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Context-dependence of fungal community responses to dominant tree mycorrhizal types in Northern hardwood forests

Andrew C. Eagar [a,*], Kurt A. Smemo [b], Richard P. Phillips [c], Christopher B. Blackwood [a]

[a] Department of Biological Sciences, Kent State University, Kent, OH, 44240, USA
[b] Environmental Studies and Science Program, Skidmore College, Saratoga Springs, NY, 12866, USA
[c] Department of Biology, Indiana University, Bloomington, IN, 47405, USA

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ABSTRACT

Dominant tree community mycorrhizal associations can influence soil biogeochemistry and nutrient cycling, suggesting a prominent role of mycorrhizas in shaping belowground microbial community composition and function. The degree to which the mycorrhizal type of dominant trees interacts with natural environmental gradients to influence belowground microbial communities is, however, unclear. Likewise, it is unknown if community-level mycorrhizal associations can influence the local microbial community encountered by an individual tree through spillover effects. To address these questions, we studied fungal communities from soil, roots, and leaf litter surrounding individual arbuscular (AM) and ectomycorrhizal (ECM) trees embedded in gradients of tree mycorrhizal dominance from three climatically distinct locations in the Adirondack Mountains, NY, USA. We found that dominant tree mycorrhizal types interact with site location to explain more variation in fungal community composition, richness, and function than specific soil properties, such as pH. This finding was consistent for all three sample types, but soil-associated fungi demonstrated the largest amount of explainable variation compared to root- and leaf litter-associated fungi. The relative abundance of plant pathogens was especially responsive to tree mycorrhizal dominance, increasing with AM dominance around individual AM trees but not around ECM trees in the same forests. These "mycorrhizal-spillover" effects on AM trees were also strongest in our warmest, driest site and weakest in our coolest, wettest site, indicating that the strength of mycorrhizal spillover is context-dependent in mixed-mycorrhizal forests.

1. Introduction

Plant mycorrhizal associations affect various terrestrial ecosystem processes, such as nutrient cycling rates and soil carbon (C) dynamics (Cornelissen et al. 2001; Read and Perez-Moreno 2003; Lin et al. 2017), yet the effects of mycorrhizal dominance on soil microbial communities are less well-described. Because different types of mycorrhizal associations vary in their nutrient acquisition strategies (Smith and Read 2008; Brundrett 2009), hypotheses that generalize these associations as drivers of plant-soil interactions have been proposed (e.g., Phillips et al. 2013; Bennett et al. 2017; Tedersoo et al. 2020). For example, under the mycorrhizal-associated nutrient economy (MANE) framework, 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 (Phillips 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. Given these hypothesized biogeochemical differences between forest stands dominated by AM and ECM trees, plant-microbe interactions may also be strongly affected by the dominant mycorrhizal type of tree communities (Bahram et al. 2020; Netherway et al. 2021; Eagar et al. 2022).

Spillover effects, where certain plant populations serve as reservoirs for pathogens that "spill over" and affect less susceptible populations, play an important role in plant population ecology (Power and Mitchell 2004; Mordecai 2011). Once thought to result from species-specific interactions between plants and pathogens, there is now increasing recognition that generalist pathogens capable of infecting multiple host species are central in creating cross-species spillover effects among plant

* Corresponding author.
E-mail addresses: aeagar1@kent.edu, eagarand@msu.edu (A.C. Eagar), ksmemo@skidmore.edu (K.A. Smemo), rpp6@indiana.edu (R.P. Phillips), cblackwo@kent.edu, blackw79@msu.edu (C.B. Blackwood).

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community members (Semchenko et al. 2022). Likewise, mutualisms between plants and microorganisms demonstrate similar dynamics to infectious diseases (Hawkes et al. 2020), suggesting spillover may occur with mutualists as well as pathogens – especially from plant species that dominate community composition. This broader application of the spillover effect concept requires new, generalizable frameworks in order to test emerging hypotheses in this field.

Recently, tree mycorrhizal associations have been implicated as potential drivers of spillover effects in both experimental (Bennett et al. 2017; Liang et al. 2020) and observational (Eagar et al. 2020, 2022; Bahram et al. 2020) studies. Notably, soil fungal plant pathogens appear sensitive to the presence of AM trees in a community (Bahram et al. 2020; Eagar et al. 2022). Fungal saprotrophs, some of which can function as facultative plant pathogens (Smith et al. 2017), also demonstrate similar responses to changes in mycorrhizal dominance consistent with the Gadgil effect (Bahram et al. 2020; Carteron et al., 2021; Eagar et al. 2022) – where direct competition between ECM fungi and fungal saprotrophs leads to competitive suppression of saprotrophic fungal activity (Gadgil and Gadgil 1971; Averill et al. 2014). However, the nature of these relationships has yet to be compared in the context of different fungal habitat types or across climatic gradients.

Interactions between soil, roots, and leaf litter are integral to the MANE framework, but it is reasonable to expect that fungal communities associated with these habitat types will respond to changes in mycorrhizal dominance to different degrees. Soil, roots, and leaf litter all represent unique environments with distinct microbiomes where microorganisms compete for different resources (Turner et al. 2013; 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). Mycorrhizal dominance might have stronger effects on root-associated microbial communities (relative to litter and soil-associated microbial communities) due to roots being the site of mycorrhiza formation. Alternatively, dominant mycorrhizal effects may have the strongest influence on leaf litter fungal communities due to differences in leaf litter chemical quality (Averill et al. 2019) and decay rates (Keller and Phillips 2019) between AM and ECM trees. However, because soil is the medium that links leaf litter and roots, soil communities may be more responsive to shifts in mycorrhizal dominance. To our knowledge, no study to date has compared fungal communities in these compartments in the context of dominant mycorrhizal associations.

Fungal distribution patterns are often dependent on regional climatic factors, such as mean annual precipitation and temperature (e.g., Tedersoo et al. 2014). Nevertheless, several studies have shown that dominant tree community mycorrhizal associations can explain more variation in fungal community composition than soil characteristics, such as moisture and soil organic matter (SOM) content, or pH (Bahram et al. 2020; Eagar et al. 2022). Furthermore, while the effect of microclimatic variation due to topography has been studied extensively for aboveground vegetation, fungal community responses to topographic variation are relatively unexplored (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 lessen or mask the effects of mycorrhizal dominance on fungal community composition. Thus, studying how climatic and mycorrhizal gradients interact to influence fungal community composition is critical to our understanding of global change outcomes.

We propose the term “mycorrhizal-spillover effects” to describe the influence of dominant plant mycorrhizal types on microbial communities surrounding individual plants. Our work here had three goals. First, we tested the hypothesis that the mycorrhizal dominance of a surrounding tree community affects the taxonomic and functional composition of the local fungal community encountered by an individual tree (a.k.a, the mycorrhizal-spillover effect). Our experimental design at three sites in the Adirondack Mountains, USA, allowed us to separate influences of the mycorrhizal type of a large individual tree from the dominant mycorrhizal type of the surrounding neighborhood, directly testing this hypothesis. Second, we investigated if topographic and regional variation affected the strength of these mycorrhizal-spillover effects through context-dependent interactions. Third, we sampled soil, roots, and leaf litter to see which associated fungal communities are more sensitive to mycorrhizal dominance and to test if general plot characteristics (e.g., tree species diversity, soil pH) better explain variation in these fungal communities than mycorrhizal dominance.

2. Methods

2.1. Study site and design

We established twenty-four 15 m radius plots in each of three forested sites at the northern edge of the temperate forest biome in the Adirondack (ADK) region of upstate New York, USA. The region includes mostly mixed northern forest ecosystems and exhibits distinct climatic gradients between warm and dry to cool and wet sites, illustrated by the increase in average annual precipitation and decrease in average annual temperature from the southeast to the northwest (Appendix A: Fig. 1). Specifically, Lake George Wild Forest (43.661, −73.545) is a warmer, drier location compared to our colder, wetter location at Shingle Shanty Preserve (43.894, −74.732). Huntington Wildlife Forest (43.987, −74.245) represents an intermediate location between the other two sites, with precipitation patterns similar to Lake George Wild Forest and temperature ranges similar to Shingle Shanty Preserve (Appendix A: Table 1).

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 > 2 cm 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 types and aspects.

Soils in our study sites are primarily spodosols (haplorthods), with some inceptisols (dystrochrepts) in the southeastern sites. Overall tree species richness is low in the ADK region and AM tree 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). Understory herbaceous vegetation cover is sparse, but includes *Viburnum lantanoides* (hobblebush), *Oxalis montana* (wood sorrel), *Cornus canadensis* (bunchberry), and *Clintonia borealis* (yellow clintonia).

2.2. Field sampling

All samples for this study 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, which were used to create one composite sample. All soil probes were cleaned with 70% EtOH and allowed to dry between plots. At each spot, we also collected composite leaf litter samples (Oi + Oe horizons) prior to coring and directly above where coring would occur 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 bulk soil. While all cores were taken

adjacent to our plot focal trees, roots from nearby tree community members were likely present in these soil samples due to root system overlap. Thus, roots included in this study may not have been from a plot focal tree, *per se*, but were still roots from trees influenced by the localized MANE effect of the focal tree. Roots were not washed prior to DNA extraction, but soil adhering to root surfaces was removed passively during sieving. DNA extracted from these root samples therefore represents microbial communities associated with both root tissue and a small portion of the immediate rhizosphere environment. All sample types were then stored at −80 °C.

Plot and soil variables measured around each focal tree were obtained independently of our samples described above and included: rarefied tree species richness and evenness (Hill's ${}^{0}D$ and ${}^{2}D$, or richness and the inverse Simpson index, respectively; Chao et al. 2014), forest floor leaf litter 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.

2.3. 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 litter samples, which were homogenized for each sample prior to extraction, 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 using ITS3ngs1-3 and ITS3ngs4-5 as forward primers paired with the ITS4ngsUni reverse primer (Tedersoo and Lindahl, 2016). This primer set captures most groups of fungi very well, although AM fungi are often in low abundance in sequence datasets due to their low biomass and ITS copy number (Tedersoo et al. 2015; AM fungi were not analyzed in this study for this reason). In PCRs, we used a 100 μM total of each primer mixture with an annealing temp of 55 °C. The cycle number (between 28 and 35 cycles) and genomic DNA dilution factor (1:20 or 1:100) varied among samples and sample types to achieve a 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 μl 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 2 × 300 bp MiSeq Illumina sequencing at the Ohio State University's Molecular and Cellular Imaging Center (Wooster, OH, USA).

2.4. 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. November 18, 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. Assignments listed as "probable" were accepted and likewise further verified. 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). Analysis of functional group distributions was conducted on the lowest taxonomic level assigned to each ASV (often genus or species), but these results were aggregated at the family level for presentation and interpretation.

2.5. 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). After rarefaction, sequences were grouped into 9864 unique ASVs and assigned to 1449 different taxonomic groups. To test our hypothesis about mycorrhizal associations influencing local fungal communities, mixed effect models were used to evaluate mycorrhizal effects on fungal 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 combined model using AIC scores for model comparison (Burnham and Anderson, 2004) with the R packages *lme4* (Bates et al., 2014) and *lmerTest* (Kuznetsova et al. 2017). Adjusted R2 values were obtained with the R package *MuMIn* (Bartoń, 2009). Model 1 was a location-based model testing the effects of site location (capturing our climate gradient), aspect, and a site × aspect interaction. Model 2 was a mycorrhizal-based model that included plot % ECM BA, focal tree mycorrhizal type (FTMT), and a % ECM BA × FTMT interaction that directly tested our mycorrhizal-spillover hypothesis. 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 geographic and mycorrhizal-based effects consistent with our second goal. In all three models, the species identity of plot focal trees was included as a random effect. Variance partitioning of modeled explanatory terms for richness and relative abundance values was achieved by analyzing each explanatory term separately while including the other terms as random effects.

Our statistical modeling of group relative abundances including both geographic and tree community terms (model 3) consistently resulted in the lowest AIC score for all functional groups and sample types (Appendices B – D: Table 4). For each sample type we report general relative abundance changes for fungal functional groups, as well as the families likely responsible for those trends, below. Site was identified as a significant variable in all analyses ($P < 0.001$), and detailed results for analyses of each site separately are shown in Appendices B – D.

To examine how mycorrhizal effects change 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, 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; Peres-Neto et al. 2006) of each modeled variable on fungal community composition consistent with our study goals, 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). 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 and to see if these variables explained more, or less, variation in fungal community composition compared to mycorrhizal effects. Lastly, to determine if tree species identity explained more variation in fungal community composition compared to tree species' mycorrhizal associations, a second redundancy analysis with focal tree species (FTS) included as the main effect and FTMT included as a conditional term was used.

To identify which fungal families were responsible for changes in the functional composition of our fungal communities (i.e., which fungal families may be influenced by mycorrhizal-spillover effects), we use the goodness() command on the family-level RDAs to obtain adjusted R^2 values for all fungal taxa. Fungal families were chosen for summarizing taxonomic patterns among guilds because ecological function roles at lower taxonomic levels are relatively well-conserved among groups of fungi (Zanne et al. 2020). 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.

3. Results

3.1. Fungal richness and mycorrhizal associations across an environmental gradient

For fungal richness, the model including interactions between both mycorrhizal and geographic terms (Model 3) was consistently selected through AIC comparison (Appendix A: Table 2). Overall, the amount of variation in ASV richness explained by the combined mycorrhizal + geographic model was similar for soil, root, and leaf litter fungal communities, although the variance explained by each modeled term differed substantially depending on sample type (Fig. 1a). When compared to one another, root samples demonstrated the lowest average fungal ASV richness (91.1 ± s.d. = 30.8) among all three sample types while soil and leaf litter sample fungal ASV richness averages were comparable (115.4 ± 24.6 vs. 124.6 ± 38.5, respectively). However, there were no significant terms identified in model 3 for root fungal ASV richness (Appendix A: Table 2). Aspect and an aspect × % ECM BA interaction were significant terms for both soil and leaf litter fungal ASV richness, while focal tree mycorrhizal type was also a significant term for soil fungal ASV richness (Appendix A: Table 2).

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 (Fig. 1b–d). Primary saprotroph ASV richness (Fig. 1b) in soil was the least-well explained among all functional group + sample type combinations. Notably, saprotroph richness did not decrease with increasing % ECM BA (Fig. 2a–c) as seen in previous studies (Bahram et al. 2020; Eagar et al. 2022). 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 (Fig. 1c). 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 compared to plots with AM focal trees (Fig. 2d and e). The variation in plant pathogen ASV richness in soil was best explained by mycorrhizal factors, but in roots and leaf litter site or interactions between mycorrhizal effects and site were more important (Fig. 1d). 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 (Fig. 2g–i). Supporting data (P-values, AIC scores) can be found in Appendix B Table 3 (soil samples), Appendix C Table 3 (root samples), and Appendix D Table 3 (leaf litter samples).

3.2. Fungal community composition, mycorrhizal associations, and environmental gradient interactions

Site was consistently identified as a driver of community composition for all sample types (Fig. 3), while the remaining terms and two-way interactions varied in significance depending on taxonomic level/guild and sample type (Appendix A: Table 3). 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 not at the ASV level (Fig. 3a and b). However, mycorrhizal effects in soil and root habitats were strongest for guild composition (Fig. 3c). The reverse was true in leaf litter, where mycorrhizal effects were strongest at the ASV level. Variation explained in the composition of fungal guilds was greatest in soil-associated communities, where mycorrhizal effects explained as much variation as geographic effects (Fig. 3c). Focal tree species identity was also consistently significant (in all cases except guild composition in leaf litter), and was particularly important for ASV and Family composition (Fig. 3a–c, Appendix A: Table 3), although it explained less variation compared to mycorrhizal effects. 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: Table 1).

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 4; Fig. 3a–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 4). 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: Table 2).

Table 1
Soil-associated fungal families with a total adjusted R^2 value $> 10\%$ and relative abundance $>1\%$ from the RDA modeling that included community data from all three sites. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively.

Soil fungi			Adj. R^2 value %		
Phylum	Family	Family member functional role(s)	Total	% ECM BA	FTMT
Ascomycota	Geoglossaceae	Primary saprotroph	13.7	9.9	8.8
	Herpotrichiellaceae	Endophyte, primary saprotroph, animal pathogen, plant necrotroph, or unknown	16.2	12.3	12.0
Basidiomycota	Amanitaceae	Ectomycorrhizal	18.4	14.3	1.9
	Boletaceae	Ectomycorrhizal	13.9	4.3	0.0
	Clavariaceae	Primary saprotroph or various	11.8	5.9	9.6
	Cortinariaceae	Ectomycorrhizal	11.8	1.0	10.5
	Entolomataceae	Primary saprotroph, ectomycorrhizal, or various	32.9	20.8	12.7
	Hydnodontaceae	Primary saprotroph	10.7	0.0	7.3
	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various, or unknown	32.6	28.2	20.3
	Russulaceae	Ectomycorrhizal	21.8	17.2	15.3

Table 2
Root-associated fungal families with a total adjusted R^2 value > 10% and relative abundance >1% from the RDA modeling that included community data from all three sites. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively.

Root fungi			Adj. R^2 value %		
Phylum	Family	Family member functional role(s)	Total	% ECM BA	FTMT
Ascomycota	Gloniaceae	Ectomycorrhizal	11.9	8.0	8.7
	Herpotrichiellaceae	Endophyte, primary saprotroph, animal pathogen, plant necrotroph, or unknown	17.8	14.3	10.4
Basidiomycota	Clavariaceae	Primary saprotroph or various	10.5	0.9	9.9
	Entolomataceae	Primary saprotroph, ectomycorrhizal, or various	14.6	10.7	7.8
	Hygrophoraceae	Ectomycorrhizal, plant biotroph, various, or unknown	22.7	17.3	14.2
	Russulaceae	Ectomycorrhizal	15.3	8.1	12.6
	Sebacinaceae	Ectomycorrhizal	11.7	11.4	1.4

Table 3
Leaf litter-associated fungal families with a total adjusted R^2 value > 10% and relative abundance >1% from the RDA modeling that included community data from all three sites. % ECM and FTMT refer to the portion of variation explained by the mycorrhizal gradient and focal tree mycorrhizal type, respectively.

Leaf fungi			Adj. R^2 value %		
Phylum	Family	Family member functional role(s)	Total	% ECM BA	FTMT
Ascomycota	Chaetomellaceae	Primary saprotroph, plant necrotroph, or unknown	12.9	12.8	4.4
	Cryphonectriaceae	Plant biotroph	20.7	17.1	13.6
	Hypocreales[a]	Primary saprotroph	17.1	4.3	16.9
	Mytilinidiaceae	Primary or wood saprotroph	14.2	0.0	10.6
	Pseudeurotiaceae	Primary saprotroph, animal pathogen, or various	26.9	24.7	9.3
	Sporocadaceae	Plant necrotroph	10.1	4.3	2.7
	Tuberaceae	Ectomycorrhizal	10.3	0.0	4.4
Basidiomycota	Cantharellales[b]	Ectomycorrhizal or lichen	11.2	0.3	0.2
	Ceratobasidiaceae	Plant necrotroph	11.9	0.2	5.9
	Clavulinaceae	Ectomycorrhizal or various	14.6	2.4	14.4
	Mycenaceae	Various	10.2	2.8	8.0
Zygomycota	Mortierellaceae	Primary saprotroph	12.0	1.4	0.0

[a] - Taxa within the Hypocreales (*inc. sed.*) include Barbatosphaeria, Brachysporium, Ciliciopodium, and Cylindrium.
[b] - Taxa within the Cantharellales (*inc. sed.*) include Minimedusa, Multiclavula, and Sistotrema.

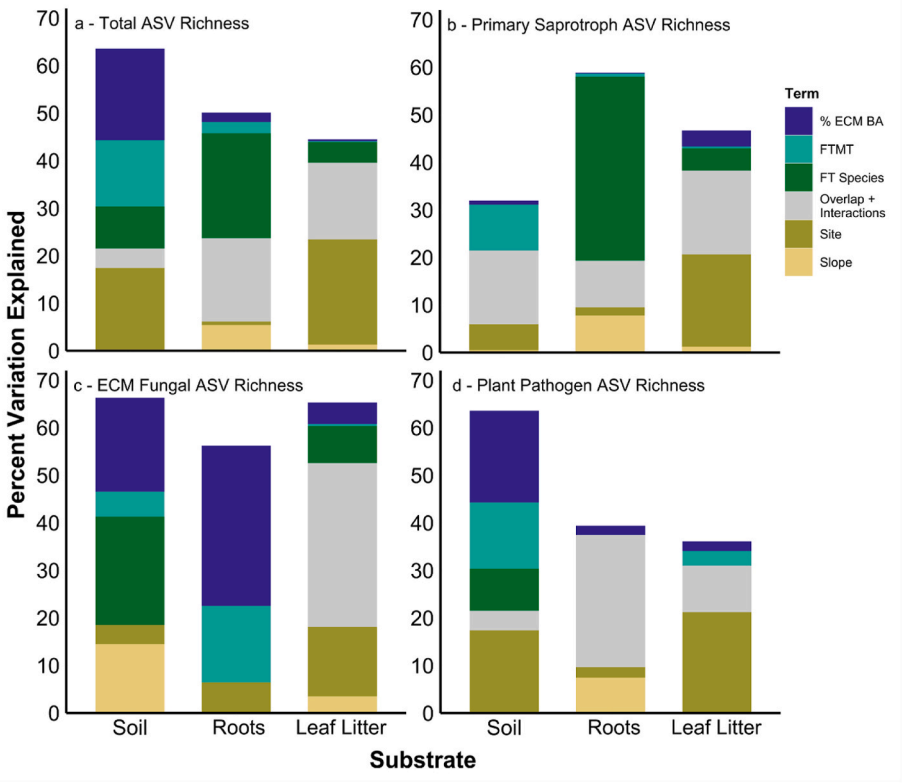

Fig. 1. Variance partitioning (Adj. R^2) of a) overall fungal richness and b – d) specific functional groups of fungi. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type; FT Species = plot focal tree species.

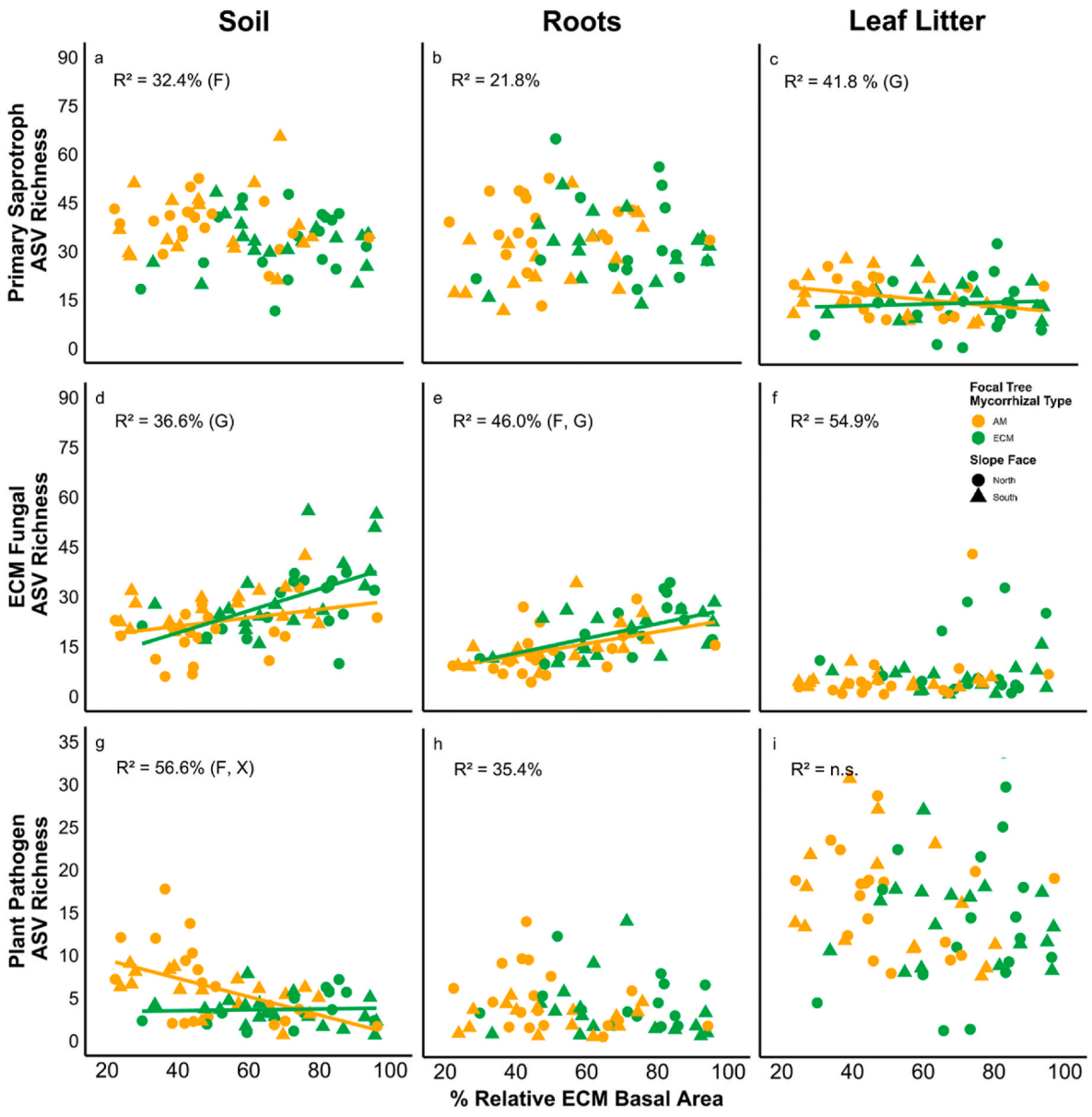

Fig. 2. Fungal functional group ASV richness reported for soil, root, and leaf litter samples. Colors correspond to plot focal tree mycorrhizal type (gold = AM focal trees, green = ECM focal trees), shapes correspond to slope aspect (circles = northern-facing slopes, triangles = southern-facing slopes), and R^2 values correspond to the most parsimonious model selected through AIC comparison (combined model 3 in all cases; significance of all model terms including site, aspect, and their interactions can be found in Appendices B – D: Table 3). Letters after an R^2 value denote significance of the model terms focal tree mycorrhizal type (F), % ECM BA gradient (G), and the interaction between the two (X).

3.3. *Mycorrhizal-spillover effects from AM-dominant communities*

In all three habitat types, plant pathogen relative abundance displayed a strong negative correlation with increasing % ECM BA, but only surrounding AM focal trees (Fig. 4g–i). Plant pathogen relative abundance remained uniformly low surrounding ECM focal trees. In soil and root samples, the Herpotrichiellaceae (Ascomycota) and Hygrophoraceae (Basidiomycota) were families identified as having pathogenic members involved with these patterns, although both families are known to contain some taxa that are not plant pathogens (Tables 1 and 2). In leaf litter samples, only the Cryphonectriaceae (Ascomycota) were associated with these patterns (Table 3).

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 1) and roots (Gloniaceae, Suillaceae; Table 2). South-facing slopes also had generally higher ectomycorrhizal fungal relative abundances (Fig. 4d and e). In contrast, there were no prominent trends in leaf litter-associated ectomycorrhizal fungal relative abundances correlated with % ECM BA or focal tree mycorrhizal type (Fig. 4f). Also as expected, the AM fungal family Glomeraceae declined in relative abundance due to both % ECM BA and surrounding ECM focal trees (from an average of 0.2% around AM trees in AM communities to 0.05% around ECM trees in ECM communities), although this group was very low in abundance as is typical in broad fungal surveys (Tedersoo et al. 2015).

Primary saprotroph relative abundances were similar in each sample type and demonstrated no notable trends with % ECM BA (Fig. 4a–c).

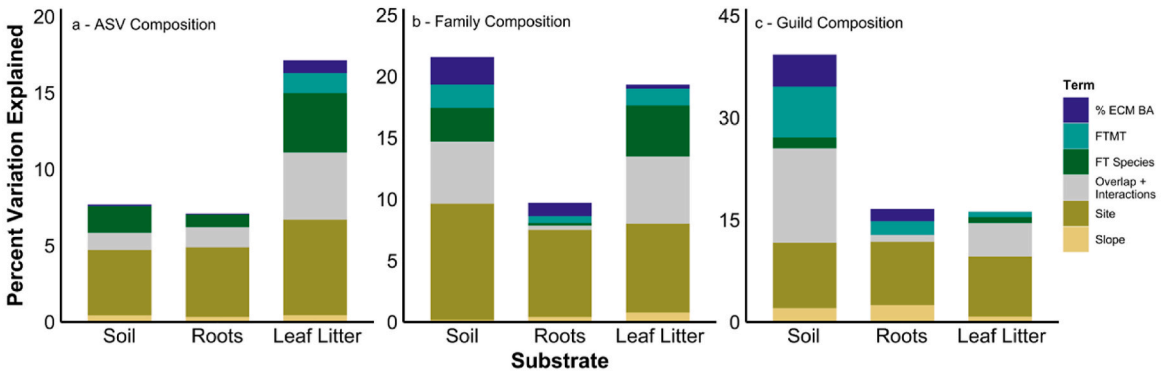

Fig. 3. Variance partitioning (Adj. R^2) of fungal community composition. % ECM BA = tree community ECM BA proportion; FTMT = plot focal tree mycorrhizal type; FT Species = plot focal tree species.

However, the families Geoglossaceae (Ascomycota), Hypocreales (Ascomycota), Clavariaceae (Basidiomycota), and saprotrophic members of Entolomataceae (Basidiomycota) demonstrated shifts in relative abundance dependent on mycorrhizal factors (Tables 1–3).

3.4. *Interactions between mycorrhizal-spillover effects and environmental gradients*

Across our climate gradient, we observed the strongest patterns between mycorrhizal effects and fungal community relative abundances at our warmer, drier site (Lake George Wild Forest) and the weakest patterns at our cooler, wetter site (Shingle Shanty Preserve) for all habitat types (Appendices B – D: Fig. 1). Notably, there were diminishing mycorrhizal-spillover effects between tree community mycorrhizal associations and soil-borne plant pathogen relative abundances across our climate gradient, mostly around AM trees (Fig. 5).

4. Discussion

Our results demonstrate that increasing ECM tree dominance corresponds to lower plant pathogen species richness and relative abundance, similar to Bahram et al. (2020) and Eagar et al. (2022), and we show that mycorrhizal associations are better predictors of fungal community composition and function than soil characteristics or individual tree species identity. We also found stronger effects of mycorrhizal dominance on fungal communities in our warmer, drier site compared to our cooler, wetter site, and these effects were more prominent in soil, rather than root and leaf litter, samples. Collectively, we provide evidence of context-dependent effects from dominant mycorrhizal associations on local fungal communities that spill over onto individual trees within forest ecosystems.

We found general support for our hypothesis that the dominance of mycorrhizal types in the surrounding tree community affects the community composition and function of local fungi associated with individual trees. Interestingly, mycorrhizal-spillover effects from the neighboring tree community may be particularly strong for plant pathogens surrounding individual AM trees (Figs. 3 and 5). Adjacent to AM focal trees, plant pathogen richness and relative abundance decreased with ECM-tree dominance; however, adjacent to ECM focal trees, plant pathogen richness and relative abundance was uniformly low, even when the surrounding neighborhood was dominated by AM trees. Both AM and ECM fungi are known to provide defensive benefits to their hosts (Pozo et al. 2002; Smith and 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 have been hypothesized to be better protected from pathogens than AM trees, owing to the fungal mantle that covers ectomycorrhizal root tips and blocks pathogen entry into root cells (Bennett et al. 2017). Such protection would potentially insulate ECM trees from spillover effects from an AM-dominant tree community, thereby creating localized low-pathogen patches within AM-dominant communities.

Our findings also revealed that environmental gradients and geographic context can alter the strength of mycorrhizal influences on fungal communities. Of note, the relationship between ECM dominance and saprotrophic fungi may be especially weak in cooler climates such as the Adirondack Mountains, as indicated by a lack of trend in all three sites in Fig. 3a–c and 5a – c. These findings were surprising, considering that competition between ECM and saprotrophic fungi is believed to suppress saprotroph activity through competitive exclusion (Gadgil and Gadgil 1971; Averill et al. 2014; Averill and Hawkes 2016; Netherway et al. 2021) and previous studies have reported results in support of this idea (Bahram et al. 2020; Carteron et al., 2021; Eagar et al. 2022). Work conducted parallel to this study at our Adirondack sites has found that our soils do not consistently reflect MANE-related biogeochemical predictions. Here, soil % C, %N, C:N ratio, pH, respiration rate, plant available NH_4^+ and NO_3^-, and net nitrification rates do not appear variable between AM- and ECM-dominant communities (unpublished data). These findings may be explained by our documented lack of relationship between ECM tree dominance and fungal saprotroph richness and relative abundance, but work at these sites is ongoing to confirm this hypothesis. Colder climates generally slow rates of decomposition (Zhang et al. 2008), potentially to an extent where the degree of soil organic matter accumulation reduces 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 in the ADK region. Thus, our findings suggest that the strength of mycorrhizal-spillover effects, and potentially other components of the MANE framework, are influenced by regional climate conditions the Adirondack Mountains.

The small amount of variation explained by soil variables in our study suggests that 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), although fungal communities in soil demonstrated the strongest responses to surrounding mycorrhizal associations. Interestingly, several fungal families demonstrated strong correlations with tree mycorrhizal associations both in soils from the Adirondacks and temperate forests in southcentral Indiana, USA (Eagar et al. 2022): saprotrophic members of the Clavariaceae and Entolomataceae, ectomycorrhizal members of the Boletaceae, Cortinariaceae, Entolomataceae, and Russulaceae, 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

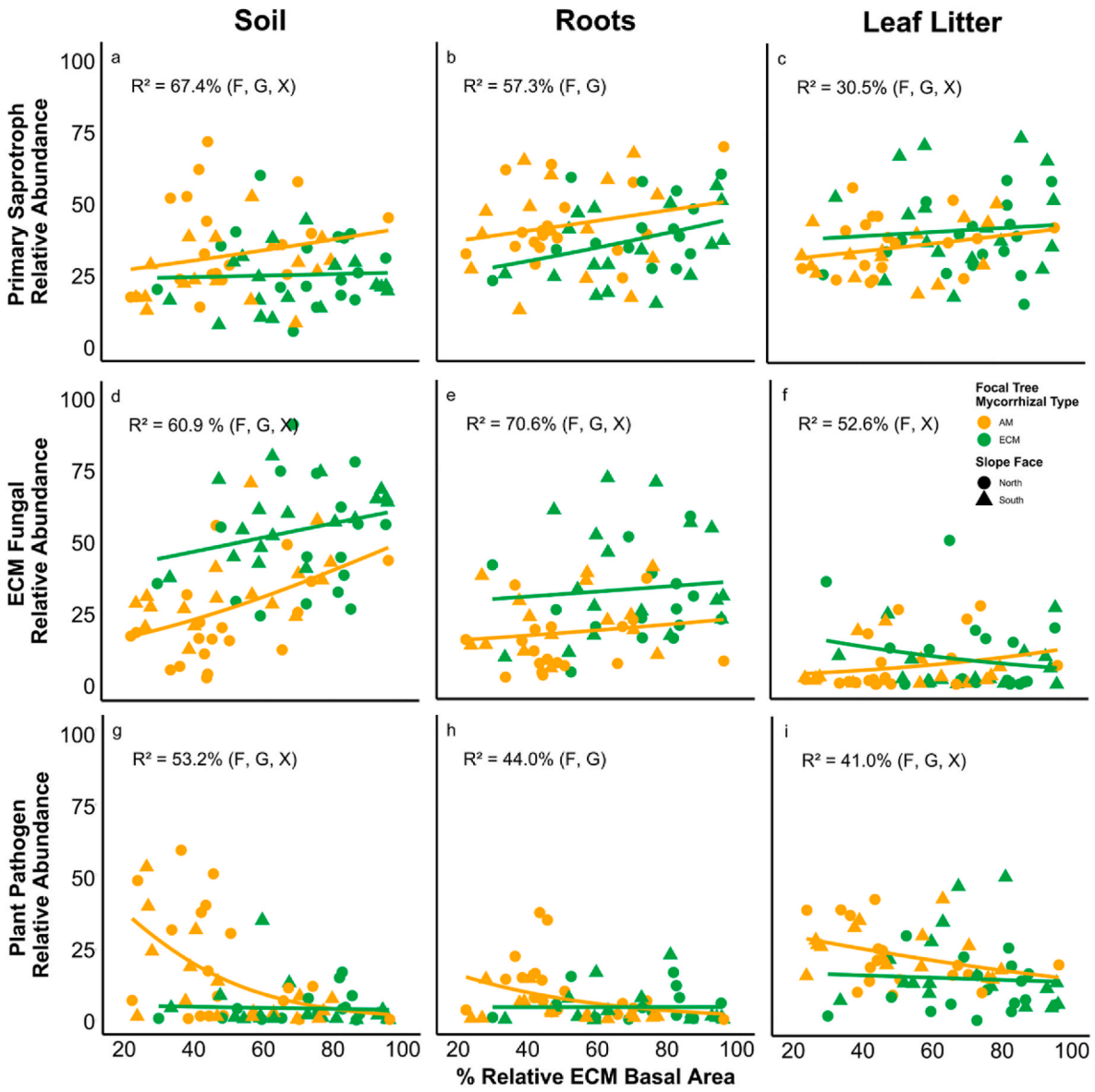

Fig. 4. Relative abundance changes among functional groups of fungi along a gradient of mycorrhizal dominance for soil, root, and leaf litter samples. Relative abundance values are displayed as percentages (0–100%). Colors correspond to plot focal tree mycorrhizal type (gold = AM focal trees, green = 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; significance of all model terms including site, aspect, and their interactions can be found in Appendices B – D: Table 3). Letters after an R^2 value denote significance of the model terms focal tree mycorrhizal type (F), % ECM BA gradient (G), and the interaction between the two (X).

relationship between fungal community composition and dominant tree mycorrhizal associations, but more comparisons at consistent taxonomic ranks are needed in future works.

In conclusion, our results support our 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 for pathogen communities surrounding individual AM trees and in warmer, drier environments. These patterns were consistent, albeit variable in strength, across soil, root, and leaf litter samples. Across much of the temperate region, tree species' ranges are shifting due to global changes (Steidinger et al. 2019). In the eastern US, many AM trees are increasing in dominance whereas in the northern hardwood forests, many forests are becoming increasingly ECM-dominant (Jo et al. 2019). Whether the turnover of tree communities is buffered or enhanced by pressures from fungal pathogens is an open question. Mycorrhizal-spillover effects of fungal pathogens due to global shifts towards AM dominance (Steidinger et al. 2019) 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.

Author contributions

ACE, CBB, RPP, and KAS designed the field study, while ACE, CBB, and KAS designed the sampling approach. ACE collected the molecular

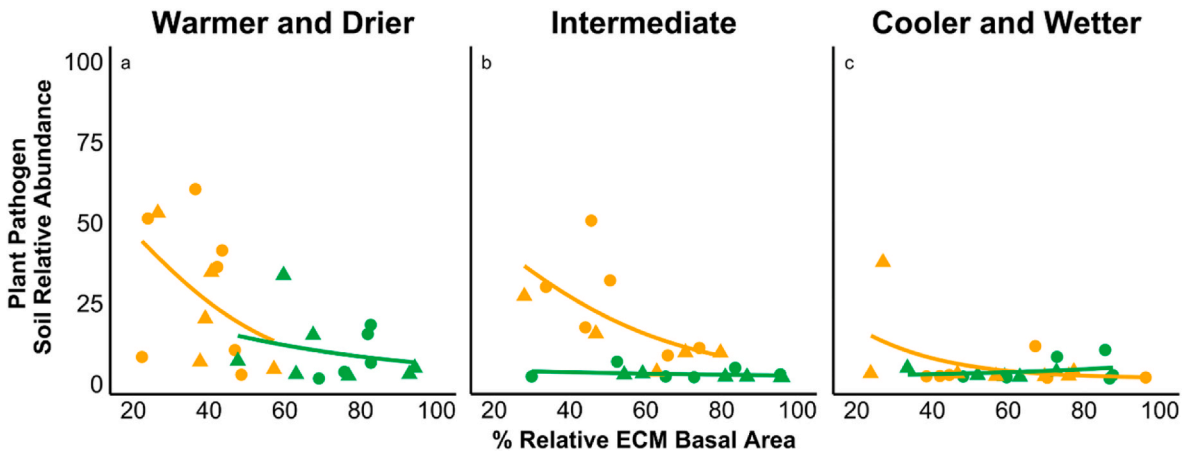

Fig. 5. Relative abundance changes of plant pathogens inhabiting bulk soil across the temperature and moisture gradient of the ADK region, exemplifying a decrease in spillover effect strength surrounding AM trees from a to c. Relative abundance values are displayed as percentages (0–100%). Colors correspond 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). More details are provided in Appendix B.

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.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

A link to our public data repository is included in the manuscript

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2023.108971.

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