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RESEARCH ARTICLE

Loss of dominant tree-mycorrhizal mutualism increases soil fungal diversity and alters community structure

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Abstract

1. Due to their mutualistic partnership with trees, mycorrhizal fungi are often important components of soil microbial communities. Mortality of tree hosts can have dramatic effects on mycorrhizal populations, but how these shifts impact the remaining soil microbial community and ecosystem function remains poorly understood.
2. Using a long-term oak girdling experiment at Black Rock Forest in New York, USA, we looked at changes in fungal community composition over 10 years following simulated large-scale oak mortality to understand the interactions between canopy tree composition, soil fungal diversity and forest function. We collected soil samples in treatment plots of 100% oak girdling (OG_{100}), 50% oak girdling (OG_{50}), non-oak girdling and a control without girdling. We sequenced the fungal community using the ITS1 forward and ITS2 reverse primers and classified the communities using the UNITE fungal reference and FUNguild databases.
3. Fungal alpha diversity significantly increased by 32% and 17% in OG_{100} and OG_{50}, respectively, compared to the control, largely driven by decreased ectomycorrhizal fungi (ECM) and increased saprophytic fungal abundance in OG_{100} and OG_{50}. ECM showed a strong negative correlation with Archaeorhizomyetes (rho = −0.48) suggesting that these saprotrophic fungal taxa replaced ECM following the loss of oak trees. Girdling treatments, soil nitrogen, carbon: nitrogen ratios and soil pH explained over 20% of the soil fungal community variation.
4. The removal of oaks led to a shift in the fungal community from ECM to more saprophytic fungi. Increases in soil pH with oak girdling, likely from tannic acid decreases from oak leaves, and the effect of pH on fungal diversity highlight the complex feedbacks and co-determined successional dynamics of the tree and fungal communities.
5. *Synthesis*. The removal of a dominant plant species, such as oaks in the northeastern US, can have cascading effects on the soil microbial community composition. Changes in the fungi community following disturbance can have significant impacts on ecosystem functions and properties such as decomposition, soil respiration,

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biodiversity and nutrient cycling. Together, this work improves our understanding of these forests' vulnerability to pathogen pressure and the impact these disturbances have not just on the focal species but on the whole ecosystem.

KEYWORDS
competitive release, deer herbivory, ectomycorrhizae, pathogens, saprotrophic fungi

1 | INTRODUCTION

The ecological links between aboveground and belowground components of ecosystems influence community to ecosystem-level attributes, such as biodiversity and biogeochemical cycling (Wardle et al., 2004). Soil fungal communities play a particularly important role, as they serve as decomposers and mutualistic partners, affecting how carbon and nutrients flow through ecosystems. Further, soil fungi act as a connection between plants and soil dynamics, such that plants and soil microbes affect each other's community population structure and dynamics (Tedersoo et al., 2020). The symbiosis between ectomycorrhizal fungi (ECM) and common plant partners like oaks (*Quercus* spp.) is thought to promote the success of both partners through positive density dependence and lead to their dominance in the ecosystems where they are found (Tedersoo et al., 2020).

Within United States' and Canadian forests, oak-dominated forests are facing significant pathogenic pressure (Carrero et al., 2020). One pathogen, the fungal disease oak wilt (caused by *Bretziella fagacearum*), which has led to large-scale oak mortality in several US states, poses a threat to the oak-dominated forests common across eastern North America. Pathogen pressure and other threats (increased herbivory of the red oak borer (*Enaphalodes rufulus*) and white-tailed deer, root rot, anthropogenic disturbances, increased drought frequency etc.) are contributing to a shift away from oaks as dominant canopy tree species in many of these forests (Haavik et al., 2015; Kruger & Reich, 1997; Lorimer, 1993; Rooney & Waller, 2003). Despite the cited importance of soil fungal communities on plant community structure and biogeochemical cycling, we have a poor understanding of how soil fungal communities shift following large-scale mortality of a dominant ECM-associated tree species.

Dominant fungal communities can have different implications for nutrient cycling, carbon storage, plant community dynamics and how forests may respond to a changing climate and disturbance. Forests dominated by trees associated with ECM fungi—one of the two most common types of mycorrhizal fungi—have slower nutrient cycling rates (Courty et al., 2010; Orwin et al., 2011) compared to forests dominated by arbuscular mycorrhizal (AM) fungi (Averill & Hawkes, 2016; Barceló et al., 2022; Midgley et al., 2015; Phillips et al., 2013; Read, 1991). Ectomycorrhizal fungi can break down soil organic matter by producing hydrolytic and oxidative extracellular enzymes, and thus access nutrient pools that AM fungi cannot (Courty et al., 2010). However, the competition between ECM fungi and free-living decomposers for soil nitrogen slows decomposition and carbon cycling (Averill, 2016). Ectomycorrhizal fungi also influence plant community dynamics, as ECM fungi tend to make the soil environment more advantageous for their plant partners and lower tree species diversity (Bennett et al., 2017; Phillips et al., 2013). Rapid loss of dominant oak species will likely lead to diminished dominance of ECM fungi, as found in California forests with an ECM host tree, California tanoak (*Neotholithocarpus densiflorus*), that experienced mortality as a result of sudden oak death caused by the introduction of the invasive pathogen *Phytophthora ramorum* (Bergemann et al., 2013). Given the strong interactions between ECM, AM and decomposers, diminished dominance of ECM following oak loss is hypothesized to have strong impacts on the structure and function of the entire soil microbial community.

Loss of the dominant fungal species may lead to competitive release within the fungal community, as observed in other organisms (Kunte, 2008; Segre et al., 2016). Under certain conditions, ECM fungi compete with and exclude a diversity of fungi from various trophic groups –saprotrophic (Gadgil & Gadgil, 1970; Peay, 2016), pathogenic (Newsham et al., 1995) and other symbiotic fungi (Peay, 2016)—through mechanisms including mycoparasitism, chemical inhibition and general resource competition (Fernandez & Kennedy, 2016). Given the dominance of ECM in intact oak forests, we hypothesized a reduction of this fungal group following oak mortality may free niche space, allowing species from other trophic groups to proliferate, potentially increasing both community evenness and richness.

In addition to the effects of competitive release, dominant tree die-off causes large-scale disturbance, changing belowground resource availability and fungal economies. Fungal community composition following tree mortality and general disturbance events can drive an increase in the ratio of saprotrophic to symbiotic fungal functional groups, due to the reduction in live tree partner roots for symbiotic fungi and the simultaneous increase in coarse woody debris serving as a carbon source for saprotrophs (Brinkmann et al., 2019; Kohout et al., 2018; Šťursová et al., 2016). In tree girdling experiments, the immediate loss of photosynthate supply to roots has been observed to decrease ECM biomass or diversity (Pena et al., 2010; Romell, 1939), with an immediate increase then recovery of soil respiration within 3 years (Levy-Varon et al., 2012, 2014). Tree loss can have a large and long-term impact, significantly decreasing ECM presence and increasing that of saprotrophs. In one experiment, the ratio of saprotroph to ECM fungi continued to increase 2 years after tree die-off events (Kohout et al., 2018), though the persistence of this effect for longer timescales remains uncertain.

Replacement of ECM with saprotrophic fungal guilds resulting from oak loss has the potential to alter ecosystem structure and function. Increasing fungal richness has been found to enhance soil respiration (Levy-Varon et al., 2014; Liu et al., 2018; Setälä & McLean 2004) and shifts from mycorrhizal fungi to saprotrophs could enhance litter

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decomposition rates (Bödeker et al., 2016). This may be from the release of the Gadgil effect, where competition between saprotrophs and mycorrhizae suppresses decomposition rates (Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1970). Release of saprotrophs from ECM mycorrhizal competition could accelerate decomposition rates, increasing rates of nutrient cycling and potentially paving the way for future colonization by AM trees and fungal species. However, a study on allelopathic chemicals from invasive garlic mustard (*Alliaria petiolara*) found a shift from ECM to saprotrophic fungi that was also linked to increases in soil organic carbon levels, suggesting slower decomposition rates (Anthony et al., 2017). Thus, the net ecosystem effects of decreasing ECM dominance remain unclear.

Effects on ecosystem-level function have been documented in many forests that have experienced oak die-off in the western United States (Bergemann et al., 2013; Cobb et al., 2013). The shift in plant species composition has led to changes in litterfall chemistry and biomass and increased availability of soil nitrogen (Cobb et al., 2013). Changes mediated by fungal composition should be expected given the outsized effect of ECM in forest nutrient cycles and may be influenced by competitive release and the transition from symbiotic to saprophytic dominated communities. The strong link between oak trees and ECM fungi provides both a reason and system in which to explore their coregulation of ecosystem function. Given large differences in the dominant plant communities (Cobb et al., 2013) and pressure on trees from other sources such as deer browsing (Côté et al., 2014; Walters et al., 2020) between western and eastern U.S. temperate forests, there is reason to expect that effects of large-scale oak mortality in eastern U.S. forests may have different impacts on forest function and community dynamics.

Here we leverage a large-scale oak girdling experiment to understand how dramatic changes in the dominant tree species alter soil fungal community structure and the implications this has for ecosystem function. We use this experiment to ask: (1) How does large-scale oak loss impact fungal diversity? (2) Does fungal community composition and function shift following oak mortality? (3) Do differences in fungal communities relate to measured differences in abiotic (edaphic) and biotic (open forest vs. deer exclusion) conditions among experimental treatments? We hypothesized that the loss of the dominant plant host, oaks, will reduce the contribution of ECM fungi to the soil fungal community. The reduction in ECM fungi and the increase in dead biomass from girdling treatments will increase saprotrophic fungi abundances in the soil. Soil characteristics that vary on small spatial scales, such as pH and soil N availability, may further explain variation in the fungal community.

2 | MATERIALS AND METHODS

2.1 | Site and experiment design

Our study was conducted in the Future of Oak Forests experimental plots at Black Rock Forest (41.41° N, 74.02° W) located in Cornwall, NY, USA, which has a mean annual temperature of 9.7°C and a mean annual precipitation of 1200 mm year^{-1} (NOAA, 2002). There is strong temperature seasonality at this site, with monthly temperature averages ranging from −2.7°C to 23.4°C (NOAA, 2002). Oak species (primarily *Quercus rubra* L. and *Q. montana* Willd. at this site) comprise approximately two thirds of the canopy tree basal area, with the understory dominated by red maple (*Acer rubrum* L.), black gum (*Nyssa sylvatica* Marsh.), black birch (*Betula lenta* L.), sugar maple (*Acer saccharum* Marsh.) and witch-hazel (*Hamamelis virginiana* L.) (Levy-Varon et al., 2012; Schuster et al., 2008). The study was reviewed and approved by Black Rock Forest.

In 2008, the Future of Oak Forests experiment initiated tree girdling and deer manipulation (employing fenced exclosures) to investigate the effects of simulated large-scale pathogen mortality of the dominant oak trees in northeastern hardwood forests. The experiment consists of twelve 75 m by 75 m plots arranged into three rows of four plots each, with rows serving as an experimental blocking factor to account for the position of plots along the hillslope of the experimental site (Figure S1). To simulate large-scale tree mortality, plots were assigned to one of four girdling treatments in such a way that each row of 4 plots contained a representative from each of the four girdling treatments, and treatments were randomly arranged within each row (Figure S1). Girdling treatments consisted of: 100% oaks girdled (OG_{100}), 50% oaks girdled (OG_{50}), non-oaks girdled (N) and control (C) plots that received no girdling. The five most common non-oak-girdled species that were girdled in the N plots included *Nyssa sylvatica*, *Acer rubrum*, *Acer saccharum*, *Fagus grandifolia* and *Betula lenta* with diameter at breast height (DBH) ranging from 2 to 35.3 cm. The DBH of girdled oaks in OG_{50} and OG_{100} plots ranged from 1.9 to 86.1 cm. About 14 years after girdling, in 2022, oaks made up 74%, 92%, 38% and 0% of the individual trees in C, N, OG_{50} and OG_{100} plots, respectively. A complete list of girdled and non-girdled individuals with their species ID and DBH, both at the start of the experimental treatments and at annual timepoints, is publicly available (Schuster et al., 2024). In 2008, trees were girdled using a chainsaw cutting 3–5 cm into the bark and severing the phloem and cambium of the tree, mimicking how many pathogens block the flow of nutrients through the phloem and cambium. Girdled trees were left standing if greater than 10 cm in diameter at breast height and felled if they were smaller. Trees that continued to leaf out after 2010 were girdled a second time. This form of girdling simulates the delayed mortality typically associated with tree death due to pathogens. In 2009, the average fraction of the total basal area girdled in OG_{100}, OG_{50}, N and C plots was 78.1%, 35.5%, 21.4% and 0%, respectively (Schuster et al., 2024).

Each plot was divided into nine 25 m by 25 m subplots. In 2009, 2 m tall deer exclusion fences were established in the southern portion of the northern subplot of each plot to exclude large-bodied herbivores from a 10 m × 15 m area. Exclosure fences exclude all herbivores larger than approximately 0.5 kg, but small rodent and insect herbivores can gain access inside exclosures through the fence mesh. To avoid edge effects of adjacent girdling treatments, soil sampling took place in the central part of each subplot. Sampling took place inside (fenced) and outside (unfenced) of deer exclosures to examine the role of deer herbivory in forest recovery.

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2.2 | Soil DNA collection and preparation

In 2021, we took eight 2.6 cm diameter 0–10 cm soil cores in each plot (4 cores outside and inside of each deer exclosure), totalling 24 cores in each girdling treatment. To best preserve the DNA in these samples, soils were then placed in a refrigerator at 4°C for less than 14 days. We then placed the samples in a −80°C freezer until they were further processed (Clasen et al., 2020). Frozen soils were freeze-dried for 48 h (1 mbar at −50°C; Labconco, Kansas City, MO, USA) before being sieved at 0.5 mm and thoroughly homogenized. DNA was extracted using a Qiagen DNeasy PowerSoil Pro kit.

2.3 | DNA sequencing and bioinformatics

A portion of the internal transcribed spacer (ITS) of nuclear DNA was PCR amplified from each genomic DNA sample using the ITS1-F and ITS2 reverse primers. Both forward and reverse primers also contained a 5' adaptor sequence to allow for subsequent indexing and Illumina sequencing. Each 25 μL PCR reaction was mixed according to the Promega PCR Master Mix specifications (Promega catalogue # M5133, Madison, WI) and PCR amplified. Amplicons were then cleaned by incubating amplicons with Exo1/SAP for 30 min at 37°C, followed by inactivation at 95°C for 5 min and stored at −20°C. A second round of PCR was performed to give each sample a unique 12-nucleotide index sequence. The indexing PCR included Promega Master mix, 0.5 μM of each primer and 2 μL of template DNA (cleaned amplicon from the first PCR reaction). Final indexed amplicons from each sample were cleaned and normalized using SequalPrep Normalization Plates (Life Technologies, Carlsbad, CA).

Sample library pools were sent for sequencing on an Illumina NovaSeq 6000 (San Diego, CA) at the Texas A&M Agrilife Genomics and Bioinformatics Sequencing Core facility using the SP Reagent Kit v1.5 (500 cycles). Raw sequence data were demultiplexed using pheniqs v2.1.0, enforcing strict matching of sample barcode indices (i.e. no errors). Cutadapt v3.4 was then used to remove gene primers from the forward and reverse reads, discarding any read pairs where one or both primers were not found at the expected location (5′) with an error rate <0.15. Read pairs were then merged using vsearch v2.15.2, discarding resulting sequences with a length of <100 bp, or with a maximum expected error rate >0.5 bp. For each sample, reads were then clustered using the unoise3 denoising algorithm as implemented in vsearch, using an alpha value of 5 and discarding unique raw sequences observed less than 8 times. Counts of the resulting amplicon sequence variants (ASVs) based on 100% sequence similarity were then compiled and putative chimeras were removed using the uchime3 algorithm, as implemented in vsearch (Figure S2). To standardize sequencing depths across samples, we rarefied the ASV table to the minimum library size, 2509 reads per sample, using the rrarefy function from the vegan package (Oksanen et al., 2020). All fungal alpha and beta diversity analyses were conducted using the rarefied dataset.

For each final ASV, a consensus taxonomy was assigned using a custom best-hits algorithm and the UNITE fungal reference database. Reference database searching used an exhaustive semi-global pairwise alignment with vsearch, and match quality was quantified using a custom, query-centric approach, where the % match ignores terminal gaps in the target sequence, but not the query sequence. The consensus taxonomy was then generated using either all 100% matching reference sequences or all reference sequences within 1% of the top match, accepting the reference taxonomy for any taxonomic level with >90% agreement across the top hits. We used FUNGuild to classify OTUs as arbuscular mycorrhizae, ectomycorrhizae and/or saprotrophs. Library prep, sequencing and taxonomy generation was handled by Jonah Ventures, Boulder, CO, USA.

2.4 | Soil data

We took soil samples for chemical analyses in the same locations as the soil DNA sampling using a 2.6 cm diameter soil core. All samples were collected in August 2021 from the surface 0–10 cm of soil. Soil was analysed for pH, inorganic nitrogen (NH_4^+ and NO_3^-), total C and nitrogen and moisture. Soil inorganic nitrogen was extracted immediately using 5 g of soil in 30 mL of 2 M KCl. Samples were agitated manually for 3 h and then filtered after 24 h. Extracts were frozen and then analysed on a SmartChem 200 discrete analyser at Harvard University, using the salicylate (no distillation) and cadmium coil methods for ammonium and nitrate, respectively. Total soil C and nitrogen were measured on dry soil using a FlashSmart 2000 Soil CN analyser at Harvard University. We assessed soil moisture (%) as the percent difference between the wet soil weight and the dry soil weight after air drying for 1 week in the lab.

2.5 | Replication statement

Scale of inference	Scale at which the factor of interest is being applied	Number of replicates at the appropriate scale
Oak-girdling treatments	Plot (75 m by 75 m)	3 plot replicates per treatment (8 soil cores per plot, 4 inside and 4 outside each exclosure with 3 lost soil samples removed from analyses)
Deer exclusion treatment	Subplot (10 m by 15 m) nested within oak-girdling treatment plots	24 subplots (12 fenced, 12 unfenced, two per oak-girdling treatment plot)

2.6 | Statistical analysis

To determine if soil fungal diversity was altered with oak loss and/or deer exclusion treatments, we performed linear mixed effect models with fixed effects of oak-girdling treatments and deer exclusion with an interaction term for these two treatment

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types. Plot row was included in the models as a random effect. Pairwise comparisons of the estimated marginal means for each of the oak-girdling treatments (as deer exclusion was not found to be significant) for fungal ASV richness and Shannon diversity indices were determined using the emmeans function adjusted with a Tukey's HSD from the emmeans R package (Lenth, 2017). We examined the effect of the experimental treatments on the absolute and relative abundance of ECM fungi, as these are the primary mycorrhizal symbionts of oaks. We tested for significant differences in ECM fungi and *Archaeorhizomycetes* abundance among the oak loss treatments using linear mixed effects models with oak-girdling treatment as a fixed effect and plot row as a random effect. We calculated estimated marginal means for pairwise comparisons between girdle treatments with Tukey's HSD correction for multiple comparisons. To examine if the abundances of ectomycorrhizal fungi and *Archaeorhizomycetes* are correlated, we used Spearman correlation tests.

Finally, to assess compositional variation of the fungal community among the different treatments, we performed a redundancy analysis (RDA) using an individual soil core location (paired cores for fungal sequencing and soil chemistry) as the sample unit. We only included 93 soil core locations of the 96 soil samples we sequenced for DNA due to loss of nitrogen data for three samples. Soil chemistry was fitted to the RDA to evaluate how these variables are associated with fungal community composition. We used an ANOVA permutation test with 999 permutations to test the significance of the model and the terms (soil variables, girdling and deer treatments) using the anova.cca function from the vegan R package (Oksanen et al., 2023). All statistical analyses were conducted in R version 3.6.3 (R Development Core Team, 2020).

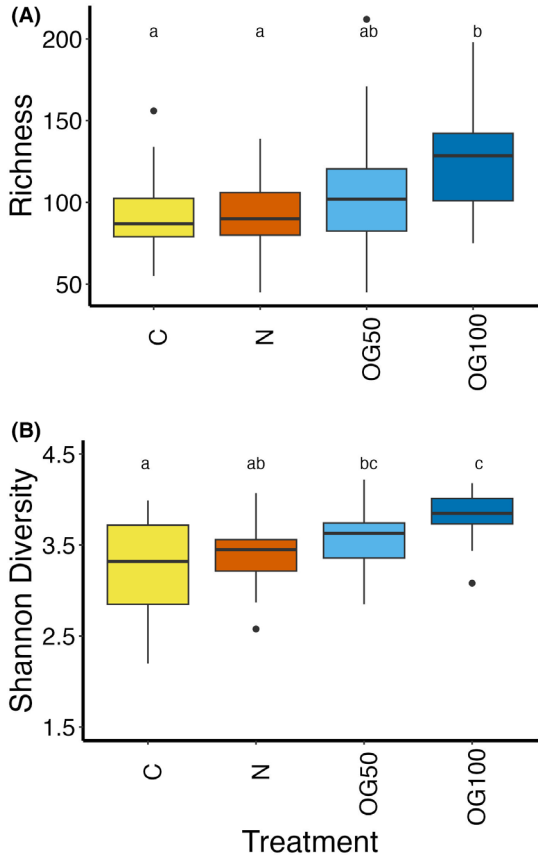


FIGURE 1 Differences in soil fungal (A) richness and (B) Shannon diversity indices among the four canopy tree girdling treatments (C—control, N—non-oak girdled, OG_{50}–50% oak girdled, OG_{100}–100% oak girdled). Boxes represent the interquartile range, the line is the median, and the whiskers are the lowest or highest value within 1.5 times the interquartile range. All points are beyond 1.5× the interquartile range. Significant differences determined by post-hoc Tukey tests are denoted by different letters.

3 | RESULTS

3.1 | Oak girdling increased fungal diversity

Oak loss increased ASV richness (32%) and Shannon diversity index metrics (17%) of fungal alpha diversity, while non-oak girdling did not affect fungal alpha diversity (Figure 1). Total oak girdling (OG_{100}) increased both richness and Shannon diversity more than 50% oak girdling (OG_{50}). OG_{50} treatments significantly increased Shannon diversity relative to control plots (Figure 1B) but did not significantly increase fungal ASV richness.

3.2 | Oak girding altered fungal community composition

The decrease in ECM fungi in OG_{100} plots coincides with the disappearance of Agaricomycetes, the class of fungi including most forest ECM symbionts (Martin et al., 2016), from the top 15 fungal taxa (Figure 2). Oak girdling decreased the absolute and relative abundance of ECM fungi (Figure 3c), with OG_{100} plots exhibiting significantly lower ECM ASV abundance than OG_{50} plots. Non-oak-girdled plots did not affect ECM abundance relative to control plots (Figure 3c). In OG_{100} plots, Agaricomycetes are largely replaced by Archaeorhizomycetes (Figures 2d and 3c), a class of fungi that is thought to be saprotrophic. We found negative relationships between the absolute abundances (Figure 3a), relative abundances (Figure S3) and abundance rank (Figure 3b) of ECM ASVs and Archaeorhizomycetes.

3.3 | Fungal composition changes in response to abiotic variables

Overall, soil edaphic properties (Table 1) were significantly correlated with fungal community composition ($p < 0.001$) with the variables included in the RDA explaining 21% of the variation in the fungal community. Specifically, we found pH was the most important variable driving fungal community composition ($R^2 = 0.73$, $p < 0.001$; Table S1). Soil C:N ratio ($R^2 = 0.28$, $p = 0.001$) and soil

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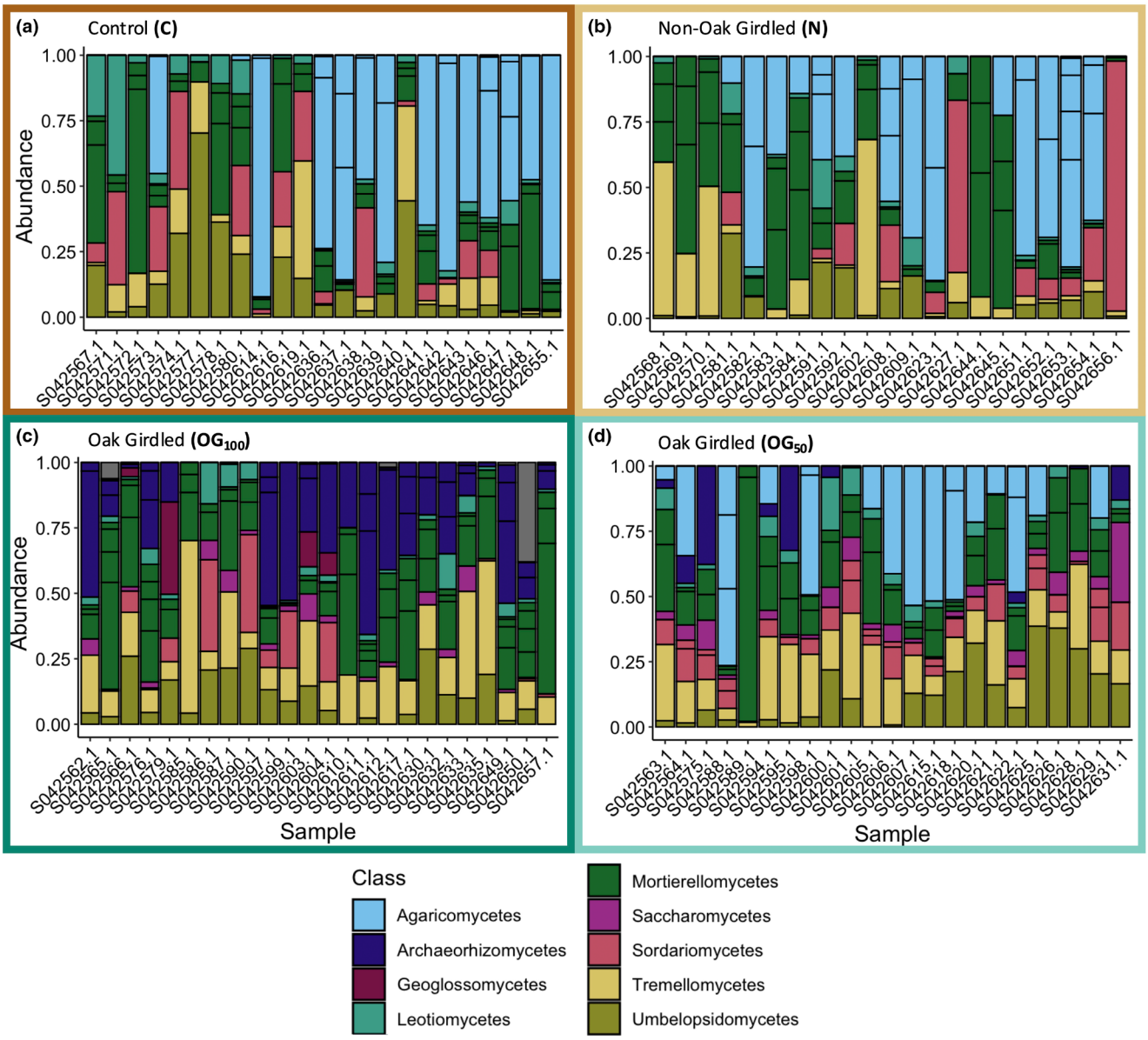


FIGURE 2 Relative abundance of the top 15 fungal taxa in each of the experimental girdling treatments, (a) control (C), (b) non-oak girdled (N), (c) 50% oak girdled (OG_{50}) and (d) oak girdled (OG_{100}). Each bar represents an individual soil sample and within each bar the relative abundance of the fungal taxa are shown. The bars are coloured by the fungal order. Sample bars that have multiple boxes of the same colour mean there are multiple fungal taxa in that order present in that sample. Coloured squares around each plot correlate with girdle treatments with yellow, orange, light blue and dark blue for control (C), non-oak girdled (N), 50% oak girdled (OG_{50}) and oak girdled (OG_{100}), respectively.

NH_4^+ ($R^2 = 0.14$, $p = 0.01$) also showed significant effects (Figure 4), but NO_3 and soil moisture had no significant impact on fungal community composition. The main effect of the girdling treatment and the interaction between girdling and deer exclusion also influenced the fungal community ($p < 0.001$ for both; Table S1). The interaction between girdling and deer exclusion was such that the influence of deer exclusion was only significant in the N girdling treatment ($p = 0.028$; Table S1). The first axis of the RDA (CAP1) was strongly correlated with pH, while the second axis (CAP2) was related to nitrogen availability, with high NH_4^+ corresponding with high soil nitrogen availability and high soil C:N corresponding with low soil nitrogen availability. Plots with oak girdling (OG_{100} and OG_{50}) differed from non-oak girdled and control plots (N and C) along the CAP1 axis, with OG_{100} and OG_{50} plots having higher pH.

4 | DISCUSSION

Overall, we found strong evidence that oak girdling, after 13 years, increased the diversity of the soil fungal community (Figure 1), shifting fungal composition away from ECM taxa toward a more diverse community that had a higher proportion of saprotrophs (Figures 2 and 3). While multiple abiotic changes impacted the fungal communities across the experimental treatments, soil

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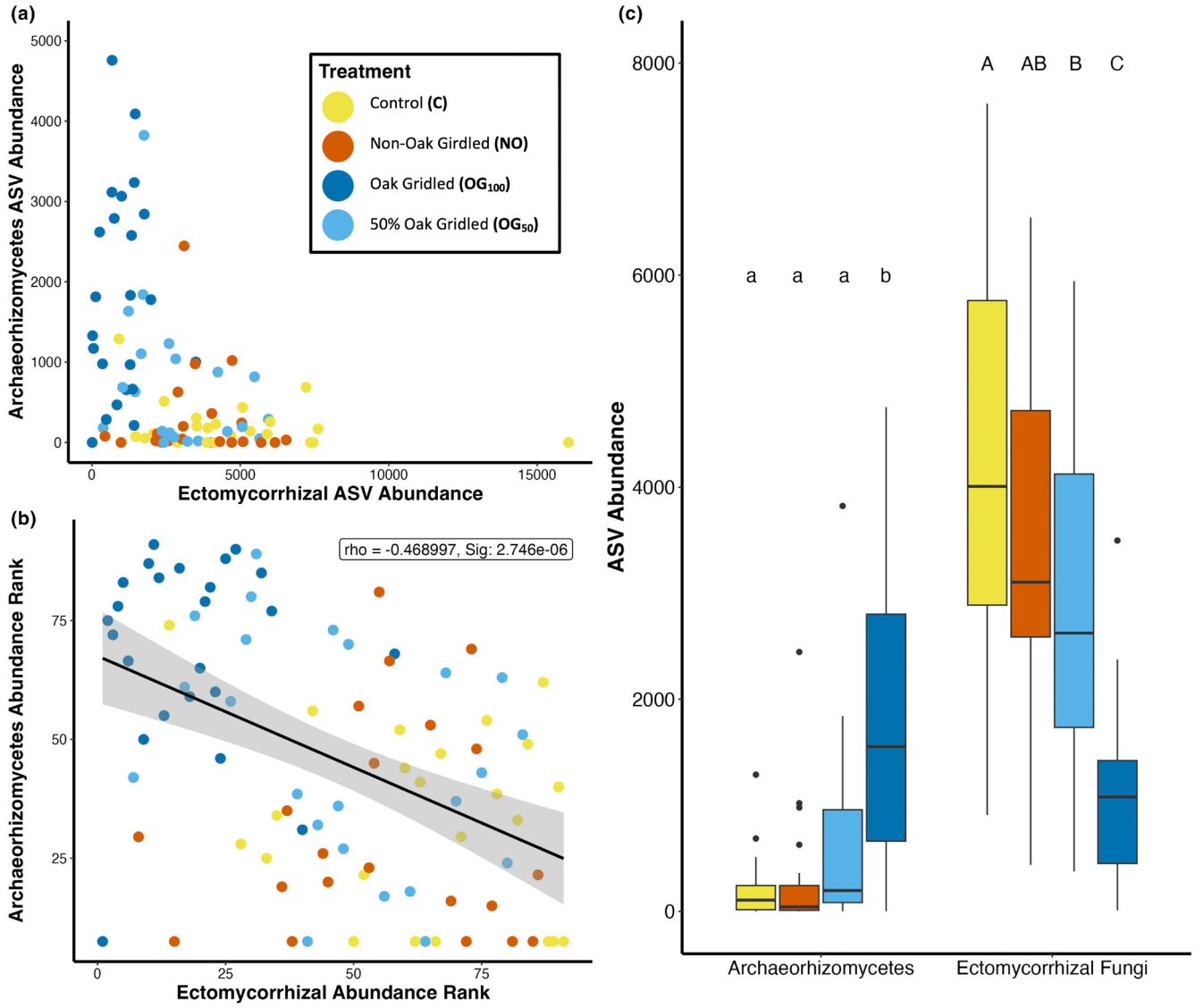


FIGURE 3 Negatively correlated relationships among ectomycorrhizae and Archaeorhizomycetes based on (a) raw ASV abundances and (b) ASV abundance Spearman correlation ranks and (c) ASV abundances for ectomycorrhizae and Archaeorhizomycetes showed opposing trends across the four girdling treatments. Treatments are shown in yellow, orange, light blue and dark blue for control (C), non-oak girdled (N), 50% oak girdled (OG_{50}) and oak girdled (OG_{100}), respectively. Boxes in (c) represent the interquartile range, the line is the median, and the whiskers are the lowest or highest value within 1.5 times the interquartile range. All points are beyond 1.5× the interquartile range. Significant differences determined by post-hoc Tukey tests are denoted by different letters.

pH was most strongly correlated with the changes in the fungal community in the oak-girdled (OG_{100} and OG_{50}) plots (Figure 4). Together, these results demonstrate the potential for unseen belowground effects of large-scale canopy tree mortality events and the important ecosystem effects that changes to the soil fungal community can have.

The experimental design of the Future of Oak Forests study—particularly the inclusion of the non-oak-girdled treatment—allows us to assess whether changes in the fungal community are due to the disturbance effects of canopy tree mortality or the mortality of oak trees specifically. Fungal taxa richness and Shannon diversity both increased (Figure 1) and community composition shifted (Figure 4) significantly in the OG_{50} and OG_{100} plots compared to control, but showed no changes in the non-oak (N) girdled plots. Because oak trees make up approximately two thirds of the basal area at our study site, the mean proportion of total basal area girdled was roughly similar between the OG_{50} and N plots (35% and 21%, respectively). This suggests that the changes in fungal diversity and community composition in oak-girdled plots were likely driven by the loss of oaks specifically, rather than disturbance to the canopy tree community in general.

Control and N plots where oaks remained intact had significantly lower soil pH than oak girdled plots (possibly due to high tannic acid content in oak leaf litter), which correlated with shifts in fungal community composition. Beyond the general effects of pH, tannins from oak leaf litter have been shown to inhibit the

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TABLE 1 Summary of soil variables collected in Black Rock Forest by girdle and deer treatment.

Girdle treatment	Deer treatment	pH	NO_3^- (mg/L)	NH_4^+ (mg/L)	C:N	Soil moisture (%)
C	EXC	4.15 ± 0.12	0.10 ± 0.09	1.11 ± 0.19	26.90 ± 1.40	10 ± 1
C	INC	4.36 ± 0.12	0.03 ± 0.02	1.24 ± 0.18	25.54 ± 1.28	6.0 ± 5.0
N	EXC	4.82 ± 0.23	0.01 ± 0.01	0.96 ± 0.19	25.36 ± 1.52	8.0 ± 4.0
N	INC	4.49 ± 0.24	0.01 ± 0.001	1.22 ± 0.18	20.58 ± 2.52	14.0 ± 1.0
OG_{100}	EXC	5.05 ± 0.19	0.03 ± 0.01	0.97 ± 0.15	25.17 ± 1.34	15.0 ± 2.0
OG_{100}	INC	5.55 ± 0.16	0.04 ± 0.02	0.86 ± 0.15	22.52 ± 0.81	9.0 ± 3.0
OG_{50}	EXC	4.95 ± 0.18	0.01 ± 0.01	1.00 ± 0.18	20.22 ± 1.62	11.0 ± 2.0
OG_{50}	INC	4.73 ± 0.18	0.01 ± 0.001	0.97 ± 0.20	25.16 ± 0.51	8.0 ± 1.0

Note: Numbers represent each variable means (±1 SE) of 10–12 samples of 0–10 cm depth. Deer treatments are denoted as deer inclusion plots (INC) where no fences were present and circles represent data from deer exclusion plots (EXC) where the area was fenced.

growth of a wide range of soil fungi (Harrison, 1971), which may have been released from this inhibition following the likely reduction of oak leaf litter in the OG_{100} and OG_{50} plots with oak girdling. The substantial sample-scale variation in fungal community composition explained by soil nitrogen metrics (Figure 4) also suggests that nitrogen availability is significantly related to fungal community composition at our site, but treatment effects on nitrogen availability were largely transient in this experiment and confined to the first 2 years following girdling implementation (Taylor et al., 2017). This suggests that girdling treatments do not significantly alter nitrogen availability long-term, but the smaller-scale heterogeneity of nitrogen availability within a given treatment strongly relates to fungal community composition.

In addition to altering soil conditions, girdling treatments could impact light dynamics in these plots. Although we did not directly measure light, previous work in these plots showed canopy openness (%) was, on average, 29% greater in OG_{100} plots (17% openness) compared to control plots (12% openness) after the first 4 years of this study (Taylor et al., 2017). Given the additional recovery time since girdling treatment (~9 years since last canopy openness measurements), we assume the light effect was markedly diminished at the time of our sampling. Importantly, understory temperatures should have a more direct impact on soil fungal communities than light itself, and even during the first 4 years of treatment implementation (when canopy openness was measured) there was no significant effect of girdling on understory temperatures (Taylor et al., 2017).

Shifts in diversity and community composition in OG_{100} and OG_{50} plots were primarily the product of a large reduction in ECM abundance, coinciding with the loss of oak roots for ECM to colonize in these plots. Our results suggest this created an ecological release allowing other fungal taxa and functional groups to proliferate in replacement of ECM—the primary replacement being the fungal class Archeorhizomycetes. Archeorhizomycetes can often be associated with roots and are thought to be non-pathogenic; they are most likely saprotrophs rather than mycorrhizae (Pinto-Figueroa et al., 2019; Rosling et al., 2011). Further, Archeorhizomycetes are potentially important for biological rock weathering (Pinto-Figueroa et al., 2019), which could further alter ecosystem-level nutrient cycling following oak loss. Previous work in these plots showed an increase in soil respiration after girdling treatments (Levy-Varon et al., 2012) that returns to pretreatment levels within 3 years (Levy-Varon et al., 2014). Additionally, Djukic et al. (2013) found a significant reduction in fungal biomarkers in both oak-girdled treatments just 1 year after the girdling treatments. It is possible that this peak in soil respiration in the first 3 years of treatment and reduction of fungal biomarkers represents a large dieback of ECM in the soil after the girdling of their oak host plant, with stabilization reached within 3 years by a different soil fungal community. If Archeorhizomycetes represent the potential successors to ECM following large-scale oak mortality, as our data suggest, this creates a strong case for better understanding their ecological roles in forest soils.

As expected, one of the primary fungi replacing ECM in OG_{100} and OG_{50} plots was a saprotrophic fungus. The combination of a reduction in competition from ECM and the addition of large amounts of coarse woody debris in the plots receiving oak girdling provides ideal conditions for saprotrophs. Indeed, a trade-off between ECM and saprotrophic fungi is commonly seen following disturbance in ECM-dominated forests (Netherway et al., 2021; Pinto-Figueroa et al., 2019) and the particular trade-off between ECM and Archeorhizomycetes has been reported elsewhere (Pinto-Figueroa et al., 2019). Prior work at Black Rock Forest has shown that shifts from ECM to saprotroph-dominated fungal communities (induced by invasive garlic mustard) correspond to increases in soil C (Anthony et al., 2017), suggesting that the shifts in fungal functional groups we report here will likely have important biogeochemical impacts during the process of forest recovery. Saprotroph dominance is likely to be a transient state lasting years to decades while substantial coarse woody debris remains on the forest floor following canopy tree die-off, after which the re-establishment of mycorrhizal fungi will likely be dictated by whether AM or ECM-associated tree species colonize the canopy following oak loss.

It is important to note that we did not introduce any pathogens to our system. While our girdling treatment isolates the effects of oak mortality from the confounding influence of introduced pathogens, natural oak decline is often driven by pathogenic fungi that may alter soil fungal communities through direct competition or shifts in host–microbe interactions (Du et al., 2022; van Ruijven et al., 2020). As such, our results may not fully capture the biotic complexity of

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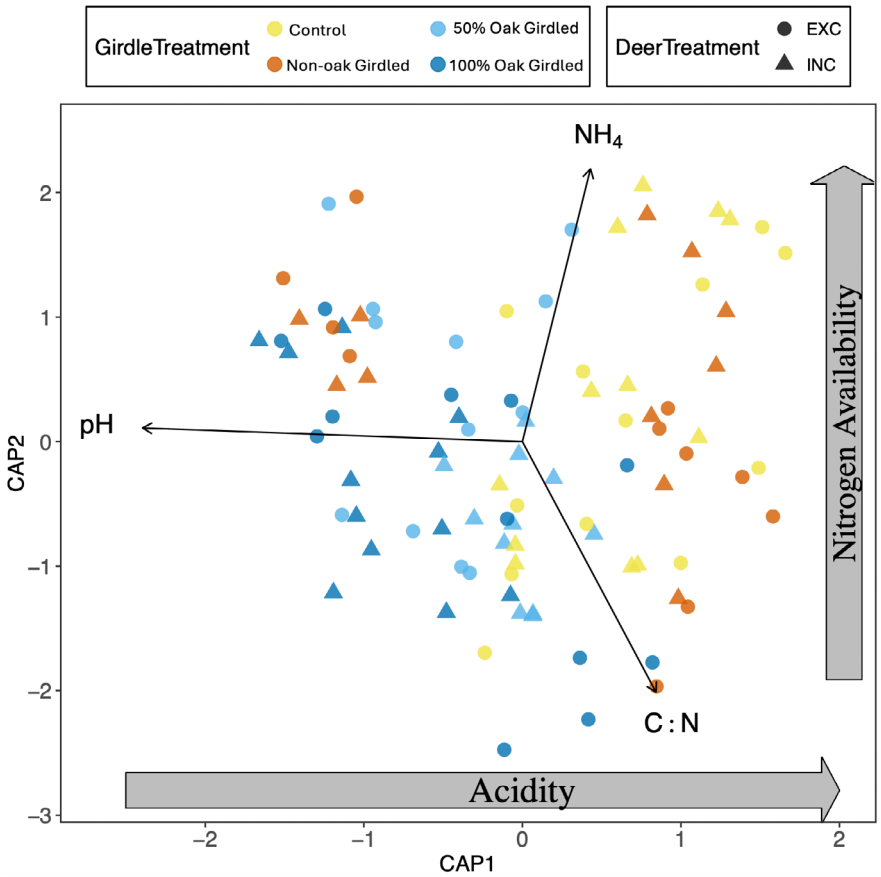


FIGURE 4 Redundancy analysis (RDA) showing the influence of soil properties on fungal community composition of 93 soil samples. Environmental variables explained 20.8% of the variation across the site samples. Blue arrows represent the variables with significant effects ($p < 0.05$) on the fungal community. Thick grey arrows represent soil characteristics that coincide with changes in the soil fungal community. Each point represents the fungal community of a soil sample, with points spatially closer having more similar fungal community composition than points further away in multivariate space. Treatments are shown in yellow, orange, light blue and dark blue for control (C), non-oak girdled (N), 50% oak girdled (OG_{50}) and oak girdled (OG_{100}), respectively. Triangles represent data from deer inclusion plots (INC) where no fences were present and circles represent data from deer exclusion plots (EXC) where the area was fenced.

pathogen-driven oak loss, and future work explicitly incorporating pathogenic introductions could provide valuable insights into these dynamics.

Counter to our expectations, we did not find evidence for replacement of ECM fungi by AM fungi following oak girdling. Of the 96 samples in our dataset, only seven contained ASVs identified as AM taxa. Although oak is, by far, the dominant genus of canopy trees at our study site, and other ECM-associated genera such as *Betula*, *Carya* and *Fagus* are common canopy trees, AM-associated maples comprise 14% of the canopy trees at our site (Schuster et al., 2008). This suggests that the low AMF ASV found may be a result of a combination of low AM-associated tree abundance and/or poor amplification of AM fungal DNA by the primers we used. While the ITSF-1 and ITS2 primers are often used for broad censusing of soil fungal communities (Gora et al., 2019; McGuire et al., 2013), these primers are much more effective at amplifying Basidiomycota and Ascomycota (Bellemain et al., 2010) than the AM phylum Glomeromycota. Thus, while we would not expect AM taxa to be dominant in the soil fungal community given the relative scarcity of AM-associated canopy trees, we caution that the lack of a response of AM fungi abundance to oak loss may be partially due to the primers used in our sequencing. Further, our data do not distinguish between active and dormant fungi but rather characterize all the fungi present in the soil. Future studies using more fine temporal sampling and RNA-based or functional assays would further elucidate the dynamics and activity of soil fungi communities in response to these disturbances.

Girdling treatments showed significant effects on fungal diversity, but we did not find strong or consistent effects of the deer exclusion treatments on the soil fungal community, despite documented effects of white-tail deer herbivory on forest ecosystem composition, structure and productivity (Rooney & Waller, 2003; Russell et al., 2017; White, 2012). If deer have an effect on the soil fungal community, it is likely this effect is indirect—deer browsing habits and preferences influence plant community composition (White, 2012), which can affect plant–soil feedbacks. It is also possible the feedbacks between plants and soil fungal communities extend beyond the boundaries (Simard & Durall, 2004) of the exclusion plots and thus are not possible to observe in this study, but given the effects of deer exclusion on understory vegetation (personal observation), we deem this possibility unlikely.

Together, our results provide an important view into the future of soil fungal communities if oak pathogens invade the eastern U.S. oak-dominated forests and drive large-scale canopy tree mortality. In such a scenario, our results suggest that soil pH will rise due to the likely reduction of acidic oak leaf litter and the substantial coarse woody debris will provide ample carbon sources for decomposers. This, along with the ecological release of competition from ECM, may initially create a more diverse soil fungal community that has a higher proportion of saprotrophic taxa. Complexities of different plant–soil feedbacks (relationships between litter quality, soil chemistry, fungal partnerships and tree growth rates) between AM- and ECM-associated trees will be important for determining the

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long-term outcome of post-disturbance tree and fungal communities in these forests—complexities that will require studies on multi-decadal timescales post disturbance. Still, our results highlight the important ties between forest tree and soil fungal communities and underscore that the species of tree lost from the canopy can be as important as the amount of canopy disturbance in determining soil chemical and fungal community responses.

AUTHOR CONTRIBUTIONS

Lindsay A. McCulloch, Benton N. Taylor, Nikhil Chari and William Schuster conceived the ideas and designed the methodology; Lindsay A. McCulloch, Carina Berlingeri, Nikhil Chari, Lauren Church, Katherine P. Terlizzi and Benton N. Taylor collected the data; Lindsay A. McCulloch, Nikhil Chari, Lauren Church, Cecilia M. Prada and Benton N. Taylor analysed the data. Lindsay A. McCulloch and Benton N. Taylor led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data and code for this paper are available on figshare: https://doi.org/10.6084/m9.figshare.27020668.v2 (McCulloch, 2024).

STATEMENT OF INCLUSION

This work was done in collaboration between researchers at Harvard University and Black Rock Forest, including local staff and scientists of the research consortium. All authors were engaged early on with the research and development of sample collection. The project was reviewed and approved by Black Rock Forest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Result table for permutation tests of RDA analysis.

Figure S1. Map of experimental plot design.

Figure S2. Rarefaction curve of amplicon sequence variants (ASV) for each soil sample.

Figure S3. Correlation between relative ASV abundances of ectomycorrhizae and Archaeorhizomycetes.

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