Title: 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.

Keywords

Fungal functional diversity, mycorrhizal associated nutrient economy (MANE), nitrogen deposition, plant-microbe interactions, temperate hardwood forests, spillover effects

1. 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 (1). In temperate forests, the decomposition of labile leaf litter from arbuscular mycorrhizal (AM) trees by saprotrophic fungi induces greater soil mineral nutrient availability (2, 3) and greater amounts of N-rich mineral-associated organic matter (4, 5) compared to lignin-rich, high C:N leaf litter from ectomycorrhizal (ECM) trees (6, 7). The direction of plant-soil feedback is also structured by mycorrhizal type, with ECM trees experiencing positive feedback and AM trees experiencing negative feedback (8, 9, 10). 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 (11, 12) 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 (13, 14). Conversely, many ECM fungi have saprotrophic capabilities and produce extracellular enzymes that decompose plant tissue to acquire organic forms of nutrients (15, 16). 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 (17, 18, 19). 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 (20, 21).

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 (2, 3, 7). Higher available soil resources such as N can affect fungal diversity (22, 23) and biomass (24, 25), leading to notable increases in fungal species richness (26). Furthermore, a positive relationship has been observed between soil resource availability and plant disease severity, particularly for AM trees (27; 28), 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 (29).

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 (11), and also alters soil organic matter (SOM) content in different ways depending on dominant tree species (30, 31). Importantly, increased anthropogenic N deposition has been shown to alter soil fungal community composition (32, 33), leading to increased saprotroph diversity and decreased ECM fungal diversity in forest soil (34, 35). Furthermore, increases in soil N availability may increase plant pathogen diversity (27, 26). 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.

2. Materials and Methods

2.1 Site Descriptions

2.1.1 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 which species are dominant (i.e., abundant) and 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 (36). 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*) (37). 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 (38). Trees were assigned a mycorrhizal type based on information from Brundrett (39) and Maherali *et al*. (40).

2.1.2 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 (41, 42). 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.

2.2 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 (see *2.3 Abiotic Soil Property Measurements*). 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 (43) 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.* (44) 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 (45) by clustering sequences into operational taxonomic units (OTUs) based on a 97% sequence similarity threshold using the UCLUST algorithm (46). 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 (47) 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 (43) 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*. (48) 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 (49;

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*. (50). 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. Pathogens of animals and fungi 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.* (51) regardless of primer choice.

2.3 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 (41). 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).

2.4 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 (~2% of all sequences). OTU abundance data were rarified and Hellinger-transformed before analysis using the vegan package (52). We performed redundancy analysis (RDA) to examine how fungal community composition changed in response to our mycorrhizal dominance gradient. RDAs were performed for each 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 (53). Thus, soil

249 moisture, soil organic matter, soil pH, and nitrification rate were tested as abiotic predictor
250 variables. Other abiotic variables were eliminated before the analysis using a variance inflation
251 factor cutoff of < 10 to detect confounded predictor variables (54) through the vegan command
252 vif.cca(). The adjusted R^2 values from the RDAs with mycorrhizal percent and the stepwise
253 RDAs were used to assess the fit of significant models (55).

254 Our first prediction, that AM soil will have greater fungal taxonomic diversity compared
255 to ECM soil (**P1**), was tested using the full community as well as separately for each functional
256 group of interest. For each plot, OTUs were used to calculate the first three Hill numbers (56),
257 representing a gradient of emphasis on evenness: ${}^0D$ or richness, ${}^1D$ or the exponentiated
258 Shannon-Wiener diversity index, and ${}^2D$ or the inverse Simpson index. To test for an effect of
259 mycorrhizal dominance on these diversity measures, we performed mixed-effects linear
260 modeling using the nlme package (57) after testing for normality. Forest site (GW, LDW, and
261 MMSF) was used as a random factor while percent AM basal area (0% - 100%) was tested as the
262 predictor. In order to test our second prediction that AM soil has higher relative abundances of
263 pathogenic and saprotrophic fungal taxa compared to ECM soil (**P2**), we again used linear
264 modeling. For each functional group of interest (biotrophs, necrotrophs, and primary
265 saprotrophs), relative abundances were used as the response variable, percent AM basal area of
266 the plots as the predictor variable, and location was used as a random effect. R^2 values were used
267 to assess the fit of each linear model for each taxonomic and functional group of interest and
268 were obtained using the MuMIn package (58).

269 In addition to testing **P1** and **P2**, samples from the nitrogen fertilization experiment were
270 used to test our third prediction that chronic inorganic N addition will increase the relative
271 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.

2.5 Data Availability

Sequence data for GW, LDW, and MMSF has been deposited in the Sequence Read Archive (SRR13120641) (59), while sequence data for MC has been deposited in the Joint Genome Institute Genome Portal (1182214) (60). GW, LDW, and MMSF data are available from doi 10.111/nph.14343. MC data are available from doi 10.1002/ecy.1595.

3. Results

3.1 Fungal Community Response to the Gradient in Mycorrhizal Types

For samples from the mycorrhizal gradient sites, 133,824 sequences (after rarefaction) 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; $P < 0.005$; Fig. 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 ($P < 0.02$; Fig. 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 ($P < 0.001$; $R^2 = 24.7\%$; Fig. 2d), while ^1D and ^2D were not significantly correlated.

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 ($P < 0.001$; $R^2 = 50.0\%$).

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 ($P < 0.05$; Fig. 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%).

3.2 Dominant mycorrhizal type × nitrogen amendment factorial experiment

For samples from the nitrogen amendment experiment, 7,570,288 sequences (after rarefaction) 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).

OTU richness was significantly higher in AM-tree dominant soil ($P = 0.0001$; $R^2 = 59.4\%$; Fig. 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 ($P < 0.008$; Fig. 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 $P = 0.003$; Fig. 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 in ECM plots compared to AM plots 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 plot 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 ($P < 0.05$; Fig. 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.

4. Discussion

4.1 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 that many groups of non-mycorrhizal fungi are affected by the mycorrhizal associations of dominant trees through controls on nutrient availability, which likely have important consequences for forest community dynamics and ecosystem processes. Within all four forests, areas with increased AM tree

386 dominance were associated with increased fungal diversity and increased relative abundances of
387 biotrophic plant pathogens, necrotrophic plant pathogens, and primary saprotrophs (Figs. 1 – 3).
388 Additionally, percent AM tree basal area consistently explained as much or more variation in
389 fungal community composition as soil properties, such as SOM content and nitrification rate,
390 sampling depth, and mineral N availability (Table 1). Mycorrhizal type is increasingly viewed as
391 a key trait with cascading effects that go well beyond nutrient acquisition, potentially affecting
392 global patterns in soil biogeochemistry and plant-soil feedbacks (3, 61, 1). Such broad effects
393 imply that tree mycorrhizal types must consistently influence non-mycorrhizal fungi, as
394 demonstrated here across four forest stands. Indeed, our findings are similar to Bahram *et al.*
395 (29), who demonstrated comparable patterns in relative abundance of plant pathogens and
396 saprotrophs in Baltic temperate forests based on mycorrhizal dominance, and support the ideas
397 offered by Netherway *et al*. (62) regarding differences between plant pathogen and saprotroph
398 abundance between AM- and ECM-dominant systems.

399 Plant-soil feedbacks tend to be more negative for AM trees than ECM trees (8, 28),
400 including at Lilly-Dickey Woods (38), and this pattern has recently been associated with greater
401 accumulation of potentially pathogenic fungi on AM tree roots vs. ECM tree roots (21, 10). Our
402 data on bulk soil fungal communities suggests that this effect on biotrophic and necrotrophic
403 plant pathogen abundances may create a “mycorrhizal spillover” effect that influences the fungal
404 functional groups responsible for plant-soil feedback encountered by other trees within the
405 community (9). Due to the increased diversity of plant biotrophs and necrotrophs in AM-tree
406 dominated stands, both heterospecific and conspecific plants may experience a greater likelihood
407 of encountering a pathogenic fungal strain capable of causing an infection. Increased relative
408 abundances of fungal biotrophic and necrotrophic plant pathogens also suggests that infectious

409 populations encountered may be a larger fraction of the community, increasing the likelihood of
410 plant disease (63). Hence, these patterns should result in more negative plant-soil feedback in
411 AM-dominated stands, helping to explain how juvenile tree recruitment, regardless of the
412 juvenile species mycorrhizal type, can be strongly influenced by the mycorrhizal type of
413 surrounding dominant trees (38, 21, 9).

414 Plant pathogen relative abundances may be greater in AM-dominant soil because of the
415 greater association of pathogens with AM roots as noted above, but other factors are likely to
416 drive increased primary saprotroph relative abundance and diversity, as well as contribute to
417 specialized necrotrophic plant pathogens that are facultatively saprotrophic (62). ECM-dominant
418 tree communities are known to induce slower rates of nutrient and SOM cycling compared to
419 AM-dominant tree communities (64, 2, 5, 65), which may be explained by the lower primary
420 saprotroph relative abundances observed in our study. AM leaf litter also tends to be more labile
421 than ECM leaf litter due to increased nutrient and polyphenol contents (3, 66, 7), creating more
422 favorable conditions for fungal plant pathogens and saprotrophs that rely on plant litter for
423 carbon and energy (22, 23). Increased labile carbon and energy availability may also drive
424 enhanced saprotrophic fungal diversity (67, 23), which may be tied to plant diversity through
425 controls on available types of leaf litter (i.e., labile vs. recalcitrant). Furthermore, reduced
426 saprotroph relative abundance (and necrotrophic plant pathogen relative abundance) in ECM-
427 dominant tree communities may also be a consequence of competitive interactions with ECM
428 fungi (68, 19). Although ECM fungi obtain most of their carbon from their host tree, they
429 compete with free-living fungi for nitrogen and other resources, including access to leaf litter.

430 While dominant mycorrhizal types have emerged as a convenient framework by which to
431 classify forests, shifts in fungal community composition have also been attributed to many other

factors, such as soil organic matter (69) or the species identity of dominant trees (70), 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* (71), 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 (71). 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.

4.2 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 (72), with depth interacting with tree mycorrhizal dominance to influence the relative abundances of saprotrophic and mycorrhizal fungi (73). While sampling depth explained some variation in OTU richness of our various functional groups in our experimental plots, we found this depth x mycorrhizal type interaction to only be significant for plant necrotroph OTU

455 richness. This appears to suggest that plant necrotroph diversity is primarily associated with the
456 more organic horizons of AM soil, but further work is needed to fully explain the drivers behind
457 this result. Additionally, sampling depth did not significantly affect fungal relative abundances,
458 either as a main effect or as an interaction with dominant mycorrhizal type. Dominant
459 mycorrhizal type consistently explained more than twice as much variation in plant biotroph,
460 plant necrotroph, and primary saprotroph OTU richness compared to sampling depth,
461 demonstrating the strong influence different mycorrhizal associations have on soil fungal
462 communities.

463 Contrary to our third prediction, mineral N addition did not increase the relative
464 abundances of plant pathogenic and saprotrophic soil fungi in our study. Neither the relative
465 abundance of fungal taxa and functional groups, nor fungal OTU richness, were affected by the
466 six years of inorganic N addition at Moores Creek. Only plant necrotroph OTU evenness
467 appeared to be weakly influenced by a mycorrhizal dominance x mineral N treatment interaction
468 (P = 0.07), with N treatment slightly increasing necrotroph OTU evenness in ECM soil while
469 having no effect in AM soil. While some studies on the effects of simulated mineral N deposition
470 on temperate hardwood forest soils have demonstrated changes to overall fungal community
471 composition (e.g., 74, 75, 76), other studies have shown that fungi may instead alter the
472 expression of extracellular enzyme genes when community composition remains unchanged (32,
473 33, 77, 78). Additionally, in relation to dominant mycorrhizal associations, extracellular enzyme
474 production has been documented to shift from C-degrading to N-degrading enzymes with
475 increasing ECM dominance (79). These variable responses of soil fungi to changes in mineral N
476 availability suggest that our fungal communities may have altered their activity instead of
477 composition, as seen in ECM-dominant plots from Midgley and Phillips (41). Alternatively,

larger amounts of N than those applied at Moores Creek can induce changes in fungal community composition, as observed at Harvard Forest (76, 80). It is also possible our plots may be limited by resources other than N or co-limited by multiple nutrients (81, 82). For example, DeForest *et al.* (81) 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.* (22) 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.* (83) 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 (83). 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.

4.3 Conclusions

Our study and those from Bahram *et al.* (29) and Netherway *et al.* (62) 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 (2, 84) and plant-soil feedback (8, 9). 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 (11, 12), 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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AUTHOR CONTRIBUTIONS

CBB, RPP, and KAS designed the study. ACE, RMM, and ALH collected the data, with ACE and ALH handling samples from GW, LDW, and MMSF and RMM handling samples from MC. ACE performed the bioinformatic and statistical analyses. ACE and CBB wrote the manuscript with input from all authors.

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763 **TABLES**

764 Table 1: Adjusted R^2 values from the RDAs conducted on fungal community composition in the
765 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	-

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

768 a. Nitrification identified as significant during the stepwise, forward selection RDA.

769 b. b. SOM + nitrification identified as significant during the stepwise, forward selection
770 RDA.

771 Table 2: Fungal families with an average relative abundance > 1% from the mycorrhizal gradient across Griffy Woods, Lilly-Dickey
772 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

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

779 Table 3: Adjusted R^2 values from the RDAs conducted on the fungal community data from the
780 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	-	-	-	-	-	-	-

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

782 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**	**R2**	**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.

FIGURE CAPTIONS

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.

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.

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.