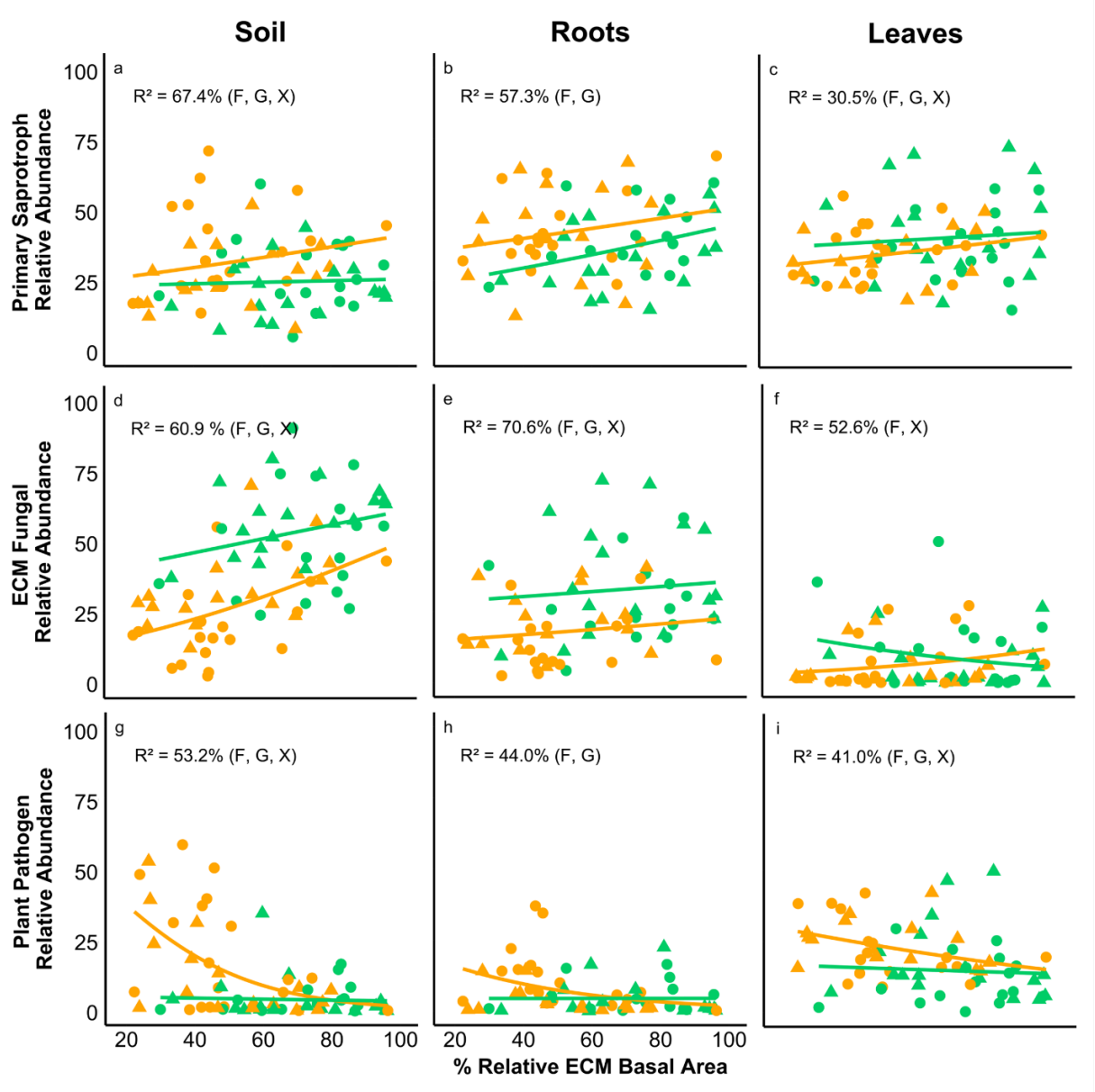

Figure 8. Relative abundance changes among functional groups of fungi along a gradient of mycorrhizal dominance for soil, root, and leaf litter samples. Relative abundance values are displayed as percentages (0 – 100%). Colors correspond to plot focal tree mycorrhizal type (gold = AM focal trees, green = ECM focal trees), shapes correspond to slope aspect (circles = northern-facing slopes, triangles = southern-facing slopes), and R^2 values correspond to the most parsimonious model selected through AIC comparison (combined model 3 in all cases). Trend lines are displayed for visualization purposes and do

not indicate significance. (F), (G), and (X) after an R^2 value denote significant model terms focal tree mycorrhizal type, % ECM BA (gradient), and the interaction between the two, respectively. Supporting data for significant model terms can be found in Appendices B – D.

Table 5. Soil-associated fungal families with a total adjusted R^2 value > 10% in the RDA modeling that included community data from all three sites. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Soil			Adj. R^2 value %			Relative abundance %			
Phylum	**Family**	**Functional role**	**Total**	**% ECM**	**FTMT**	**AM plot, AM tree**	**AM plot, ECM tree**	**ECM plot, AM tree**	**ECM plot, ECM tree**
Ascomycota	Archaeorhizomycetaceae	Primary saprotroph	10.7	0.4	6.2	0.49 ± 0.77	0.34 ± 0.68	0.59 ± 0.73	0.25 ± 0.47
	Chaetomiaceae	Primary or dung saprotroph	11.0	8.0	8.6	0.2 ± 0.48	0 ± 0	0.03 ± 0.06	0.02 ± 0.08
	Elaphomycetaceae	Primary saprotroph or ectomycorrhizal	10.5	2.7	9.6	0.32 ± 0.92	0.08 ± 0.17	0.02 ± 0.09	0.75 ± 1.32
	Geoglossaceae	Primary saprotroph	13.7	9.9	8.8	2.65 ± 2.67	0.21 ± 0.36	1.6 ± 3.58	1.15 ± 2.35
	Herpotrichiellaceae	Endophyte, primary saprotroph, animal pathogen, plant necrotroph, or unknown	16.2	12.3	12.0	2.28 ± 1.44	1.88 ± 2.46	1.68 ± 1.02	1.19 ± 1.12
	Melanommataceae	Wood saprotroph	14.5	6.2	8.7	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.07
	Mycosphaerellaceae	Plant necrotroph, lichen, or various	11.9	0.4	5.4	0.02 ± 0.06	0 ± 0	0.01 ± 0.03	0 ± 0
Basidiomycota	Amanitaceae	Ectomycorrhizal	18.4	14.3	1.9	1.17 ± 2.06	0.74 ± 1.27	6.81 ± 8.52	4.35 ± 4.93
	Boletaceae	Ectomycorrhizal	13.9	4.3	0.0	0.43 ± 0.94	0.43 ± 0.03	1.44 ± 0.95	0.89 ± 1.34
	Clavariaceae	Primary saprotroph or various	11.8	5.9	9.6	7.36 ± 7.58	6.47 ± 9.93	8.76 ± 14.07	3.34 ± 9.04
	Cortinariaceae	Ectomycorrhizal	11.8	1.0	10.5	2.23 ± 2.75	22.1 ± 26.51	2.07 ± 3.32	5.91 ± 10.47
	Cyphellaceae	Primary saprotroph	15.3	8.4	5.7	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.06
	Entolomataceae	Primary saprotroph, ectomycorrhizal, or various	32.9	20.8	12.7	2.54 ± 3.11	3.85 ± 7.36	2.34 ± 2.69	0.84 ± 2.13
	Hydnodontaceae	Primary saprotroph	10.7	0.0	7.3	1.78 ± 4.27	0.11 ± 0.16	1.25 ± 1.74	0.3 ± 0.48
	Hygrophoraceae	Ectomycorrhizal, plant biotroph	32.6	28.2	20.3	25.21 ± 19.2	5.83 ± 4.81	6.43 ± 8.64	4.88 ± 11.53
	Russulaceae	Ectomycorrhizal	21.8	17.2	15.3	6.26 ± 5.59	20.47 ± 14.3	16.17 ± 11.1	19.6 ± 13.43
	Sporidiobolaceae	Primary saprotroph	13.1	4.1	0.1	0.04 ± 0.13	0.11 ± 0.21	0 ± 0	0.01 ± 0.03
Glomeromycota	Glomeraceae	Arbuscular mycorrhizal	15.0	12.5	7.3	0.21 ± 0.38	0.13 ± 0.26	0.07 ± 0.11	0.05 ± 0.17

Table 6. Root-associated fungal families with a total adjusted R^2 value > 10% in the RDA modeling that included community data from all three sites. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Roots			Adj. R^2 value %			Relative abundance %			
Phylum	**Family**	**Functional role**	**Total**	**% ECM**	**FTMT**	**AM plot, AM tree**	**AM plot, ECM tree**	**ECM plot, AM tree**	**ECM plot, ECM tree**
Ascomycota	Chaetomiaceae	Primary or dung saprotroph	11.1	9.4	3.7	0.46 ± 1.48	0 ± 0	0.06 ± 0.12	0.07 ± 0.15
	Gloniaceae	Ectomycorrhizal	11.9	8.0	8.7	1.32 ± 2.23	1.79 ± 0.71	2.08 ± 2.58	2.99 ± 3.4
	Herpotrichiellaceae	Endophyte, primary saprotroph, animal pathogen, plant necrotroph, or unknown	17.8	14.3	10.4	4.68 ± 3.69	4.63 ± 5.01	3.09 ± 1.79	2.11 ± 1.82
	Orbiliaceae	Primary or wood saprotroph	13.2	4.9	1.5	0 ± 0	0 ± 0	0.01 ± 0.02	0 ± 0
	Pleomassariaceae	Primary saprotroph or various	10.1	5.2	1.2	0.2 ± 0.8	0 ± 0	0 ± 0	0.02 ± 0.06
	Tuberaceae	Ectomycorrhizal	14.6	7.4	4.9	0.07 ± 0.24	0 ± 0	0 ± 0	0.2 ± 0.48
Basidiomycota	Clavariaceae	Primary saprotroph or various	10.5	0.9	9.9	2.37 ± 2.45	0.95 ± 1.1	4.86 ± 9.06	1.1 ± 2.23
	Crepidotaceae	Wood saprotroph	10.2	0.4	0.9	0.02 ± 0.1	0.07 ± 0.13	0 ± 0	0.01 ± 0.03
	Entolomataceae	Primary saprotroph, ectomycorrhizal, or various	14.6	10.7	7.8	1.59 ± 3.57	0.65 ± 1.03	0.93 ± 1.22	0.53 ± 1.31
	Hydnangiaceae	Ectomycorrhizal	17.4	7.3	7.1	0.03 ± 0.12	0 ± 0	0 ± 0	0.08 ± 0.16
	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various	22.7	17.3	14.2	8.96 ± 9.39	1.61 ± 1.92	2.15 ± 3.31	1.57 ± 3.91
	Lycoperdaceae	Primary saprotroph	13.2	4.9	1.5	0 ± 0	0 ± 0	0.01 ± 0.02	0 ± 0
	Malasseziaceae	Animal pathogen	12.2	3.6	1.6	0 ± 0	0.02 ± 0.04	0 ± 0	0 ± 0
	Porotheleaceae	Wood saprotroph	11.2	5.8	3.3	0 ± 0.02	0 ± 0	0 ± 0	0.13 ± 0.5
	Russulaceae	Ectomycorrhizal	15.3	8.1	12.6	4.71 ± 3.82	17.57 ± 13.7	9.89 ± 7.8	11.5 ± 7.98
	Schizoporaceae	Primary or wood saprotroph	13.3	3.6	2.8	0 ± 0	0 ± 0	0.08 ± 0.23	0 ± 0
	Sebacinaceae	Ectomycorrhizal	11.7	11.4	1.4	0.69 ± 0.89	0.82 ± 1.63	1.45 ± 2.21	1.46 ± 1.67
	Suillaceae	Ectomycorrhizal	10.0	4.6	4.0	0 ± 0	0 ± 0	0 ± 0	0.13 ± 0.53

Table 7. Leaf-associated fungal families with a total adjusted R^2 value > 10% in the RDA modeling that included community data from all three sites. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown. Taxa within the Hypocreales (inc. sed.) included Barbatosphaeria, Brachysporium, Ciliciopodium, and Cylindrium. Taxa within the Saccharomycetales (inc. sed.) included Candida, Myxozyma, and Nadsonia. Taxa within the Cantharellales (inc. sed.) included Minimedusa, Multiclavula, and Sistotrema.

Leaves			**Adj. R^2 value %**			**Relative abundance %**			
Phylum	**Family**	**Functional role**	**Total**	**% ECM**	**FTMT**	**AM plot, AM tree**	**AM plot, ECM tree**	**ECM plot, AM tree**	**ECM plot, ECM tree**
Ascomycota	Chaetomellaceae	Primary saprotroph, plant necrotroph, or unknown	12.9	12.8	4.4	1.09 ± 2	0.22 ± 0.45	0.2 ± 0.34	0.33 ± 1.12
	Chaetomiaceae	Primary or dung saprotroph	10.2	2.1	2.9	0 ± 0	0.05 ± 0.09	0 ± 0	0 ± 0.02
	Cryphonectriaceae	Plant biotroph	20.7	17.1	13.6	2.51 ± 4.65	0.27 ± 0.26	1.22 ± 3.53	0.17 ± 0.53
	Didymellaceae	Necrotroph or various	11.5	3.0	1.8	0.21 ± 0.73	0.28 ± 0.49	0.08 ± 0.15	0.26 ± 0.54
	Dothideaceae	Primary saprotroph, plant necrotroph, or various	10.9	1.8	3.8	0.19 ± 0.26	0.03 ± 0.05	0.2 ± 0.32	0.1 ± 0.15
	Hypocreales (inc. sed.)	Primary saprotroph	17.1	4.3	16.9	6.35 ± 4.23	1.88 ± 1.76	8.46 ± 9.75	2.69 ± 2.39
	Lasiosphaeriaceae	Primary or dung saprotroph	15.3	9.4	9.6	0.01 ± 0.06	0.1 ± 0.19	0 ± 0	0.4 ± 1.14
	Micropeltidaceae	Lichen	13.9	2.6	9.9	0.03 ± 0.05	0.02 ± 0.05	0.04 ± 0.08	0 ± 0
	Mytilinidiaceae	Primary or wood saprotroph	14.2	0.0	10.6	0.11 ± 0.48	1.91 ± 3.83	0.02 ± 0.09	0.76 ± 2.41
	Pezizaceae	Primary saprotroph, ectomycorrhizal, or various	14.8	11.7	5.4	0.03 ± 0.1	0 ± 0	0.16 ± 0.46	0.21 ± 0.38
	Phaeosphaeriaceae	Primary saprotroph, plant necrotroph, or various	12.1	11.4	5.9	0.01 ± 0.05	0.03 ± 0.06	0.08 ± 0.23	0.22 ± 0.54

	Pseudeurotiaceae	Primary saprotroph, animal pathogen, or various	26.9	24.7	9.3	1.24 ± 1.32	0.44 ± 0.51	0.21 ± 0.55	0.22 ± 0.37
	Saccharomycetales (inc. sed.)	Primary saprotroph	12.7	7.2	8.3	0 ± 0	0.12 ± 0.25	0.01 ± 0.03	0.34 ± 0.94
	Schizoparmaceae	Unknown	12.6	7.4	9.4	0.47 ± 0.91	0 ± 0	0.05 ± 0.17	0.05 ± 0.26
	Septorioideaceae	Endophyte	10.2	4.8	4.3	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.05
	Sporocadaceae	Plant necrotroph	10.1	4.3	2.7	0.35 ± 0.59	0.48 ± 0.66	0.91 ± 1.22	1.12 ± 1.7
	Sympoventuriaceae	Primary saprotroph	21.0	4.5	5.0	0.36 ± 0.72	0.2 ± 0.4	0.25 ± 0.58	0.52 ± 0.52
	Teratosphaeriaceae	Primary saprotroph, plant necrotroph, various, or unknown	16.5	14.8	6.1	0.46 ± 0.52	0.18 ± 0.3	0.25 ± 0.45	0.18 ± 0.26
	Tuberaceae	Ectomycorrhizal	10.3	0.0	4.4	0 ± 0.02	3.36 ± 6.71	0 ± 0	0.13 ± 0.44
	Xylariaceae	Primary saprotroph	10.6	0.1	4.2	0 ± 0	0.07 ± 0.15	0 ± 0	0.05 ± 0.21
Basidiomycota	Cantharellales (inc. sed.)	Ectomycorrhizal or lichen	11.2	0.3	0.2	2.34 ± 6.12	3.05 ± 6.1	0.71 ± 1.42	1.41 ± 5.37
	Ceratobasidiaceae	Plant necrotroph	11.9	0.2	5.9	0.61 ± 0.98	0.56 ± 0.81	0.27 ± 0.69	1.39 ± 3.53
	Clavulinaceae	Ectomycorrhizal or various	14.6	2.4	14.4	0.79 ± 0.95	0.03 ± 0.05	3.56 ± 6.61	0.37 ± 1.42
	Cortinariaceae	Primary saprotroph or ectomycorrhizal	13.3	5.0	0.7	0.26 ± 0.89	0.02 ± 0.04	0.88 ± 2.06	0.24 ± 0.63
	Ganodermataceae	Wood saprotroph or various	10.8	4.3	0.2	0 ± 0	0 ± 0	0.02 ± 0.07	0 ± 0.02
	Hydnangiaceae	Ectomycorrhizal	14.4	12.9	1.2	0 ± 0.02	0 ± 0	0.04 ± 0.12	0.07 ± 0.24
	Hymenochaetaceae	Primary saprotroph, ectomycorrhizal, or plant necrotroph	12.6	4.5	1.6	0 ± 0	0 ± 0	0.08 ± 0.31	0 ± 0
	Pseudomicrostroma (Microstromatales inc. sed.)	Unknown	10.6	5.9	0.0	0 ± 0	0 ± 0	0.02 ± 0.08	0.01 ± 0.05
	Mycenaceae	Various	10.2	2.8	8.0	1.09 ± 3.23	0 ± 0	3.47 ± 10.53	0 ± 0
	Porotheleaceae	Wood saprotroph	10.8	6.0	4.1	0 ± 0	0 ± 0	0 ± 0	0.09 ± 0.31
	Sebacinaceae	Ectomycorrhizal	12.1	7.8	7.3	0.02 ± 0.08	0.02 ± 0.05	0.18 ± 0.66	0.36 ± 0.78
	Trimorphomycetaceae	Fungal parasite	18.3	6.1	0.0	0.03 ± 0.13	0 ± 0	0.1 ± 0.25	0.08 ± 0.21
Zygomycota	Mortierellaceae	Primary saprotroph	12.0	1.4	0.0	1.27 ± 1.95	2.59 ± 2.16	2.66 ± 4.19	1.48 ± 2.09

DISCUSSION

Extending the MANE framework to microbial communities represents a convenient way to generalize traits that drive plant-soil feedback outcomes under different environmental conditions in temperate hardwood forests (Bennett *et al.* 2017, Netherway *et al.* 2021). We tested the hypothesis that fungal communities change in relation to dominant tree mycorrhizal associations and that the strength of these interactions varies based on environmental context. In support of this, we demonstrate that increasing ECM tree dominance results in lower plant pathogen species richness and relative abundance, similar to Bahram *et al.* (2020) and Eagar *et al.* (2022), and confirm that mycorrhizal associations are better predictors of fungal community composition and function than soil characteristics or properties (Eagar *et al.* 2022). We also provide evidence of the mycorrhizal spillover effect, where tree community mycorrhizal associations affect the fungal community encountered by an individual tree.

Our findings also show that environmental gradients and geographic context can alter the strength of mycorrhizal influences on fungal communities. Of note, our results indicate that the relationship between ECM dominance and saprotrophic fungi may be especially weak in cooler climates such as the Adirondack Mountains given the absence of negative trends in Figs. 3 and 5. These findings were surprising, considering that competition between ECM and saprotrophic fungi is believed to suppress saprotroph activity through competitive exclusion (Gadgil & Gadgil 1971, Averill *et al.* 2014, Averill & Hawkes 2016, Netherway *et al.* 2021) and the supporting microbial evidence of this provided by Bahram *et al.* (2020) and Eagar *et al.* (2022). Additional work at our Adirondack sites has found that our soils do not reflect MANE-related biogeochemical predictions (Smemo *et al. in prep*), which may be explained by the lack of a relationship between ECM tree dominance and fungal saprotroph richness/relative abundance.

Colder climates slow rates of litter decomposition (Zhang *et al.* 2008), potentially to an extent where the degree of soil organic matter accumulation alleviates competitive interactions between ectomycorrhizal and saprotrophic fungi. This climate-driven suppression of competition may facilitate saprotroph activity despite the presence of ECM trees, leading to similar rates of nutrient cycling between AM and ECM soil contrary to the MANE hypothesis. Thus, our findings suggest that mycorrhizal spillover effects, and potentially the entire MANE framework, may be dependent on environmental factors controlled by regional climate patterns.

We found general support for the spillover hypothesis that dominance of mycorrhizal type in the surrounding tree community affects the local soil microbiome of individual trees. However, the effects of the surrounding tree community on plant pathogens may be particularly important for individual AM trees (Figs. 3 & 5). Plant pathogen richness and relative abundance decreased with ECM-tree dominance surrounding AM focal trees, but was low near all ECM focal trees even when the surrounding community was dominated by AM trees. Both AM and ECM fungi are known to provide defensive benefits to their hosts (Pozo *et al.* 2002, Smith & Read 2008, Kanekar *et al.* 2018), but no study to date has directly compared the defensive benefits conferred by AM vs. ECM fungi. ECM trees may have stronger defenses than AM trees, potentially insulating them from spillover effects from an AM-dominant tree community, and creating localized low-pathogen patches within AM-dominant communities. This suggests that negative feedback experienced by AM trees can be weakened through ECM-dominant spillover effects, but not *vice versa* for positive feedback experienced by ECM trees.

Despite showing that the strength of mycorrhizal spillover effects can vary with climate, in many cases mycorrhizal associations explained as much or more variation in fungal community composition compared to geographic considerations (i.e., site location and plot

aspect) in each of our soil, root, and leaf litter sample types. While dispersal limitation and environmental filtering influences fungal community composition across broad geographic scales (Kivlin *et al.* 2014, Zhang *et al.* 2017), it is apparent that mycorrhizal associations are also strong biotic drivers structuring fungal communities in systems where multiple mycorrhizal types are present. The lack of biogeochemical MANE syndromes in our soils and the small amount of variation explained by soil variables suggests mycorrhizal influences on pathogenic and ectomycorrhizal fungi are primarily driven by biotic interactions rather than abiotic influences or soil biogeochemistry. These observations were consistent between soil, root, and leaf litter samples despite their uniqueness as microbial habitats (Turner *et al.* 2013, Fu *et al.* 2017, Hassani *et al*. 2018).

Interestingly, several fungal families demonstrated strong correlations with tree mycorrhizal associations here in the Adirondacks as well as in midwestern temperate forests in southcentral Indiana, USA (Eagar *et al.* 2022): saprotrophic members of the Clavariaceae, Mortierellaceae, and Entolomataceae, ectomycorrhizal members of the Boletaceae, Cortinariaceae, Entolomataceae, and Russulaceae, plant pathogenic members of the Ceratobasidiaceae, and various functional groups within the Herpotrichiellaceae and Hygrophoraceae. This observation suggests that a handful of fungal families may be responsible for global trends in the relationship between fungal community composition and dominant tree mycorrhizal associations, but more comparisons at consistent taxonomic ranks are needed in future work.

Collectively, our results support the hypothesis that dominant tree community mycorrhizal associations influence the distribution and composition of fungal communities in predictable ways, with increasing dominance of AM trees leading to greater richness and relative

abundance of fungal pathogens. These shifts in fungal community composition appear especially strong surrounding individual AM trees and in warmer, drier environments. Considering that AM trees are predicted to replace ECM trees as species' ranges shift northward due to climate change (Jo *et al.* 2019, Steidinger *et al.* 2019), spillover effects from ECM communities may contribute to AM tree range expansion by lessening top-down pressures from fungal pathogens. Accumulation of fungal pathogens due to shifts towards AM dominance may also contribute to the increases in mortality and younger stand ages observed in forests worldwide (McDowell *et al.* 2020). However, more work linking environmental conditions to mycorrhizal influences on fungal community composition and function is needed to evaluate this unexpected potential contributor to changing forest dynamics. A concerted effort to identify the fungi involved in these community shifts may also yield pertinent information for the management of forested ecosystems under global change.

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CHAPTER IV

DOMINANT COMMUNITY MYCORRHIZAL TYPES INFLUENCE LOCAL SPATIAL STRUCTURE BETWEEN ADULT AND JUVENILE TEMPERATE FOREST COMMUNITIES

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ABSTRACT

Plant-soil feedback (PSF) is known to influence plant community composition, and recent work suggests that these effects may be regulated by traits related to mycorrhizal associations and phylogenetic relationships. However, there is a critical need to test the usefulness of these traits in predicting PSF outcomes in natural plant communities. To test for evidence of mycorrhizal and phylogenetic controls over PSF at both the species and community level, we examined the spatial relationship between adult and juvenile trees in stem-mapped hardwood forest plots using

point pattern analyses and linear mixed-effect models. We found that spatial patterns of adult and juvenile trees, as well as overall adult tree recruitment, was significantly affected by the dominant mycorrhizal type of our forested communities, but was not influenced by the phylogenetic relationship between adult and juvenile trees. Additionally, PSF experienced by individual species was dependent on the mycorrhizal dominance of the surrounding community. Spatial patterns in communities dominated by arbuscular mycorrhizal trees reflected overdispersion between adult and juvenile trees (suggestive of negative PSF), while communities dominated by ectomycorrhizal trees reflected clustering (suggestive of positive PSF). Our findings indicate that PSFs are driven by the mycorrhizal associations of dominant trees, with effects of dominant community member traits on soil microorganisms and biogeochemistry "spilling over" onto less abundant individuals in the community. Our research supports the use of whole-community, mycorrhizal-based frameworks for studying PSF in plant communities where multiple mycorrhizal types are present.

INTRODUCTION

Plant-soil feedback (PSF) is thought to be a key driver of plant population size (Hovatter *et al*. 2013), community diversity (LaManna *et al*. 2016, Teste *et al*. 2017) and ecosystem function (Kulmatiski *et al*. 2012, Lange *et al*. 2015). Negative PSF effects are attributed to the growth of a plant resulting in buildup of plant pathogens that subsequently reduce the growth of conspecific plants grown in the same soil (Packer & Clay 2000, Bever *et al.* 2015). Negative PSF can increase plant diversity by preventing common species from competitively excluding rarer species (Connell 1971, van der Putten *et al*. 1993), increasing fecundity in rare species through compensatory responses (Bradley *et al*. 2008), and increasing plant productivity through the promotion of niche complementarity (Petermann *et al.* 2008, Schnitzer *et al*. 2011). Conversely,

positive PSF can have the opposite effect on plant communities by creating favorable conditions for dominant species, ultimately reducing plant community diversity (Connell & Lowman 1989, Teste *et al*. 2017). These positive PSF effects result from plants creating unique soil conditions that select for their own specific resource acquisition strategies (Wurzburger & Hendrick 2009) or beneficial microbial species (Mangan *et al*. 2010). Since both positive and negative PSF are influenced by plant-microbe interactions, changes in microbial community composition caused by differences in plant functional traits (e.g., root and leaf tissue chemistry) should influence the strength and direction of PSF in a plant community (Wardle *et al*. 1999). However, a convenient framework for summarizing traits associated with the drivers of PSF remains elusive despite the ecological significance of these interactions (van der Putten *et al.* 2016).

Recently, the type of mycorrhizal association engaged in by a plant has been recognized as a potential indicator for a suite of integrated leaf and root traits that influence soil nutrient cycling (Cornelissen *et al*. 2001, Phillips *et al*. 2013), thus providing a predictive framework for soil biogeochemistry and microbial community composition that may also be important for PSF. Ectomycorrhizal (ECM) and ericoid mycorrhizal (ERM) plants typically have recalcitrant leaf litter that decomposes more slowly than the leaf litter of arbuscular mycorrhizal (AM) plants, thereby reducing decomposition rates in communities dominated by ECM and ERM plants (Wurzburger & Hendrick 2009, Averill & Hawkes 2016). Furthermore, some ECM and ERM fungi can directly decompose recalcitrant, senesced tissues and take up organic forms of nutrients, leading to competition with the larger saprotrophic microbial community, reducing rates of soil nutrient mineralization, and lowering soil pH (Gadgil & Gadgil 1971, Read & Perez-Moreno 2003, Averill *et al*. 2014, Tedersoo *et al.* 2020). The different nutrient acquisition strategies and microbial communities associated with AM versus ECM trees suggest that AM-

associating species promote greater growth of non-mycorrhizal saprotrophic fungi, many of which may also be capable of facultative plant pathogen activity (Smith *et al.* 2017, Chen *et al.* 2019, Bahram *et al.* 2020). Because negative PSF is often associated with fungal pathogens (Bagchi *et al.* 2010, Liu *et al.* 2012, Liang *et al.* 2016), it seems likely that AM associations promote a microbial community that is more conducive to development of negative PSF. Indeed, Bennett *et al.* (2017) recently performed greenhouse experiments to measure feedback and observed that AM tree species largely experience negative PSF and ECM species largely experience positive PSF. However, signs of different mycorrhizal-associated PSF effects still need to be investigated in natural, established plant communities.

If the propensity for positive or negative PSF is influenced by mycorrhizal effects on soil biogeochemistry and the microbial community, there is the potential for effects of dominant plant species to "spill over" in natural settings and influence PSF mechanisms across the entire community. More abundant or larger community members have a greater effect on soil microbial communities and biogeochemical cycles than less abundant or smaller community members, as demonstrated by the strong influence of dominant mycorrhizal type (AM or ECM) on soil biogeochemical processes (Phillips *et al*. 2013). Thus, dominant community members may influence the direction and strength of PSF in less common community members. However, few studies have considered aggregated effects of entire plant communities when studying PSF (but see Eppinga *et al*. 2018), and only a handful of studies have explicitly considered species' mycorrhizal types as a primary driver of PSF processes within entire plant communities (Johnson *et al.* 2018, Chen *et al.* 2019, Tedersoo *et al.* 2020). Given the differences in litter chemistry, microbial communities, and species level PSF based on the different mycorrhizal associations described above, we predict that negative PSF effects should become stronger with increasing

AM dominance in a forested community. For example, even though an individual ECM tree might tend to experience positive feedback because of coupling between its ECM fungi and recalcitrant leaf litter, we reason this positive feedback would be lessened or nullified by dominant nearby AM trees having an overriding effect on the surrounding soil microbial community and biogeochemistry.

In addition to specific traits such as mycorrhizal type, evolutionary relationships can have a strong influence over ecological interactions, and thus may serve as an additional factor structuring PSF (Liu *et al.* 2012, Anacker *et al*. 2014, Parker *et al*. 2015). According to Darwin's naturalization hypothesis, closely related species may occupy similar ecological niches and share similar natural enemies due to an overlap in traits associated with resource acquisition and defense (Cavender-Bares *et al*. 2009, Cadotte *et al.* 2017). Traits that are shared between closely related plant species may be similarly exploitable by generalist pathogens or mutualists, causing the effects of PSF to expand from conspecific individuals to nearby, closely related plant species (Parker & Gilbert 2004, Metz *et al.* 2010, Zambrano *et al*. 2017). If the drivers of PSF operate beyond the conspecific level, PSF between closely related species should be stronger than PSF between distantly related species (Liu *et al.* 2012). Despite this potential, evidence of phylogenetic structure in PSF remains mixed. For example, Liu *et al.* (2012) and Gilbert *et al*. (2015) found that pairs of closely related plant species experience stronger negative PSF compared to pairs of distant relatives, while Anacker and Strauss (2016) demonstrated that closely related plant species experience weaker negative PSF compared to distant relatives. Furthermore, other studies have concluded that phylogenetic relationships have no influence on PSF at all (Mehrabi & Tuck 2015, Fitzpatrick *et al*. 2017). These conflicting results require further investigation to determine if phylogenetically structured PSF effects are occurring in

natural plant communities.

Point pattern analyses are powerful analytical tools that can compare the observed spatial patterns of plants against models of spatial randomness to identify if plants are growing closer to, or further away from, one another than expected (e.g., He & Duncan 2000, Calabrese *et al*. 2010, Johnson *et al*. 2018). For example, these analyses have identified interactions between shrub species in relation to patterns of fire-driven mortality (Biganzoli *et al*. 2009) and patterns in survival related to inter and intraspecific competition in an old-growth forest (He & Duncan 2000). Additionally, these analyses can detect signs of PSF in the fine-scale spatial structure found between plant community members (Brown *et al*. 2016). If PSF is an important driver of plant community dynamics, negative PSF should result in patterns of overdispersion between adult plants and their progeny, driven by the presence of pathogens near established adult individuals, while positive PSF should result in patterns of clustering due to advantageous conditions being found near conspecific plants (Martínez *et al.* 2013). Furthermore, if PSF is affected by the soil microbial community and biogeochemical environment, then traits of dominant tree species should dictate the strength and direction of PSF that spills over onto less common community members found nearby. Due to the distribution of mycorrhizal types and diverse assemblage of species in temperate hardwood forests (Steidinger *et al.* 2019), these communities are ideal for testing for spatial patterns consistent with PSF spillover effects based on community mycorrhizal types and phylogenetic relationships.

In this study, we explored the spatial structure of a temperate hardwood forest community with varying mycorrhizal dominance using stem-mapped plots and point pattern analyses. Our goal was to identify spatial patterns consistent with our overarching hypothesis that the strength of PSF is affected by factors extending beyond the presence of conspecifics, including spillover

effects of dominant community members. We tested tree communities of varying mycorrhizal dominance for spatial patterns consistent with the following, specific hypotheses: **(H1)** Under a "mycorrhizal spillover" hypothesis, PSF between juvenile and adult trees is expected to be affected by the mycorrhizal associations of dominant community members, becoming more positive in ECM dominated communities and more negative in AM communities. This hypothesis leads to the prediction that adult trees in ECM-dominant communities will have more juvenile trees and more conspecific trees in close proximity than will adult trees in AM-dominant communities, regardless of individual tree species identity. **(H2)** Under an "individual species mycorrhizal type" hypothesis, dominant community members are less important, and PSF is affected by each individual species mycorrhizal type, with AM species experiencing negative PSF and ECM species experiencing positive PSF regardless of surrounding community composition (Bennett *et al.* 2017; Johnson *et al.* 2018). According to this hypothesis, we expect that ECM adult trees will have more juvenile trees and more conspecific trees in close proximity than will AM adult trees, with these patterns being found irrespective of the mycorrhizal associations of the surrounding community. In addition, we tested **(H3)** that PSF is affected by the phylogenetic relationships between adult and juvenile individuals within a community, with more closely related individuals experiencing stronger PSF than distantly related individuals. These three hypotheses are not mutually exclusive, and effects may be additive. For example, if PSF is structured by both phylogenetic and mycorrhizal effects, we expect to find that ECM species or ECM-dominant communities will have more closely related juvenile trees in close proximity to adult trees, while AM species or AM-dominant communities will have more distantly related juvenile trees in close proximity to adult trees. In addition to point-pattern analyses, we examined how soil abiotic properties, adult and juvenile abundances, and species

diversity change with community mycorrhizal dominance. Demographic information, such as adult recruitment and mortality over an 8-year time period, was also explored based on community mycorrhizal dominance.

MATERIALS AND METHODS

Study site

Jennings Woods is a 30-hectare temperate hardwood forest owned by Kent State University in Northeastern Ohio, USA (41°10.4' N, 81°12.1' W). It contains 29 tree species (14 AM and 15 ECM), with sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), shagbark hickory (*Carya ovata*), American elm (*Ulmus americana*), red oak (*Quercus rubra*), and American hornbeam (musclewood; *Carpinus caroliniana*) accounting for >75% of the total abundance of all adult trees in the forest (Blackwood *et al*. 2013). It has remained undisturbed since 1973 and experienced selective harvesting prior to that, resulting in dominant, naturally regenerated canopy tree ages between 60 to 100 years old. Ninety-five circular plots 30 m in diameter (706.5 m^2) were established in 2008 when an initial survey of adult trees ≥ 10 cm diameter at breast height (DBH) and soil properties (percent C, percent N, total extractable P, percent moisture, and pH) was conducted (Figure 9, Blackwood *et al.* 2013). These plots are an appropriate size to test for spatial patterns associated with PSF in local tree neighborhoods because these distance-dependent processes are known to act at local scales < 30 m (Hubbell *et al*. 2001, Wang *et al*. 2015).

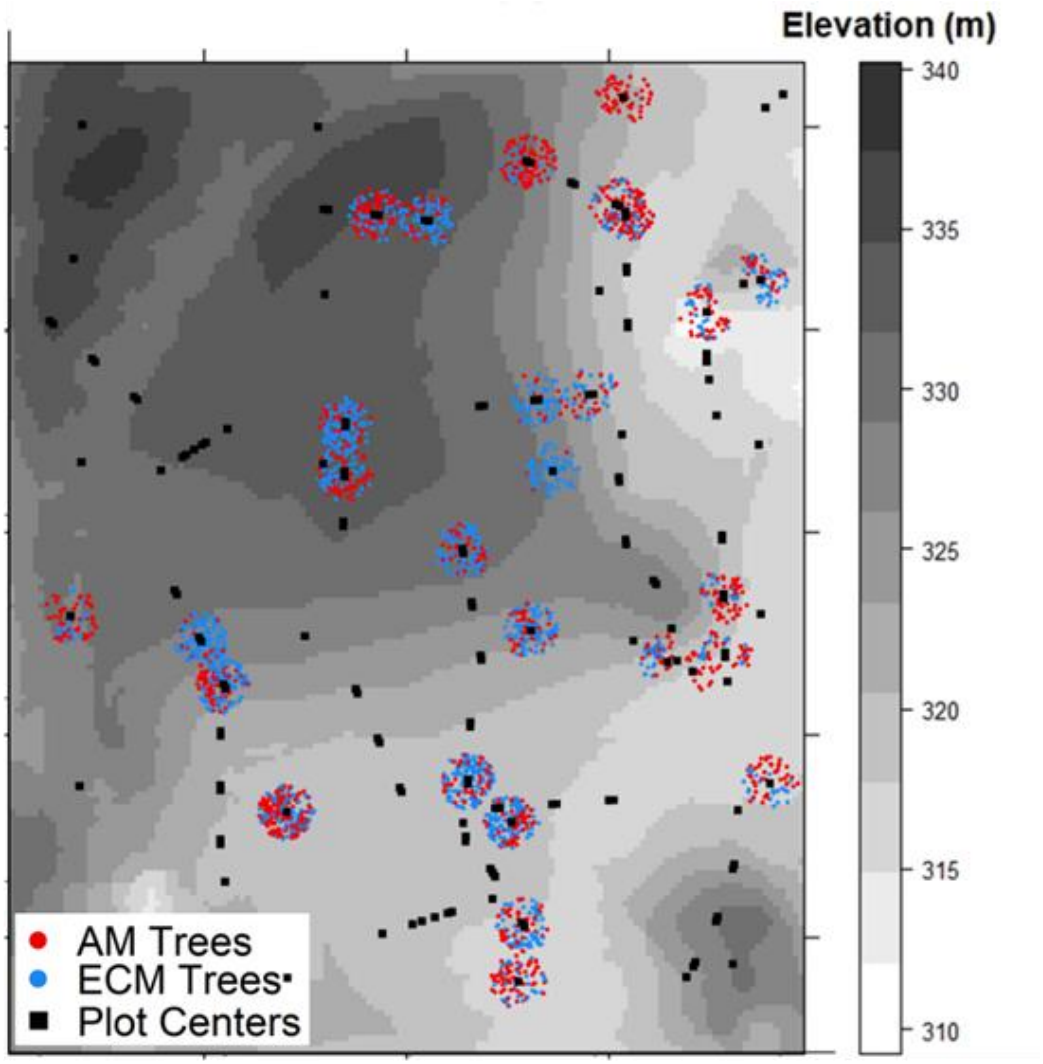

Figure 9. Map of Jennings Woods. Colored points include the juvenile and adult trees that had their spatial locations mapped during our 2016 survey. Black squares represent the center of each plot included in our 2008 and 2016 demographic surveys. Comprehensive site information can be found in Blackwood *et al.* (2013).

Adult and juvenile tree inventory and mapping

In May-August 2016, individual trees above 1.4 m in height across 28 plots were identified to species and their locations were mapped from the center of each plot using a range finder (Sonin Multi-Measure Combo Pro 10300, Sonin, Inc., Charlotte, NC) and compass (Silva Lensatic 360; Johnson Outdoors Gear, Inc., Racine, WI). Trees with a DBH ≥ 5 cm were recorded as adult trees, while trees with a smaller DBH were recorded as juvenile trees. This resulted in a total of 1025 adult and 2254 juvenile trees across all plots. Tree mycorrhizal associations were assigned based on Brundrett (2009) and Maherali *et al*. (2016). Adult tree basal area (m^2) was calculated using the formula $\pi(DBH/2)^2 \times 10^{-4}$. Species and mycorrhizal type basal areas were calculated by summing the basal areas of individuals in each plot. The relative basal areas of AM and ECM trees were obtained for each plot by dividing a summed mycorrhizal type basal area by the total summed basal area of the plot. Thus, the AM relative basal area across our plots ranged from 92.1% (i.e., dominated by AM trees) to 7.9% (i.e., dominated by ECM trees). In addition to this spatial survey, we resurveyed all original 95 plots for growth, recruitment, and mortality of adult trees.

Statistical approach and packages

To test our specific hypotheses, we conducted a series of analyses to examine spatial patterns in juvenile trees. First, point pattern analyses were performed to examine overall densities, heterospecific/conspecific ratios, and phylogenetic structure of juveniles at differing distances from adult trees. Results were then aggregated in two ways. First, plots were divided into two groups, one with >50% relative AM basal area and one with <50% relative AM basal area, and results were aggregated across plots within each group. Second, results were aggregated across species within each mycorrhizal type. We then performed similar analyses

separately for several common species. We also used linear mixed models to explicitly test for differences in juvenile density and heterospecific/conspecific ratios driven by plot mycorrhizal type. Finally, we tested for effects of dominant mycorrhizal types on tree community demographics and soil characteristics. Considering these analyses together provides a detailed examination of the spatial structure between adult and juvenile trees to determine the consistency of observed patterns with predicted PSF outcomes.

All point pattern analyses were conducted in Programita (Wiegand & Moloney 2004, 2013) using circular windows to account for the shape of our plots (Wiegand *et al*. 2006). Generalized linear mixed-effect models (GLMMs) were performed in R version 3.3.0 (R Development Core Team 2017) using the packages nlme (Pinheiro *et al.* 2017) and lme4 (Bates *et al.* 2014). R^2 values for significant GLMMs were obtained using the MuMIn package from Bartoń (2009).

Within-plot point pattern functions aggregated by community or species mycorrhizal type

Point pattern analyses involve assessment of a response variable (in this case, based on characteristics of juvenile trees) at different distance intervals from focal points (adult trees). The observed response variable is then compared to results of a simulation under an appropriate null model of spatial randomness. Edge effects will occur when part of a distance interval around an individual focal point falls outside the plot where data was collected, resulting in undercounts of surrounding points. To correct for edge effects, we used the Wiegand-Moloney edge correction method, which applies a weighted correction to each calculation based on the area analyzed for each focal point at a given distance interval, with the maximum distance interval less than half the diameter of a plot (Wiegand & Moloney 2004, 2013). For example, for a given adult tree near the edge of a plot, the number of surrounding juvenile trees is divided by the proportion of

the area sampled to obtain an estimate of total juvenile trees surrounding this adult point within and outside of the plot.

To test for spatial patterns consistent with PSF, we first examined the distribution of juvenile trees relative to adult trees considering only adult tree mycorrhizal type and not species identity. Tests of spatial randomness were used to determine if juvenile trees were distributed randomly around adult trees, or if juveniles were clustered or overdispersed around adults. We used the neighborhood density function (i.e., bivariate O-ring statistic), which measures the probabilistic density of points surrounding a focal point at a given distance class (Wiegand & Moloney 2004), to determine the spatial distribution of juvenile trees surrounding adult trees. For each plot, the observed location of juvenile trees relative to adults was compared to a random distribution obtained under the null model of spatial randomness generated by 199 Monte Carlo simulations randomizing the spatial location of juvenile trees in each plot. Values above the null model simulation envelopes indicate significantly higher densities of juvenile trees surrounding adult trees (i.e., clustering with adult trees, suggesting positive PSF), while values below these envelopes indicate significantly lower densities than expected (i.e., overdispersion from adult trees, suggesting negative PSF). Values within these envelopes indicate conformity with spatially random models and signify no patterns of clustering or overdispersion occur between adult and juvenile individuals.

To test **H1** (PSF is influenced by the dominant mycorrhizal type of the surrounding community), individual plot neighborhood density statistics were aggregated by community-dominant mycorrhizal type (binning plots according to > 50% and < 50% AM relative basal area) to obtain an average observed statistic and null model distribution. To test **H2** (PSF is influenced by species' mycorrhizal types regardless of surrounding community mycorrhizal

associations), the neighborhood density point pattern analysis was repeated at the plot level with only tree species of a single mycorrhizal type included. These species-specific results were then aggregated by mycorrhizal type across all plots. This procedure resulted in an average statistic and null model distribution for AM and ECM tree species and their juvenile communities irrespective of the dominant mycorrhizal type of our plots. The use of spatial randomness as a null hypothesis assumes that the intensity of points (i.e., mean number of points per unit area) is homogeneous across the study area (Wiegand & Moloney 2013). Inhomogeneous intensities caused by environmental gradients or geographic features can create false observations of clustering or overdispersion if unaccounted for. To test for homogeneous intensities in our plots, we used the homtest() function in the R packages Spatstat and Spatstat.local from Baddeley & Turner (2004). Of our 28 plots, 24 demonstrated homogeneity in their pattern intensity. Including four plots with inhomogeneous intensities had no qualitative influence on the outcome of our aggregated results, and so we present analysis of the full dataset.

We also examined the ratio of heterospecific-to-conspecific juveniles surrounding adults without varying the spatial position of juvenile points, with larger than expected ratios nearby adults suggesting negative PSF, and smaller ratios suggesting positive. To test for patterns in the distribution of conspecific individuals consistent with PSF, we used the mark correlation function (Illian *et al*. 2008) to calculate the ratio of heterospecific-to-conspecific juvenile trees surrounding adult trees. Mark correlation functions were calculated for each species in each plot, with these results being aggregated by dominant plot mycorrhizal type (**H1**) or by species' mycorrhizal type (**H2**). Random labelling of juvenile points was used to construct null model envelopes from 199 Monte Carlo simulations in which the heterospecific/conspecific labeling of juvenile individuals was randomly shuffled (Illian *et al*. 2008, Jacquemyn *et al*. 2010). Observed

values above this simulation envelope indicate significantly higher proportions of heterospecific juveniles surrounding adult trees (a pattern consistent with negative PSF), while values below the simulation envelope indicate significantly higher proportions of conspecific juveniles (a pattern consistent with positive PSF).

To test for spatial patterns consistent with phylogenetically structured PSF between adult and juvenile trees (**H3**), the phylogenetic mark correlation function was calculated for each species in each plot (Shen *et al*. 2013, Wiegand & Moloney 2013). For this function, a similar analytical approach to the mark correlation function was taken using a phylogenetic distance matrix constructed in Phylocom (Webb *et al*. 2008) using Phylomatic (Webb & Donoghue 2005) and data from Zanne *et al*. (2014) (see Appendix E for detailed methods).

In order to further explore PSF effects on individual species, we conducted three additional point pattern analyses on the seven most abundant adult tree species in our forest, comprising >75% relative abundance. This included three AM species (*A. saccharum*, *A. rubrum*, and *U. americana*) and four ECM species (*F. grandifolia*, *C. ovata*, *C. caroliniana*, and *Q. rubra*). We used the neighborhood density and mark correlation functions to examine the density of conspecific juveniles and heterospecific juveniles surrounding adult focal trees of each species, following the same spatially random modeling approach mentioned above for the neighborhood density function and random labelling modeling approach for the mark correlation function. These species-level results were aggregated by plot mycorrhizal dominance to see if patterns observed in these analyses are consistent within a species across plots of different mycorrhizal types.

Effects of dominant community mycorrhizal type on average point pattern statistics

The aggregation approach of our point pattern analyses described above resulted in a qualitative comparison of the significant spatial patterns in communities dominated (>50%) by AM or ECM trees. To directly explore how community mycorrhizal dominance changed plot-level spatial patterns, we used generalized linear mixed-effect models (GLMMs). We used the plot-level neighborhood density statistic or mark correlation function at each distance class as the response variable, with "plot" included as a random effect to account for non-independence of different distances within each plot. Percent AM basal area (7.9% to 92.1% AM), distance, and an interaction term (mycorrhizal type × distance) were supplied as fixed effects. After detection of a significant "mycorrhizal type × distance" interaction, this analysis was also repeated for the neighborhood density statistic after separating plots into four groups based on mycorrhizal dominance: 0 – 25%, 25 – 50%, 50 – 75%, and 75 – 100% relative AM basal area plots. These four models were analyzed with distance as the only fixed effect.

Effects of dominant mycorrhizal types on tree community and soil characteristics

GLMMs were also used to test for responses in plot-level community characteristics to the continuous mycorrhizal type gradient (7.9% to 92.1% relative AM basal area) and the discrete, majority mycorrhizal type of each plot (AM or ECM). Response variables included data from the 2016 juvenile and adult inventory for 28 plots (number of adults, number of juveniles, rarified species diversity) as well as demographic variables calculated by comparison of the 2008 and 2016 adult inventories for 95 plots (adult growth rates, recruitment of new adult trees ≥ 10 cm DBH, and percent mortality of adult trees). The number of adult and juvenile individuals, in addition to the recruitment data, were analyzed using a Poisson error distribution, while percent

mortality data were analyzed using a binomial distribution with a logistic model. We used additional GLMMs to test for an effect of the mycorrhizal gradient and majority mycorrhizal type on soil percent C, percent N, total extractable P, percent moisture, and pH (see Blackwood *et al*. 2013 for description of soil measurements).

RESULTS

Within-plot point pattern functions aggregated by community or species mycorrhizal type

The average distance between adult and juvenile trees was 2.7 (±1.5) m in AM plots and 2.1 (±0.7) m in ECM plots. Across all plots surveyed, the neighborhood density function indicated that densities of juvenile trees surrounding adult individuals were greater than expected according to the null model for all distances ≥ 2 m ($P < 0.05$; Figure 10A). Aggregating plots by dominant mycorrhizal type (to test **H1**) resulted in a notable change to this pattern, consistent with our prediction of patterns suggesting more positive PSF in ECM-dominant communities and more negative PSF in AM-dominant communities. Juvenile tree densities in AM-dominant communities shifted towards a more random pattern and were less dense than expected ~ 2 m from adult trees. Juvenile densities were greater than expected only for distances ≥ 8 m in AM-dominant communities ($P < 0.05$; Figure 10B). Meanwhile, juvenile densities in ECM-dominant communities were greater than expected for most distances ≥ 2 m ($P < 0.05$; Figure 10C). To test for effects of mycorrhizal type of individual trees regardless of community mycorrhizal dominance (**H2**), the neighborhood density function was aggregated according to tree species' mycorrhizal associations. This test revealed no deviations from the null model envelope in juvenile distribution between either AM- or ECM-associating adult tree species ($P > 0.05$; Figure 10D and E).

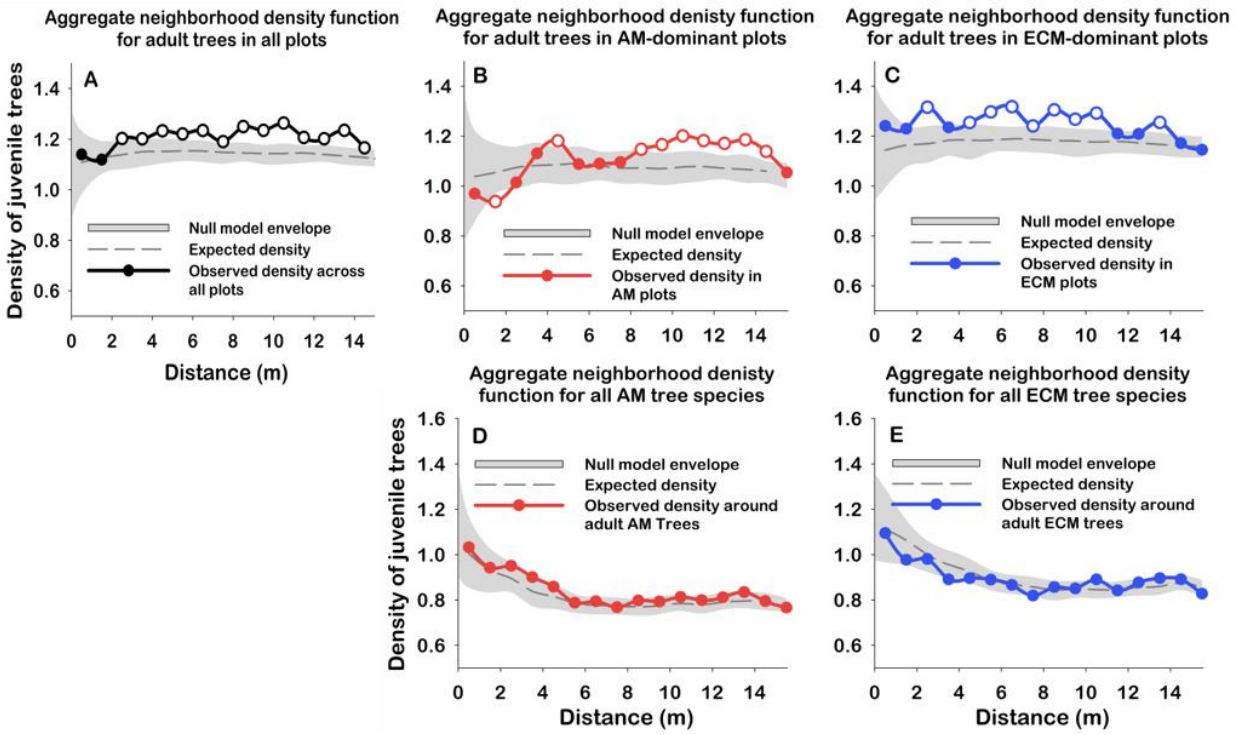

Figure 10. Neighborhood density function showing the density of juvenile trees surrounding adult trees. Results are aggregated across all plots (A), by dominant community mycorrhizal type (B and C), or by individual species mycorrhizal type (D and E). Significant deviations in the observed neighborhood density function from the random null model envelope are indicated by hollow points.

Across all plots, the mark correlation function (i.e., the heterospecific/conspecific ratio of juvenile trees surrounding adult trees) revealed fewer heterospecific juvenile individuals surrounding adult trees than expected under the null model for most distances ≤ 6 m ($P < 0.05$; Figure 11A). When plots were aggregated by dominant mycorrhizal type (**H1**), patterns were again consistent with our predictions. The heterospecific/conspecific ratio in AM-dominant communities shifted towards a more random pattern and only deviated from the null model envelope at 11 m ($P < 0.05$; Figure 11B). Conversely, ECM-dominant communities had more conspecific juvenile trees than expected under the null model for most distances ≤ 6 m ($P < 0.05$; Figure 11C). However, when aggregating the mark correlation function by species mycorrhizal type (**H2**), results were similar for both AM and ECM species, with fewer heterospecific juveniles found at distances ≤ 1 m from adult trees ($P < 0.05$; Figure 11D & E).

The phylogenetic mark correlation function, which was used to test for a phylogenetic signal in the spatial pattern of adult and juvenile trees (**H3**), did not deviate from the random null model across all distances when aggregated across all plots ($P > 0.05$). This pattern did not change when plots were aggregated by their dominant mycorrhizal type ($P > 0.05$) or when individual adult tree species were aggregated by their mycorrhizal associations ($P > 0.05$).

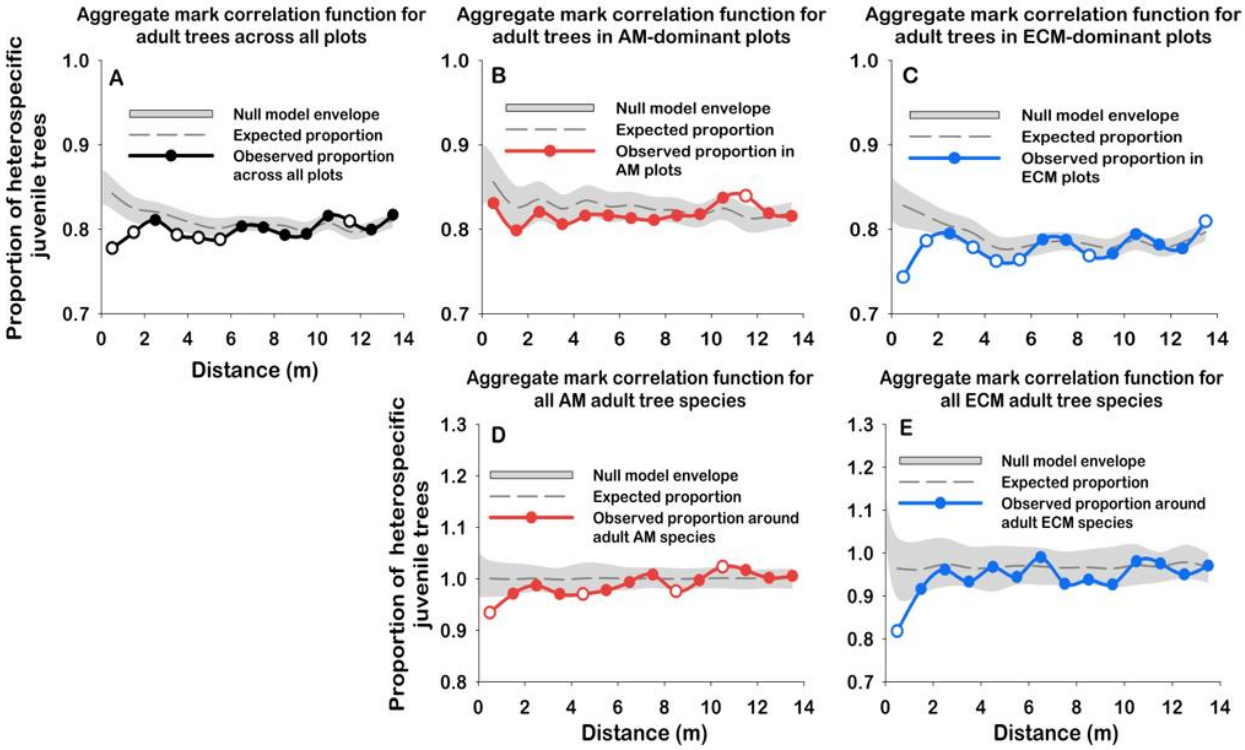

Figure 11. Mark correlation function showing the heterospecific/conspecific ratio of juvenile trees surrounding adult trees. Results are aggregated across all plots (A), by dominant community mycorrhizal type (B and C), or by individual species mycorrhizal type (D and E). Values above the null model envelope indicate higher proportions of heterospecific juvenile trees, while values below the null model envelope indicate higher proportions of conspecific juvenile trees. Significant deviations in the mark correlation function from the random null model envelope are indicated by hollow points.

Results of the point pattern analyses conducted for individual tree species

We found that individual species often exhibited different results in AM and ECM-dominated plots, but there is a consistent trend of patterns being more indicative of negative feedback in AM plots and positive feedback in ECM plots. For AM-associated species, the neighborhood density function revealed that both *A. saccharum* and *U. americana* exhibited no spatial structure of conspecific juveniles in AM plots, but had higher densities of conspecific juveniles in ECM plots at short distances (1 – 4m) (Appendix E: Figure 17). *A. rubrum* conspecific juveniles did not deviate from random spatial models in ECM plots, but in AM plots there were too few conspecific juvenile individuals to analyze. However, since *A. rubrum* adults were often present in AM plots, this could be indicative of negative feedback. Additionally, there were higher densities of heterospecific juveniles around *A. saccharum* at short distance intervals, but only in ECM plots (Appendix E: Figure 17). The ratio of heterospecific to conspecific juveniles around adult trees for all three species did not deviate from models of random labeling in AM plots, while both *A. rubrum* and *U. americana* exhibited lower ratios at short distances between adult and juvenile trees in ECM plots (Appendix E: Figure 19).

Trends were similar for ECM-associated species, with more signs of negative feedback in AM plots and positive feedback in ECM plots. The neighborhood density function indicated that *F. grandifolia* had higher densities of conspecific juvenile trees at moderate distances (5 – 7 m) between adult and juvenile trees in ECM plots, and lower densities around 6m in AM plots. *F. grandifolia* also appeared to have a negative effect on heterospecific juveniles at short distances in both plot types, with lower densities of heterospecific juvenile trees than expected under the null model of spatial randomness (Appendix E: Figure 18). *F. grandifolia* adults had lower ratios of heterospecific to conspecific juveniles at ~1m, but only in ECM plots (Appendix E: Figure

20). In ECM plots, *Q. rubra* showed higher densities of conspecific juveniles surrounding adults at short distances (Appendix E: Figure 18). There were too few of *Q. rubra* or *C. ovata* juveniles in AM plots to analyze their structure, again indicative of negative feedback. All other combinations of species and plots did not deviate from the simulated models of spatial randomness (Appendix E: Figure 17 – 20).

Effects of dominant community mycorrhizal type on average point pattern statistics

Across all 95 plots, linear modeling indicated that the neighborhood density function was affected by a significant interaction between distance and percent AM basal area ($P < 0.001$; $R^2 = 0.07$), but the main effects of the mycorrhizal gradient and distance were not significant. Furthermore, when distance from adult tree was tested as a predictor for plots separated into different AM dominance categories, the effect of distance from adult trees on juvenile densities notably shifted from a positive relationship in plots with a majority AM basal area to a negative relationship in plots with a majority ECM basal area (Figure 12). This result suggests that as ECM dominance increases, juvenile densities shift from being farther away from adult trees to closer to them, consistent with **H1**.

The mark correlation function was significantly affected by the distance between adult and juvenile trees ($P < 0.001$; $R^2 = 0.03$), but not by the mycorrhizal gradient or the interaction between the mycorrhizal gradient and distance. While this suggests that overall average values of the mark correlation function are similar in AM- and ECM-dominant plots, the previous comparison to spatial null models found that AM- and ECM-dominant plots do differ in the spatial arrangement of conspecific juvenile trees when constrained by each plot's neighborhood density (Figure 11).

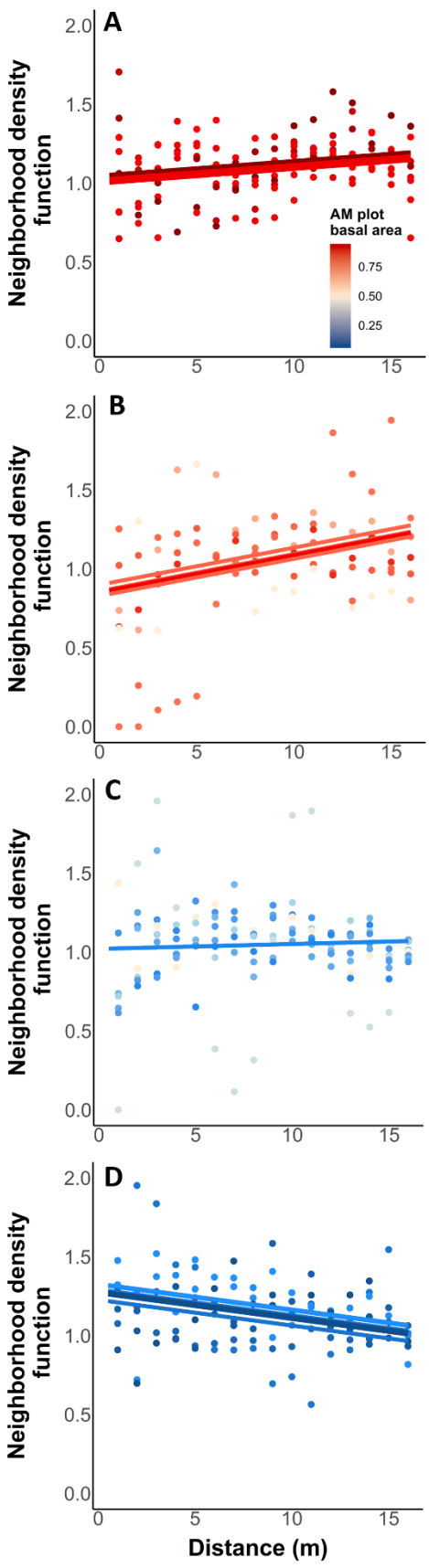
A
B
C
D
Neighborhood density function
2.0
1.5
1.0
0.5
0.0
0
5
10
15
AM plot basal area
0.75
0.50
0.25
Distance (m)

Figure 12. Generalized linear mixed-effect modeling results demonstrating the significant changes in juvenile density with distance from adult trees. Separate analyses were conducted for **A)** plots with a relative percent AM basal area between 75-100% (few ECM trees present; P = 0.01; R^2 = 0.076), **B)** plots with a relative percent AM basal area between 50-75% (P = 0.001; R^2 = 0.125), **C)** plots with a relative percent AM basal area between 25-50% (P = 0.5748), and **D)** plots with a relative percent AM basal area between 0-25% (few AM trees but many ECM trees present; P = 0.002; R^2 = 0.122). Points indicate values for the neighborhood density function at a specific distance interval for each plot, while colors correspond to the relative AM/ECM basal area percent of a plot. Lines represent the predicted model values for each plot in our forest and highlight the shifts in spatial patterns occurring in the juvenile community along the mycorrhizal gradient. Plot was held as a random effect to account for non-independence of neighborhood densities within the same plot, resulting in different intercepts for each plot.

Effects of dominant mycorrhizal types on tree community and soil characteristics

Recruitment of new adult trees between 2008 and 2016 significantly decreased with increasing AM dominance along the mycorrhizal gradient ($P < 0.05$; $R^2 = 0.05$; Appendix E: Figure 21). Additionally, recruitment of new adult trees between 2008 and 2016 was significantly higher in ECM-dominant plots, nearly double that of adult recruitment in AM-dominant plots ($P < 0.05$; Appendix E: Table 35). GLMMs indicated that mycorrhizal type had no effects on other demographic or community parameters (adult and juvenile abundances, species richness, adult growth rates, and adult mortality) or abiotic soil variables (percent C, Percent N, C:N ratio, total P, percent moisture, and pH) (Appendix E: Table 35).

DISCUSSION

Our analyses indicate that dominant community mycorrhizal associations influence the local structure of tree recruitment in forest communities, with ECM-dominant and AM-dominant communities exhibiting different spatial relationships between adult and juvenile individuals. These patterns are consistent with our hypothesis that the mycorrhizal type of dominant community members can result in PSF effects that spill over onto less common individuals and affect the entire tree community (**H1**). ECM-dominant communities had greater densities of juvenile trees (Figure 10) and more conspecific individuals (Figure 11) near adult trees than expected, in contrast to AM-dominant communities, which also exhibited lower recruitment of adult trees generally (Appendix S1: Figure 21, Table 35). These spatial patterns support the idea that soils of varying mycorrhizal dominance reflect important differences in the way arbuscular and ectomycorrhizas cycle soil nutrients and interact with soil microbial communities (Phillips *et al*. 2013, Averill *et al*. 2014, Lin *et al.* 2017), thereby influencing the recruitment of juvenile trees near established adults at the community level. ECM fungal activity can suppress

saprotrophs through competition, reduce soil mineral nutrient availability, and increase acidity in ECM soil (Phillips *et al*. 2013, Averill *et al.* 2014, Averill & Hawkes 2016, Tedersoo *et al.* 2020), which may reduce pathogen activity (LaManna *et al.* 2016, Smith *et al.* 2017) and create soil conditions conducive for positive PSF in ECM-dominant communities. This mechanism has recently been supported at the species level by Chen *et al.* (2019), who found that tree species that experience stronger negative density dependence also more rapidly accumulate pathogenic soil fungi, while trees that experience weaker negative density dependence more rapidly accumulate ECM fungi. Our findings expand on these mechanisms by documenting their influence across entire forest communities.

Collectively, our analyses show no differences between spatial patterns of AM and ECM species when considered independent from their surrounding community mycorrhizal associations (**H2**). This lack of influence of individual species' mycorrhizal associations on adult and juvenile spatial structure, in contrast to the effect from the dominant mycorrhizal type of the community, indicates that spillover effects from dominant community mycorrhizal associations may be the overriding factor influencing PSF in other individuals found nearby. Recent work by Bennett *et al.* (2017) demonstrated that the mycorrhizal associations of different species can result in different feedback outcomes, with ECM species largely experiencing positive feedback and AM species largely experiencing negative feedback when grown on soil conditioned by conspecific individuals. However, we found that community-level context, explored here as dominant mycorrhizal type, is also a key driver of feedback patterns. For example, we found no pattern in both *A. saccharum* and *U. americana* in AM plots, but clustering of conspecific juveniles and lower heterospecific/conspecific ratios nearby adults in ECM plots. This positive feedback signal in ECM plots for *A. saccharum* was unexpected, since Bennett *et al.* (2017)

indicated that *A. saccharum* experiences little feedback in either direction. For *A. rubrum*, the presence of conspecific juveniles in ECM plots and lack of conspecific juveniles in AM plots implies that the negative feedback identified in Bennett *et al.* 2017 is only strong in AM plots. Of our ECM species, *F. grandifolia* and *Q. rubra* showed patterns of positive feedback consistent with Bennett *et al.* (2017) only in ECM plots. *Q. rubra* juveniles in AM plots were nearly absent, pointing to potential negative feedback for *Q. rubra* when the dominant community members are AM trees. Because tree species grow at different rates, future analyses could be improved by tracking individual juveniles over time or reconsidering the general size cutoff between adult and juvenile individuals of each species (Detto *et al.* 2019). However, taken holistically, the results of our analyses at the community and species levels support our overarching hypothesis that dominant community members have a dramatic influence on the local environment based on their mycorrhizal associations, resulting in PSF effects spilling over onto less common individuals in the community.

PSF is just one of several explanations that has been put forward for explaining the spatial distribution of plants in a community (Tilman 1988, Jones *et al*. 2008), but it is difficult to explain the patterns we have observed using alternative mechanisms. For example, strong intraspecific and interspecific competition can lead to non-random patterns of mortality, with surviving plant species being regularly spaced throughout a community (He & Duncan 2000). Specifically, competition for soil resources can create uniform or overdispersed spatial patterns between individual trees when resource availabilities are low (Getzin *et al*. 2006). ECM tree communities have been shown to induce lower inorganic nutrient availabilities (Read & Perez-Moreno 2003, Averill *et al*. 2014), which should lead to stronger competitive interactions between trees within these communities. However, our results show a pattern that is opposite to

expectations from increased competition for soil nutrients in ECM communities, with all juvenile trees clustering around adults instead of being overdispersed in ECM plots (Figure 10C). This suggests that ECM associations can reduce the negative effects of competition and low inorganic nutrient availability through positive PSF between tree community members, likely driven by the ability of ECM fungi to obtain organic nutrients from host plant leaf litter (Read & Perez-Moreno 2003, Wurzburger & Hendrick 2009). Additionally, some saprotrophs may function as facultative biotrophic or necrotrophic pathogens (Olson *et al.* 2012, Smith *et al.* 2017). Under conditions of low mineral nutrient availability, pathogen populations may be suppressed by competition for organic resources from ECM fungi (Averill & Hawkes 2016). Conversely, weaker effects of competition between trees might be expected in AM communities because mineral nutrient availability is frequently higher under AM trees (Lin *et al*. 2017, Lin *et al*. 2018). Again, we observed the opposite pattern, with overdispersion at short distances between adult and juvenile trees in our AM communities, as well as lower overall recruitment rates. Larger pathogen populations may be a consequence of greater soil mineral nutrient availability (LaManna *et al*. 2016), which can lead to stronger pathogen-driven negative PSF and override the benefits of greater soil nutrient availability in AM communities. Therefore, the contrasting PSF outcomes of different mycorrhizal communities observed in our study are likely contingent on the ability of ECM communities to overcome the negative effects of reduced mineral nutrient availability and to suppress the growth of saprotrophs/facultative pathogens. We did not find any differences between abiotic soil properties of different mycorrhizal types, although the variables we measured may not represent the specific mineral and organic forms of nutrients expected to differ between soil of different mycorrhizal types (Phillips *et al.* 2013, Averill *et al*. 2014, Lin *et al*. 2017).

Dispersal strategies can also dictate where plants grow relative to one another (Howe & Smallwood 1982). Individuals of a species that exhibits limited dispersal capabilities are typically found clustered together, while species that can disperse greater distances are more randomly distributed throughout a community (Jacquemyn & Hermy 2001). If seed dispersal alone controlled the spatial distribution of trees in our sites, we would expect random distributions between adult and juvenile individuals throughout our community due to the size of our plots (30 m diameter) and the high likelihood of dispersal at these scales (Nathan & Muller-Landau 2000). Thus, post-dispersal filters, both abiotic and biotic, ultimately influence where plants establish within a community and therefore play a larger role than dispersal in influencing plant community structure at this spatial scale (Leck *et al*. 2008, Wang *et al*. 2015). Furthermore, we are unaware of any trait-based link between mycorrhizal associations and dispersal that can explain the community-wide, mycorrhizal-associated spatial patterns observed at the scale in our study, though dispersal colimitation of plants and mycorrhizal fungi may be an important consideration (Tedersoo *et al.* 2020).

For evolutionary relationships to play a role in driving PSF, trait dissimilarity and evolutionary distance need to be positively correlated so that closely related species overlap in traits that drive PSF (**H3**; Anacker *et al*. 2014, Parker *et al*. 2015, Cadotte *et al.* 2017). The random phylogenetic spatial structure observed in our analysis of both AM- and ECM-associating tree communities do not suggest this level of phylogenetic conservatism of traits that are associated with PSF. While our results agree with several other published studies that suggest phylogenetic relatedness is a poor predictor of PSF strength and direction (e.g., Mehrabi *et al*. 2015, Fitzpatrick *et al*. 2017), our study only considers aggregate phylogenetic distances between species with no consideration for specific traits. Furthermore, although Jennings Woods

includes several pairs of congeneric species and five species of *Quercus*, greater species sampling may be necessary to detect a subtle phylogenetic signal in PSF (e.g., Liu *et al.* 2012). Additional work is needed to identify and evaluate more plant traits associated with PSF that are related to species' mycorrhizal types and how these relationships have shaped plant evolutionary history. Mycorrhizal fungi are thought to have played a significant role in plant niche differentiation (Gerz *et al*. 2018) and, while the evolution of mycorrhizas has been well studied across many plant clades (Brundrett 2002, Valverde-Barrantes *et al*. 2016, Brundrett & Tedersoo 2018), the implications of these symbiotic relationships for speciation rates and the evolution of traits connected to PSF are still poorly understood. Gaining a better understanding of these relationships, such as identifying differences in the defensive benefits conferred by AM vs. ECM fungal structures, should yield important insights into the evolutionary consequences of PSF and the mechanisms that shape these relationships through time.

Although additional studies are needed to fully establish the mechanisms behind the patterns observed here, our results indicate that community-level mycorrhizal dominance is an important factor that structures spatial patterns and demography in natural forests. The patterns we identified are consistent with mycorrhizal type differences in leaf litter and root traits driving variation in PSF by influencing the abundance of pathogenic microbial functional groups and soil mineral nutrient availability. Our research highlights the prominent role of mycorrhizas in structuring community-level interactions through spillover PSF effects from dominant community members. We recommend more PSF work adopt a holistic, community-level approach in order to expand from the perspective of species-specific interactions in communities where multiple mycorrhizal types are present.

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CHAPTER V

OVERVIEW, CHAPTER SYNTHESIS, AND FUTURE DIRECTIONS

OVERVIEW

Feedback experienced between plants, the soil environment, and their associated microbiota is understood to be a fundamental driver of plant community composition (Mills & Bever 1998, Teste *et al.* 2017), trait evolution (Lau & Lennon 2011, terHorst & Zee 2016), and ecosystem function (Schnitzer *et al.* 2011, Van Nuland *et al.* 2016). The field of plant-soil feedback research is growing rapidly, but there are several underexplored areas that need to be addressed to advance the field (e.g., Smith-Ramesh & Reynolds 2017, Forero *et al.* 2019, Gundale & Kardol 2021). First, the majority of plant-soil feedback work has been conducted with grassland species or in grassland ecosystems (Kulmatiski *et al.* 2008, Forero *et al.* 2019), which represent a small fraction of global plant biodiversity (Kreft & Jetz 2007). Exploring how plant-soil feedback operates in other systems is therefore important for generalizing its mechanisms and outcomes. Second, despite the recognized importance of expanding plant-soil feedback research from species-focused studies to the community scale, the number of published studies doing so is low (Kulmatiski *et al.* 2008, Revillini *et al.* 2016, Forero *et al.* 2019). Alarmingly, in their meta-analysis comparing greenhouse and field experiments, Forero *et al.* (2019) concluded that "greenhouse-measured plant-soil feedbacks that predominate in the literature both overestimate and provide little direct inference into plant-soil feedback effects in the field." The lack of agreement between study types was attributed to the overriding influence of stressful growing

conditions, but the authors stress the need for more field studies to substantiate their conclusions (Forero *et al.* 2019). Lastly, plant-soil feedback across communities appears dependent on environmental context (Hovatter et al. 2013, Smith-Ramesh & Reynolds 2017), highlighting the need for studying these interactions across temporal and environmental gradients (Thakur *et al.* 2020, Gundale & Kardol 2021).

In addition to expanding the scope of plant-soil feedback work, it is essential to identify generalizable trends in feedback patterns to understand their significance in the context of increasing global temperatures, changing precipitation patterns, and anthropogenic N deposition (van der Putten *et al.* 2013, Gundale & Kardol 2021). Conceptual frameworks predicting feedback strength and direction in plant communities are difficult to achieve, however, because many feedback drivers are thought to be species-specific (Bezemer *et al.* 2006, van der Putten *et al.* 2013, Yan *et al.* 2015) and variable across biotic and abiotic gradients (Revillini *et al.* 2016, Smith-Ramesh *et al*. 2017). In spite of these context-dependencies, mycorrhizal relationships represent contrasting trait-based plant nutrient acquisition strategies that influence plant-soil interactions from both biotic and abiotic perspectives (Phillips *et al.* 2013, Averill *et al.* 2019), are species-specific (Brundrett 2009, Soudzilovskaia *et al.* 2020), and stable over recent geological time (Taylor *et al.* 2009, Brundrett & Tedersoo 2018). Thus, plant mycorrhizal associations represent a reliable trait to use when integrating plant nutrient economics into plant-soil feedback research (Bahram *et al.* 2020, Netherway *et al.* 2021). They also represent a novel way to explore plant-soil feedback effects outside grassland systems, which strictly form arbuscular mycorrhizal symbioses (Smith & Read 2010, Soudzilovskaia *et al.* 2020).

My work here sought to explore plant-soil feedback relationships in temperate hardwood forests through the mycorrhizal-associated nutrient economy (MANE) framework (Phillips *et al*.

2013). Specifically, I focused on the relationship between tree community mycorrhizal composition and soil fungal community species and functional composition across multiple forested gradients. Although this approach is reductive (viewing a diverse assemblage of plants and their traits as mycorrhizal types), it has the potential to be useful in predicting plant-soil interactions due to the balanced distribution of different mycorrhizal syndromes within these systems (Phillips *et al.* 2013). By simplifying complex dynamics in this way, it becomes easier to understand how plants interact with soil microbial communities and how these relationships drive evolutionary processes and shift with global change. My work addressed several knowledge gaps in current plant-soil feedback research by **1)** studying plant-soil feedback in non-grass species/non-grassland ecosystems; **2)** approaching plant-soil feedback at the community, rather than the individual species, level; and **3)** exploring plant-soil feedback drivers along environmental gradients and outside of greenhouse settings. Here, I present an integrated discussion of my chapters II, III, and IV and the support for my spillover hypothesis (detailed in chapter I), as well potential future research directions in these areas under climate change.

CHAPTER SYNTHESIS

The MANE framework makes clear predictions regarding soil processes, such as carbon and nutrient cycling, and proposes general shifts in soil bacterial:fungal ratios between arbuscular (AM) and ectomycorrhizal (ECM) trees, but is not specific about mycorrhizal effects on soil microbial community composition (Phillips *et al.* 2013, Netherway *et al.* 2021). Thus, MANE outcomes on microbial community function need to be investigated in forest communities of mixed mycorrhizal composition where competing nutrient acquisition strategies and other trait differences between AM and ECM trees interact (Netherway *et al.* 2021). I hypothesized that dominant (i.e., large or abundant) tree community members affect other

community members in predictable ways by influencing fungal community composition and function through their mycorrhizal associations. I proposed that these mycorrhizal "spillover effects" are a net result of both direct (mycorrhizas interacting with soil microbes) and indirect (tree mycorrhizal traits influencing overall soil nutrient availability) drivers operating in communities of mixed mycorrhizal types. My spillover hypothesis leverages the MANE framework to understand plant-soil feedback effects in these systems using information about entire tree community mycorrhizal types. My three data chapters tested parts of this hypothesis by examining relationships between soil fungal and tree communities across three study systems in the midwestern and northeastern United States.

Chapters II and III demonstrate that tree community mycorrhizal types are better predictors of fungal community dynamics than edaphic conditions (pH, C:N ratio, etc.), revealing that the diversity and relative abundances of saprotrophic, plant pathogenic, and ECM fungi change in consistent ways with tree community mycorrhizal composition. As ECM tree dominance increased, the diversity and relative abundances of saprotrophs (Figs. 2 & 3) and plant pathogens decreased while ECM fungal diversity and relative abundance increased (Figs. 2, 3, 6, & 8). Chapter II also consisted of a sampling design covering multiple areas in each plot to achieve a consensus microbial community profile, thereby demonstrating the net effect of tree community mycorrhizal dominance on soil microbial community composition (compared to localized effects from an individual tree, a concept explored explicitly in chapter III). These results are remarkably similar to those of Bahram *et al.* (2020), who studied gradients of mycorrhizal dominance in boreal and temperate forests of the Baltic region and found the same patterns among functional group relative abundances and mycorrhizal dominance. They also

support the commentary offered by Netherway *et al*. (2021), suggesting there is a global pattern between these relationships in these systems.

Although chapters II and III do not directly test for typical plant-soil feedback outcomes (e.g., changes in biomass between different cohorts/generations), they do provide circumstantial evidence of potential feedback directions because fungal mutualists and soil-borne pathogens are key drivers of plant-soil feedback effects (Mangan *et al.* 2010, Bever *et al.* 2015). Additionally, plant-pathogen interactions appear stronger in soils with greater mineral nutrient availability (LaManna *et al.* 2016, Segnitz *et al.* 2020); a characteristic hypothesized of AM-dominant forest soils (Read & Perez-Moreno 2003, Phillips *et al.* 2013). It is therefore reasonable to expect that greater pathogen abundance and diversity would translate to stronger negative plant-soil feedback patterns in AM-dominant forests, similar to the individual species-level observations from Bennett *et al.* (2017). Likewise, greater ECM fungal abundances and diversity that reduces fungal pathogen abundance and diversity should simultaneously weaken negative feedback effects while strengthening positive feedback effects in ECM-dominant forests. Although AM trees in ECM-dominant stands would not directly benefit from greater ECM fungal presence, they would encounter lower amounts of pathogens in these communities. This type of indirect benefit to AM trees in ECM stands likely explains the spatial patterns consistent with plant-soil feedback outcomes among individual vs community mycorrhizal types observed in chapter IV.

Pathogen-driven negative feedback is associated with decreases in biomass as plants either allocate resources from growth to defense or lose biomass to necrosis (Cipollini & Heil 2010, De Coninck *et al.* 2015, Lemmermeyer *et al.* 2015). In cases of high pathogen loads or during vulnerable stages of development, such as seed germination and seedling establishment, plant-pathogen interactions often lead to mortality (Packer & Clay 2000, Liang *et al.* 2016).

Strong negative feedback induced by adult plants can therefore decrease survivorship in their progeny, with these effects decreasing with distance between parents and offspring in an extension of the Janzen-Connell hypothesis (Janzen 1970, Connell 1971, Packer & Clay 2000). My chapter IV (Title) tested for observational spatial evidence of this effect between adult and juvenile trees within forested communities consistent with the microbial evidence detailed in chapters II and III. Unlike previous work by Johnson *et al.* (2018), who examined the spatial structure between adults and juveniles of either mycorrhizal type but did not consider surrounding mycorrhizal community contexts in their study, my study explicitly considered the mycorrhizal type of the surrounding tree community when evaluating adult/juvenile recruitment relationships.

This context provided additional support for my spillover hypothesis and was critical in revealing discrepancies between the greenhouse-based, species-level results from Bennett *et al*. (2017) and *in situ* community-level feedback patterns in this system. Here, trees in AM-dominant communities reflected patterns between adult and juvenile individuals consistent with negative feedback regardless of their species or mycorrhizal identity. My work provides evidence that the relationship between adult and juvenile ECM trees, which should reflect patterns of positive feedback according to Bennett *et al.* (2017) and Johnson *et al.* (2018), can instead be negative in communities with a high presence of AM trees. My conclusion - that tree species reported to demonstrate positive or negative feedback can experience different feedback outcomes based on surrounding tree community mycorrhizal associations - also reinforces the opinion of Forero *et al.* (2019) that greenhouse experiments of plant-soil feedback miss important *in situ* considerations that affect feedback outcomes.

While the work presented in chapter IV took place in a third forest independent from those sampled in chapters II and III, it is likely that similar relationships between forest mycorrhizal community composition and soil fungal community composition exist in all three locations. Our forest in NE Ohio (chapter IV) has a similar tree community composition to our sites in south-central Indiana (chapter II) and shares several dominant tree species with our Adirondack, New York sites (e.g., *Acer rubrum* and *Fagus grandifolia*; chapter III). Geographically, our Ohio forest represents an intermediate climate type between the other two locations; it experiences fewer days with below-freezing temperatures and infrequent snowpack compared to our Adirondack sites, but has lower average monthly temperatures and higher yearly precipitation than our Indiana sites (NOAA National Centers for Environmental Information). The microbial patterns seen at each end of our geographic extent suggest that these trends should be similar in soil from our middling Ohio forests. Additionally, Bahram *et al.* (2020) provide evidence of similar patterns in fungal community composition with forest mycorrhizal dominance in both boreal and temperate Baltic hardwood forests, and Netherway *et al*. (2021) make predictions consistent with these observations without caveats concerning specific geographic considerations. Together, the results presented in chapters II and III, along with evidence and commentary supplied by Bahram *et al.* (2020) and Netherway *et al*. (2021), provide a satisfactory explanation of the responsible drivers behind the spatial patterns observed in chapter IV.

It is likely the occurrence of these mycorrhizally-associated plant-soil feedback effects are widespread in forests around the globe. My research in midwestern and northeastern U.S. forests arrived at conclusions that were similar to those from Baltic temperate and boreal forests (Bahram *et al.* 2020) and from subtropical forests from southern China (Liang *et al*. 2020).

Together, these studies, along with mine, represent the first steps in expanding plant-soil feedback research into *in situ* community settings in forested ecosystems. The potentially ubiquitous nature of these relationships has broad implications for understanding the consequences of shifts in tree community composition on plant-soil interactions driven by global change factors. Studying the consequences of global change through plant-soil feedback therefore represents an important direction for future work in this area, which I discuss below in my final section.

FUTURE DIRECTIONS

Anthropologically-driven global change factors that affect temperate hardwood forests include increased temperature, shifted precipitation patterns leading to wetter habitats, and increased atmospheric N deposition (Soudzilovskaia *et al.* 2015, Jo *et al.* 2019, McDowell *et al.* 2020). While it is generally understood that climate change will lead to plant species' range shifts from lower to higher latitudes (Hughes 2000, Walther *et al.* 2001, McCarty 2001), many predictions do not consider changes in plant-soil feedback patterns when assessing the outcomes of global change (Rudgers *et al.* 2020). Climate-driven changes in mycorrhizal composition are expected to increase decomposition rates and demonstrate northward shifts in arbuscular mycorrhizal dominance (Steidinger *et al.* 2019, Jo *et al.* 2019). For example, over the last three decades global change factors have increased AM tree presence and decreased ECM tree presence in the Eastern United States (Jo *et al.* 2019). Furthermore, warming temperatures are increasing AM tree influences and decreasing ECM tree influences on carbon cycling, decreasing soil C stocks in mixed mycorrhizal systems (Soudzilovskaia *et al.* 2015). Thus, as colder, drier habitats in the Northern hemisphere become warmer and wetter, AM trees are expected to replace ECM trees and alter soil biogeochemistry across these ecosystems (Jo *et al.*

2019, Steidinger *et al.* 2019). These studies also indicate that changes in soil biogeochemical cycling are consistent with the MANE hypothesis, which implicates plant-microbe interactions as responsible drivers. Consequently, increasing AM dominance and decreasing ECM dominance should lead to weakened positive and strengthened negative feedback effects in these systems through changes in microbial community composition.

Altered plant-soil feedback dynamics congruent with shifts in mycorrhizal dominance will likely exacerbate the effects of climate change and further reinforce global change outcomes in temperate hardwood forest ecosystems. AM trees have traits associated with mineral N uptake and will benefit more than ECM trees from increased atmospheric N deposition (Averill *et al.* 2019), speeding up N cycling rates as they become more dominant (Mushinski *et al.* 2020, Lin *et al.* 2021). Likewise, soil carbon in colder climates, which are more ECM-dominant (Tedersoo *et al.* 2014, Tedersoo *et al.* 2022), is more sensitive to warming (Koven *et al.* 2017). Losses of soil carbon in colder climates will be accelerated by the replacement of ECM trees with AM trees, with these losses reinforcing AM establishment as mineral nutrient availability increases (Phillips *et al.* 2013, Mushinski *et al.* 2020). Most importantly, the expansion of AM tree species ranges into more northern, ECM-dominant systems represents a specific case of enemy escape from top-down controls on fitness because there are less soil-borne pathogens in these systems (Roos *et al.* 2011, Bahram *et al*. 2020, Eagar *et al.* 2022, Eagar *et al.* in prep). Relieving AM trees from the largest driver of negative plant-soil feedback (Mills & Bever 1998) early in their establishment will further encourage the expansion of AM tree species ranges, as it takes time for pathogens that would otherwise hinder these trees to develop in newly colonized regions (Flory & Clay 2013).

The same factors promoting the expansion of AM tree ranges will also enhance plant-pathogen interactions and strengthen negative plant-soil feedback relationships. For example, increased atmospheric N deposition coupled with greater AM tree dominance will increase soil mineral nutrient availability, which is connected to greater soil pathogen activity (LaManna *et al.* 2016) and diversity (Castaño *et al.* 2019). Likewise, increases in soil moisture can drive seed mortality through controls on pathogenesis (Allen *et al.* 2018) and make pathogens more detrimental to plants (Hersh *et al*. 2012). Thus, increases in soil moisture due to shifting precipitation patterns will increase the strength of negative plant-soil feedback through enhanced plant-pathogen interactions. Collectively, global change-driven increases in AM dominance at the expense of ECM dominance will lead to more plant-pathogen interactions, less belowground carbon, and more rapid N cycling that will further contribute to, and be strengthened by, global change. These factors have consequences on the relationship between trees and their progeny (Eagar *et al.* 2020) and will result in increased tree mortality, disease severity, and overall younger forests across the Northern hemisphere (McDowell *et al*. 2020).

Plant-soil feedback effects are also known to drive evolution in plants and their associated microorganisms (Gilbert & Parker 2010, Schweitzer *et al.* 2014, Frantzeskakis *et al.* 2020). While we know that global change is disrupting established plant-microbe interactions both spatially and temporally (Rudgers *et al.* 2020), our understanding of the consequences of these changes as they relate to evolutionary interactions in temperate forests remains scarce. The period of time between AM tree establishment and pathogen response in ECM-dominant systems presents an opportunity for novel plant-microbe interactions to occur (Parker & Gilbert 2004, Gilbert & Parker 2010). This lag time resulting from enemy escape could create selective pressures on AM tree species favoring genotypes better suited for nutrient uptake rather than

defense (Dawson 2015). If selection for traits related to nutrient uptake in AM trees occurs at the cost of defensive traits, the eventual adaption of pathogens may cause greater disease susceptibility in AM trees. Additionally, microbial pathogens can evolve quickly in response to new plant hosts because novel genotypes represent strong selective forces (Gilbert & Parker 2010). Adaptation of pathogens to new AM tree hosts may result in ECM trees encountering pathogens they are ill-equipped to defend against, eventually leading to stronger negative plant-soil feedback experienced in the future by both AM and ECM trees.

From a macroevolutionary perspective, plant-soil feedback has the potential to influence plant species diversification and may be responsible for the differences in species richness between different plant mycorrhizal groups. Negative plant-soil feedback influences meta-community diversity (Loeuille & Leibold 2014) and has the potential to drive speciation through the arms race/ Red Queen hypothesis (Haldane 1949, Clay & Kover 1996, Loeuille & Leibold 2014). Here, plant-pathogen interactions select for pathogen traits that can overcome plant defenses and for plant traits that successfully defend against pathogen attack. This relationship may have contributed to generating the high diversity of AM plants seen across the globe (Brundrett 2009, Brundrett & Tedersoo 2018). Conversely, positive plant-soil feedback reinforces specific traits associated with beneficial plant-microbe interactions that reduce other selection pressures, such as those associated with stress tolerance (Hawkes *et al.* 2020). Given that ECM symbioses are phylogenetically constrained (Brundrett 2009), and ECM plant clades are less numerous and diverse than AM clades (Brundrett & Tedersoo 2018), it is reasonable to hypothesize that positive feedback generated through ECM associations decreased diversification rates in these clades through the reduction of other selective pressures. Considering that range expansion can be a substantial driver of speciation (Vamosi *et al.* 2018), I

expect that the replacement of ECM trees by AM trees will influence the coevolution between plants and their microbiome in ways that increase rates of diversification through stronger negative plant-soil feedback effects.

While the work presented in my dissertation studied several specific components of plant-soil feedback in identified areas of need, many other complex relationships in this field remain underexplored. Work in various systems, especially those with long-lived individuals such as trees, still needs to investigate explicit spatial and temporal components in plant-soil interactions to answer questions related to global change and evolution. Leveraging existing environmental gradients, as suggested by Thakur *et al.* (2020) and Gundale & Kardol (2021), represents a promising avenue for gauging community feedback responses to the introduction of new species or mycorrhizal associations and their long-term consequences. These processes are inherently linked to plant-microbial co-evolution through plant-soil feedback effects (Van Nuland *et al.* 2016), the environmental context of which is being altered by global change factors (Dostál 2021). Understanding the role that plant-soil feedback plays in structuring the effects of global change on plant and microbial communities presents a substantial challenge, but is one that can be studied by creatively integrating and applying concepts from multiple sub-disciplines across ecology and evolutionary biology.

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APPENDIX A

CHAPTER III METHODS & DATA FOR SITE CLIMATE DATA, PLOT TREE COMMUNITY DATA, AND SOIL VARIABLES

Climate

We obtained 2017 and 2018 daily mean, maximum, and minimum temperature and precipitation data from PRISM Climate Group (PRISM Climate Group 2021) for our three primary study site regions. The PRISM (Parameter-elevation Regressions on Independent Slopes Model) models are constructed from observations from monitoring networks and modeled at a spatial resolution of 800 m. This resolution provides good separation of our study sites, but it does not allow us to resolve localized information regarding slope aspect and topography. The remoteness of our sampling locations, annual snowpack, and dense tree canopy cover all present substantial barriers for consistent monitoring of climate and weather data of each established plot. We created five unique bioclimatic zones across the Adirondack Park using a Kmeans unsupervised clustering algorithm on three raster layers (4 km resolution) from the PRISM data with each layer representing minimum monthly temperature, mean monthly temperature, or mean monthly precipitation.

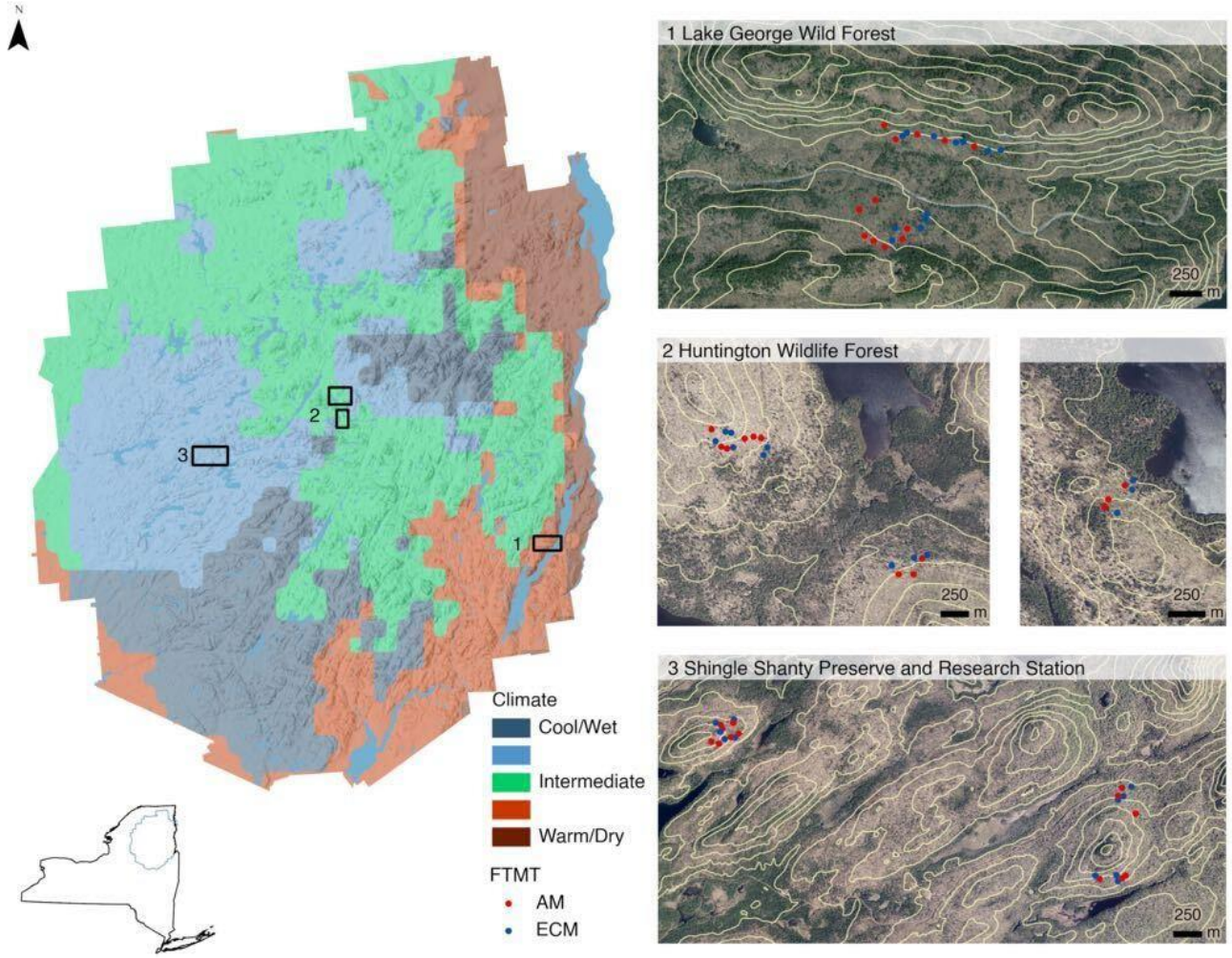

Figure 13. Climate map of the Adirondack Park region and sampling plot locations. Plots are denoted by their focal tree's mycorrhizal type (FTMT).

Tree community and forest floor sampling

Tree abundance data were rarefied to 62 counts per plot using the R (ver. 4.1.1; R Core Team 2021) package *vegan* (Oksanen *et al.* 2013). Plot mycorrhizal basal areas were obtained by calculating each tree's individual basal area using the formula $2\pi(DBH/2) \times 10^{-4}$, summing the basal areas of each mycorrhizal type, then dividing by the total basal area of each plot. Six replicate forest floor (FF) samples were taken within 5 m of each focal tree by randomly tossing a 25 x 25 cm PVC frame and collecting all litter above the O horizon using a serrated knife. Samples were placed in paper bags, dried at 105° C for 72 hours, and weighed to obtain average FF mass for each plot. One composite soil sample was collected by combining 10 replicate, 5cm diameter PVC cores taken within 5 m of the focal tree after removal of the leaf litter layer. Samples were divided into 0-5 cm and 5-10 cm depths. All soil samples were transported to the lab in coolers on ice and stored at 4° C until processing. All composite soil samples were homogenized through a 2 mm mesh sieve to separate roots from soil.

Soil variables

Fresh composite root samples taken from each soil core were dried at 60° C for 72 hours and weighed to determine the average fine root biomass from 0-10 cm depth. A subsample of ~ 20 g soil was dried at 105° C for 72 hours to calculate soil moisture content and was pulverized in a SPEX ball mill (SPEX Sample Prep, Metuchen, NJ USA) for determining total and percent soil C and N content on an elemental analyzer (Costech Analytical, Valencia, CA USA). Soil pH was measured using a 1:2 dilution of field moist soil and deionized water. Soil respiration rates were determined using PVC soil collars and a LI-COR 6400XT with soil chamber kit (LI-COR Environmental, Lincoln, Nebraska USA) over a one-week period in July of 2018. Mean respiration rates were calculated by averaging plot level measurements from 6 random locations

within 5 m of a plot focal tree. Inorganic N concentrations were measured by shaking fresh soil samples in a 1:5 dilution of soil and 1 M KCl for 1 h, centrifuging at 3000 rpm for 10 minutes, and filtering the supernatant which was analyzed colorimetrically in 96 well-plates (Smemo *et al*. 2021). Ammonium (NH_4^+) concentrations were obtained using a salicylate-hypochlorite procedure (Kempers & Zweers 1986), while nitrate plus nitrite (reported as NO_3^-) concentrations were obtained using a VCl_3/Griess procedure (Miranda *et al*. 2001). Net N mineralization and nitrification rates were measured from soil subsamples incubated at 20°C for 14 days before extraction with 1M KCl (Robertson *et al.* 1999) and analyzed for NH_4^+ and NO_3^- with the same methods described above. The difference between final and initial ion concentrations was used to calculate net N mineralization and nitrification rates.

Tables and figures

Table 8. Results of the mixed-effect linear modeling (P-values and AIC scores) comparing the three models analyzed for fungal ASV richness. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P < 0.07).

Model	**Terms**	**Soil**		**Roots**		**Leaves**	
		P-value	**AIC**	**P-value**	**AIC**	**P-value**	**AIC**
Geographic	Site	**0.043**	653.7	0.773	633.9	**0.0003**	674.7
	Aspect	**0.008**		**0.062**		0.180	
	Site x Aspect	**0.017**		0.102		0.946	
Mycorrhizal	% ECM BA	0.817	644.2	0.536	609.3	0.756	659.0
	FTMT	0.195		0.157		0.329	
	% ECM BA x FTMT	0.378		0.207		0.362	
Combined	Site	0.087	**513.3**	0.304	**462.6**	0.623	**493.7**
	Aspect	**0.013**		0.108		**0.053**	
	FTMT	**0.031**		0.301		0.638	
	% ECM BA	0.236		0.361		0.113	
	Site x Aspect	0.490		0.448		0.105	
	Site x FTMT	0.209		0.763		0.168	
	Aspect x FTMT	0.137		0.625		0.389	
	Site x % ECM BA	0.222		0.263		0.308	
	Aspect x % ECM BA	**0.060**		0.167		**0.015**	
	FTMT x % ECM BA	0.097		0.439		0.852	
	Site x FTMT x % ECM BA	0.359		0.614		0.160	
	Aspect x FTMT x % ECM BA	0.304		0.826		0.091	
	Site x Aspect x % ECM BA	0.281		0.245		0.119	
	Site x Aspect x FTMT	0.107		0.459		0.200	

Table 9. Results (P-values) of the RDA on overall fungal community composition. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type; FT Species = plot focal tree species. Bold values indicate significant or marginally significant terms (P< 0.07).

Term	**Soil**			**Root**			**Leaf**		
	ASV	**Family**	**Guild**	**ASV**	**Family**	**Guild**	**ASV**	**Family**	**Guild**
FT species	**0.001**	**0.021**	**0.056**	**0.001**	**0.001**	**0.003**	**0.001**	**0.001**	0.154
Site	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
Aspect	**0.015**	0.352	**0.024**	**0.032**	0.120	**0.016**	**0.060**	**0.055**	0.184
FTMT	0.423	**0.003**	**0.001**	0.561	**0.051**	**0.018**	**0.010**	**0.017**	0.108
% ECM BA	0.179	**0.003**	**0.002**	0.293	**0.022**	**0.062**	**0.001**	0.183	0.647
Site x Aspect	**0.043**	0.065	0.149	**0.014**	0.388	0.533	**0.004**	**0.010**	0.079
Site x FTMT	0.230	0.244	**0.040**	0.291	0.198	0.209	0.079	**0.045**	0.412
Aspect x FTMT	0.972	0.950	0.575	0.779	0.943	0.360	0.327	0.110	0.406
Site x % ECM BA	0.749	0.309	0.326	**0.025**	0.062	0.413	0.062	**0.036**	**0.065**
Aspect x % ECM BA	0.186	0.267	0.523	0.497	0.764	0.449	0.273	0.422	0.729
FTMT x % ECM BA	0.838	0.166	0.231	0.924	0.753	0.807	0.731	0.771	0.069
Site x FTMT x % ECM BA	0.294	0.303	0.253	0.249	0.061	0.230	0.137	0.114	0.201
Aspect x FTMT x % ECM BA	0.160	0.911	0.556	0.554	0.938	0.909	0.381	0.718	0.320
Site x Aspect x % ECM BA	0.500	0.464	0.377	0.293	0.537	0.418	0.662	0.525	0.634
Site x Aspect x FTMT	0.767	0.458	0.494	0.810	0.687	0.890	0.720	0.426	0.937

Table 10. Results from the forward selection RDA with soil variables conducted on fungal community composition.

Sample Type	Taxon Level	P-value	Adj. R^2	Terms
Soil				
	Guild	0.002	8.1%	C:N
	Family	0.001	10.4%	pH + C:N
	ASV	0.001	3.9%	pH + C:N + Tree species evenness
Root				
	Guild	0.006	3.7%	Forest floor mass
	Family	0.001	5.9%	pH + C:N
	ASV	0.001	4.3%	pH + C:N + Tree species evenness + Forest floor mass
Leaf				
	Guild	0.001	9.5%	pH + Fine root biomass + Soil respiration
	Family	0.001	4.6%	pH + Fine Root Biomass
	ASV	0.001	6.4%	pH + NH_4^+ + NO_3^- + C:N + Fine root biomass + Tree species evenness

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APPENDIX B

CHAPTER III SUPPORTING DATA FOR SOIL FUNGI

Table 11. Results (P-values and Adj. R^2-values) from the RDA on soil fungal community composition for each site. Letters with the Adj. R^2-values indicate: a – variation explained by focal tree species when controlling for species mycorrhizal identity; b – variation explained by the combined mycorrhizal + geographic model excluding focal tree species identity. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type; FT Species = plot focal tree species. Bold values indicate significant or marginally significant terms ($P < 0.07$).

Lake George	ASV		Family		Guild	
	P-value	Adj. R^2	P-value	Adj. R^2	P-value	Adj. R^2
FT species	0.258	0.0%[a]	**0.02**	18.9%[a]	0.393	0.0%[a]
Aspect	0.183	0.0%[b]	0.731	12.3%[b]	0.581	29.1%[b]
FTMT	0.929		0.354		**0.03**	
% ECM BA	0.996		0.14		0.118	
Aspect x FTMT	0.948		0.319		0.388	
Aspect x % ECM BA	0.966		0.377		0.269	
FTMT x % ECM BA	0.951		**0.018**		0.198	
Aspect x FTMT x % ECM BA	0.798		0.168		0.198	
Huntington Forest						
FT species	**0.01**	7.6%[a]	0.305	21.9%[a]	0.845	2.3%[a]
Aspect	**0.025**	6.4%[b]	**0.038**	21.4%[b]	**0.023**	52.9%[b]
FTMT	**0.007**		0.1		**0.001**	
% ECM BA	**0.039**		**0.009**		**0.052**	
Aspect x FTMT	0.801		0.805		0.485	
Aspect x % ECM BA	**0.033**		0.223		0.66	
FTMT x % ECM BA	0.087		0.518		0.139	
Aspect x FTMT x % ECM BA	**0.002**		0.174		0.485	

Shingle Shanty

FT species	0.121	3.4%[a]	0.222	0.0%[a]	0.166	0.0%[a]
Aspect	**0.039**	1.9%[b]	0.076	1.5%[b]	**0.012**	10.6%[b]
FTMT	0.69		0.075		0.25	
% ECM BA	0.311		0.092		0.227	
Aspect x FTMT	0.825		0.673		0.951	
Aspect x % ECM BA	0.706		0.882		0.224	
FTMT x % ECM BA	0.657		0.986		0.63	
Aspect x FTMT x % ECM BA	0.298		0.911		0.354	

Table 12. Selected soil physiochemical properties identified as drivers of soil fungal community composition at each sampling site. Bold values indicate significant or marginally significant terms (P< 0.07).

Site	Taxon Level	P-value	Adj. R^2	Terms
Lake George				
	Guild	**0.045**	7.5%	Tree species richness
	Family	**0.018**	1.8%	C:N
	ASV	**0.004**	0.7%	C:N
Huntington Forest				
	Guild	n.s.	0.0%	
	Family	n.s.	0.0%	
	ASV	n.s.	0.0%	
Shingle Shanty				
	Guild	n.s.	0.0%	
	Family	n.s.	0.0%	
	ASV	n.s.	0.0%	

Table 13. Results (P-values, R^2-values, and AIC scores) from the mixed effect linear modeling for fungal richness in each functional group studied. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph ASV Richness			**ECM Fungal ASV Richness**			**Plant Pathogen ASV Richness**		
	P-value	R^2	AIC	P-value	R^2	AIC	P-value	R^2	AIC
Site	0.230	9.3%	522.7	0.394	15.5%	525.6	**0.001**	28.9%	345.7
Aspect	0.758			**0.005**			0.149		
Site x Aspect	0.137			0.310			**0.008**		
% ECM BA	0.767	9.1%	503.6	**0.000**	25.3%	490.4	**0.004**	32.2%	330.3
FTMT	0.265			0.192			**0.001**		
% ECM BA x FTMT	0.612			0.132			**0.001**		
Site	0.098	32.4%	**401.7**	0.721	36.6%	**387.8**	**0.041**	56.6%	**249.3**
Aspect	0.089			0.275			0.128		
FTMT	**0.050**			0.888			**0.003**		
% ECM BA	0.751			**0.005**			0.109		
Site x Aspect	0.321			0.795			0.133		
Site x FTMT	0.359			0.748			0.623		
Aspect x FTMT	0.153			0.717			0.104		
Site x % ECM BA	0.258			0.312			0.088		
Aspect x % ECM BA	0.129			0.683			0.110		
FTMT x % ECM BA	0.223			0.804			**0.001**		
Site x FTMT x % ECM BA	0.635			0.483			0.668		
Aspect x FTMT x % ECM BA	0.305			0.832			0.122		
Site x Aspect x % ECM BA	0.466			0.696			0.266		
Site x Aspect x FTMT	0.420			0.845			0.349		

Table 14. Results (P-values, R^2-values, and AIC scores) of the generalized mixed effect modeling using a binomial logit distribution for the relative abundance of soil primary saprotrophs, ECM fungi, and plant pathogens. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph Relative Abundance	**ECM Fungal Relative Abundance**	**Plant Pathogen Relative Abundance**
Model	**AIC Score**		
Site-based	5797	17214	14723
Mycorrhizal-based	6265	8726	9357
Combined	**3291**	**5697**	**5594**
R^2-value	67.4%	60.9%	53.2%
Terms	**P-value**		
Site	**< 0.001**	**< 0.001**	**< 0.001**
Aspect	**< 0.001**	**< 0.001**	**0.005**
FTMT	**< 0.001**	**< 0.001**	**< 0.001**
% ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Site x Aspect	**0.008**	**< 0.001**	**< 0.001**
Site x FTMT	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT	**< 0.001**	**0.003**	**< 0.001**
Site x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Site x FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	**< 0.001**	**< 0.001**	**0.006**
Site x Aspect x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**

Table 15. Results (P-values, R^2-values, and AIC scores) of the generalized mixed effect modeling using a binomial logit distribution for the relative abundance of soil primary saprotrophs, ECM fungi, and plant pathogens at each study site. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph Relative Abundance	**ECM Fungal Relative Abundance**	**Plant Pathogen Relative Abundance**
Lake George			
R^2-value	84.9%	74.5%	19.2%
Terms	P-value		
Aspect	**< 0.001**	**< 0.001**	**< 0.001**
FTMT	**< 0.001**	**< 0.001**	**0.007**
% ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
FTMT x % ECM BA	**< 0.001**	**< 0.001**	**0.003**
Aspect x FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Huntington Forest			
R^2-value	66.9%	86.5%	96.3%
Terms	P-value		
Aspect	**< 0.001**	**< 0.001**	**< 0.001**
FTMT	**< 0.001**	**< 0.001**	**< 0.001**
% ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT	**< 0.001**	**< 0.001**	0.873
Aspect x % ECM BA	**< 0.001**	**< 0.001**	0.061
FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	**< 0.001**	**< 0.001**	0.316
Shingle Shanty			
R^2-value	75.1%	31.9%	58.1%
Terms	P-value		
Aspect	**< 0.001**	**< 0.001**	**< 0.001**
FTMT	0.985	**< 0.001**	0.129
% ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**

FTMT x % ECM BA	0.246	**< 0.001**	0.802
Aspect x FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**

Table 16. Soil-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Lake George. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Lake George			Adj. R^2 value %				Relative abundance %			
Phylum	Family	Functional role	Total	% ECM	FTMT	Aspect	AM plot, AM tree	AM plot, ECM tree	ECM plot, AM tree	ECM plot, ECM tree
Ascomycota	Amphisphaeriaceae	Primary saprotroph or plant necrotroph	18.1	2.1	8.8	8.8	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.05
	Archaeorhizomycetaceae	Primary saprotroph	18.8	0.7	0.1	17.3	0.2 ± 0.46	0 ± 0	0 ± 0	0.22 ± 0.56
	Aspergillaceae	Primary Saprotroph	16.5	8.5	9.1	9.1	0.02 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	Chaetomiaceae	Primary or dung saprotroph	23.5	12.8	16.4	3.8	0.19 ± 0.46	0 ± 0	0 ± 0	0 ± 0
	Dermateaceae	Primary saprotroph, plant necrotroph, various, or unknown	17.0	1.2	0.1	12.4	0.04 ± 0.12	0 ± 0	0 ± 0	0.05 ± 0.18
	Geoglossaceae	Primary saprotroph	43.5	33.1	42.0	0.0	3 ± 1.7	0.74 ± 0	2.65 ± 0	0.69 ± 0.69
	Gloniaceae	Ectomycorrhizal	20.7	16.0	17.5	4.5	0.7 ± 0.58	1.65 ± 0	1.17 ± 0	1.86 ± 1.58
	Helotiaceae	Primary or wood saprotroph, ectomycorrhizal, plant necrotroph, endophyte, ericoid mycorrhizal, various, or unknown	39.3	25.0	8.4	8.1	0.58 ± 0.74	0 ± 0	0.16 ± 0	1.35 ± 1.28
	Herpotrichiellaceae	Primary saprotroph, endophyte, animal pathogen, plant necrotroph, or unknown	24.4	3.5	16.4	2.0	2.17 ± 1.34	0.16 ± 0	2.1 ± 0	1.36 ± 1.27
	Lasiosphaeriaceae	Primary or dung saprotroph	31.9	7.2	0.1	5.7	0.24 ± 0.59	0 ± 0	0 ± 0	0.14 ± 0.27
	Lipomycetaceae	Primary saprotroph	17.1	11.2	4.4	4.4	0.06 ± 0.2	0 ± 0	0 ± 0	0 ± 0
	Orbiliaceae	Primary or wood saprotroph	17.9	10.7	8.8	8.8	0.07 ± 0.17	0 ± 0	0 ± 0	0 ± 0
	Plectosphaerellaceae	Plant necrotroph	17.1	11.2	4.4	4.4	0.01 ± 0.03	0 ± 0	0 ± 0	0 ± 0
	Pleomassariaceae	Primary saprotroph or various	16.8	1.6	7.9	7.9	0 ± 0	0 ± 0	0 ± 0	0.13 ± 0.36
	Pleosporaceae	Plant necrotroph	17.1	11.2	4.4	4.4	0.02 ± 0.07	0 ± 0	0 ± 0	0 ± 0
	Rhytismataceae	Plant necrotroph or various	17.1	11.2	4.4	4.4	0.09 ± 0.3	0 ± 0	0 ± 0	0 ± 0
	Trichocomaceae	Primary saprotroph	30.0	27.5	13.6	0.4	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.08
	Trichomeriaceae	Dung saprotroph, epiphyte, or endophyte	15.6	6.8	0.4	0.4	0.1 ± 0.33	0 ± 0	0 ± 0	0.02 ± 0.05
Basidiomycota	Amanitaceae	Ectomycorrhizal	35.1	30.5	18.9	6.1	0.04 ± 0.09	0 ± 0	0.7 ± 0	2.45 ± 5.28
	Atheliaceae	Primary saprotroph, ectomycorrhizal, plant necrotroph, or various	39.0	29.3	31.6	10.0	1.18 ± 2.2	3.22 ± 0	1.25 ± 0	14.82 ± 21.8

	Clavariaceae	Primary saprotroph or various	29.7	6.0	22.1	0.4	9.05 ± 8.26	3.79 ± 0	9.59 ± 0	3.82 ± 4.14
	Clavulinaceae	Ectomycorrhizal or various	18.4	12.4	10.5	3.8	0.24 ± 0.62	0 ± 0	0 ± 0	1.93 ± 4.77
	Cyphellaceae	Primary saprotroph	24.7	13.2	9.1	9.1	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.1
	Entolomataceae	Primary saprotroph, ectomycorrhizal, or various	37.1	31.5	35.0	0.0	1.77 ± 1.68	0 ± 0	0.94 ± 0	0.46 ± 0.6
	Exidiaceae	Primary saprotroph	22.2	20.3	9.1	0.0	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Ganodermataceae	Wood saprotroph or various	24.9	22.1	18.4	4.2	0.09 ± 0.15	0 ± 0	0 ± 0	0 ± 0
	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various, or unknown	34.9	33.5	17.9	0.0	31.1 ± 20.1	8.33 ± 0	1.79 ± 0	12.19 ± 17.2
	Omphalotaceae	Primary or wood saprotroph	18.1	10.7	9.1	9.1	0.08 ± 0.18	0 ± 0	0 ± 0	0 ± 0
	Russulaceae	Ectomycorrhizal	34.0	23.0	19.8	6.7	5.11 ± 4.43	9.15 ± 0	10.91 ± 0	16.43 ± 15.01
	Schizoporaceae	Primary or wood saprotroph	19.4	12.6	4.4	4.4	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.07
	Strophariaceae	Primary or wood saprotroph, various, or unknown	21.2	13.6	4.4	4.4	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.12
	Suillaceae	Ectomycorrhizal	22.9	20.7	12.4	1.1	0.1 ± 0.35	0 ± 0	0 ± 0	0.45 ± 0.61
	Trichosporonaceae	Primary saprotroph, animal pathogen, or unknown	17.7	2.6	9.1	9.1	0.01 ± 0.03	0 ± 0	0 ± 0	0 ± 0
	Trimorphomycetaceae	Fungal parasite	30.5	2.0	1.7	29.3	0.2 ± 0.29	0 ± 0	0 ± 0	0.13 ± 0.27
	Tritirachiaceae	Primary saprotroph	21.2	13.6	4.4	4.4	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.12
Chytridiomycota	Chytridiaceae	Various	16.5	8.5	9.1	9.1	0.02 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	Rhizophydiaceae	Plant necrotroph	16.1	14.4	10.3	2.7	0.93 ± 2.14	0 ± 0	0 ± 0	0.02 ± 0.05
Glomeromycota	Diversisporaceae	Arbuscular mycorrhizal	16.9	7.0	6.9	6.9	0.09 ± 0.27	0 ± 0	0 ± 0	0 ± 0
	Glomeraceae	Arbuscular mycorrhizal	18.7	16.1	10.6	3.7	0.31 ± 0.51	0 ± 0	0 ± 0	0.06 ± 0.14
Kickxellomycota	Kickxellaceae	Primary saprotroph	24.8	11.7	14.1	14.1	0.03 ± 0.05	0 ± 0	0 ± 0	0 ± 0
Zygomycota	Mortierellaceae	Primary saprotroph	26.1	0.2	7.4	3.3	6.88 ± 2.12	4.29 ± 0	49.34 ± 0	6.45 ± 5.88
Mucoromycota	Umbelopsidaceae	Primary saprotroph	33.5	18.3	15.2	10.9	0.47 ± 0.56	0.25 ± 0	0.62 ± 0	1.03 ± 0.66

Table 17. Soil-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Huntington Forest. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Huntington Forest			Adj. R^2 value %				Relative abundance %			
Phylum	Family	Functional role	Total	% ECM	FTMT	Aspect	AM plot, AM tree	AM plot, ECM tree	ECM plot, AM tree	ECM plot, ECM tree
Ascomycota	Amorosiaceae	Unknown	22.2	14.2	10.3	8.7	0.04 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	Archaeorhizomycetaceae	Primary saprotroph	18.7	7.5	11.3	7.6	0.59 ± 0.24	1.32 ± 0	1.02 ± 1.09	0.4 ± 0.58
	Aspergillaceae	Primary saprotroph	16.3	1.0	4.2	5.0	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Beltraniaceae	Primary saprotroph	20.3	3.3	1.5	7.5	0 ± 0	0 ± 0	0.07 ± 0.17	0.01 ± 0.03
	Cephalothecaceae	Primary or wood saprotroph	15.8	5.8	14.7	0.1	0.07 ± 0.15	0 ± 0	0.03 ± 0.05	0 ± 0
	Chaetomellaceae	Primary saprotroph, plant necrotroph, or unknown	26.1	9.3	22.7	3.7	0.08 ± 0.11	0 ± 0	0.09 ± 0.13	0 ± 0
	Chaetosphaeriaceae	Primary or wood saprotroph, or unknown	26.7	0.6	17.2	0.3	0.03 ± 0.07	0 ± 0	0.2 ± 0.11	0.05 ± 0.15
	Cyphellophoraceae	Animal pathogen or unknown	24.9	14.3	5.0	5.0	0.02 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	Debaryomycetaceae	Primary saprotroph	20.0	1.6	9.7	0.4	0 ± 0	0 ± 0	0.06 ± 0.1	0 ± 0
	Didymellaceae	Plant necrotroph or various	25.8	3.3	1.0	25.0	0.06 ± 0.14	0.26 ± 0	0.07 ± 0.11	0.03 ± 0.1
	Elaphomycetaceae	Primary saprotroph or ectomycorrhizal	35.3	18.1	29.9	0.1	0 ± 0	0.26 ± 0	0.13 ± 0.31	1.29 ± 1.85
	Fenestellaceae	Primary saprotroph	24.5	18.8	9.5	1.0	0.07 ± 0.12	0 ± 0	0 ± 0	0 ± 0
	Geoglossaceae	Primary saprotroph	26.3	2.4	5.3	21.6	2.21 ± 2.42	0.09 ± 0	2.66 ± 6.19	1.42 ± 3.21
	Gloniaceae	Ectomycorrhizal	25.5	23.9	9.9	0.2	0.35 ± 0.51	0.79 ± 0	1.7 ± 2.41	1.77 ± 1.86
	Helotiales (inc. sed.)	Primary saprotroph, ectomycorrhizal, plant necrotroph, endophyte, various, or unknown	21.3	0.0	3.0	17.4	0.73 ± 0.7	0.18 ± 0	1.93 ± 1.57	1.11 ± 1.63
	Herpotrichiellaceae	Primary saprotroph, plant necrotroph, animal pathogen, endophyte, or unknown	16.8	8.6	14.5	1.2	2.51 ± 1.76	0.44 ± 0	2.25 ± 1.28	1.44 ± 1.16
	Hyaloscyphaceae	Primary saprotroph, fungal parasite, endophyte, or various	18.1	2.0	5.6	7.5	1.42 ± 1.15	0 ± 0	1.99 ± 1.97	0.98 ± 0.68
	Hypocreaceae	Primary saprotroph	30.4	13.2	0.0	21.6	0 ± 0	0 ± 0	0.13 ± 0.15	0.08 ± 0.14
	Hypocreales (inc. sed.)	Primary saprotroph	51.6	16.1	0.0	42.7	0.02 ± 0.04	0 ± 0	0.33 ± 0.38	0.21 ± 0.41
	Lasiosphaeriaceae	Primary or dung saprotroph	19.0	15.8	8.4	0.1	0.26 ± 0.35	0 ± 0	0.01 ± 0.03	0.01 ± 0.05

	Melanommataceae	Wood saprotroph	22.1	13.5	8.7	10.4	0 ± 0	0 ± 0	0 ± 0	0.06 ± 0.14
	Mycosphaerellaceae	Plant necrotroph, lichen, or various	44.3	4.6	28.0	13.8	0.07 ± 0.08	0 ± 0	0.06 ± 0.11	0 ± 0
	Myxotrichaceae	Ericoid mycorrhizal or various	19.1	0.2	1.9	16.3	0.13 ± 0.17	0.35 ± 0	0.17 ± 0.42	0.03 ± 0.07
	Pezizaceae	Primary saprotroph, ectomycorrhizal, or various	37.3	30.0	22.8	0.3	0.15 ± 0.24	0 ± 0	0.21 ± 0.37	1.36 ± 1.83
	Pyronemataceae	Primary saprotroph, ectomycorrhizal, various, or unknown	32.6	0.5	4.3	26.2	0.63 ± 0.86	1.5 ± 0	0.75 ± 0.87	0.39 ± 0.73
	Sordariomycetes (inc. sed.)	Unknown	17.6	15.2	8.7	0.0	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.03
	Sporocadaceae	Plant necrotroph	19.8	9.0	17.4	1.8	0 ± 0	0 ± 0	0 ± 0	0.06 ± 0.11
	Sporormiaceae	Primary saprotroph	16.3	1.0	4.2	5.0	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.05
	Taphrinaceae	Plant biotroph	21.2	5.0	8.4	8.4	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.05
	Tuberaceae	Ectomycorrhizal	21.3	2.7	5.9	12.2	0.04 ± 0.08	0 ± 0	0.03 ± 0.07	0.26 ± 0.61
	Tubeufiaceae	Primary or wood saprotroph, various, or unknown	28.9	3.1	10.1	10.1	0 ± 0	0 ± 0	0.04 ± 0.07	0 ± 0
	Xylariales (inc. sed.)	Primary saprotroph, plant necrotroph, or unknown	15.1	2.0	0.3	10.0	0.05 ± 0.11	0 ± 0	0.07 ± 0.17	0.27 ± 0.9
Basidiomycota	Agaricaceae	Primary saprotroph	32.7	0.0	4.4	27.2	0.17 ± 0.37	0 ± 0	0.15 ± 0.27	0.05 ± 0.1
	Amanitaceae	Ectomycorrhizal	27.3	27.2	5.6	1.1	2.33 ± 3.04	2.65 ± 0	4.55 ± 5.49	4.79 ± 3.54
	Atheliaceae	Primary saprotroph, ectomycorrhizal, plant necrotroph, or various	19.9	6.2	0.3	8.5	0.25 ± 0.24	0 ± 0	1.02 ± 0.96	1.37 ± 2.27
	Boletaceae	Ectomycorrhizal	36.4	1.0	0.2	36.0	0.69 ± 0.81	0.26 ± 0	1.15 ± 0.69	1.33 ± 1.31
	Bulleribasidiaceae	Fungal parasite	30.1	12.9	4.2	4.2	0 ± 0	0.35 ± 0	0 ± 0	0 ± 0
	Cantharellales (inc. sed.)	Ectomycorrhizal or lichen	18.2	15.9	4.3	5.6	0 ± 0	0 ± 0	0.01 ± 0.03	0.15 ± 0.44
	Clavariaceae	Primary saprotroph or various	21.2	8.1	1.7	17.5	4.79 ± 4.28	20.72 ± 0	5.58 ± 6.21	5.57 ± 15.75
	Clavariaceae	Various	21.2	8.1	1.7	17.5	4.79 ± 4.28	20.72 ± 0	5.58 ± 6.21	5.57 ± 15.75
	Clavulinaceae	Ectomycorrhizal or various	34.8	1.0	25.6	6.4	0.3 ± 0.34	0.26 ± 0	0.65 ± 0.86	6.25 ± 10.05
	Cortinariaceae	Primary saprotroph or ectomycorrhizal	24.3	16.3	18.6	0.3	2.17 ± 4.31	0.97 ± 0	1.1 ± 2.34	4.88 ± 5.37
	Crepidotaceae	Wood saprotroph	25.7	17.5	0.0	8.7	0.06 ± 0.14	0.44 ± 0	0 ± 0	0 ± 0
	Cyphellaceae	Primary saprotroph	19.5	10.9	4.2	4.2	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Entolomataceae	Primary saprotroph, ectomycorrhizal, or various	42.6	16.3	28.7	6.0	2.51 ± 3.09	0.53 ± 0	3.82 ± 3.33	0.68 ± 0.63
	Hebelomataceae	Ectomycorrhizal	16.8	1.1	5.0	4.2	0 ± 0	0 ± 0	0.04 ± 0.1	0 ± 0
	Hyaloriaceae	Wood saprotroph	35.3	26.1	0.0	0.3	0.02 ± 0.04	0 ± 0	0.14 ± 0.24	0.12 ± 0.26
	Hydnangiaceae	Ectomycorrhizal	22.1	21.0	2.1	3.8	0.49 ± 1.1	0 ± 0	0.19 ± 0.34	0.44 ± 0.58
	Hydnodontaceae	Primary or wood saprotroph	34.6	0.1	28.0	0.8	0.56 ± 1.02	0 ± 0	1.51 ± 1.64	0.05 ± 0.09

	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various, or unknown	74.0	45.2	58.4	6.2	29.8 ± 12.5	10.93 ± 0	11.95 ± 10.4	1.45 ± 3.04
	Hymenochaetaceae	Primary saprotroph, ectomycorrhizal, or plant necrotroph	16.8	1.1	5.0	4.2	0 ± 0	0 ± 0	0.06 ± 0.14	0 ± 0
	Hymenogastraceae	Ectomycorrhizal	34.3	18.1	8.7	7.7	0.03 ± 0.07	0 ± 0	0 ± 0	0.72 ± 1.65
	Inocybaceae	Ectomycorrhizal	15.0	4.3	5.0	10.5	1.57 ± 3.1	18.87 ± 0	5.62 ± 6.54	7.53 ± 9.22
	Lachnocladiaceae	Primary saprotroph	19.5	10.9	4.2	4.2	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.24
	Malasseziaceae	Animal pathogen	19.7	0.6	5.6	13.0	0.07 ± 0.1	0 ± 0	0.06 ± 0.1	0.05 ± 0.15
	Piskurozymaceae	Unknown	24.7	7.4	21.7	1.3	1.71 ± 1.49	0.09 ± 0	1.29 ± 1.17	0.55 ± 0.42
	Porotheleaceae	Wood saprotroph	18.8	7.3	6.0	6.0	0 ± 0	0 ± 0	0 ± 0	0.76 ± 2.4
	Russulaceae	Ectomycorrhizal	29.0	13.3	13.8	14.5	6.43 ± 8.81	15.61 ± 0	12.31 ± 7.26	19.2 ± 15.16
	Sebacinaceae	Ectomycorrhizal	24.5	11.8	22.2	0.3	1.06 ± 2.22	0.35 ± 0	1.4 ± 1.61	5.2 ± 6.35
	Sporidiobolaceae	Primary saprotroph or plant necrotroph	35.0	20.9	1.2	7.2	0.02 ± 0.04	0.53 ± 0	0 ± 0	0 ± 0
	Thelephoraceae	Primary saprotroph, ectomycorrhizal, or various	29.8	0.8	12.3	16.1	1.8 ± 1.13	0.18 ± 0	2.02 ± 1.34	1.23 ± 1.21
	Trichosporonaceae	Primary saprotroph, animal pathogen, or unknown	18.8	0.0	10.0	4.6	0.04 ± 0.1	0 ± 0	0.15 ± 0.13	0.04 ± 0.11
	Trimorphomycetaceae	Fungal parasite	15.7	0.8	14.5	0.3	0.37 ± 0.44	0.53 ± 0	0.44 ± 0.43	0.11 ± 0.22
Chytridiomycota	Chytriomycetaceae	Various	33.5	0.3	13.7	16.3	0 ± 0	0 ± 0	0 ± 0	0.11 ± 0.19
	Lobulomycetaceae	Fungal parasite	21.5	14.4	7.2	2.3	0 ± 0	0 ± 0	0.04 ± 0.09	0.06 ± 0.1
Glomeromycota	Archaeosporaceae	Arbuscular mycorrhizal	19.5	10.9	4.2	4.2	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
Zygomycota	Mortierellaceae	Primary saprotroph	23.2	13.1	19.4	0.0	18.69 ± 5.7	18.34 ± 0	21.07 ± 5.86	14.8 ± 5.14
Mucoromycota	Umbelopsidaceae	Primary saprotroph	35.4	12.7	17.1	9.2	0.23 ± 0.24	0 ± 0	0.07 ± 0.13	0.03 ± 0.08

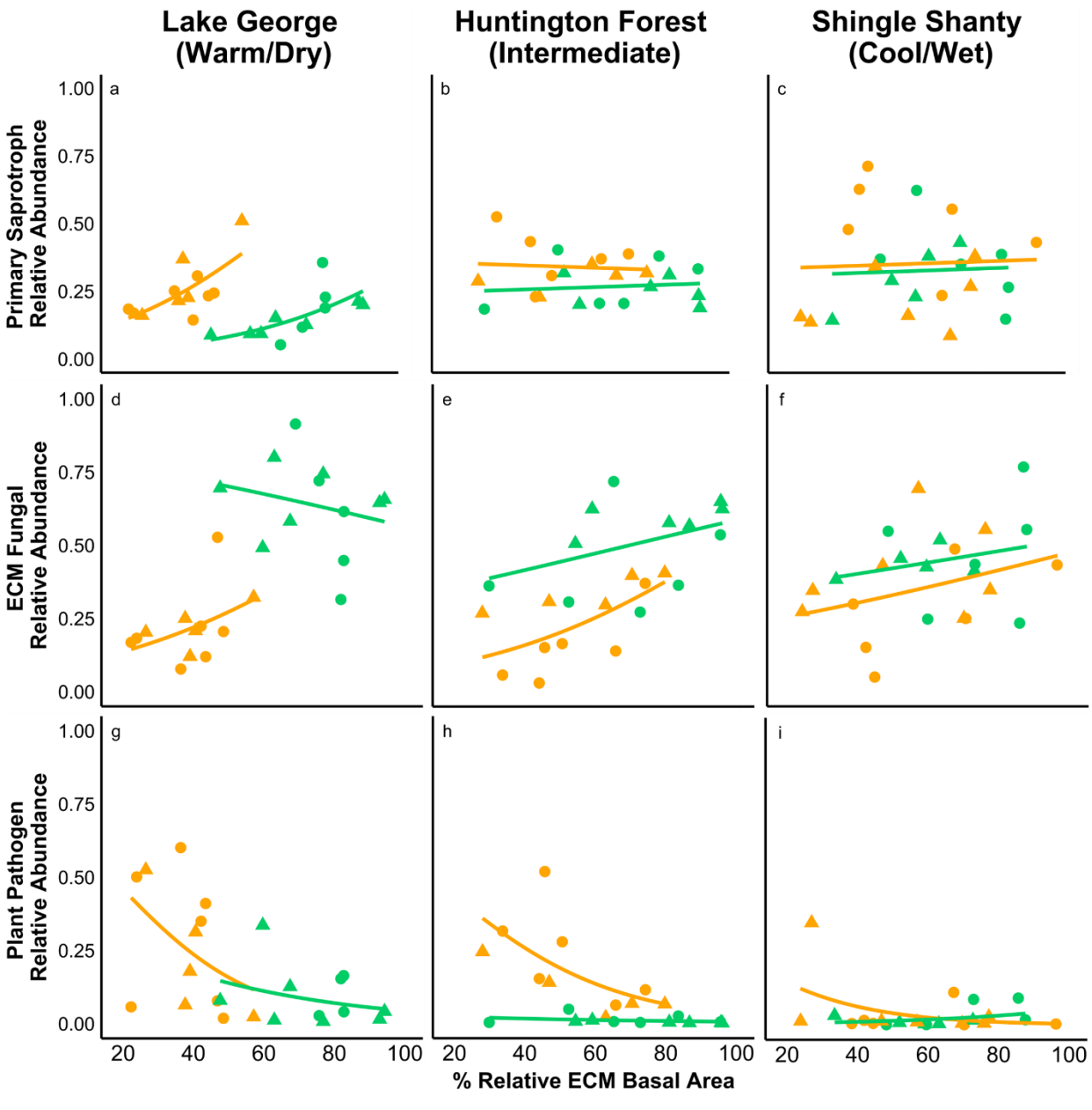
Table 18. Soil-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Shingle Shanty. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Shingle Shanty			Adj. R^2 value %				Relative abundance %			
Phylum	Family	Functional role	Total	% ECM	FTMT	Aspect	AM plot, AM tree	AM plot, ECM tree	ECM plot, AM tree	ECM plot, ECM tree
Ascomycota	Archaeorhizomycetaceae	Primary saprotroph	24.8	0.4	3.6	17.4	0.78 ± 1.47	0.06 ± 0.08	0.26 ± 0.35	0.22 ± 0.24
	Bionectriaceae	Primary saprotroph or unknown	25.4	4.4	0.2	13.9	0.03 ± 0.05	0 ± 0	0 ± 0	0.02 ± 0.05
	Chaetomiaceae	Primary or dung saprotroph	27.2	2.4	0.8	17.9	0.07 ± 0.13	0 ± 0	0.02 ± 0.06	0.05 ± 0.16
	Clavicipitaceae	Primary saprotroph or animal pathogen	16.8	5.2	4.1	7.6	0.02 ± 0.05	0.12 ± 0.17	0.01 ± 0.03	0.03 ± 0.06
	Cordycipitaceae	Primary saprotroph or animal pathogen	29.8	0.6	3.1	24.9	0.03 ± 0.07	0 ± 0	0.01 ± 0.03	0.06 ± 0.1
	Cryphonectriaceae	Plant biotroph	17.8	0.1	16.4	0.0	0.03 ± 0.07	0 ± 0	0.05 ± 0.07	0 ± 0
	Dermateaceae	Primary saprotroph, plant necrotroph, various, or unknown	18.5	0.4	18.4	0.0	0.15 ± 0.38	0.08 ± 0.11	0 ± 0	0.55 ± 0.85
	Elaphomycetaceae	Primary saprotroph or ectomycorrhizal	19.2	0.0	17.6	0.3	0.46 ± 0.72	0 ± 0	0 ± 0	1.14 ± 1.25
	Helminthosphaeriaceae	Primary saprotroph	19.2	8.5	5.1	4.4	0 ± 0	0.06 ± 0.08	0 ± 0	0 ± 0
	Helotiaceae	Primary or wood saprotroph, ectomycorrhizal, ericoid mycorrhizal, plant necrotroph, endophyte, various, or unknown	27.9	8.8	12.7	1.4	1.61 ± 1.11	2.13 ± 1.19	1.01 ± 0.57	2.07 ± 1.51
	Herpotrichiellaceae	Primary saprotroph, plant necrotroph, animal pathogen, endophyte, or unknown	42.5	38.7	8.2	9.6	2.28 ± 1.61	3.46 ± 2.84	1.14 ± 0.43	0.67 ± 0.79
	Hypocreaceae	Primary saprotroph	23.6	21.8	0.7	0.0	0.51 ± 0.58	0.18 ± 0.25	0.04 ± 0.06	0.27 ± 0.52
	Melanommataceae	Wood saprotroph	19.5	0.1	16.9	1.6	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.04
	Pezizaceae	Primary saprotroph, ectomycorrhizal, or various	28.6	7.9	7.3	8.7	0.1 ± 0.17	0 ± 0	0 ± 0	0 ± 0
	Rhytismataceae	Plant necrotroph or various	16.3	7.3	10.6	0.1	0 ± 0	0 ± 0	0 ± 0	0.08 ± 0.16
	Saccharomycetales (inc. sed.)	Primary saprotroph	16.6	10.4	6.0	7.1	0.14 ± 0.33	0 ± 0	0.01 ± 0.03	0 ± 0
	Sarcosomataceae	Primary or wood saprotroph	19.5	12.5	8.9	6.1	0.33 ± 0.52	0 ± 0	0.01 ± 0.03	0.01 ± 0.03
	Sordariales (inc. sed.)	Primary saprotroph	15.3	2.7	3.7	4.4	0 ± 0	0 ± 0	0.05 ± 0.13	0 ± 0
	Sympoventuriaceae	Primary saprotroph	24.4	14.4	0.6	17.3	0.12 ± 0.28	0.06 ± 0.08	0.04 ± 0.09	0.02 ± 0.06
	Taphrinaceae	Plant biotroph	19.2	8.5	5.1	4.4	0 ± 0	0.06 ± 0.08	0 ± 0	0 ± 0

	Tuberaceae	Ectomycorrhizal	22.1	15.6	2.5	1.4	0 ± 0	0 ± 0	0.06 ± 0.1	0.01 ± 0.03
	Venturiaceae	Primary saprotroph, plant necrotroph, various, or unknown	21.1	2.9	1.0	18.8	0.14 ± 0.19	0.06 ± 0.08	0.05 ± 0.08	0.11 ± 0.13
	Xylariales (inc. sed.)	Primary saprotroph, plant necrotroph, or unknown	17.8	17.7	0.6	1.0	0.06 ± 0.14	0.04 ± 0.06	0 ± 0	0 ± 0
Basidiomycota	Amanitaceae	Ectomycorrhizal	15.0	1.4	0.6	9.2	2.29 ± 2.18	0.16 ± 0.11	9.62 ± 10.57	6.13 ± 5.63
	Boletaceae	Ectomycorrhizal	26.1	7.7	0.5	9.3	1.19 ± 1.79	0.82 ± 0.36	2.03 ± 0.97	1.35 ± 1.3
	Chrysozymaceae	Primary saprotroph	17.5	15.6	3.7	4.4	0.02 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	Clavulinaceae	Ectomycorrhizal or various	24.9	13.8	1.1	2.2	0.72 ± 1.11	0.42 ± 0.59	3.36 ± 3.88	1.45 ± 2.09
	Coniophoraceae	Wood saprotroph	15.4	13.1	3.7	4.4	0.01 ± 0.03	0 ± 0	0 ± 0	0 ± 0
	Cortinariaceae	Primary saprotroph or ectomycorrhizal	16.2	0.1	14.6	0.1	1.79 ± 2.18	13.01 ± 10.0	1.18 ± 0.72	6.87 ± 10.76
	Entolomataceae	Primary saprotroph, ectomycorrhizal, or various	46.0	30.0	2.2	29.9	3.97 ± 4.85	7.44 ± 10.52	1.28 ± 1.62	1.52 ± 3.9
	Exidiaceae	Primary saprotroph	15.3	2.7	3.7	4.4	0 ± 0	0 ± 0	0.01 ± 0.03	0 ± 0
	Hyaloriaceae	Wood saprotroph	18.7	0.4	16.7	2.5	0 ± 0	0.24 ± 0.34	0 ± 0	0.11 ± 0.22
	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various, or unknown	32.5	18.1	18.0	9.1	10.6 ± 16.0	2.02 ± 2.86	2.35 ± 4.19	0.13 ± 0.39
	Hymenogastraceae	Ectomycorrhizal	15.4	1.8	5.1	4.4	0 ± 0	0.24 ± 0.34	0 ± 0	0 ± 0
	Jaapiaceae	Primary saprotroph	21.8	15.7	7.6	0.1	0.05 ± 0.07	0 ± 0	0 ± 0	0 ± 0
	Kriegeriaceae	Unknown	17.1	7.0	1.1	4.8	0.23 ± 0.5	0 ± 0	0 ± 0	0.05 ± 0.16
	Meruliaceae	Primary or wood saprotroph	16.5	0.1	6.8	8.1	0.05 ± 0.11	0 ± 0	0.17 ± 0.44	0 ± 0
	Omphalotaceae	Primary or wood saprotroph	21.4	11.5	0.1	15.9	0.27 ± 0.66	0 ± 0	0.01 ± 0.03	0.05 ± 0.09
	Podoscyphaceae	Primary saprotroph	21.8	5.3	16.5	1.0	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.08
	Russulaceae	Ectomycorrhizal	33.5	16.2	20.7	0.2	8.24 ± 4.74	28.56 ± 18.2	20.22 ± 13.5	23.95 ± 8.49
	Sebacinaceae	Ectomycorrhizal	17.7	16.4	0.0	2.3	1.12 ± 2.58	0 ± 0	2.25 ± 3.09	2.33 ± 3.44
	Strophariaceae	Primary or wood saprotroph, various, or unknown	30.3	17.7	3.8	20.5	0.53 ± 0.78	1.13 ± 1.6	0.35 ± 0.76	0.11 ± 0.26
	Tremellaceae	Fungal parasite	16.1	7.4	4.9	10.2	0.02 ± 0.04	0 ± 0	0 ± 0	0.11 ± 0.29
	Xenasmataceae	Primary saprotroph	21.8	21.2	0.3	3.7	0.23 ± 0.22	0.18 ± 0.25	0.07 ± 0.12	0.09 ± 0.12
Chytridiomycota	Rhizophydiaceae	Plant necrotroph	15.4	10.2	8.6	1.7	0 ± 0	0 ± 0	0 ± 0	0.17 ± 0.45
	Powellomycetaceae	Unknown	15.4	1.8	5.1	4.4	0 ± 0	0.04 ± 0.06	0 ± 0	0 ± 0
Glomeromycota	Archaeosporaceae	Arbuscular mycorrhizal	15.3	2.7	3.7	4.4	0 ± 0	0 ± 0	0.01 ± 0.03	0 ± 0
	Glomeraceae	Arbuscular mycorrhizal	34.0	15.0	25.6	4.1	0.12 ± 0.13	0 ± 0	0.02 ± 0.04	0 ± 0
Zygomycota	Mortierellaceae	Primary saprotroph	37.2	1.7	2.7	35.3	26.5 ± 16.0	26.3 ± 11.43	20.87 ± 11.9	25.66 ± 7.91

Mucoromycota	Umbelopsidaceae	Primary saprotroph	44.4	2.8	19.3	17.2	0.38 ± 0.6	0 ± 0	0.08 ± 0.09	0.04 ± 0.07
Rozellomycota	Rozellomycotina (inc. sed.)	Various	21.0	0.3	10.3	8.7	0 ± 0	0.06 ± 0.08	0 ± 0	0.03 ± 0.09

Figure 14. Relative abundance changes among functional groups of soil-associated fungi along a gradient of mycorrhizal dominance at each study site. Relative abundance values are displayed as decimals (0 – 1). Colors correspond to plot focal tree mycorrhizal type (gold = AM focal trees, green = ECM focal trees) and shapes correspond to slope aspect (circles = northern-facing slopes, triangles = southern-facing slopes).



APPENDIX C

CHAPTER III SUPPORTING DATA FOR ROOT FUNGI

Table 19. Results (P-values and Adj. R^2-values) from the RDA on root fungal community composition for each site. Letters with the Adj. R^2-values indicate: a – variation explained by focal tree species when controlling for species mycorrhizal identity; b – variation explained by the combined mycorrhizal + geographic model excluding focal tree species identity. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type; FT Species = plot focal tree species. Bold values indicate significant or marginally significant terms (P< 0.07).

Lake George	ASV		Family		Guild	
	P-value	Adj. R^2	P-value	Adj. R^2	P-value	Adj. R^2
FT species	0.404	0.8%[a]	0.423	0.0%[a]	0.251	0.0%[a]
Aspect	0.083	1.1%b	0.216	12.6%b	0.087	7.0%b
FTMT	0.984		0.166		**0.024**	
% ECM BA	0.719		**0.059**		0.406	
Aspect x FTMT	0.939		0.443		0.533	
Aspect x % ECM BA	0.73		0.25		0.331	
FTMT x % ECM BA	0.32		**0.018**		0.524	
Aspect x FTMT x % ECM BA	0.077		0.1		0.73	
Huntington Forest						
FT species	**0.019**	4.3%[a]	0.173	0.0%[a]	0.207	20.5%[a]
Aspect	**0.006**	3.9%[b]	0.099	2.6%[b]	0.205	20.3%[b]
FTMT	0.086		**0.023**		**0.02**	
% ECM BA	0.062		0.675		0.621	
Aspect x FTMT	0.679		0.793		0.851	
Aspect x % ECM BA	0.126		0.771		0.757	
FTMT x % ECM BA	0.117		0.685		0.182	
Aspect x FTMT x % ECM BA	0.255		0.838		0.484	

Shingle Shanty

FT species	0.123	3.4%[a]	0.173	3.7%[a]	0.979	0.0%[a]
Aspect	**0.05**	2.2%[b]	0.848	0.0%[b]	0.601	0.0%[b]
FTMT	0.146		0.49		0.944	
% ECM BA	**0.036**		**0.015**		0.176	
Aspect x FTMT	0.852		0.89		0.233	
Aspect x % ECM BA	0.488		0.855		0.703	
FTMT x % ECM BA	0.987		0.808		0.329	
Aspect x FTMT x % ECM BA	0.308		0.968		0.643	

Table 20. Selected soil physiochemical properties identified as drivers of root fungal community composition at each sampling site. Bold values indicate significant or marginally significant terms (P< 0.07).

Site	Taxon Level	P-value	Adj. R^2	Terms
Lake George				
	Guild	n.s.	0.0%	
	Family	n.s.	0.0%	
	ASV	**0.009**	0.9%	C:N
Huntington Forest				
	Guild	n.s.	0.0%	
	Family	n.s.	0.0%	
	ASV	n.s.	0.0%	
Shingle Shanty				
	Guild	n.s.	0.0%	
	Family	n.s.	0.0%	
	ASV	n.s.	0.0%	

Table 21. Results (P-values, R^2-values, and AIC scores) from the mixed effect linear modeling for fungal richness in each functional group studied. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph ASV Richness			**ECM Fungal ASV Richness**			**Plant Pathogen ASV Richness**		
	P-value	R^2	AIC	P-value	R^2	AIC	P-value	R^2	AIC
Site	0.461	9.6%	503.5	0.146	6.6%	458.1	0.386	22.3%	316.0
Aspect	**0.036**			0.922			**0.012**		
Site x Aspect	0.729			0.776			**0.017**		
% ECM BA	0.547	2.0%	485.2	**0.000**	34.4%	417.3	0.255	2.4%	319.1
FTMT	0.380			0.984			0.823		
% ECM BA x FTMT	0.337			0.739			0.757		
Site	0.354	21.8%	**378.5**	0.464	46.0%	**329.0**	0.240	35.4%	**249.2**
Aspect	**0.028**			0.492			0.759		
FTMT	0.312			**0.051**			0.527		
% ECM BA	0.437			**0.001**			0.710		
Site x Aspect	0.390			0.223			0.243		
Site x FTMT	0.223			0.130			0.770		
Aspect x FTMT	0.422			0.513			0.557		
Site x % ECM BA	0.282			0.559			0.220		
Aspect x % ECM BA	**0.058**			0.508			0.845		
FTMT x % ECM BA	0.332			**0.063**			0.397		
Site x FTMT x % ECM BA	0.142			**0.066**			0.922		
Aspect x FTMT x % ECM BA	0.571			0.931			0.258		
Site x Aspect x % ECM BA	0.242			0.252			**0.051**		
Site x Aspect x FTMT	0.215			0.241			0.551		

Table 22. Results (P-values, R^2-values, and AIC scores) of the generalized mixed effect modeling using a binomial logit distribution for the relative abundance of root primary saprotrophs, ECM fungi, and plant pathogens. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph Relative Abundance	**ECM Fungal Relative Abundance**	**Plant Pathogen Relative Abundance**
Model	AIC Score		
Site-based	6578	9871	6458
Mycorrhizal-based	5527	7490	5443
Combined	**4356**	**4447**	**3279**
R^2-value	57.3%	70.6%	44.0%
Terms	P-value		
Site	**< 0.001**	**0.03**	**< 0.001**
Aspect	**0.01**	**< 0.001**	**< 0.001**
FTMT	**0.01**	**< 0.001**	**0.04**
% ECM BA	**< 0.001**	**0.04**	**< 0.001**
Site x Aspect	**< 0.001**	**< 0.001**	**< 0.001**
Site x FTMT	0.66	**< 0.001**	**< 0.001**
Aspect x FTMT	0.26	0.74	**< 0.001**
Site x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x % ECM BA	0.42	0.64	0.64
FTMT x % ECM BA	0.78	**< 0.001**	0.62
Site x FTMT x % ECM BA	**0.03**	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	**0.01**	0.53	**< 0.001**
Site x Aspect x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**

Table 23. Results (P-values, R^2-values, and AIC scores) of the generalized mixed effect modeling using a binomial logit distribution for the relative abundance of root primary saprotrophs, ECM fungi, and plant pathogens at each study site. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph Relative Abundance	**ECM Fungal Relative Abundance**	**Plant Pathogen Relative Abundance**
Lake George			
R^2-value	52.3%	57.0%	31.1%
Terms	P-value		
Aspect	**< 0.001**	**< 0.001**	0.820
FTMT	**< 0.001**	**< 0.001**	**< 0.001**
% ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**< 0.001**	**< 0.001**	**0.032**
FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Huntington Forest			
R^2-value	45.9%	40.4%	56.0%
Terms	P-value		
Aspect	**< 0.001**	**< 0.001**	0.165
FTMT	**< 0.001**	**0.002**	**< 0.001**
% ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**< 0.001**	**0.011**	**< 0.001**
FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	**< 0.001**	**0.009**	**< 0.001**
Shingle Shanty			
R^2-value	89.3%	69.2%	61.4%
Terms	P-value		
Aspect	**< 0.001**	**0.001**	**< 0.001**
FTMT	0.069	0.783	0.057
% ECM BA	**< 0.001**	0.262	**< 0.001**
Aspect x FTMT	0.153	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**< 0.001**	0.143	**< 0.001**

FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	**0.034**	**< 0.001**	**< 0.001**

Table 24. Root-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Lake George. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Lake George			Adj. R^2 value %				Relative abundance %			
Phylum	**Family**	**Functional role**	**Total**	**% ECM**	**FTMT**	**Aspect**	**AM plot, AM tree**	**AM plot, ECM tree**	**ECM plot, AM tree**	**ECM plot, ECM tree**
Ascomycota	Chaetomiaceae	Primary or dung saprotroph	23.5	17.0	7.1	5.4	1.04 ± 2.54	0.08 ± 0	0 ± 0	0.16 ± 0.45
	Chaetosphaeriaceae	Primary or wood saprotroph, or unknown	21.7	13.8	4.6	5.5	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Cordycipitaceae	Primary saprotroph or animal pathogen	23.6	16.3	5.5	4.6	0.1 ± 0.3	0 ± 0	0 ± 0	0 ± 0
	Didymellaceae	Plant necrotroph or various	15.5	10.9	8.3	3.2	0.19 ± 0.53	0 ± 0	0 ± 0	0 ± 0
	Dissoconiaceae	Various	23.6	16.3	5.5	4.6	0.03 ± 0.1	0 ± 0	0 ± 0	0 ± 0
	Elaphomycetaceae	Primary saprotroph or ectomycorrhizal	16.2	8.2	1.0	1.6	0.04 ± 0.13	0 ± 0	0 ± 0	0.19 ± 0.6
	Geoglossaceae	Primary saprotroph	32.9	29.1	29.7	0.0	2.02 ± 2.78	0.8 ± 0	1.3 ± 0	0.19 ± 0.4
	Gloniaceae	Ectomycorrhizal	46.7	40.8	33.1	8.4	0.53 ± 0.66	1.52 ± 0	1.21 ± 0	3.43 ± 4.06
	Melanommataceae	Wood saprotroph	17.7	5.3	6.1	13.4	0.17 ± 0.37	0 ± 0	0 ± 0	0.02 ± 0.06
	Pezizaceae	Primary saprotroph, ectomycorrhizal, or various	21.6	14.1	14.2	3.8	0.34 ± 0.4	0.4 ± 0	0.08 ± 0	0.65 ± 0.64
	Pleomassariaceae	Primary saprotroph or various	26.1	15.2	7.2	11.1	0.46 ± 1.29	0 ± 0	0 ± 0	0.02 ± 0.06
	Pycnoraceae	Lichen	23.6	16.3	5.5	4.6	0.03 ± 0.1	0 ± 0	0 ± 0	0 ± 0
	Rutstroemiaceae	Primary saprotroph	21.8	1.1	10.4	1.3	0.01 ± 0.03	0 ± 0	0.32 ± 0	0 ± 0
	Saccharomycetales (inc. sed.)	Primary saprotroph	15.4	8.7	10.1	6.9	0.01 ± 0.03	0.16 ± 0	0 ± 0	0.42 ± 1.16
	Sordariomycetes (inc. sed.)	Unknown	16.8	4.7	10.3	8.5	0.05 ± 0.11	0 ± 0	0 ± 0	0 ± 0
	Stictidaceae	Primary saprotroph or lichen	16.6	8.0	10.3	8.5	0.09 ± 0.22	0 ± 0	0 ± 0	0 ± 0
	Sympoventuriaceae	Primary saprotroph	24.5	1.7	0.1	14.4	0.02 ± 0.07	0 ± 0	0 ± 0	0.02 ± 0.04
	Teratosphaeriaceae	Primary saprotroph, plant necrotroph, various, or unknown	23.6	16.3	5.5	4.6	0.04 ± 0.13	0 ± 0	0 ± 0	0 ± 0
	Trichomonascaceae	Primary saprotroph	21.7	13.8	4.6	5.5	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Xylariaceae	Primary saprotroph	17.1	0.0	4.6	5.5	0 ± 0	0 ± 0	0 ± 0	0.08 ± 0.26
Basidiomycota	Atheliaceae	Primary saprotroph, ectomycorrhizal, plant necrotroph, or various	52.4	19.6	27.1	32.5	2.17 ± 3.88	2.96 ± 0	0.65 ± 0	11.4 ± 11.65
	Bolbitiaceae	Primary saprotroph	28.2	27.1	23.4	0.0	3.63 ± 5.39	0 ± 0	0 ± 0	0.06 ± 0.18

	Cantharellales (inc. sed.)	Ectomycorrhizal or lichen	19.0	4.2	2.1	13.5	2.82 ± 8.29	0 ± 0	0 ± 0	0.47 ± 1.36
	Clavariaceae	Primary saprotroph or various	36.4	3.5	21.5	0.7	3.91 ± 3.26	2.32 ± 0	11.98 ± 0	1.51 ± 1.79
	Cortinariaceae	Primary saprotroph or ectomycorrhizal	24.8	0.1	5.8	3.7	0.73 ± 1.63	48.48 ± 0	20.73 ± 0	5.57 ± 11.01
	Cyphellaceae	Primary saprotroph	27.6	12.0	18.3	5.6	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.19
	Exidiaceae	Primary saprotroph	23.8	14.9	4.6	5.5	0 ± 0	0 ± 0	0 ± 0	0.37 ± 1.16
	Geminibasidiaceae	Primary saprotroph	22.0	20.3	9.4	0.1	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.15
	Hydnangiaceae	Ectomycorrhizal	55.8	45.8	32.8	6.3	0 ± 0	0 ± 0	0 ± 0	0.12 ± 0.13
	Hydnodontaceae	Primary or wood saprotroph	20.6	18.6	13.5	1.0	0.12 ± 0.32	1.2 ± 0	0 ± 0	1.78 ± 3.87
	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various, or unknown	34.0	33.3	19.7	1.0	10.8 ± 7.43	4.33 ± 0	1.46 ± 0	3.7 ± 5.91
	Marasmiaceae	Primary or wood saprotroph, or various	23.4	0.1	5.5	5.5	0 ± 0	0 ± 0	0.16 ± 0	0 ± 0
	Omphalotaceae	Primary or wood saprotroph	19.0	17.4	8.8	0.5	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.08
	Russulaceae	Ectomycorrhizal	35.9	20.4	20.7	9.3	3.55 ± 2.48	7.85 ± 0	7.13 ± 0	9.89 ± 8.74
	Sebacinaceae	Ectomycorrhizal	23.9	3.1	0.1	13.1	1.05 ± 1.13	2.96 ± 0	0.24 ± 0	0.97 ± 1.35
	Sporidiobolaceae	Primary saprotroph or plant necrotroph	36.2	1.6	4.6	5.5	0 ± 0	0.08 ± 0	0 ± 0	0 ± 0
	Suillaceae	Ectomycorrhizal	31.4	16.9	11.6	11.6	0 ± 0	0 ± 0	0 ± 0	0.39 ± 0.96
	Thelephoraceae	Primary saprotroph, ectomycorrhizal, or various	39.9	34.8	17.1	2.3	1.08 ± 0.85	1.28 ± 0	0.81 ± 0	2.86 ± 2.48
	Tricholomataceae	Primary saprotroph, ectomycorrhizal, or plant necrotroph	16.7	3.8	0.2	0.3	20.2 ± 19.7	3.53 ± 0	12.06 ± 0	17.3 ± 13.36
	Trichosporonaceae	Primary saprotroph, animal pathogen, or unknown	18.7	3.5	0.3	2.8	0.11 ± 0.22	0 ± 0	0.24 ± 0	0.09 ± 0.12
	Trimorphomycetaceae	Fungal parasite	16.8	13.8	11.1	1.6	0.04 ± 0.13	0 ± 0	0 ± 0	0.29 ± 0.47
Chytridiomycota	Lobulomycetaceae	Fungal parasite	23.6	16.3	5.5	4.6	0.01 ± 0.03	0 ± 0	0 ± 0	0 ± 0
Glomeromycota	Claroideoglomeraceae	Arbuscular Mycorrhizal	23.6	16.3	5.5	4.6	0.01 ± 0.03	0 ± 0	0 ± 0	0 ± 0
	Glomeraceae	Arbuscular Mycorrhizal	21.1	1.0	0.4	20.0	0.71 ± 0.74	0 ± 0	0.24 ± 0	1.38 ± 3.59
Mucoromycota	Cunninghamellaceae	Primary saprotroph	21.7	13.8	4.6	5.5	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.15
	Mucoraceae	Primary saprotroph	26.4	5.7	1.3	18.3	0 ± 0	0 ± 0	0.16 ± 0	0.03 ± 0.07
	Umbelopsidaceae	Primary saprotroph	41.7	28.4	13.7	13.6	0.23 ± 0.31	0 ± 0	1.13 ± 0	0.91 ± 0.78

Table 25. Root-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Huntington Forest. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Huntington Forest			Adj. R^2 value %				Relative abundance %			
Phylum	**Family**	**Functional role**	**Total**	**% ECM**	**FTMT**	**Aspect**	**AM plot, AM tree**	**AM plot, ECM tree**	**ECM plot, AM tree**	**ECM plot, ECM tree**
Ascomycota	Amphisphaeriaceae	Primary saprotroph or plant necrotroph	19.6	2.4	1.6	12.6	0.16 ± 0.37	0 ± 0	0.02 ± 0.04	0.51 ± 1.51
	Chaetomiaceae	Primary or dung saprotroph	20.6	19.4	7.6	0.0	0.05 ± 0.08	0 ± 0	0.09 ± 0.19	0.02 ± 0.05
	Didymellaceae	Plant necrotroph or various	43.2	23.4	27.0	3.4	0 ± 0	0 ± 0	0 ± 0	0.22 ± 0.36
	Geoglossaceae	Primary saprotroph	33.3	0.6	0.2	28.8	0.68 ± 0.93	0 ± 0	1.96 ± 4.05	1.93 ± 4.02
	Gloniaceae	Ectomycorrhizal	23.1	14.0	19.8	0.2	0.39 ± 0.72	1.91 ± 0	1.28 ± 2.2	2.73 ± 3.26
	Helotiaceae	Primary or wood saprotroph, ectomycorrhizal, ericoid mycorrhizal, plant necrotroph, endophyte, various, or unknown	34.1	6.6	3.4	16.9	10.5 ± 5.98	25.75 ± 0	7.57 ± 6.72	11.18 ± 6.9
	Herpotrichiellaceae	Primary saprotroph, plant necrotroph, animal pathogen, endophyte, or unknown	54.9	29.5	43.1	0.9	6.2 ± 5.05	1.64 ± 0	3.98 ± 0.66	1.54 ± 1.09
	Hyaloscyphaceae	Primary saprotroph, endophyte, fungal parasite, or various	46.3	0.2	30.4	6.2	7.68 ± 3.16	0.45 ± 0	5.88 ± 2.14	3.63 ± 2.31
	Lasiosphaeriaceae	Primary or dung saprotroph	26.9	24.3	9.4	0.1	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.22
	Lentitheciaceae	Wood saprotroph	15.4	1.3	4.6	4.6	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.08
	Leotiaceae	Primary saprotroph, ericoid mycorrhizal, or unknown	15.9	0.6	0.1	13.4	1.15 ± 2.56	0 ± 0	0.33 ± 0.39	0.71 ± 1.11
	Melanommataceae	Wood saprotroph	17.6	0.0	0.0	16.6	0.84 ± 1.72	0 ± 0	0 ± 0	0.35 ± 0.91
	Pleosporaceae	Plant necrotroph	20.9	11.8	4.6	4.6	0 ± 0	0 ± 0	0 ± 0	0.13 ± 0.4
	Rhytismataceae	Plant necrotroph or various	22.9	9.3	7.0	7.0	0 ± 0	0 ± 0	0 ± 0	0.26 ± 0.76
	Saccharomycetales (inc. sed.)	Primary saprotroph	18.1	1.3	5.5	4.6	0 ± 0	0 ± 0	0.1 ± 0.22	0 ± 0
	Sclerotiniaceae	Primary saprotroph or plant necrotroph	18.7	11.5	0.8	3.1	0 ± 0	0 ± 0	0.03 ± 0.07	0.03 ± 0.06
	Sordariomycetes (inc. sed.)	Unknown	18.9	0.4	8.0	8.0	0 ± 0	0.09 ± 0	0 ± 0	0.05 ± 0.17
	Sporocadaceae	Plant necrotroph	15.9	5.6	2.6	6.5	0 ± 0	0 ± 0	0.03 ± 0.07	0.38 ± 1.21
	Teratosphaeriaceae	Primary saprotroph, plant necrotroph, various, or unknown	19.5	1.3	9.6	0.0	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.07
	Thelebolaceae	Primary saprotroph	16.2	0.9	4.6	5.5	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.15
	Tuberaceae	Ectomycorrhizal	33.0	17.1	10.1	7.4	0 ± 0	0 ± 0	0.08 ± 0.12	0.4 ± 0.68

Basidiomycota	Amanitaceae	Ectomycorrhizal	24.3	19.2	14.9	0.0	0.72 ± 0.72	1.36 ± 0	0.58 ± 0.86	1.73 ± 1.76
	Bulleribasidiaceae	Fungal parasite	15.4	1.3	4.6	4.6	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Chrysozymaceae	Primary saprotroph	25.7	5.0	6.8	2.8	0 ± 0	0.09 ± 0	0.02 ± 0.05	0.06 ± 0.13
	Clavariaceae	Primary saprotroph or various	25.7	1.2	6.1	21.5	1.58 ± 1.65	1.46 ± 0	2.74 ± 3.34	1.49 ± 2.87
	Clavulinaceae	Ectomycorrhizal or various	21.7	0.1	10.7	9.6	0.02 ± 0.04	0 ± 0	0.16 ± 0.32	2 ± 5.38
	Cortinariaceae	Primary saprotroph or ectomycorrhizal	23.5	20.7	8.3	0.2	0.8 ± 1.79	0.27 ± 0	1.08 ± 2.42	1.64 ± 1.6
	Crepidotaceae	Wood saprotroph	17.2	4.2	0.0	13.7	0.15 ± 0.33	0.18 ± 0	0 ± 0	0.03 ± 0.09
	Entolomataceae	Primary saprotroph, ectomycorrhizal, or various	46.8	3.2	35.9	5.2	0.9 ± 1.31	0 ± 0	1.83 ± 1.14	0.22 ± 0.26
	Ganodermataceae	Wood saprotroph or various	15.4	1.3	4.6	4.6	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various, or unknown	53.1	33.5	41.2	10.1	15.1 ± 12.4	1.55 ± 0	3.67 ± 3.95	0.68 ± 1.69
	Hymenogastraceae	Ectomycorrhizal	40.1	15.3	0.6	15.0	0 ± 0	0 ± 0	0.5 ± 1.12	0.33 ± 0.71
	Inocybaceae	Ectomycorrhizal	22.6	3.8	21.5	2.4	0.44 ± 0.58	10.56 ± 0	0.42 ± 0.89	3.23 ± 4.01
	Malasseziaceae	Animal Pathogen	35.7	12.7	4.6	4.6	0 ± 0	0.09 ± 0	0 ± 0	0 ± 0
	Phaeotremellaceae	Fungal parasite	15.4	1.3	4.6	4.6	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.06
	Piskurozymaceae	Unknown	25.5	16.7	17.7	0.3	2.05 ± 1.49	0.91 ± 0	0.9 ± 0.48	0.77 ± 0.36
	Porotheleaceae	Wood saprotroph	31.3	13.8	9.0	9.0	0 ± 0	0 ± 0	0 ± 0	0.26 ± 0.62
	Psathyrellaceae	Wood or dung saprotroph	21.6	1.3	9.2	9.2	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.06
	Russulaceae	Ectomycorrhizal	27.0	4.4	7.5	22.7	5.69 ± 6.19	33.94 ± 0	9.42 ± 7.04	10.93 ± 9.26
	Sebacinaceae	Ectomycorrhizal	46.2	43.5	16.7	0.0	0.33 ± 0.63	0 ± 0	1.42 ± 2.05	2.2 ± 1.39
	Sporidiobolaceae	Primary saprotroph or plant necrotroph	22.4	1.9	9.5	9.5	0 ± 0	0 ± 0	0 ± 0	0.11 ± 0.23
	Steccherinaceae	Primary or wood saprotroph	15.8	1.1	2.6	9.0	0 ± 0	0 ± 0	0.52 ± 1.16	0.03 ± 0.08
	Strophariaceae	Primary or wood saprotroph, various, or unknown	58.2	6.3	48.6	13.1	0.42 ± 0.4	0 ± 0	0.65 ± 0.83	0 ± 0
	Tremellaceae	Fungal parasite	18.9	0.5	10.5	8.7	0.09 ± 0.2	0 ± 0	0.33 ± 0.73	0 ± 0
Chytridiomycota	Lobulomycetaceae	Fungal parasite	25.1	14.1	5.5	5.5	0.05 ± 0.12	0 ± 0	0 ± 0	0 ± 0
	Rhizophydiaceae	Plant necrotroph	22.4	3.8	0.1	12.8	0 ± 0	0 ± 0	0.08 ± 0.19	0.02 ± 0.04
Kickxellomycota	Kickxellaceae	Primary saprotroph	17.8	6.4	0.0	11.6	0 ± 0	0 ± 0	0.05 ± 0.11	0.03 ± 0.08
Mucoromycota	Umbelopsidaceae	Primary saprotroph	19.1	0.0	9.6	5.4	0.38 ± 0.52	0 ± 0	0.25 ± 0.35	0.11 ± 0.14

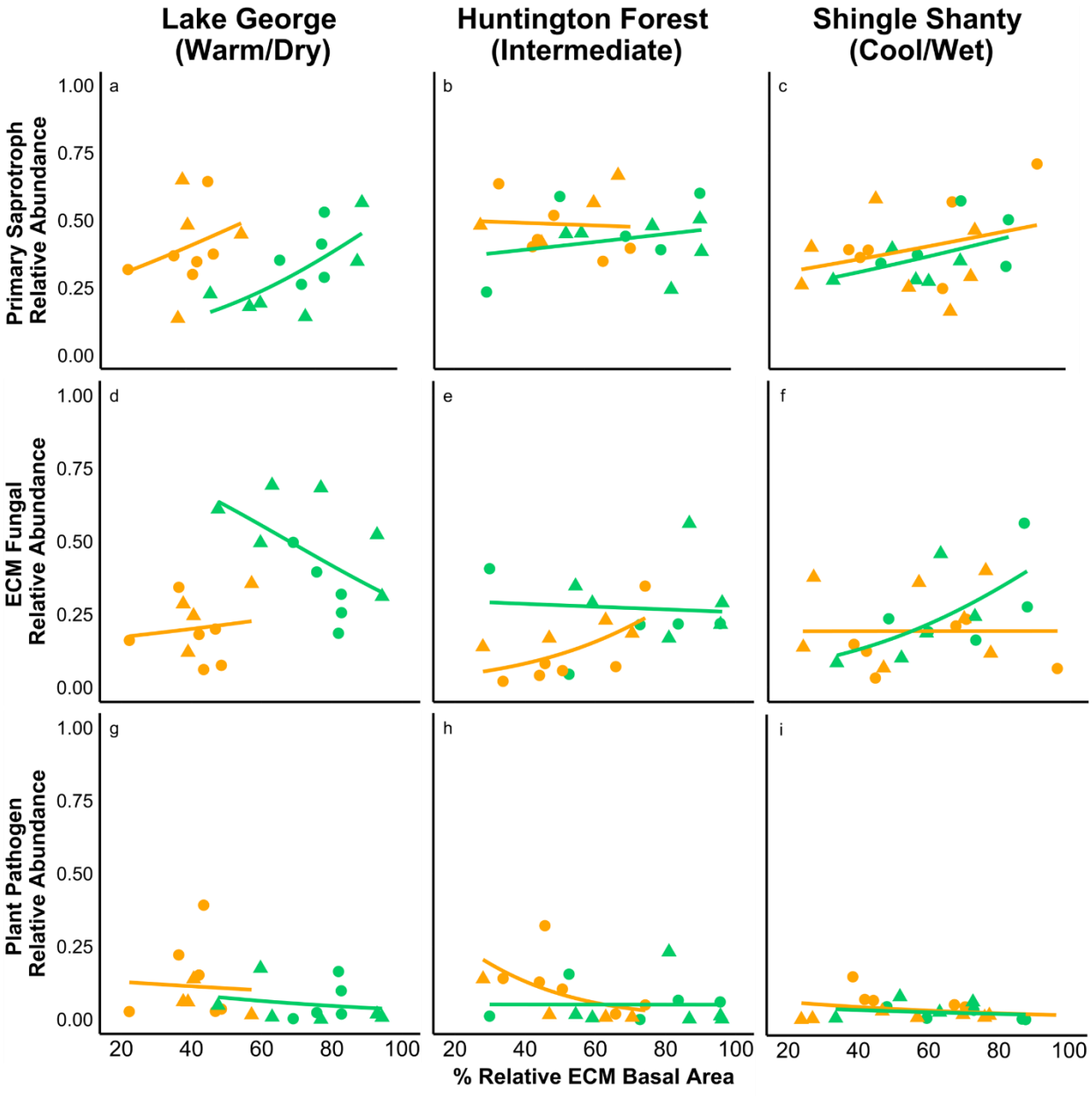
Table 26. Root-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Shingle Shanty. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Shingle Shanty			Adj. R^2 value %				Relative abundance %			
Phylum	**Family**	**Functional role**	**Total**	**% ECM**	**FTMT**	**Aspect**	**AM plot, AM tree**	**AM plot, ECM tree**	**ECM plot, AM tree**	**ECM plot, ECM tree**
Ascomycota	Archaeorhizomycetaceae	Primary saprotroph	16.3	5.5	3.5	5.0	0.09 ± 0.22	0 ± 0	0 ± 0	0 ± 0
	Chaetosphaeriaceae	Primary or wood saprotroph or unknown	21.5	21.2	0.2	2.3	0.69 ± 1.46	0 ± 0	0.01 ± 0.03	0.18 ± 0.27
	Clavicipitaceae	Animal Pathogen	19.1	8.4	5.9	4.2	0 ± 0	0.22 ± 0.31	0 ± 0	0 ± 0
	Clavicipitaceae	Primary saprotroph	19.1	8.4	5.9	4.2	0 ± 0	0.22 ± 0.31	0 ± 0	0 ± 0
	Cucurbitariaceae	Plant necrotroph or various	18.4	1.2	18.2	0.3	0 ± 0	0.05 ± 0.07	0 ± 0	0.04 ± 0.09
	Dermateaceae	Primary saprotroph, plant necrotroph, various, or unknown	24.7	22.8	1.9	0.0	8.09 ± 8.98	1.13 ± 0.43	1.44 ± 1.68	3.03 ± 4.41
	Didymellaceae	Plant necrotroph or various	22.3	2.3	10.9	7.7	0 ± 0	0 ± 0	0 ± 0	0.06 ± 0.13
	Didymosphaeriaceae	Primary saprotroph or plant necrotroph	15.5	9.7	5.9	5.0	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Dothideaceae	Primary saprotroph, plant necrotroph, or various	16.4	6.3	12.4	0.0	0.41 ± 0.61	0 ± 0	0.03 ± 0.07	0 ± 0
	Helotiaceae	Primary or wood saprotroph, ectomycorrhizal, ericoid mycorrhizal, plant necrotroph, endophyte, various, or unknown	19.2	16.6	3.5	0.0	17.9 ± 12.4	16.88 ± 11.8	10.83 ± 7.54	9.58 ± 8.37
	Herpotrichiellaceae	Primary saprotroph, plant necrotroph, animal pathogen, endophyte, or unknown	36.9	35.8	4.1	3.9	5.79 ± 3.55	6.67 ± 7.54	1.87 ± 0.96	2.03 ± 2.26
	Lasiosphaeriaceae	Primary or dung saprotroph	29.0	17.9	11.2	9.4	0 ± 0	0 ± 0	0 ± 0	0.09 ± 0.21
	Lentitheciaceae	Wood saprotroph	16.1	1.6	5.9	5.0	0 ± 0	0.1 ± 0.15	0 ± 0	0 ± 0
	Leotiaceae	Primary saprotroph, ericoid mycorrhizal, or unknown	16.6	0.1	14.2	2.0	0.14 ± 0.21	0 ± 0	0.58 ± 1.08	2.96 ± 4.52
	Lophiostomataceae	Primary saprotroph or unknown	16.3	5.5	3.5	5.0	0.02 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	Melanommataceae	Wood saprotroph	19.8	1.0	1.6	13.5	0.03 ± 0.07	0 ± 0	0.02 ± 0.06	0.01 ± 0.03
	Myxotrichaceae	Ericoid Mycorrhizal or various	20.2	0.2	1.5	15.8	0.39 ± 0.67	0.59 ± 0.1	0.14 ± 0.21	0.13 ± 0.14
	Pycnoraceae	Lichen	22.4	0.2	12.4	8.7	0 ± 0	0 ± 0	0 ± 0	0.07 ± 0.13
	Pyronemataceae	Primary saprotroph, ectomycorrhizal, various, or unknown	27.2	18.5	0.3	15.8	1.11 ± 1.27	1.26 ± 0.54	0.71 ± 0.89	0.47 ± 0.56
	Sporocadaceae	Plant necrotroph	32.6	4.8	1.8	19.7	0 ± 0	0 ± 0	0.1 ± 0.17	0.16 ± 0.37
	Sympoventuriaceae	Primary saprotroph	51.3	0.8	20.3	26.9	0 ± 0	0.55 ± 0.78	0.15 ± 0.21	0.41 ± 0.48

	Taphrinaceae	Plant biotroph	16.1	3.8	3.5	4.2	0 ± 0	0 ± 0	0.04 ± 0.11	0 ± 0
	Teratosphaeriaceae	Primary saprotroph, primary saprotroph, various, or unknown	17.7	1.5	0.6	12.4	0 ± 0	0 ± 0	0.05 ± 0.14	0.03 ± 0.07
	Thelebolaceae	Primary saprotroph	16.1	3.8	3.5	4.2	0 ± 0	0 ± 0	0.01 ± 0.04	0 ± 0
	Tuberaceae	Ectomycorrhizal	25.0	16.6	3.5	5.0	0 ± 0	0 ± 0	0.03 ± 0.09	0 ± 0
	Tubeufiaceae	Primary or wood saprotroph, various, or unknown	16.1	3.8	3.5	4.2	0 ± 0	0 ± 0	0.01 ± 0.04	0 ± 0
	Vibrisseaceae	Primary saprotroph or endophyte	19.2	7.3	3.0	14.4	1.14 ± 1.84	0.26 ± 0.36	0.88 ± 1.83	0.28 ± 0.43
	Xylariaceae	Primary saprotroph	16.3	5.5	3.5	5.0	0.02 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	Xylariales (inc. sed.)	Primary saprotroph, plant necrotroph, or unknown	19.8	3.5	1.2	11.2	0.03 ± 0.07	0 ± 0	0.15 ± 0.39	0.15 ± 0.29
Basidiomycota	Amanitaceae	Ectomycorrhizal	21.2	5.8	3.7	5.6	0.88 ± 0.95	0 ± 0	3.91 ± 3.46	1.9 ± 2.03
	Ceratobasidiaceae	Plant necrotroph	15.7	0.5	10.4	2.6	0 ± 0	1.9 ± 2.69	0.01 ± 0.03	0.03 ± 0.05
	Cerrenaceae	Primary saprotroph	15.1	9.1	5.9	5.0	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Clavariaceae	Primary saprotroph or various	18.0	0.0	15.4	2.1	0.85 ± 0.98	0 ± 0	5.87 ± 12.38	0.02 ± 0.04
	Clavulinaceae	Ectomycorrhizal or various	18.6	12.4	2.0	0.2	0.13 ± 0.15	0.06 ± 0.08	1.58 ± 3.37	0.44 ± 0.6
	Cortinariaceae	Primary or wood saprotroph, or ectomycorrhizal	21.9	7.5	17.5	1.5	0.31 ± 0.35	3.02 ± 0.53	1.4 ± 1.71	6.13 ± 10.42
	Entolomataceae	Primary saprotroph	41.8	24.5	0.9	28.2	1.06 ± 1.62	1.65 ± 2.34	0.27 ± 0.23	0.28 ± 0.47
	Entolomataceae	Ectomycorrhizal	41.8	24.5	0.9	28.2	1.06 ± 1.62	1.65 ± 2.34	0.27 ± 0.23	0.28 ± 0.47
	Entolomataceae	Various	41.8	24.5	0.9	28.2	1.06 ± 1.62	1.65 ± 2.34	0.27 ± 0.23	0.28 ± 0.47
	Erythrobasidiaceae	Primary saprotroph	16.3	5.5	3.5	5.0	0.11 ± 0.26	0 ± 0	0 ± 0	0 ± 0
	Ganodermataceae	Wood saprotroph or various	27.7	2.4	15.9	4.1	0.03 ± 0.07	0.81 ± 0.42	0.05 ± 0.09	0.06 ± 0.07
	Hyaloriaceae	Wood saprotroph	15.5	9.7	5.9	5.0	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.06
	Hymenogastraceae	Ectomycorrhizal	16.1	1.6	5.9	5.0	0 ± 0	0.77 ± 1.09	0 ± 0	0 ± 0
	Jaapiaceae	Primary saprotroph	15.2	3.3	3.5	4.2	0 ± 0	0 ± 0	0.01 ± 0.03	0 ± 0
	Omphalotaceae	Primary or wood saprotroph	22.5	6.8	4.0	13.6	0.11 ± 0.28	0 ± 0	0 ± 0	0.22 ± 0.41
	Phaeotremellaceae	Fungal parasite	16.1	3.8	3.5	4.2	0 ± 0	0 ± 0	0.04 ± 0.11	0 ± 0
	Pleurotaceae	Primary saprotroph	22.6	1.6	11.5	8.1	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.1
	Russulaceae	Ectomycorrhizal	25.7	5.2	20.2	1.4	5.64 ± 3.23	14.25 ± 13.46	10.62 ± 9.31	14.23 ± 4.95
	Schizoporaceae	Primary or wood saprotroph	24.3	10.5	6.1	1.2	0 ± 0	0 ± 0	0.17 ± 0.38	0 ± 0
	Sebacinaceae	Ectomycorrhizal	22.8	16.6	0.2	10.2	0.69 ± 1.1	0 ± 0	1.75 ± 3.2	1.3 ± 1.87
	Strophariaceae	Primary or wood saprotroph, various, or unknown	29.2	15.0	0.2	21.6	3.84 ± 6.45	0.66 ± 0.93	0.46 ± 1.07	2.18 ± 4.89
	Tricholomataceae	Primary saprotroph, ectomycorrhizal, or plant necrotroph	26.0	23.5	5.5	0.6	6.34 ± 10.4	15.86 ± 3.9	13.25 ± 17.2	16.34 ± 18.4

Chytridiomycota	Rhizophydiaceae	Plant necrotroph	15.5	9.7	5.9	5.0	0 ± 0	0 ± 0	0 ± 0	0.06 ± 0.18
Glomeromycota	Acaulosporaceae	Arbuscular Mycorrhizal	18.3	15.8	3.5	4.2	0.06 ± 0.16	0 ± 0	0 ± 0	0 ± 0
	Archaeosporaceae	Arbuscular Mycorrhizal	15.2	3.3	3.5	4.2	0 ± 0	0 ± 0	0.01 ± 0.03	0 ± 0
Zygomycota	Mortierellaceae	Primary saprotroph	24.0	0.3	1.1	22.2	9.15 ± 5.3	9.8 ± 8.1	11.14 ± 7.33	8.57 ± 3.25
Mucoromycota	Mucoraceae	Primary saprotroph	19.5	0.4	7.3	10.4	0.01 ± 0.04	0 ± 0	0.01 ± 0.03	0 ± 0

Figure 15. Relative abundance changes among functional groups of root-associated fungi along a gradient of mycorrhizal dominance at each study site. Relative abundance values are displayed as decimals (0 – 1). Colors correspond to plot focal tree mycorrhizal type (gold = AM focal trees, green = ECM focal trees) and shapes correspond to slope aspect (circles = northern-facing slopes, triangles = southern-facing slopes).



APPENDIX D

CHAPTER III SUPPORTING DATA FOR LEAF LITTER FUNGI

Table 27. Results (P-values and Adj. R^2-values) from the RDA on leaf fungal community composition for each site. Letters with the Adj. R^2-values indicate: a – variation explained by focal tree species when controlling for species mycorrhizal identity; b – variation explained by the combined mycorrhizal + geographic model excluding focal tree species identity. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type; FT Species = plot focal tree species. Bold values indicate significant or marginally significant terms (P< 0.07).

Lake George	ASV		Family		Guild	
	P-value	Adj. R^2	P-value	Adj. R^2	P-value	Adj. R^2
FT species	**0.02**	16.6%[a]	**0.016**	4.1%[a]	0.306	4.6%[a]
Aspect	0.136	8.6%[b]	**0.031**	19.0%[b]	0.355	8.9%[b]
FTMT	**0.007**		0.126		0.403	
% ECM BA	0.152		**0.01**		**0.061**	
Aspect x FTMT	0.586		0.074		0.659	
Aspect x % ECM BA	0.725		0.19		0.678	
FTMT x % ECM BA	0.383		**0.043**		0.187	
Aspect x FTMT x % ECM BA	0.333		**0.029**		0.745	
Huntington Forest						
FT species	**0.001**	14.3%[a]	**0.006**	9.8%[a]	0.088	0.8%[a]
Aspect	**0.012**	10.7%[b]	**0.008**	10.1%[b]	**0.057**	6.6%[b]
FTMT	**0.039**		0.094		0.332	
% ECM BA	**0.049**		0.596		0.445	
Aspect x FTMT	0.414		0.462		0.67	
Aspect x % ECM BA	0.117		0.204		0.448	
FTMT x % ECM BA	0.231		0.597		0.428	
Aspect x FTMT x % ECM BA	0.144		0.395		0.384	

Shingle Shanty

FT species	**0.019**	10.6%[a]	**0.061**	6.7%[a]	0.399	4.1%[a]
Aspect	0.085	3.7%[b]	0.737	0.5%[b]	0.429	3.8%[b]
FTMT	0.364		0.103		0.432	
% ECM BA	**0.018**		0.233		0.507	
Aspect x FTMT	0.514		0.598		0.71	
Aspect x % ECM BA	0.417		0.583		0.939	
FTMT x % ECM BA	0.322		0.207		**0.041**	
Aspect x FTMT x % ECM BA	0.921		0.796		0.982	

Table 28. Selected soil physiochemical properties identified as drivers of leaf fungal community composition at each sampling site. Bold values indicate significant or marginally significant terms (P< 0.07).

Site	Taxon Level	P-value	Adj. R^2	Terms
Lake George				
	Guild	**0.001**	33.6%	C:N + NO_3^- + N mineralization + Net nitrification + Tree species evenness
	Family	**0.001**	14.4%	C:N + NO_3^- + Fine root biomass
	ASV	**0.006**	4.5%	C:N + NO_3^-
Huntington Forest				
	Guild	n.s.	0.0%	
	Family	n.s.	0.0%	
	ASV	n.s.	0.0%	
Shingle Shanty				
	Guild	n.s.	0.0%	
	Family	n.s.	0.0%	
	ASV	**0.001**	3.8%	Tree species evenness

Table 29. Results (P-values, R^2-values, and AIC scores) from the mixed effect linear modeling for fungal richness in each functional group studied. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph ASV Richness			**ECM Fungal ASV Richness**			**Plant Pathogen ASV Richness**		
	P-value	R^2	AIC	P-value	R^2	AIC	P-value	R^2	AIC
Site	**0.001**	25.1%	532.3	**0.003**	34.1%	423.8	**0.003**	19.9%	435.5
Aspect	0.440			0.080			0.885		
Site x Aspect	0.890			**0.001**			0.198		
% ECM BA	0.208	3.7%	522.8	0.075	5.9%	426.9	0.423	8.5%	427.9
FTMT	0.327			0.631			0.072		
% ECM BA x FTMT	0.275			0.390			0.101		
Site	0.527	41.8%	**398.4**	0.856	54.9%	**315.9**	0.471	38.8%	**330.3**
Aspect	**0.050**			0.530			0.162		
FTMT	0.451			0.326			0.149		
% ECM BA	**0.042**			0.102			0.759		
Site x Aspect	0.144			0.277			0.721		
Site x FTMT	0.172			0.368			0.849		
Aspect x FTMT	0.641			0.217			0.884		
Site x % ECM BA	0.240			0.160			0.456		
Aspect x % ECM BA	**0.015**			0.234			0.155		
FTMT x % ECM BA	0.677			0.223			0.243		
Site x FTMT x % ECM BA	0.187			0.440			0.995		
Aspect x FTMT x % ECM BA	0.124			0.178			0.429		
Site x Aspect x % ECM BA	0.163			**0.027**			0.626		
Site x Aspect x FTMT	0.158			0.886			0.325		

Table 30. Results (P-values, R^2-values, and AIC scores) of the generalized mixed effect modeling using a binomial logit distribution for the relative abundance of leaf primary saprotrophs, ECM fungi, and plant pathogens. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph Relative Abundance	**ECM Fungal Relative Abundance**	**Plant Pathogen Relative Abundance**
Model	AIC Score		
Site-based	5965	8097	6885
Mycorrhizal-based	5042	9483	5154
Combined	**3417**	**6181**	**3555**
R^2-value	30.5%	52.6%	41.0%
Terms	P-value		
Site	**< 0.001**	**0.01**	**0.03**
Aspect	0.91	**< 0.001**	**< 0.001**
FTMT	**0.01**	**< 0.001**	**< 0.001**
% ECM BA	**0.05**	0.39	**< 0.001**
Site x Aspect	**< 0.001**	**< 0.001**	**< 0.001**
Site x FTMT	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT	**< 0.001**	**< 0.001**	**< 0.001**
Site x % ECM BA	**0.01**	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Site x FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	0.28	**< 0.001**	**0.01**
Site x Aspect x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**

Table 31. Results (P-values, R^2-values, and AIC scores) of the generalized mixed effect modeling using a binomial logit distribution for the relative abundance of leaf primary saprotrophs, ECM fungi, and plant pathogens at each study site. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type. Bold values indicate significant or marginally significant terms (P< 0.07).

	Primary Saprotroph Relative Abundance	**ECM Fungal Relative Abundance**	**Plant Pathogen Relative Abundance**
Lake George			
R^2-value	30.4%	38.5%	31.0%
Terms	P-value		
Aspect	**< 0.001**	0.090	**< 0.001**
FTMT	0.350	**< 0.001**	**< 0.001**
% ECM BA	**< 0.001**	**0.001**	**< 0.001**
Aspect x FTMT	0.257	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
FTMT x % ECM BA	0.611	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	0.459	**< 0.001**	**< 0.001**
Huntington Forest			
R^2-value	42.2%	95.1%	52.8%
Terms	P-value		
Aspect	**< 0.001**	**< 0.001**	**< 0.001**
FTMT	0.563	**< 0.001**	**< 0.001**
% ECM BA	**0.005**	**< 0.001**	**< 0.001**
Aspect x FTMT	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x % ECM BA	**0.001**	**< 0.001**	**< 0.001**
FTMT x % ECM BA	**< 0.001**	**< 0.001**	**< 0.001**
Aspect x FTMT x % ECM BA	**< 0.001**	**< 0.001**	0.991
Shingle Shanty			
R^2-value	73.6%	91.4%	56.3%
Terms	P-value		
Aspect	0.574	**< 0.001**	**0.003**
FTMT	**< 0.001**	**< 0.001**	**< 0.001**
% ECM BA	**0.009**	0.221	**< 0.001**
Aspect x FTMT	0.401	0.237	0.554
Aspect x % ECM BA	0.087	0.471	**< 0.001**

FTMT x % ECM BA	**< 0.001**	**< 0.001**	**0.007**
Aspect x FTMT x % ECM BA	**0.002**	0.460	0.721

Table 32. Leaf-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Lake George. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Lake George			Adj. R^2 value %				Relative abundance %			
Phylum	**Family**	**Functional role**	**Total**	**% ECM**	**FTMT**	**Aspect**	**AM plot, AM tree**	**AM plot, ECM tree**	**ECM plot, AM tree**	**ECM plot, ECM tree**
Ascomycota	Amphisphaeriaceae	Primary saprotroph or Plant necrotroph	34.5	22.7	9.3	9.2	19.7 ± 12.9	16.96 ± 0	24.94 ± 0	13.53 ± 17.57
	Aspergillaceae	Primary saprotroph	23.9	14.0	4.0	4.8	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.02
	Capnodiales (inc. sed.)	Primary saprotroph or various	22.3	0.4	3.2	20.7	0.06 ± 0.09	0 ± 0	0 ± 0	0.04 ± 0.13
	Chaetomellaceae	Primary saprotroph, plant necrotroph, or unknown	21.0	15.3	3.6	0.0	1.64 ± 2.33	0.97 ± 0	0 ± 0	0.74 ± 1.54
	Chaetosphaeriaceae	Primary or wood saprotroph, or unknown	39.7	9.9	0.2	9.4	0 ± 0	0 ± 0	0.57 ± 0	0.13 ± 0.44
	Cryphonectriaceae	Plant biotroph	32.4	25.0	11.3	5.2	2.78 ± 5.4	0.49 ± 0	0.32 ± 0	0.25 ± 0.62
	Dermateaceae	Primary saprotroph	54.0	44.1	19.1	5.7	1.6 ± 3.92	0.49 ± 0	0.16 ± 0	4.49 ± 4.02
	Dermateaceae	Plant necrotroph	54.0	44.1	19.1	5.7	1.6 ± 3.92	0.49 ± 0	0.16 ± 0	4.49 ± 4.02
	Dermateaceae	Unknown or various	54.0	44.1	19.1	5.7	1.6 ± 3.92	0.49 ± 0	0.16 ± 0	4.49 ± 4.02
	Dissoconiaceae	Various	18.2	12.7	12.8	2.3	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.07
	Fenestellaceae	Primary saprotroph	20.3	2.5	0.0	9.8	0.01 ± 0.03	0 ± 0	0 ± 0	0.01 ± 0.04
	Helotiaceae	Primary or wood saprotroph, ectomycorrhizal, plant necrotroph, ericoid mycorrhizal, endophyte, various, or unknown	19.6	0.1	2.6	4.1	9.15 ± 5.17	11.6 ± 0	7.39 ± 0	11.42 ± 7.36
	Helotiales (inc. sed.)	Primary saprotroph, ectomycorrhizal, plant necrotroph, endophyte, various, or unknown	23.5	12.0	19.9	0.9	2.96 ± 1.58	5.46 ± 0	0.65 ± 0	4.61 ± 2.67
	Herpotrichiellaceae	Primary saprotroph, plant necrotroph, endophyte, animal pathogen, or unknown	23.3	2.5	1.6	0.3	0.7 ± 0.54	0 ± 0	0.24 ± 0	0.65 ± 0.96
	Hypocreaceae	Primary saprotroph	23.9	14.0	4.0	4.8	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.12
	Hypocreales (inc. sed.)	Primary saprotroph	42.8	23.2	41.6	0.5	8.2 ± 3.46	2.44 ± 0	12.27 ± 0	4.14 ± 2.63
	Lasiosphaeriaceae	Primary or dung saprotroph	31.9	6.5	16.7	20.1	0 ± 0	0.39 ± 0	0 ± 0	0.3 ± 0.59
	Lophiostomataceae	Primary saprotroph or unknown	21.0	2.8	11.8	9.8	0.07 ± 0.15	0 ± 0	0 ± 0	0 ± 0
	Melanommataceae	Wood saprotroph	19.4	0.3	2.8	8.3	0.07 ± 0.2	0.49 ± 0	0 ± 0	0.09 ± 0.21
	Microdochiaceae	Primary saprotroph or unknown	30.6	1.4	4.0	4.8	0 ± 0	0.1 ± 0	0 ± 0	0 ± 0
	Mytilinidiaceae	Primary saprotroph	54.8	52.2	27.1	1.0	0 ± 0	0 ± 0	0 ± 0	0.43 ± 0.8

	Mytilinidiaceae	Wood saprotroph	54.8	52.2	27.1	1.0	0 ± 0	0 ± 0	0 ± 0	0.43 ± 0.8
	Phaeosphaeriaceae	Primary saprotroph, plant necrotroph, or various	17.6	15.7	12.1	0.9	0 ± 0	0 ± 0	0 ± 0	0.21 ± 0.41
	Pleosporales (inc. sed.)	Primary saprotroph	18.0	2.2	7.3	12.9	0.09 ± 0.11	0.49 ± 0	0 ± 0	0.25 ± 0.43
	Pseudeurotiaceae	Primary saprotroph, animal pathogen, or various	63.8	61.8	49.1	3.2	2.26 ± 1.27	0.88 ± 0	0.32 ± 0	0.34 ± 0.51
	Pycnoraceae	Lichen	33.5	0.8	15.5	0.8	1.07 ± 0.57	8.19 ± 0	0.16 ± 0	2.7 ± 3.26
	Pyronemataceae	Primary saprotroph, ectomycorrhizal, unknown, or various	17.7	16.8	8.3	0.1	0 ± 0	0 ± 0	0 ± 0	0.06 ± 0.14
	Rhytismataceae	Plant necrotroph or various	24.4	0.7	0.8	23.5	10.7 ± 12.0	8.19 ± 0	1.22 ± 0	6.23 ± 6.9
	Saccharomycetales (inc. sed.)	Primary saprotroph	36.4	29.6	30.4	6.7	0 ± 0	0.29 ± 0	0 ± 0	0.9 ± 1.22
	Sarcosomataceae	Primary or wood saprotroph	15.5	8.1	5.1	6.2	0 ± 0	0 ± 0	0 ± 0	0.43 ± 1.4
	Septorioideaceae	Endophyte	22.9	11.9	7.7	9.2	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.09
	Sporocadaceae	Plant necrotroph	34.5	1.2	5.4	0.6	0.3 ± 0.29	1.46 ± 0	0 ± 0	0.69 ± 0.9
	Stictidaceae	Primary saprotroph or lichen	16.5	7.7	0.8	1.5	0.03 ± 0.09	0 ± 0	0 ± 0	0.06 ± 0.17
	Sympoventuriaceae	Primary saprotroph	19.6	15.9	10.2	4.4	0.3 ± 0.44	0 ± 0	0 ± 0	0.71 ± 0.65
	Taphrinaceae	Biotroph	24.3	14.4	8.2	9.8	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.08
	Teratosphaeriaceae	Primary saprotroph, plant necrotroph, unknown, or various	20.7	10.3	11.2	11.4	0.28 ± 0.25	0 ± 0	0 ± 0	0.13 ± 0.23
	Trichocomaceae	Primary saprotroph	23.9	14.0	4.0	4.8	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.02
	Trichomeriaceae	Dung saprotroph, endophyte, epiphyte	15.4	6.3	13.9	0.1	0.2 ± 0.33	0.1 ± 0	0 ± 0	0.48 ± 0.57
	Valsaceae	Various or unknown	26.2	0.0	5.7	4.8	0 ± 0	0 ± 0	0.16 ± 0	0 ± 0
	Vibrisseaceae	Endophyte	31.3	17.5	12.7	15.3	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.1
	Vibrisseaceae	Primary saprotroph	31.3	17.5	12.7	15.3	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.1
	Xylariaceae	Primary saprotroph	47.5	0.0	12.3	14.7	0 ± 0	0.39 ± 0	0 ± 0	0.15 ± 0.38
	Xylariales (inc. sed.)	Primary saprotroph, plant necrotroph, or unknown	15.9	2.6	7.1	11.3	0.26 ± 0.31	1.66 ± 0	0.24 ± 0	1.01 ± 1.57
Basidiomycota	Agaricaceae	Primary saprotroph	19.6	10.1	1.6	2.3	0.01 ± 0.03	0 ± 0	0 ± 0	0.1 ± 0.34
	Agaricostilbomycetes (inc. sed.)	Unknown	16.4	8.7	0.8	1.0	0.01 ± 0.04	0 ± 0	0 ± 0	0.02 ± 0.05
	Auriculariales (inc. sed.)	Primary saprotroph	37.5	0.5	7.3	8.8	0 ± 0	0.49 ± 0	0 ± 0	0.01 ± 0.03
	Botryobasidiaceae	Primary saprotroph	21.8	12.9	4.0	4.8	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.13
	Cantharellales (inc. sed.)	Ectomycorrhizal or lichen	21.4	0.0	0.0	19.9	2.59 ± 6.23	9.94 ± 0	4.79 ± 0	1.41 ± 2.42
	Chionosphaeraceae	Primary saprotroph or various	33.0	23.8	5.4	0.2	0.07 ± 0.09	0 ± 0	0 ± 0	0.13 ± 0.13
	Chrysozymaceae	Primary saprotroph	22.0	7.5	12.1	13.9	0.89 ± 0.64	0.19 ± 0	0.16 ± 0	0.42 ± 0.41
	Clavulinaceae	Ectomycorrhizal or various	36.9	28.2	35.5	0.0	0.71 ± 0.78	0 ± 0	4.47 ± 0	0.07 ± 0.25

	Cortinariaceae	Primary saprotroph or ectomycorrhizal	15.3	4.2	0.0	0.4	0.09 ± 0.2	0 ± 0	0 ± 0	0.12 ± 0.34
	Crepidotaceae	Wood saprotroph	28.5	26.5	12.0	0.0	0.02 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	Cryptococcaceae	Fungal parasite	27.1	1.3	6.1	11.9	0.12 ± 0.14	0.1 ± 0	0 ± 0	0.22 ± 0.24
	Exidiaceae	Primary saprotroph	16.1	3.0	8.3	10.0	0 ± 0	0 ± 0	0 ± 0	0.04 ± 0.09
	Hydnangiaceae	Ectomycorrhizal	47.8	28.1	8.3	9.9	0 ± 0	0 ± 0	0 ± 0	0.09 ± 0.2
	Kriegeriaceae	Unknown	34.0	1.2	2.5	33.4	0.41 ± 0.57	0.1 ± 0	0 ± 0	0.18 ± 0.16
	Leucosporidiaceae	Primary saprotroph	22.0	1.3	11.9	0.1	0.01 ± 0.04	0 ± 0	0.08 ± 0	0 ± 0
	Microbotryomycetes (inc. sed.)	Primary saprotroph or fungal parasite	38.0	4.2	15.4	26.9	0.3 ± 0.35	0 ± 0	0 ± 0	0.1 ± 0.18
	Mrakiaceae	Unknown	17.4	4.2	0.1	3.3	0.05 ± 0.12	0 ± 0	0 ± 0	0.05 ± 0.11
	Mycenaceae	Various	28.5	0.2	7.2	5.0	0.03 ± 0.06	0 ± 0	36.07 ± 0	0 ± 0
	Rhynchogastremataceae	Fungal parasite	30.6	1.4	4.0	4.8	0 ± 0	0.19 ± 0	0 ± 0	0 ± 0
	Russulaceae	Ectomycorrhizal	23.9	14.0	4.0	4.8	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.34
	Schizoporaceae	Primary or wood saprotroph	21.8	12.9	4.0	4.8	0 ± 0	0 ± 0	0 ± 0	0.12 ± 0.38
	Sebacinaceae	Ectomycorrhizal	32.7	11.2	20.0	18.6	0.05 ± 0.15	0.1 ± 0	0 ± 0	0.29 ± 0.46
	Serendipitaceae	Orchid or ericoid mycorrhizal	49.7	39.5	23.4	10.8	0 ± 0	0 ± 0	0 ± 0	0.18 ± 0.24
	Stereaceae	Primary or wood saprotroph	24.9	14.3	9.6	11.5	0 ± 0	0 ± 0	0 ± 0	0.49 ± 1.19
	Suillaceae	Ectomycorrhizal	23.9	14.0	4.0	4.8	0 ± 0	0 ± 0	0 ± 0	0.05 ± 0.17
	Tetragoniomycetaceae	Plant necrotroph	20.3	13.6	5.7	4.8	0.01 ± 0.03	0 ± 0	0 ± 0	0 ± 0
	Thelephoraceae	Primary saprotroph, ectomycorrhizal, or various	32.2	18.3	2.5	0.5	0.19 ± 0.46	0 ± 0	0.08 ± 0	0.44 ± 0.89
	Tremellaceae	Fungal parasite	23.6	1.1	12.3	3.5	0.27 ± 0.4	0 ± 0	0 ± 0	0.05 ± 0.1
	Tricholomataceae	Primary saprotroph, ectomycorrhizal, or plant necrotroph	34.6	23.6	5.7	3.6	5.49 ± 6.4	0 ± 0	1.95 ± 0	9.77 ± 9.32
Chytridiomycota	Powellomycetaceae	Unknown	21.1	14.5	18.8	4.6	0.15 ± 0.24	0 ± 0	0.16 ± 0	0.03 ± 0.09
Zygomycota	Mortierellaceae	Primary saprotroph	16.3	7.2	0.4	1.9	0.48 ± 0.55	0 ± 0	0.16 ± 0	0.6 ± 0.65
Mucoromycota	Mucoraceae	Primary saprotroph	15.5	8.4	2.0	3.0	0.02 ± 0.04	0 ± 0	0 ± 0	0.23 ± 0.74

Table 33. Leaf-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Huntington Forest. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Huntington Forest			Adj. R^2 value %				Relative abundance %			
Phylum	Family	Functional role	Total	% ECM	FTMT	Aspect	AM plot, AM tree	AM plot, ECM tree	ECM plot, AM tree	ECM plot, ECM tree
Ascomycota	Amphisphaeriaceae	Primary saprotroph or plant necrotroph	19.9	5.1	10.8	5.8	11.6 ± 11.6	0 ± 0	12.76 ± 11.5	8.22 ± 16.71
	Ascobolaceae	Dung saprotroph or various	16.8	1.1	5.0	4.2	0 ± 0	0 ± 0	0.03 ± 0.07	0 ± 0
	Aspergillaceae	Primary saprotroph	20.1	0.4	9.8	3.2	0 ± 0	0 ± 0	0.07 ± 0.17	0.23 ± 0.37
	Aureobasidiaceae	Primary saprotroph	16.8	1.1	5.0	4.2	0 ± 0	0 ± 0	0.01 ± 0.04	0 ± 0
	Cephalothecaceae	Primary or wood saprotroph	20.1	3.9	8.5	8.5	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.06
	Chaetomellaceae	Primary saprotroph, plant necrotroph, or unknown	36.7	21.7	30.6	0.5	1.6 ± 2.8	0 ± 0	0.53 ± 0.58	0.03 ± 0.09
	Chaetomiaceae	Primary or dung saprotroph	30.1	12.9	4.2	4.2	0 ± 0	0.09 ± 0	0 ± 0	0 ± 0
	Clavicipitaceae	Primary saprotroph or animal pathogen	19.5	10.9	4.2	4.2	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.06
	Cordycipitaceae	Primary saprotroph or animal pathogen	19.5	10.9	4.2	4.2	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Cryphonectriaceae	Plant biotroph	43.4	17.1	12.9	14.0	0.95 ± 0.99	0.09 ± 0	0.24 ± 0.37	0.19 ± 0.64
	Cucurbitariaceae	Plant necrotroph or various	17.6	0.9	0.9	16.0	0.04 ± 0.08	0 ± 0	0.05 ± 0.11	0.04 ± 0.12
	Dermateaceae	Primary saprotroph, plant necrotroph, various, or unknown	15.8	7.5	13.5	0.2	0.51 ± 0.68	1.28 ± 0	0.29 ± 0.41	1.33 ± 1.71
	Didymellaceae	Plant necrotroph or various	42.0	16.7	1.5	14.5	0.08 ± 0.19	0 ± 0	0.15 ± 0.24	0.27 ± 0.5
	Fenestellaceae	Primary saprotroph	43.2	16.1	2.1	16.4	0.04 ± 0.05	0 ± 0	0 ± 0	0.01 ± 0.03
	Geoglossaceae	Primary saprotroph	20.4	2.1	4.2	13.2	0.45 ± 1	0 ± 0	0.05 ± 0.13	2 ± 4.42
	Gloniaceae	Ectomycorrhizal	38.3	4.0	10.4	22.9	0 ± 0	1.65 ± 0	0.57 ± 1.39	0.71 ± 1.31
	Helotiaceae	Primary or wood saprotroph, ectomycorrhizal, plant necrotroph, ericoid mycorrhizal, endophyte, various, or unknown	22.0	6.8	0.7	19.5	12.25 ± 7.7	34.31 ± 0	11.63 ± 7.16	9.14 ± 5.38
	Hypocreaceae	Primary saprotroph	27.5	8.3	0.3	8.5	0 ± 0	0 ± 0	0.03 ± 0.07	0.01 ± 0.03
	Hypocreales (inc. sed.)	Primary saprotroph	58.1	6.4	41.5	13.9	7.06 ± 4.82	0.09 ± 0	8.46 ± 7.56	1.68 ± 1.83
	Lasiosphaeriaceae	Primary or dung saprotroph	16.1	14.0	6.7	3.1	0.06 ± 0.12	0 ± 0	0 ± 0	0.69 ± 1.79
	Melanommataceae	Wood saprotroph	32.3	22.6	22.1	0.0	0 ± 0	0 ± 0	0 ± 0	0.84 ± 1.55

	Mycosphaerellaceae	Plant necrotroph, lichen, or various	41.7	3.6	36.5	3.9	0.11 ± 0.07	0 ± 0	0.09 ± 0.1	0.01 ± 0.03
	Mytilinidiaceae	Primary or wood saprotroph	22.1	1.1	12.9	1.8	0 ± 0	0 ± 0	0.07 ± 0.17	1.35 ± 3.51
	Myxotrichaceae	Ericoid mycorrhizal or various	22.4	1.7	0.2	16.7	0.17 ± 0.38	0 ± 0	0.38 ± 0.92	0.41 ± 1.14
	Nectriaceae	Primary saprotroph or plant necrotroph	19.4	17.4	4.7	0.1	0.02 ± 0.04	0 ± 0	0.04 ± 0.11	0.19 ± 0.49
	Pezizaceae	Primary saprotroph, ectomycorrhizal, or various	43.3	42.6	13.0	3.1	0 ± 0	0 ± 0	0.44 ± 0.77	0.47 ± 0.49
	Phacidiaceae	Plant necrotroph or unknown	20.6	3.2	0.7	20.0	0 ± 0	0 ± 0	0.08 ± 0.19	0.04 ± 0.08
	Pleosporales (inc. sed.)	Primary saprotroph	28.9	21.2	4.8	14.2	0 ± 0	0 ± 0	0.02 ± 0.04	0.1 ± 0.23
	Pseudeurotiaceae	Primary saprotroph, animal pathogen, or various	25.9	18.4	9.4	10.8	0.51 ± 0.76	0 ± 0	0.38 ± 0.8	0.14 ± 0.29
	Rhytismataceae	Plant necrotroph or various	35.4	1.4	9.6	21.5	3.09 ± 4.36	0 ± 0	7.19 ± 7	2.44 ± 4.46
	Schizoparmaceae	Unknown	22.9	15.9	17.1	0.7	0.57 ± 0.78	0 ± 0	0.01 ± 0.04	0 ± 0
	Sclerotiniaceae	Primary saprotroph or plant necrotroph	35.5	10.4	20.0	9.2	1.16 ± 1.59	0 ± 0	0.21 ± 0.3	0.01 ± 0.03
	Sordariomycetes (inc. sed.)	Unknown	27.7	9.9	25.0	0.5	0.59 ± 0.48	0 ± 0	0.41 ± 0.41	0.13 ± 0.18
	Sympoventuriaceae	Primary saprotroph	40.5	10.4	11.6	30.1	0.06 ± 0.12	0.09 ± 0	0.13 ± 0.24	0.38 ± 0.48
	Teratosphaeriaceae	Primary saprotroph, plant necrotroph, various, or unknown	29.6	15.9	10.2	5.8	0.28 ± 0.21	0.09 ± 0	0.45 ± 0.59	0.18 ± 0.32
	Trichomeriaceae	Dung saprotroph, endophyte, or epiphyte	34.9	1.3	13.0	16.2	0.19 ± 0.15	0 ± 0	0.33 ± 0.68	0.09 ± 0.21
	Tubeufiaceae	Primary or wood saprotroph, various, or unknown	31.9	15.7	1.9	8.5	0.13 ± 0.29	0 ± 0	0 ± 0	0.01 ± 0.03
	Venturiaceae	Primary saprotroph, plant necrotroph, various, or unknown	38.3	2.4	10.8	27.6	1.14 ± 0.95	0.18 ± 0	1.09 ± 0.7	2.58 ± 1.8
	Vibrisseaceae	Primary saprotroph or endophyte	26.7	2.1	0.2	25.8	0.64 ± 1.42	2.2 ± 0	0.13 ± 0.32	0.13 ± 0.23
Basidiomycota	Agaricaceae	Primary saprotroph	16.8	0.4	3.8	12.3	0 ± 0	0 ± 0	0.08 ± 0.19	0.15 ± 0.33
	Agaricostilbaceae	Primary saprotroph	24.9	14.3	5.0	5.0	0.04 ± 0.08	0 ± 0	0 ± 0	0 ± 0
	Amanitaceae	Ectomycorrhizal	42.2	2.8	12.1	26.2	0.33 ± 0.73	0.37 ± 0	0.13 ± 0.32	0.99 ± 1.41
	Botryobasidiaceae	Primary saprotroph	16.3	1.0	4.2	5.0	0 ± 0	0 ± 0	0 ± 0	0.08 ± 0.25
	Bulleribasidiaceae	Fungal parasite	25.5	21.4	1.1	0.2	0 ± 0	0 ± 0	0.04 ± 0.11	0.03 ± 0.04
	Cantharellales (inc. sed.)	Ectomycorrhizal or lichen	19.2	3.8	0.7	15.3	4.66 ± 10.4	0 ± 0	0.9 ± 1.86	2.52 ± 8.25
	Ceratobasidiaceae	Plant necrotroph	18.0	0.0	0.1	16.3	1.77 ± 2.67	0 ± 0	0.42 ± 0.69	0.94 ± 0.85
	Chrysozymaceae	Primary saprotroph	25.0	6.4	0.1	10.1	0.34 ± 0.28	0 ± 0	0.25 ± 0.34	0.52 ± 0.87
	Clavariaceae	Primary saprotroph or various	25.7	0.5	1.8	21.6	0.28 ± 0.5	0.82 ± 0	0.83 ± 2.03	1.17 ± 3.15
	Cortinariaceae	Primary saprotroph or ectomycorrhizal	33.9	4.5	0.0	21.4	0.65 ± 1.46	0 ± 0	0.86 ± 2.1	0.63 ± 1.21
	Erythrobasidiaceae	Primary saprotroph	24.9	14.3	5.0	5.0	0.02 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	Filobasidiaceae	Primary saprotroph or fungal parasite	18.2	0.9	8.6	8.6	0.03 ± 0.08	0.09 ± 0	0.09 ± 0.17	0 ± 0

	Hydnangiaceae	Ectomycorrhizal	27.3	17.2	4.4	4.4	0 ± 0	0 ± 0	0.01 ± 0.04	0.07 ± 0.16
	Hydnodontaceae	Primary or wood saprotroph	22.9	0.3	9.6	12.2	0.42 ± 0.71	0.46 ± 0	0.98 ± 1.5	0.19 ± 0.56
	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various, or unknown	16.2	2.9	5.7	11.2	5.27 ± 11.8	0.91 ± 0	0.9 ± 2.2	0.04 ± 0.14
	Hymenogastraceae	Ectomycorrhizal	38.8	15.0	1.2	13.7	0 ± 0	0 ± 0	0.28 ± 0.68	0.29 ± 0.64
	Inocybaceae	Ectomycorrhizal	23.1	0.3	5.7	15.8	0.07 ± 0.15	10.16 ± 0	0.42 ± 1.03	0.82 ± 2.37
	Mycenaceae	Various	35.1	19.2	24.7	1.5	4.58 ± 6.35	0 ± 0	1.42 ± 2.32	0 ± 0
	Omphalotaceae	Primary or wood saprotroph	32.6	0.5	2.5	27.4	1.97 ± 2.86	0 ± 0	0.53 ± 0.76	0.88 ± 2.1
	Physalacriaceae	Primary saprotroph	19.5	10.9	4.2	4.2	0 ± 0	0 ± 0	0 ± 0	0.65 ± 2.16
	Piskurozymaceae	Unknown	39.4	0.1	5.0	30.6	0.35 ± 0.36	0.09 ± 0	0.55 ± 0.64	0.26 ± 0.29
	Pleurotaceae	Primary saprotroph	18.3	4.1	8.7	10.4	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.04
	Pluteaceae	Wood saprotroph	19.5	10.9	4.2	4.2	0 ± 0	0 ± 0	0 ± 0	0.01 ± 0.03
	Porotheleaceae	Wood saprotroph	28.6	12.5	8.2	8.2	0 ± 0	0 ± 0	0 ± 0	0.16 ± 0.4
	Russulaceae	Ectomycorrhizal	32.3	0.2	19.2	10.9	0.24 ± 0.36	31.75 ± 0	0.96 ± 2.01	4.32 ± 6.38
	Sebacinaceae	Ectomycorrhizal	52.2	15.1	10.7	23.5	0 ± 0	0.09 ± 0	0.42 ± 1.03	0.78 ± 1.12
	Serendipitaceae	Ericoid or orchid mycorrhizal	16.8	1.1	5.0	4.2	0 ± 0	0 ± 0	0.01 ± 0.04	0 ± 0
	Sporidiobolaceae	Primary saprotroph or plant necrotroph	20.5	0.0	14.6	2.7	0.31 ± 0.27	0 ± 0	1.38 ± 2.91	0.14 ± 0.22
	Trimorphomycetaceae	Fungal parasite	50.0	8.9	2.0	30.4	0 ± 0	0.09 ± 0	0.14 ± 0.21	0.19 ± 0.39
	Tulasnellaceae	Various	16.8	1.1	5.0	4.2	0 ± 0	0 ± 0	0.01 ± 0.04	0 ± 0
	Typhulaceae	Plant biotroph or various	17.2	13.7	6.3	5.5	0 ± 0	0 ± 0	0 ± 0	1.14 ± 3.66
	Xenasmataceae	Primary saprotroph	25.4	6.0	0.4	13.1	0 ± 0	0 ± 0	0.09 ± 0.21	0.06 ± 0.14
Chytridiomycota	Powellomycetaceae	Unknown	42.4	14.8	16.0	13.7	0.21 ± 0.21	0 ± 0	0.22 ± 0.36	0.06 ± 0.21
Glomeromycota	Glomeraceae	Arbuscular Mycorrhizal	35.9	7.4	35.8	0.0	0.15 ± 0.23	0 ± 0	0.2 ± 0.16	0.01 ± 0.03
Zygomycota	Mortierellaceae	Primary saprotroph	37.1	0.2	1.5	29.9	2.76 ± 2.5	3.75 ± 0	4.26 ± 6.17	2.39 ± 3.11
Mucoromycota	Endogonales (inc. sed.)	Ectomycorrhizal	36.9	16.6	10.4	10.4	0.04 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	Mucoraceae	Primary saprotroph	17.0	6.6	9.4	7.9	0.13 ± 0.29	0 ± 0	0.03 ± 0.07	0 ± 0
Rozellomycota	Rozellomycotina (inc. sed.)	Various	30.1	12.9	4.2	4.2	0 ± 0	0.27 ± 0	0 ± 0	0 ± 0

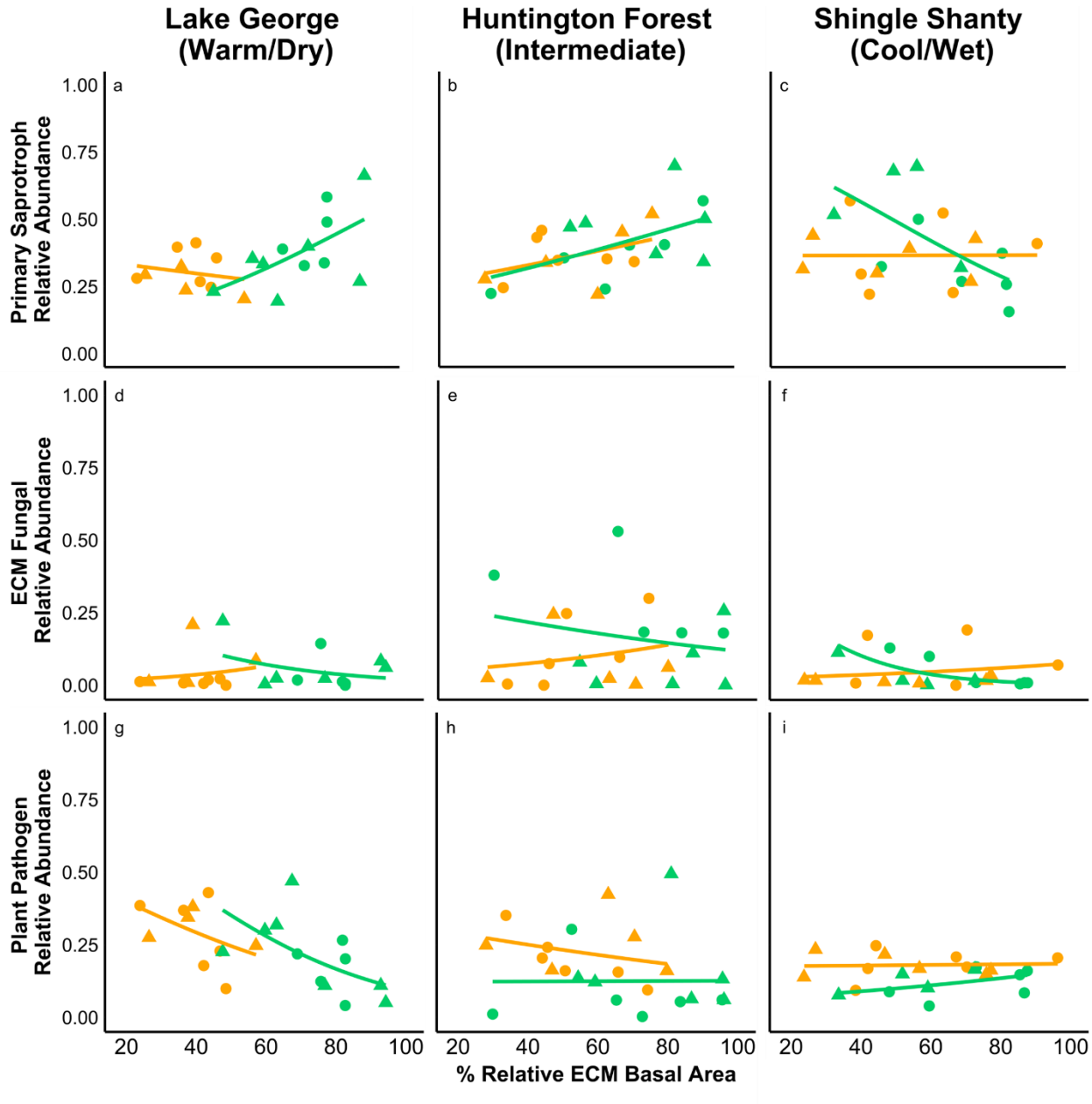
Table 34. Leaf-associated fungal families with a total adjusted R^2 value > 15% in the RDA modeling that included community data from Shingle Shanty. Relative abundance values include average and standard deviation. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively. Not all abundant taxa are shown.

Shingle Shanty			Adj. R^2 value %				Relative abundance %			
Phylum	**Family**	**Functional role**	**Total**	**% ECM**	**FTMT**	**Aspect**	**AM plot, AM tree**	**AM plot, ECM tree**	**ECM plot, AM tree**	**ECM plot, ECM tree**
Ascomycota	Ascobolaceae	Dung saprotroph or various	15.8	1.8	5.7	5.7	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.05
	Bionectriaceae	Unknown	22.1	17.5	8.3	0.3	0.03 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	Bionectriaceae	Primary saprotroph or unknown	22.1	17.5	8.3	0.3	0.03 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	Chaetothyriaceae	Primary saprotroph or unknown	15.8	1.8	5.7	5.7	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.05
	Cryphonectriaceae	Plant biotroph	31.7	12.6	19.4	1.0	3.42 ± 5.58	0.25 ± 0.36	2.35 ± 5.18	0.04 ± 0.1
	Diaporthaceae	Plant necrotroph	16.1	1.7	5.7	4.0	0 ± 0	0.06 ± 0.09	0 ± 0	0 ± 0
	Dothideaceae	Primary saprotroph, plant necrotroph, or various	21.8	0.2	12.8	8.7	0.17 ± 0.33	0 ± 0	0.32 ± 0.51	0.04 ± 0.07
	Elaphomycetaceae	Primary saprotroph or ectomycorrhizal	21.0	8.3	5.7	5.7	0 ± 0	0.05 ± 0.06	0 ± 0	0 ± 0
	Helotiaceae	Primary or wood saprotroph, ectomycorrhizal, plant necrotroph, ericoid mycorrhizal, endophyte, various, or unknown	21.2	0.1	11.1	7.4	20.8 ± 10.0	12.06 ± 6.73	23.63 ± 14.0	16.0 ± 11.67
	Helotiales (inc. sed.)	Primary saprotroph, ectomycorrhizal, plant necrotroph, endophyte, various, or unknown	19.6	6.6	15.8	3.8	1.87 ± 2.72	0.93 ± 0.3	0.93 ± 0.73	5.44 ± 6.5
	Herpotrichiellaceae	Primary saprotroph, plant necrotroph, endophyte, animal pathogen, or unknown	27.3	16.5	15.6	7.2	1.13 ± 0.75	0.95 ± 1.34	0.45 ± 0.4	0.18 ± 0.15
	Hyaloscyphaceae	Primary saprotroph, endophyte, fungal parasite, or various	39.2	19.0	24.0	0.2	12.1 ± 9.55	7.32 ± 2.44	7.19 ± 3.28	2.99 ± 2.3
	Lasiosphaeriaceae	Primary or dung saprotroph	20.5	9.1	11.9	8.3	0 ± 0	0 ± 0	0 ± 0	0.15 ± 0.28
	Lecanoraceae	Lichen	16.7	5.5	4.0	4.0	0.02 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	Leotiaceae	Primary saprotroph, ericoid mycorrhizal, or unknown	35.4	14.7	21.8	13.6	4.94 ± 3.88	7 ± 5.95	4.07 ± 1.84	8.34 ± 4.17
	Melanommataceae	Wood saprotroph	25.6	2.7	16.5	11.4	0 ± 0	0 ± 0	0 ± 0	0.11 ± 0.2
	Micropeltidaceae	Lichen	17.9	0.3	7.7	7.7	0.02 ± 0.04	0 ± 0	0.05 ± 0.12	0 ± 0
	Mycosphaerellaceae	Plant necrotroph, lichen, or various	17.5	12.5	2.7	0.5	0.4 ± 0.34	0.51 ± 0.72	0.03 ± 0.08	0.07 ± 0.19
	Mytilinidiaceae	Primary saprotroph	19.3	9.9	3.2	6.2	0.46 ± 1.12	3.25 ± 4.59	0 ± 0	0.17 ± 0.47
	Mytilinidiaceae	Wood saprotroph	19.3	9.9	3.2	6.2	0.46 ± 1.12	3.25 ± 4.59	0 ± 0	0.17 ± 0.47
	Phacidiaceae	Plant necrotroph or unknown	25.1	15.2	4.0	4.0	0 ± 0	0 ± 0	0.03 ± 0.07	0 ± 0

	Phaeosphaeriaceae	Primary saprotroph, plant necrotroph, or various	19.1	4.0	17.6	0.0	0 ± 0	0.13 ± 0.18	0 ± 0	0.14 ± 0.29
	Pyronemataceae	Primary saprotroph, ectomycorrhizal, various, or unknown	25.1	15.2	4.0	4.0	0 ± 0	0 ± 0	0.08 ± 0.19	0 ± 0
	Rhytismataceae	Plant necrotroph or various	16.5	14.6	0.0	4.9	9.67 ± 18.4	0.45 ± 0.63	5.06 ± 6.15	11.37 ± 16.5
	Saccharomycetales (inc. sed.)	Primary saprotroph	25.1	15.2	4.0	4.0	0 ± 0	0 ± 0	0.03 ± 0.07	0 ± 0
	Sporocadaceae	Plant necrotroph	34.0	19.2	0.2	4.2	0.17 ± 0.23	0.06 ± 0.09	1.63 ± 1.6	1.08 ± 0.99
	Teichosporaceae	Primary saprotroph	19.1	14.0	0.0	0.4	0 ± 0	0 ± 0	0.1 ± 0.25	0.03 ± 0.05
	Teratosphaeriaceae	Primary saprotroph, plant necrotroph, various, or unknown	26.1	21.5	0.9	13.1	0.89 ± 0.77	0.32 ± 0.45	0.1 ± 0.2	0.24 ± 0.2
	Tuberaceae	Ectomycorrhizal	15.1	0.9	6.3	4.1	0 ± 0	6.43 ± 9.1	0.02 ± 0.05	0.03 ± 0.08
	Venturiaceae	Primary saprotroph, plant necrotroph, various, or unknown	22.8	15.8	0.2	1.1	2.89 ± 2.24	2.2 ± 1.21	4.77 ± 3.48	4.1 ± 2.35
	Xylariales (inc. sed.)	Primary saprotroph, plant necrotroph, or unknown	22.2	0.4	14.9	4.7	1.07 ± 1.25	1.02 ± 1.44	1.55 ± 1.35	0.46 ± 0.56
Basidiomycota	Agaricostilbaceae	Primary saprotroph	17.6	15.4	4.0	5.7	0.02 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	Bulleraceae	Fungal Parasite	25.1	15.2	4.0	4.0	0 ± 0	0 ± 0	0.02 ± 0.04	0 ± 0
	Bulleribasidiaceae	Fungal Parasite	15.6	1.9	5.9	11.1	0.01 ± 0.03	0.06 ± 0.09	0 ± 0	0.06 ± 0.17
	Ceratobasidiaceae	Plant necrotroph	38.4	0.6	34.8	3.9	0.41 ± 0.44	1 ± 1.29	0.03 ± 0.07	0.89 ± 0.75
	Chrysozymaceae	Primary saprotroph	19.7	3.0	9.2	1.6	0.47 ± 0.38	0 ± 0	1 ± 1.62	0.47 ± 0.74
	Clavariaceae	Primary saprotroph or various	29.2	3.9	18.9	0.0	0.02 ± 0.04	0.63 ± 0.38	0 ± 0	0.06 ± 0.12
	Crepidotaceae	Wood saprotroph	19.2	0.6	8.1	11.7	0.03 ± 0.08	0 ± 0	0.06 ± 0.15	0 ± 0
	Filobasidiaceae	Primary saprotroph or fungal parasite	25.4	22.0	8.8	2.3	0.17 ± 0.26	0.05 ± 0.06	0.03 ± 0.05	0.02 ± 0.07
	Hydnodontaceae	Primary or wood saprotroph	26.8	24.2	0.0	5.9	1.35 ± 2.76	0.54 ± 0.77	0 ± 0	0.47 ± 0.89
	Hymenochaetaceae	Primary saprotroph, ectomycorrhizal, or plant necrotroph	25.1	15.2	4.0	4.0	0 ± 0	0 ± 0	0.09 ± 0.22	0 ± 0
	Hymenogastraceae	Ectomycorrhizal	16.1	1.7	5.7	4.0	0 ± 0	2.29 ± 3.24	0 ± 0	0 ± 0
	Lachnocladiaceae	Primary saprotroph	20.1	3.4	4.0	5.7	0 ± 0	0 ± 0	0.04 ± 0.1	0 ± 0
	Microstromatales (inc. sed.)	Unknown	25.1	15.2	4.0	4.0	0 ± 0	0 ± 0	0.02 ± 0.04	0 ± 0
	Paxillaceae	Ectomycorrhizal	37.2	6.4	18.8	1.3	0 ± 0	0.11 ± 0.03	0 ± 0	0.01 ± 0.03
	Phaeotremellaceae	Fungal Parasite	52.9	42.0	23.1	7.0	0.14 ± 0.1	0 ± 0	0 ± 0	0 ± 0
	Piskurozymaceae	Unknown	24.7	12.6	18.0	0.8	0.11 ± 0.12	0 ± 0	0.02 ± 0.04	0 ± 0
	Russulaceae	Ectomycorrhizal	23.0	1.2	12.7	3.9	0.36 ± 0.28	0.23 ± 0.32	0.94 ± 0.92	0.21 ± 0.17
	Schizoporaceae	Primary or wood saprotroph	19.0	2.9	4.0	5.7	0 ± 0	0 ± 0	0.81 ± 1.97	0 ± 0
	Septobasidiaceae	Animal Pathogen	16.7	5.5	4.0	4.0	0.02 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	Serendipitaceae	Ericoid or orchid mycorrhizal	15.6	12.8	4.0	5.7	0.03 ± 0.08	0 ± 0	0 ± 0	0 ± 0

	Strophariaceae	Primary or wood saprotroph, various, or unknown	31.9	1.7	24.0	1.8	0.27 ± 0.4	8.66 ± 12.24	0.05 ± 0.11	3.45 ± 5.91
	Tremellaceae	Fungal Parasite	17.9	5.8	0.0	5.6	0.04 ± 0.06	0 ± 0	0.43 ± 0.76	0.2 ± 0.29
	Wallemiaceae	Primary saprotroph	16.1	1.7	5.7	4.0	0 ± 0	0.06 ± 0.09	0 ± 0	0 ± 0
Chytridiomycota	Rhizophydiaceae	Plant necrotroph	19.4	7.5	15.4	3.3	0.08 ± 0.2	0.64 ± 0.9	0.02 ± 0.05	0.19 ± 0.25
Glomeromycota	Glomeraceae	Arbuscular mycorrhizal	23.5	4.0	0.1	11.5	0.06 ± 0.15	0.51 ± 0.72	0.03 ± 0.08	0 ± 0

Figure 16. Relative abundance changes among functional groups of leaf-associated fungi along a gradient of mycorrhizal dominance at each study site. Relative abundance values are displayed as decimals (0 – 1). Colors correspond to plot focal tree mycorrhizal type (gold = AM focal trees, green = ECM focal trees) and shapes correspond to slope aspect (circles = northern-facing slopes, triangles = southern-facing slopes).



APPENDIX E

CHAPTER IV SUPPLEMENTAL METHODS AND DATA

Supplemental methods

The phylogenetic mark correlation function calculates the average phylogenetic distance between adult and juvenile trees, excluding conspecific pairs, using a phylogenetic distance matrix (Shen *et al*. 2013, Wiegand & Moloney 2013). Our phylogenetic distance matrix was constructed in Phylocom (Webb *et al*. 2008) using Phylomatic (Webb & Donoghue 2005) and the supplied megatree from Zanne *et al*. (2014). Null model envelopes were generated from 199 Monte Carlo simulations randomizing the species identity of juvenile trees, thereby varying the average phylogenetic distance between an adult tree and the surrounding juvenile community, using random labeling (Jacquemyn *et al*. 2010). Values above this random simulation envelope indicate greater phylogenetic distances between juvenile and adult trees (a pattern consistent with phylogenetically-structured negative PSF), while values below this envelope indicate shorter phylogenetic distances (a pattern consistent with phylogenetically-structured positive PSF). These results were aggregated by plot mycorrhizal type and focal adult species mycorrhizal type.

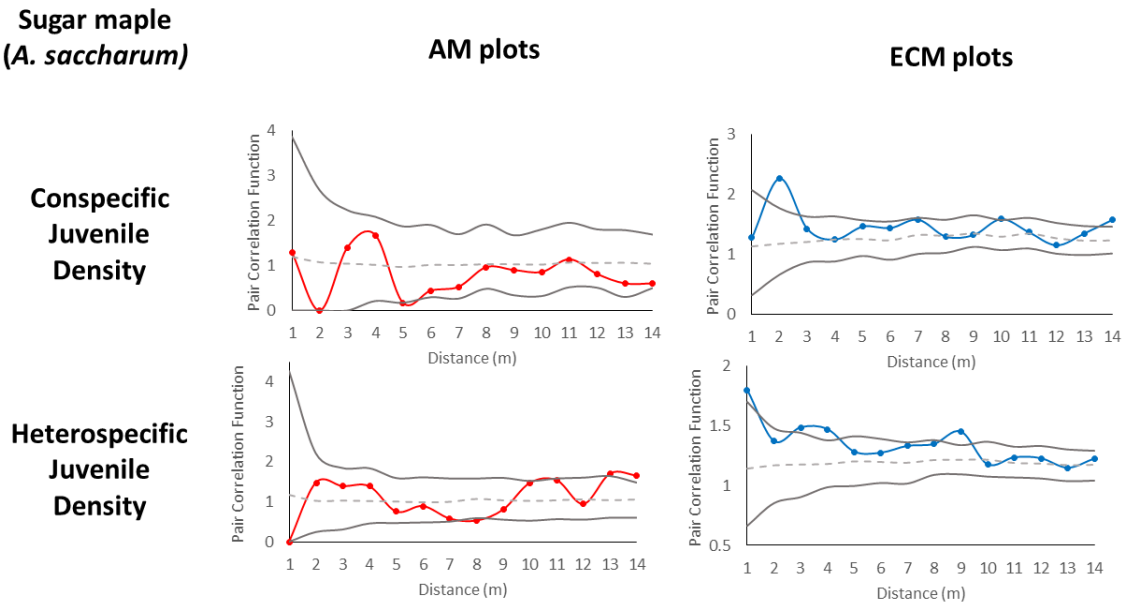
Supplemental tables

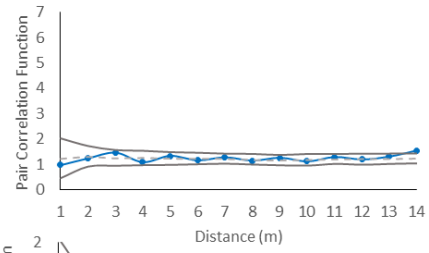
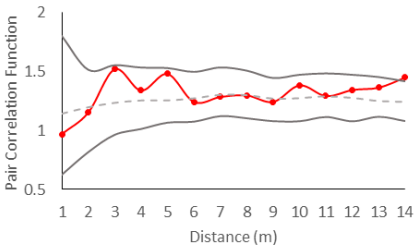
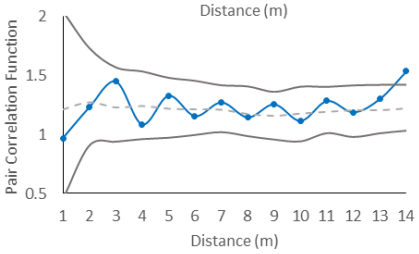
Table 35. Community properties and abiotic soil data by dominant community mycorrhizal type. Data shown are averages ± S.D. * Adult recruitment was significantly different between AM and ECM plots ($P = 0.02$).

	AM > 50%	**ECM > 50%**
Adult Recruitment *	1.4 ± 1.3	2.4 ± 2.6
Adult Abundance	33.0 ± 9.2	38.1 ± 13.1
Juvenile Abundance	71.1 ± 35.4	84.1 ± 64.6
Species Richness	14.4 ± 3.3	15.1 ± 4.4
Rarified Species Richness	10.6 ± 2.7	10.6 ± 4.0
Adult Growth Rate (cm DBH)	1.9 ± 2.1	2.1 ± 3.6
Adult Percent Mortality	14.3% ± 10.9%	14.2% ± 10.7%
Percent C	4.9% ± 2.3%	5.1% ± 3.5%
Percent N	0.3% ± 0.1%	0.3% ± 0.2%
C:N ratio	14.7 ± 2.5	14.9 ± 3.0
Extractable Total P (μg P/g soil)	185.0 ± 97.0	173.0 ± 116.0
Percent Moisture	32.1% ± 9.8%	31.2% ± 11.2%
pH	4.8 ± 0.7	4.9 ± 0.8

Supplemental figures

Figure 17. Neighborhood density function results for three AM-associated tree species across AM and ECM-dominated plots. Results were variable among species, with some species exhibiting different patterns between adult and juvenile individuals based on the dominant mycorrhizal type of the plots. Significant deviations from the grey null model occur where the colored points fall outside the grey lines ($P < 0.05$). Values above these null models indicate higher densities of juvenile trees than expected, while values below indicate lower densities of juvenile trees.



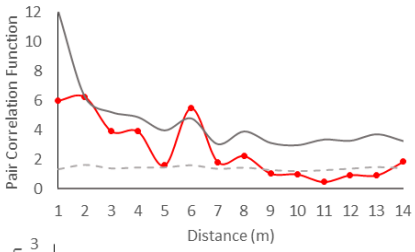
Red maple (*A. rubrum*)	**AM plots**	**ECM plots**
Conspecific Juvenile Density	**N/A (too few conspecific individuals)**	
Heterospecific Juvenile Density		

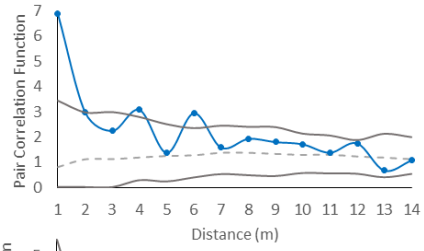
American elm
(*U. americana*)

AM plots

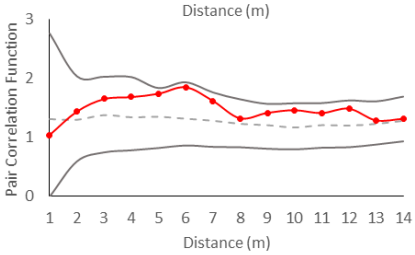
ECM plots

Conspecific Juvenile Density





Heterospecific Juvenile Density



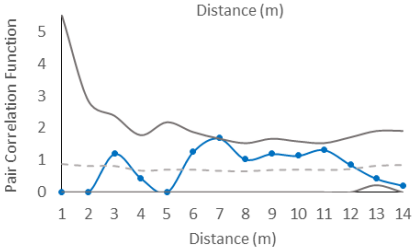
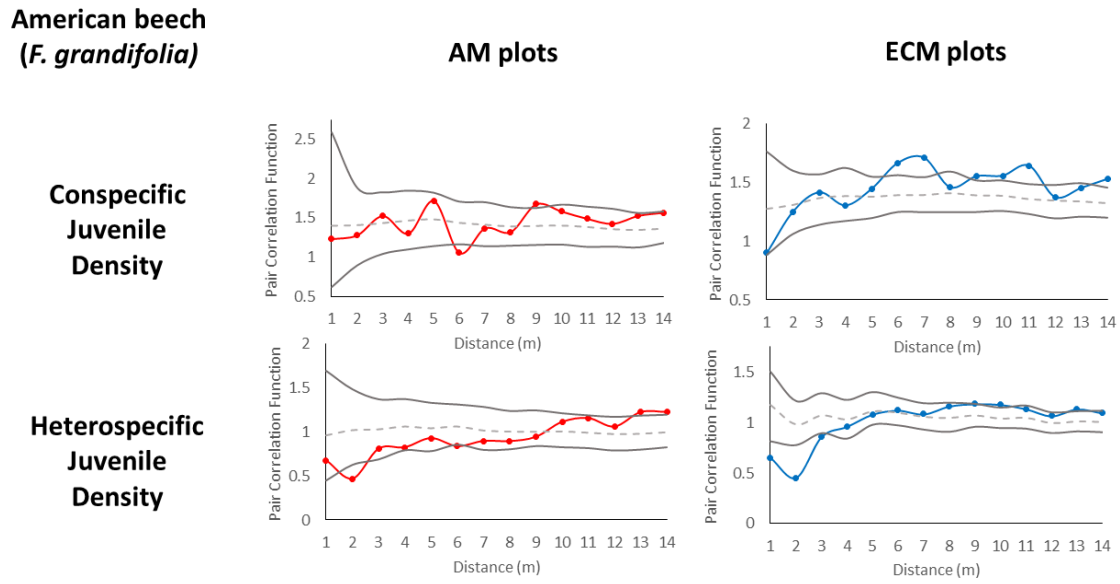
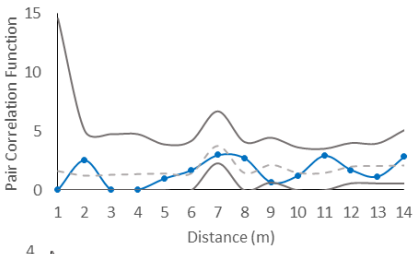
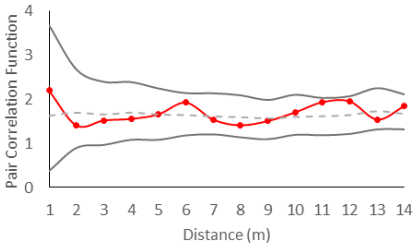
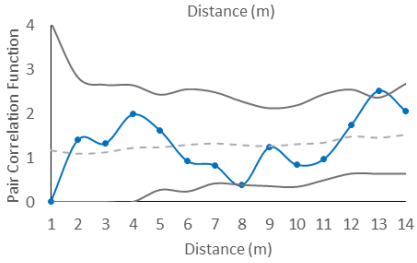


Figure 18. Neighborhood density function results for four ECM-associated tree species across AM and ECM-dominate plots. Results were variable between each species of interest, with some species exhibiting different patterns between adult and juvenile individuals based on the mycorrhizal dominance of the plots. Significant deviations from the grey null model occur when the colored points fall outside the grey lines ($P < 0.05$). Values above these null models indicate higher densities of juvenile trees than expected, while values below indicate lower densities of juvenile trees.

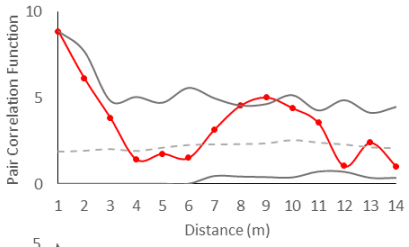


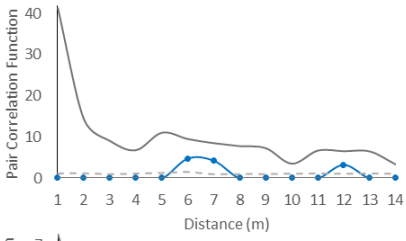
Shagbark hickory (*C. ovata*)	AM plots	ECM plots
Conspecific Juvenile Density	N/A (too few conspecific individuals)	
Heterospecific Juvenile Density		

American hornbeam (musclewood) (*C. caroliniana)*

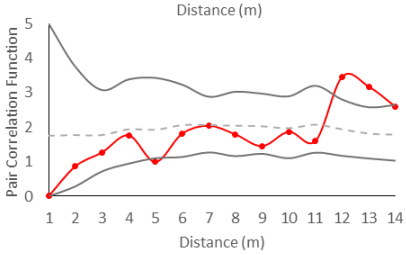
AM plots | **ECM plots**

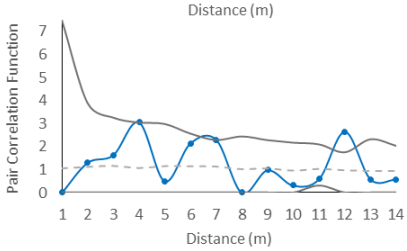
Conspecific Juvenile Density





Heterospecific Juvenile Density





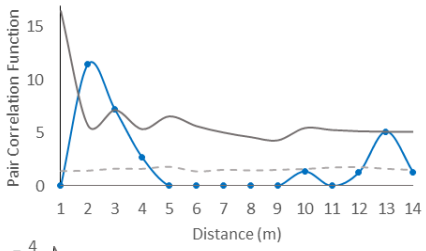
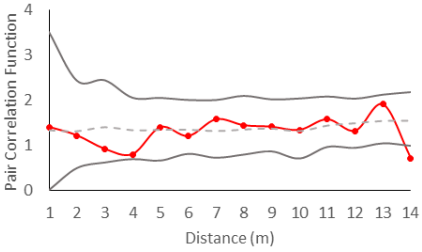
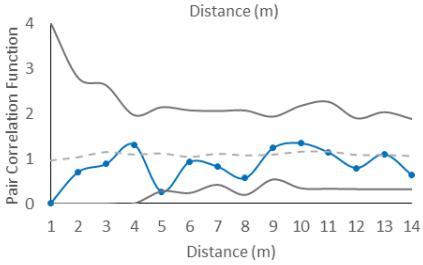
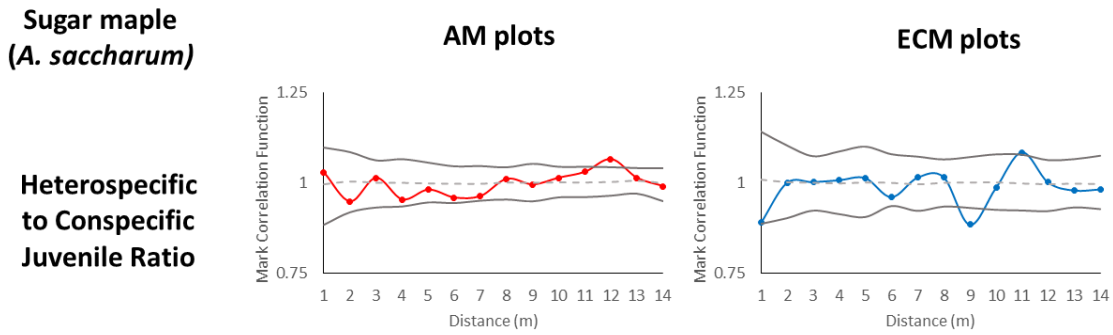
Northern red oak (*Q. rubra)*	AM plots	ECM plots
Conspecific Juvenile Density	**N/A (too few conspecific individuals)**	
Heterospecific Juvenile Density		

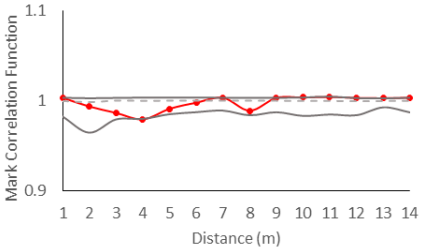
Figure 19. Mark correlation function results for three AM-associated tree species across AM and ECM-dominate plots. Results were variable among species, with some species exhibiting different patterns between adult and juvenile individuals based on the mycorrhizal dominance of the plots. Significant deviations from the grey null model occur when the colored points fall outside the grey lines ($P < 0.05$). Values above these null models indicate higher ratios of heterospecific to conspecific juvenile individuals, while values below indicate lower ratios.



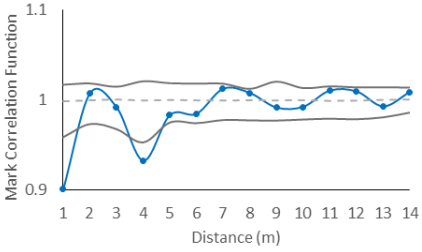
Red maple
(*A. rubrum*)

Heterospecific to Conspecific Juvenile Ratio

AM plots



ECM plots

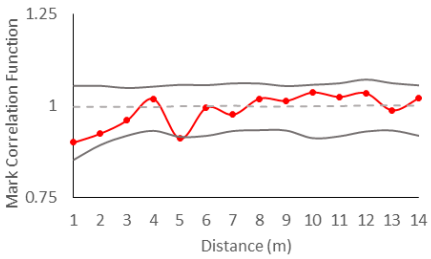


American elm
(*U. americana*)

AM plots

ECM plots

Heterospecific to Conspecific Juvenile Ratio



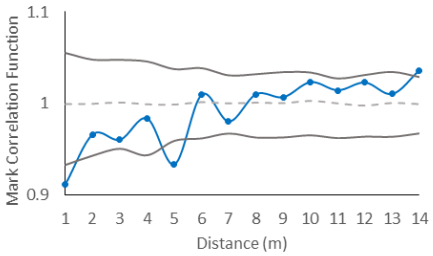
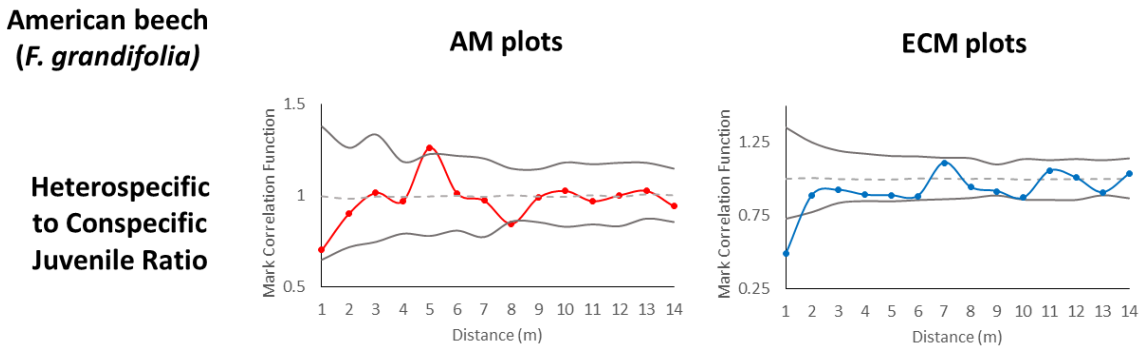


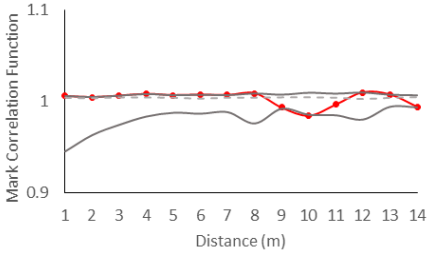
Figure 20. Mark correlation function results for four ECM-associated tree species across AM and ECM-dominate plots. Results were variable between each species of interest, with some species exhibiting different patterns between adult and juvenile individuals based on the mycorrhizal dominance of the plots. Significant deviations from the grey null model occur when the colored points fall outside the grey lines ($P < 0.05$). Values above these null models indicate higher ratios of heterospecific to conspecific juvenile individuals, while values below indicate lower ratios.



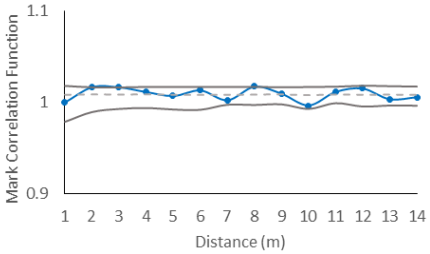
Shagbark hickory (*C. ovata)*

Heterospecific to Conspecific Juvenile Ratio

AM plots



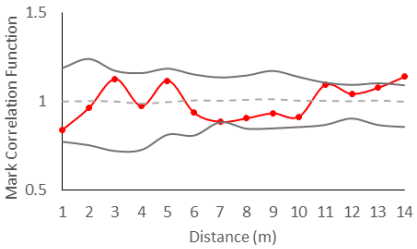
ECM plots



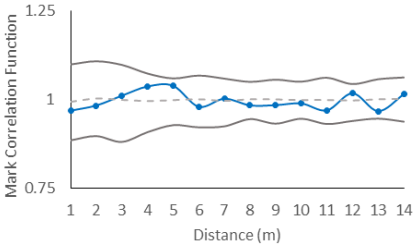
American hornbeam (musclewood) (*C. caroliniana)*

Heterospecific to Conspecific Juvenile Ratio

AM plots



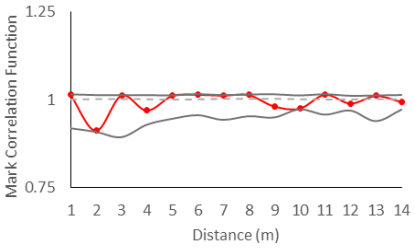
ECM plots



Northern red oak
(*Q. rubra*)

Heterospecific to Conspecific Juvenile Ratio

AM plots



ECM plots

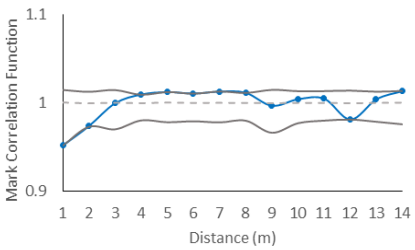
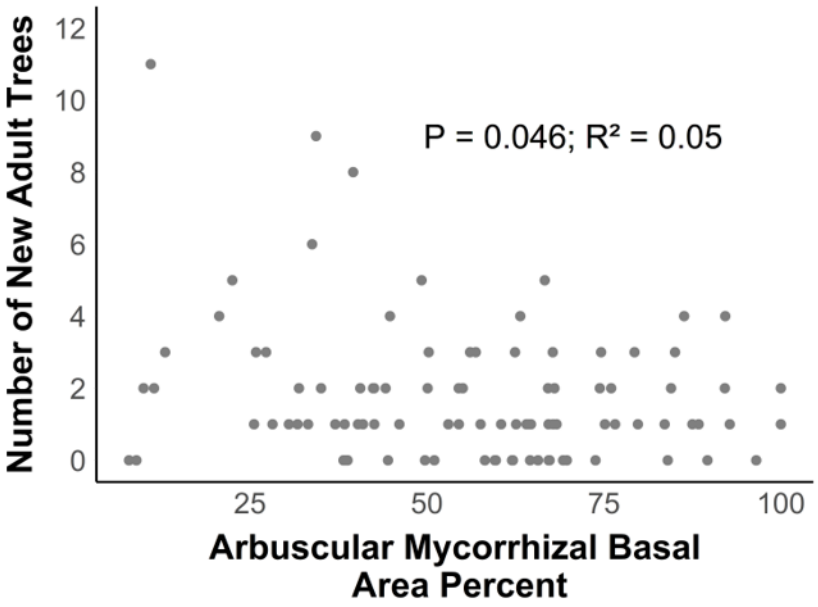


Figure 21. Recruitment of new adult trees by plot mycorrhizal basal area. Recruitment of new adult trees is significantly and negatively affected by increasing percent AM basal area, according to generalized linear modeling with Poisson error distribution (P = 0.046, R^2 = 0.05; Table 1).



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