

RESEARCH ARTICLE

Ericoid mycorrhizal shrubs alter the relationship between tree mycorrhizal dominance and soil carbon and nitrogen

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Abstract

1. Plant–fungal associations strongly influence forest carbon and nitrogen cycling. The prevailing framework for understanding these relationships is through the relative abundance of arbuscular (AM) versus ectomycorrhizal (EcM) trees. Ericoid mycorrhizal (ErM) shrubs are also common in forests and interactions between co-occurring ErM shrubs and AM and EcM trees could shift soil biogeochemical responses. Here we test hypotheses that the effects of ErM shrubs on soil carbon and nitrogen either extend or are redundant with those of EcM trees.
2. Using regional vegetation inventory data (>3,500 plot observations) we evaluated the frequency, richness and relative abundance of ErM plants in temperate forests in the eastern United States and examined their relationship with EcM plant cover. We then used surface soil (7 cm) data from 414 plots within a single forest to analyse relationships between ErM plant cover, relative EcM tree basal area and soil carbon and nitrogen concentrations while accounting for other biogeochemical controls, such as soil moisture.
3. At both scales, we found a positive relationship between ErM and EcM plants, and the majority of ErM plants were in the shrub layer. Within the forest site, ErM plants strongly modulated tree mycorrhizal dominance effects. We found negative relationships between EcM relative basal area and soil carbon and nitrogen concentrations, but these relationships were weak to negligible in the absence of ErM plants. Both EcM relative basal area and ErM plant cover were positively associated with the soil carbon-to-nitrogen ratio. However, this relationship was driven by relatively lower nitrogen for EcM trees and higher carbon for ErM plants. As such, the functional effects of ErM plants on soil biogeochemistry neither extended nor were redundant with those of EcM trees.
4. *Synthesis.* We found that ErM shrubs strongly influenced the relationship between tree mycorrhizal associations and soil biogeochemistry, and the effects of ErM shrubs and EcM trees on carbon and nitrogen were functionally distinct. Our findings suggest that ErM shrubs could confound interpretation of AM versus EcM tree effects in ecosystems where they co-occur but also bolster growing calls to consider mycorrhizal functional types as variables that strongly influence forest biogeochemistry.

KEYWORDS

arbuscular mycorrhizal fungi, ectomycorrhizal fungi, forest understorey, functional traits, fungal interactions, nutrient cycling, plant–soil (below-ground) interactions, soil organic matter

1 | INTRODUCTION

Globally, the vast majority of tree species associate with arbuscular (AM) and/or ecto- (EcM) mycorrhizal fungi (Soudzilovskaia et al., 2020), to which they provide carbon (C) in exchange for greater access to soil nutrients (Smith & Read, 2008). Whereas AM fungi increase access to dissolved, inorganic nutrients by extending the host plant root system, some EcM fungi can degrade organic matter through the production of extracellular enzymes and/or Fenton oxidation, thereby liberating organic nutrients otherwise inaccessible for plant uptake (Lindahl & Tunlid, 2015; Nicolás et al., 2019; Read & Perez-Moreno, 2003). These contrasting nutrient acquisition strategies are thought to strongly influence soil C and nitrogen (N) cycling and storage (Averill et al., 2014; Cheeke et al., 2017; Dickie et al., 2014; Read, 1991; Steidinger et al., 2019). Specifically, a high relative abundance of AM trees within an ecosystem is hypothesized to be associated with ecological traits and processes related to fast cycling, inorganic nutrient availability, whereas EcM trees are linked to slow cycling, organic nutrient pools (Chapman et al., 2006; Phillips et al., 2013). The characterization of these distinct biogeochemical syndromes has prompted widespread use of AM versus EcM relative tree basal area (hereafter referred to as AM or EcM tree dominance; Phillips et al., 2013) to help explain and predict terrestrial ecosystem processes and their responses to global change (Dickie et al., 2014; Johnson et al., 2013; Shi et al., 2019; Terrer et al., 2016, 2021). In particular, much work has focused on tree mycorrhizal dominance effects on soil C and N within temperate forests owing to the high co-occurrence of AM and EcM trees (e.g. Craig et al., 2018; Phillips et al., 2013; Zhu et al., 2018; reviewed in Tedersoo & Bahram, 2019).

One consistent finding from this body of work has been a positive association between EcM tree dominance and the soil carbon-to-nitrogen ratio (i.e. C:N; Averill et al., 2014; Cheeke et al., 2017; Cotrufo et al., 2019; Craig et al., 2018; Jo et al., 2019; Lin et al., 2017; Zhu et al., 2018), and several mechanisms are thought to contribute to this relationship. Some studies have shown that this trend is driven by relatively lower N stocks or concentrations rather than changes in C (Craig et al., 2018; Lin et al., 2017; Zhu et al., 2018) as a result of selective mining of N-bearing organic molecules by EcM fungi (Lindahl & Tunlid, 2015; Nicolás et al., 2019). Others have hypothesized that EcM fungi could increase soil C through competitive interactions with free-living saprotrophs (i.e. the Gadgil effect; Averill, 2016; Averill & Hawkes, 2016). In this instance, EcM fungi could use energy from plant photosynthate to outcompete free-living saprotrophs for limited organic N, thereby suppressing overall saprotrophic activity and reducing C losses from decomposition (Gadgil & Gadgil, 1971, 1975). Evidence in support of the Gadgil effect has, however, been limited to conditions under which EcM fungi are superior competitors for N than free-living saprotrophs, such as in ecosystems with recalcitrant

litter inputs (Fernandez & Kennedy, 2016; Fernandez et al., 2020; Smith & Wan, 2019). Mycorrhizal fungi can also stimulate microbial activity through exudation of labile C and/or turnover of fungal necromass (Kaiser et al., 2015), and differences in rhizosphere priming among the mycorrhizal groups could influence soil C:N (Brzostek et al., 2015; Keller & Phillips, 2019; Sulman et al., 2017; Wurzbürger & Brookshire, 2017; Yin et al., 2021). For instance, because AM fungi lack organic matter-degrading abilities and hence rely on free-living saprotrophs to mineralize N (Tisserant et al., 2013), they could potentially increase organic matter decomposition through priming (Frey, 2019; Keller et al., 2021). The prevalence of each of these mechanisms within an ecosystem is thought to vary with soil conditions, microbial community composition and organic substrate quality (Fernandez et al., 2020; Zak et al., 2019). Although much work has focused on understanding the context dependencies of these effects across gradients of AM versus EcM tree dominance (e.g. Craig et al., 2018; Fitch et al., 2020; Lang et al., 2021; Midgley et al., 2015; Zhu et al., 2018), it remains unclear how these mechanisms interact and cumulatively affect soil C and N in the presence of other mycorrhizal groups.

Ericoid mycorrhizal (ErM) shrubs are also common in temperate forests (Figure S1; Dudley et al., 2020; Mallik, 1995; Monk et al., 1985) and possess functional traits known to influence ecosystem biogeochemistry (Clemmensen et al., 2015; Read & Perez-Moreno, 2003; Tedersoo & Bahram, 2019; Wurzbürger & Hendrick, 2009), but their interactions with AM versus EcM trees have rarely been evaluated. Ericoid mycorrhizal foliar litters (Clemmensen et al., 2021; Cornelissen et al., 2001; Xu et al., 2020), fine roots (See et al., 2019) and fungal biomass and necromass (Clemmensen et al., 2015) generally decompose slower than those of AM and EcM plants and fungi, which could contribute to organic matter accumulation in sites in which ErM plants occur (Read, 1991). Ericoid mycorrhizal fungi also have extensive saprotrophic capabilities, enabling them to access and modify organic nutrients (Read & Perez-Moreno, 2003). Comparative genomic analyses have shown that ErM fungi possess a higher variety and abundance of extracellular enzyme-coding genes compared to EcM fungi (Martino et al., 2018; Miyauchi et al., 2020; Perotto et al., 2018; Tedersoo & Bahram, 2019). Because the ability of some EcM fungi to modify organic matter through extracellular enzyme production is thought to be one of the primary mechanisms driving differences in soil C and N in AM- versus EcM-dominated forests (Frey, 2019; Read & Perez-Moreno, 2003), ErM fungi could also have strong biogeochemical effects. Yet the influence of ErM plants on soil C and N in forests has been little explored relative to the effects of AM versus EcM trees. One potential reason for the limited research on ErM plants is that they are primarily shrubs and hence are less often surveyed in forests on account of having stem diameters that fall below tree measurement thresholds (e.g. 10- or

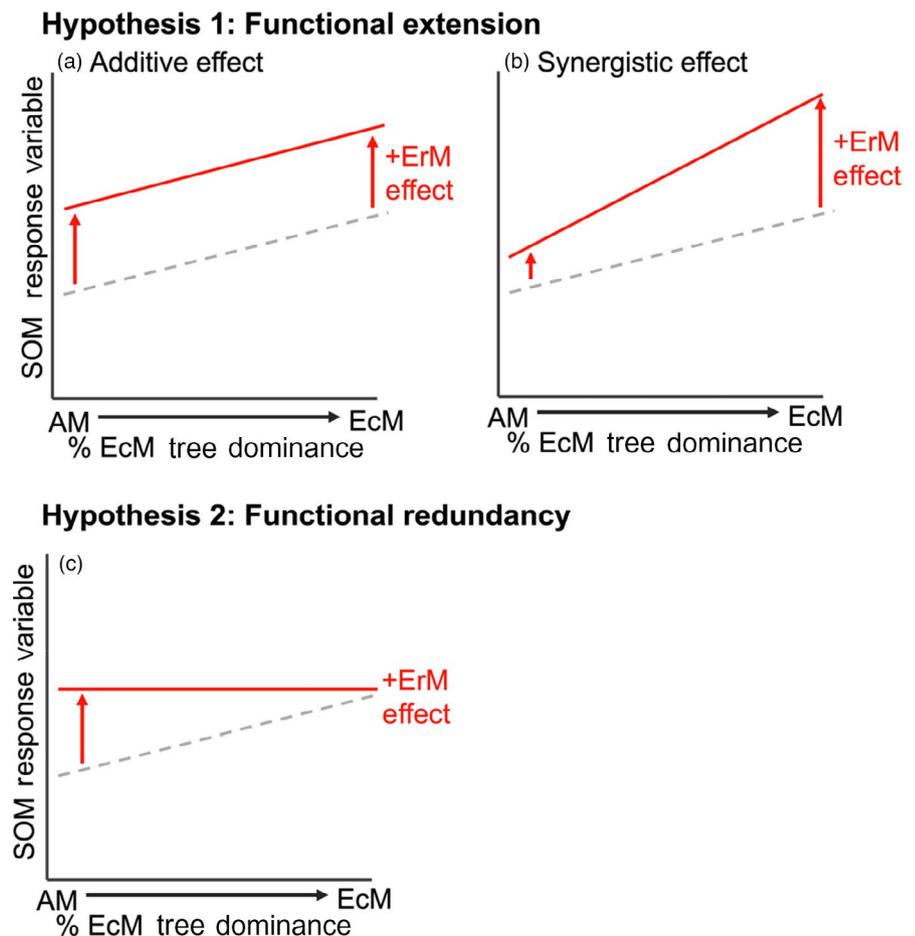
12.7-cm diameter at breast height [DBH, 130 or 137 cm above the ground]).

Yet because ErM plants are most prevalent in sub-canopy layers, they have the potential to coexist and hence interact with AM and EcM trees across gradients of mycorrhizal dominance. Specifically, the presence of ErM shrubs could functionally extend (hypothesis 1; Figure 1) EcM tree dominance effects given, for instance, the greater organic matter-degrading abilities of ErM fungi compared to EcM fungi (Martino et al., 2018; Perotto et al., 2018; Read & Perez-Moreno, 2003). In this case, complementary nutrient acquisition strategies (organic vs. mineral) or decay mechanisms that target different organic molecules could result in the partitioning of resources between co-occurring ErM and AM or EcM fungi (Wurzburger & Hendrick, 2009). The presence of ErM plants could therefore increase the magnitude of the EcM tree dominance effect in either an additive (hypothesis 1a) or synergistic (hypothesis 1b; Figure 1) way. These hypotheses are consistent with predictions of an AM-EcM-ErM trait continuum that aligns with gradients of N limitation and soil organic matter (SOM) accumulation (Cornelissen et al., 2001; Read, 1991; Read & Perez-Moreno, 2003). Alternatively, the effects of ErM fungi on soil C and N could be functionally redundant with those of EcM tree dominance (hypothesis 2; Figure 1). Wide variation in organic matter decay mechanisms exists among different lineages of EcM fungi (Miyachi et al., 2020; Pellitier & Zak, 2018; Shah et al., 2016). Therefore, at the community-level, diverse taxa of

EcM fungi could possess traits redundant with those of ErM fungi. If hypothesis 2 holds, we would expect ErM plant effects to be high in AM-dominated stands but negligible under EcM tree dominance (Figure 1). This hypothesis is consistent with previous studies that have grouped ErM and EcM fungi together owing to their shared saprotrophic capabilities (Averill et al., 2014; Orwin et al., 2011).

The potential for ErM shrubs to have additive, synergistic or redundant effects with other mycorrhizal functional types is, however, contingent on the extent to which ErM shrubs co-occur with both AM and EcM trees. Therefore, our first objective was to quantify the abundance of ErM plants in temperate forests in the eastern United States (U.S.) and evaluate their relationship with AM versus EcM plant cover. To address this objective, we used two datasets that included observations of sub-canopy as well as canopy vegetation layers, thereby addressing the relative scarcity of shrub observations in many forest inventory datasets. Because both groups are thought to be adapted to high SOM (Read, 1991; Read & Perez-Moreno, 2003) and can coexist on plant roots (Wurzburger et al., 2012), we hypothesized that ErM and EcM plant cover would be positively associated at the regional scale. To evaluate which of our competing hypotheses (Figure 1) were consistent with empirical relationships among ErM plant cover, EcM tree dominance and surface soil C and N concentrations, we analysed soil and vegetation data collected across varying levels of ErM plant cover along an AM to EcM tree dominance gradient within a forest in Connecticut (CT), U.S. Given that

FIGURE 1 Alternative hypotheses for how ericoid mycorrhizal (ErM) plants could alter the relationship between arbuscular (AM) versus ecto- (EcM) mycorrhizal tree dominance and variables indicative of the quantity and composition of soil organic matter (SOM). Solid red and grey dashed lines show the hypothesized effect of EcM relative basal area on SOM with and without ErM plants, respectively. Specifically, ErM plants could extend EcM tree dominance effects in either an (a) additive or (b) synergistic way (hypotheses 1a and 1b, respectively). This would suggest that ErM plants and fungi could be a further end member of the AM versus EcM dominance framework. Alternatively, the effects of ErM plants and fungi could be (c) redundant (hypothesis 2) with those of EcM owing to shared traits, such as the ability to degrade organic matter. In this case, we would expect the effects of ErM plant cover to be high in stands dominated by AM trees but negligible under EcM tree dominance



these data were observational and not experimental, we followed a causative statistical inference approach (see Bradford et al., 2021; Holland, 1986) that focused on identifying the relative effect sizes of ErM abundance, AM versus EcM tree dominance and their interaction within the context of other causal predictors of soil C and N concentrations.

2 | MATERIALS AND METHODS

2.1 | Regional data collation and preparation

We used vascular plant data from the U.S. National Park Service (USNPS) and U.S. Forest Service (USFS) vegetation inventory and monitoring programs to compare the frequency, species richness and relative abundance of ErM plants in eastern U.S. forests to those of AM and EcM plants. This dataset included 2,678 deciduous plots in 41 USNPS parks and 826 mixed deciduous plots in 18 USFS National Forests. We excluded one plot from the USFS dataset that included non-vascular plants only, which yielded a total of 3,503 USNPS and USFS plots (Table S1; Figure S2). We used these data since they had percent cover estimates for both canopy and sub-canopy vegetation layers and therefore included ErM shrub cover. The USNPS data, collected from 1996 to 2007, were collated from the USNPS Vegetation Inventory and Monitoring Program website (USNPS, 2014), and the USFS data, collected from 1999 to 2002, were downloaded from Vegbank (Peet et al., 2013). All analysed USNPS plots were a fixed size of 20 × 20 m, while the USFS plots were variable in size (generally 100–1,000 m²) as they aimed to capture plant species richness in different ecosystem types (Lee et al., 2008; Peet et al., 2018). Note that in the final dataset, the number of plots per site was uneven (Table S1), and the locations of the sites were not systematically distributed across the study region (Figure S2). For this reason, we did not analyse biogeographic patterns of ErM plant abundance or regional scale drivers of ErM plant cover. Instead, we focused on comparing the frequency, richness and relative abundance of AM, EcM and ErM plants.

Both the USNPS and USFS vegetation sampling protocols estimated plant cover within different vertical vegetation layers within each plot (Lee et al., 2008). Each plot could therefore include up to eight layers: emergent trees (variable height), tree canopy (variable height), tree sub-canopy (>5 m), tall shrub (2–5 m), short shrub (<2 m), herbaceous, vines and epiphytes. To better compare plots with different numbers of vegetation layers, we combined all tree (vegetation >5 m, excluding vines), shrub (woody vegetation <5 m, excluding vines) and hanging (vine and epiphyte) layers, which yielded four potential vegetation layers within each plot (tree, shrub, herbaceous and vine/epiphyte). We assigned mycorrhizal associations to each recorded vascular plant genus using the classifications in Soudzilovskaia et al. (2020). To calculate the percent cover of species with dual mycorrhizal status, we assigned half the cover value to each group (Phillips et al., 2013).

To compare the abundance of AM, EcM and ErM plants across eastern U.S. forests, we used multiple approaches to ensure that differences in sampling protocols among sites or between the USNPS and USFS datasets did not substantially influence our results. First, we analysed the mean and standard deviation of total and relative percent cover values of each mycorrhizal type within each vegetation layer across all plots. Total percent cover is the raw cover data, which can exceed 100% owing to multiple overlapping plant species within the same mycorrhizal group and/or multiple sampled vegetation layers within the same vertical stratum (e.g. tree layer). We therefore also used relative cover values, which were normalized by total vegetation cover within each plot and vegetation layer. Finally, we compared the cumulative relative cover of AM, EcM and ErM plants across all plots by dividing the sum of all plant cover affiliated with a particular mycorrhizal group by the sum of all plant species cover across all plots.

2.2 | Local field site and sampling design

To evaluate the potential effects of ErM plant cover on surface soil C and N concentrations across a tree mycorrhizal dominance gradient, we used observational soil and vegetation data collected from 420 plots arrayed across a 3,213-ha second-growth, mixed-hardwood forest in CT, U.S. (41°57'N, 72°07'W). The climate is moist and temperate with a mean January temperature of −4.6°C, a mean July temperature of 21.7°C, and a mean annual precipitation of 133 cm (National Oceanic & Atmospheric Administration [NOAA], 2021). The topography consists of rolling ridges and valleys underlain by metamorphic bedrock (Ashton et al., 1998). Soils are of glacial origin and primarily include deep, well-drained upland ablation till (Nipmuck, Brookfield, Charlton, Chatfield and Canton series), fertile, upland basal till of drumlins (Paxton, Montauk and Woodbridge series) and deep, poorly drained tills in depressions, drainageways or toe slopes (Ridgebury, Leicester and Whitman series; National Resources Conservation Service [NRCS], 2020; Table S2).

The plot arrangement consisted of 42 transects established in parallel pairs located 50 m apart. Each transect included ten 4-m radius plots located every 20 m. The placement of the transects was designed to capture variation in topography, stand age and forest cover type. Approximately 70% of the site is actively managed for timber on a rotational basis, with the remainder of the area in unmanaged reserves. Because the structure and composition of the understorey shifts during forest succession with changes in light availability (Oliver & Larson, 1996), this variation in stand structure allowed us to capture a range of canopy and sub-canopy vegetation cover as well as varied species composition.

Ectomycorrhizal tree species at the site include a mix of hardwoods and conifers, such as oaks (*Quercus* spp. L.), eastern hemlock (*Tsuga canadensis* (L.) Carrière) and eastern white pine (*Pinus strobus* L.), and AM tree species include hardwoods, such as maples (*Acer* spp. L.), white ash (*Fraxinus americana* L.) and tulip poplar (*Liriodendron tulipifera* L.; Table S3). Mountain laurel (*Kalmia latifolia* L.) makes up the

vast majority of ErM plant cover at the site (Table S3). This species is a broad-leaved evergreen shrub that can form dense, clonal thickets in temperate forest understories in the region (Figure S1b; Monk et al., 1985). Other understory plant species at the site included AM and AM/non-mycorrhizal plants, such as eastern hay-scented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore), witch hazel (*Hamamelis virginiana* L.) and sedges (*Carex* spp. L.). However, each of these other understory species makes up a lower proportion of total plant cover compared to mountain laurel.

2.3 | Soil and vegetation sampling

In May–July 2013, we estimated percent cover of all understory ErM plant species (based on Soudzilovskaia et al., 2020)—including both shrubs and herbaceous layer plants (e.g. *Gaultheria procumbens* L.)—within each 4-m radius plot using six cover classes (Daubenmire, 1959). We estimated total basal area of trees ≥ 1.37 m in height (i.e. standard breast height in the U.S.) from the plot center using variable radius plot (VRP) sampling with a 2.3 m²/ha basal area factor angle gauge (Hovind & Rieck, 1970). For each tree tallied during VRP sampling, we also identified the species and measured DBH at 1.3 m, and we used the mycorrhizal classifications from Soudzilovskaia et al. (2020) to calculate the percentage of EcM tree basal area (i.e. EcM tree dominance) using the DBH measurements (Phillips et al., 2013).

The following year in 2014, we collected and pooled twenty 2-cm diameter, 7-cm-deep soil cores within each plot after removing the litter layer. We had intended to sample to 10 cm but were unable to consistently collect samples to that depth owing to extremely rocky conditions in some plots. As such, we chose to sample to a depth of 7 cm across all 420 plots. We focused on surface soil samples since our primary objective was to investigate potential interactions between ErM and AM/EcM fungi, which are most abundant in upper horizons (Lindahl et al., 2007; Read et al., 2004; Wurzbürger et al., 2012), though we recognize that these relationships could shift in deeper horizons (Craig et al., 2018). We measured soil temperature and moisture (volumetric water content) in the field on three occasions during the 2014 growing season (May, July and September) and recorded five measurements per plot at each sampling occasion. To measure soil moisture, we used a handheld Hydrosense II Soil Water Content Measurement System (Campbell Scientific, Inc.), and for soil temperature we used a digital thermometer (Taylor Precision Products).

2.4 | Laboratory analyses

We first homogenized each soil sample and passed it through a 4-mm sieve. We measured pH on field-moist samples stored at 5°C and SOM and total C and N concentrations on dried samples. For pH, we mixed the soils and water in a 1-to-1 volumetric ratio and measured the pH of the supernatant after 10 min using a benchtop meter

(VWR symphony Sb70p; Allen, 1989). We estimated SOM by calculating mass loss of soils heated at 550°C for 12-hr in a muffle furnace. This temperature and duration are within the recommended range for loams (Hoogsteen et al., 2015) and maximized mass loss in samples with high organic matter content. We used a ball mill to grind air-dried soil samples to a fine powder and analysed total C and N concentrations using dry combustion (Leco CNS-2000; Leco Corporation).

2.5 | Data and inferential analysis

We used linear mixed models (LMMs) to analyse the relationships between ErM plant cover and EcM dominance in the regional (USNPS/USFS) and CT forest datasets as well as the relationships between ErM plant cover, EcM tree dominance and soil C and N concentrations in the CT plots. Prior to all analyses, we excluded five plots from the CT dataset that were located in standing water or swamps as well as one plot that had no overstorey trees. This yielded a total of 414 observations. In the regional dataset, one plot had no AM or EcM vegetation cover, so we had a total of 3,502 observations. Random effects included site (i.e. USFS National Forest or USNPS park) in all regional models and transect and transect pair in all CT models. We fit all LMMs using a Gaussian error distribution, calculated variance explained by fixed effects (marginal R^2) and by fixed and random effects (conditional R^2 ; Nakagawa & Schielzeth, 2013), and ran all analyses with the 'lme4' package in R (version 4.0.3; Bates et al., 2015; R Core Development Team, 2021).

First, we built models that included percent EcM dominance as a fixed effect and total percent ErM plant cover as the response variable. For the CT dataset, EcM dominance was the percentage of EcM tree basal area (Phillips et al., 2013), and in the regional dataset it was the percentage of all EcM plant cover (including sub-canopy plants) out of the sum of AM and EcM plant cover within each plot. For the regional dataset, we built a second model that included both evergreen EcM tree cover and deciduous EcM tree cover as fixed effects ($n = 2,984$). We performed this analysis since we were interested in investigating whether ErM plants were more strongly associated with deciduous versus evergreen EcM trees since this could have implications for their combined soil biogeochemical effects at the regional scale (Fernandez et al., 2020; Midgley & Sims, 2020). Through this analysis, we also evaluated the association between ErM plant cover and the total cover of EcM trees (rather than relative cover of all EcM plants as described above), which helped validate results from the previous models. Finally, we supplemented our analysis with quantile regression. Quantile regression recognizes that response variables are products of multiple controls and hence single predictor-outcome relationships likely only emerge at high or low quantile values when the influence of other controls are relaxed (Cade & Noon, 2003). For this analysis, we evaluated the relationship between ErM plant cover and EcM dominance at the 75th and 90th quantiles of the distribution of ErM plant cover using the 'QUANTREG' package in R (Koenker, 2021). To compute standard errors of the

quantile regression coefficient estimates, we used the bootstrapping method (Koenker, 2021).

Next, to analyse the relationships between ErM plant cover and EcM tree dominance and the quantity and composition of SOM in the CT forest plots ($n = 414$), we included %SOM, %C, %N and C:N as response variables. We natural log-transformed the dependent variables to meet model assumptions of normal residual distributions and homoscedasticity as well as to minimize inferential errors associated with analysing ratio response variables (Isles, 2020). Fixed effects included percent ErM plant cover, percent EcM tree dominance, total tree basal area (m^2/ha), mean soil moisture (%), mean soil temperature ($^{\circ}\text{C}$), pH, the ErM cover by EcM dominance interaction, and the EcM dominance by basal area interaction. Given the inferential challenges associated with analysing ratio response variables (Isles, 2020; Jasiński & Bazzaz, 1999), we built two additional models with C and N as response variables. Again, we natural log-transformed the response variables to meet model assumptions. In addition to the fixed effects described above, we included %N as an additional predictor in the C model and %C as an additional predictor in the N model to evaluate the effects of increasing ErM plant cover and EcM tree dominance when controlling for %N and %C, respectively. We also included second order terms for %C and %N in these models since we observed a nonlinear relationship between C and N.

Our overarching causative inferential approach was based on Holland (1986) and was developed in Bradford et al. (2021) to investigate organismal effects on SOM dynamics. The focus of this approach is on identifying the conditional effect size of a causal variable relative to other known controls. Our decision regarding which variables to include as fixed effects in our statistical models was therefore based on known biological mechanisms that relate each predictor to the response variable rather than model selection (Bradford et al., 2019; Hobbs et al., 2012). Specifically, we chose to include soil moisture, temperature and pH as fixed effects since they are known controls of SOM dynamics and microbial activity. We had also intended to include soil texture but removed it since over half (219) the plots had greater than 20% SOM and could therefore not be analysed for texture using the hydrometer method. In addition to these soil biogeochemical controls, we included total tree basal area to account for differences in management history and stand age, which varied substantially among plots (see Section 2.2) and can have strong microsite effects (Boettcher & Kalisz, 1990; Zinke, 1962). We included the interaction term between EcM tree dominance and basal area to investigate the possibility that increasing basal area could have non-additive effects on soil C and N concentrations across the tree mycorrhizal gradient. Given that our goal was to determine robust coefficient estimates and that multicollinearity was sufficiently low, we retained all terms in our models irrespective of their statistical significance. To compare the relative effect sizes of the fixed effects, we standardized and centered all variables by subtracting the mean and dividing by one standard deviation.

The square-root of the variance inflation factors for the main effects in all models were <1.4 with the exception of the expected

correlations between the first- and second-order terms, indicating sufficiently low collinearity amongst the predictor variables. We did, however, note that soil moisture and EcM tree dominance were negatively correlated ($r = -0.46$; Figure S7) at the CT site and therefore built an additional LMM with EcM tree dominance as a function of soil moisture. We also tested the sensitivity of our coefficient estimates to different model specifications to verify that our conclusions were robust (Bradford et al., 2019, 2021; Holland, 1986). Specifically, given the observed negative correlation between EcM tree dominance and soil moisture, we examined whether the size of the standardized coefficient of EcM tree dominance changed when soil moisture was removed from the model. We also ran models that included all two-way interactions between the independent variables to explore the influence of ecologically plausible interaction terms on the coefficient estimates. Finally, we ran a model that included the five plots located in standing water that we had excluded from our analysis. In all instances, the coefficient estimates for EcM tree dominance and ErM cover were robust to these changes (i.e. same sign and within the same order of magnitude).

3 | RESULTS

3.1 | Regional assessment of ErM plants in forests in the eastern U.S.

The eastern U.S. forest dataset included 69 ErM plant species, which accounted for 2.5% of the 2,769 species surveyed (see Table S4 for full ErM plant species list) and made up 6.7% of total vegetation cover (Table S5). Although ErM plants represented a relatively low proportion of total species richness and relative cover compared to AM (1,754 species, 56% of total cover) and EcM (127 species, 33% of total cover) plants, they occurred in almost half (48%) the plots (Table 1; Table S5). Differences in the relative cover of ErM plants compared to AM and EcM plants were also strongly dependent on vegetation layer (Figure 2; Figure S3; Table 1; Tables S5 and S6). We found that 84% of total ErM cover across all plots was in the shrub layer compared to only 13% in the tree layer (i.e. vegetation >5 m; Table S6). In contrast, the tree layer had the highest percentages of total AM (40%) and EcM (85%) plant cover across all plots relative to the percentages in the other vegetation layers (Table S6). In the tree layer, ErM plants included 15 species, had a relative cover of 1.7%, and occurred in 11.7% of plots (Table S5). In the shrub layer, however, all 69 ErM plant species were present, and the relative percent cover of ErM vegetation was higher (21.7%) than that of EcM plants (18.5%) despite having fewer species (Table S5).

Comparisons of the mean and variation of percent cover of each plant mycorrhizal type within each plot affirmed the results based on relative cover across all plots. Mean total ErM plant cover was relatively low (11.1%) compared to that of AM (94.0%) and EcM (55.6%) plants when all vegetation layers were considered but comparable (9.6%) to that of EcM plants (8.2%) in the shrub layer (Table 1;

TABLE 1 Species richness, frequency and the mean and standard deviation (SD) of total and relative percent cover of plants associated with each of the mycorrhizal groups across all vegetation layers ($n = 3,503$) and in the tree ($n = 3,287$), shrub ($n = 3,407$) and herbaceous ($n = 3,436$) layers. Data are from the U.S. National Park Service and U.S. Forest Service datasets. Frequency is the percentage of plots in which each plant mycorrhizal type occurs. Total cover is the sum percent cover of all plant species that form each mycorrhizal association within each layer, which can be greater than 100% owing to multiple overlapping species and multiple sampled vegetation layers (e.g. short shrubs, tall shrubs) within each layer category (see Section 2.1). Relative cover is the percentage of each plant mycorrhizal cover type within each vegetation layer divided by total plant cover within that vegetation layer

Plant mycorrhizal type ^a	Vegetation layer	Plant species richness	% Frequency	Mean (SD) % Total plant cover	Mean (SD) % relative plant cover
AM	All	1,754	99.9	94.0 (48.0)	59.6 (28.1)
	Tree	199	91.5	39.9 (38.5)	44.0 (32.6)
	Shrub	440	58.9	26.1 (30.1)	63.2 (33.0)
	Herb	1,554	82.0	29.3 (32.2)	93.5 (16.8)
EcM	All	127	92.1	55.6 (69.8)	33.8 (24.2)
	Tree	90	90.4	50.2 (43.7)	54.8 (32.3)
	Shrub	94	74.4	8.18 (14.5)	19.6 (24.0)
	Herb	83	33.7	0.565 (2.01)	4.22 (11.8)
ErM	All	69	48.2	11.1 (25.4)	6.56 (13.1)
	Tree	15	11.7	1.60 (7.71)	1.17 (4.77)
	Shrub	69	47.3	9.6 (22.0)	17.2 (28.2)
	Herb	28	8.6	0.319 (2.34)	2.23 (10.9)

^aAbbreviations are as follows: arbuscular (AM), ecto- (EcM) and ericoid mycorrhizal (ErM) plants.

Figure S3). Variation in total ErM cover among plots was also very high. The maximum total percent ErM plant cover value across all vegetation layers was 222% within a single plot, and the standard deviation across all plots was 25% in all layers and 22% in the shrub layer (Table 1; Figure S3). Likewise, when the percent cover values were normalized by total vegetation cover within each plot and layer (i.e. relative cover), we found that, on average, ErM plants made up ~17% of total vegetation cover in the shrub layer but only ~6.6% of total vegetation cover across all layers in a plot (Table 1; Figure S3). Again, variation among plots was high. Relative ErM plant cover within each plot ranged from 0% to 100% and had a standard deviation of 28% in the shrub layer and 13% across all layers (Table 1; Figure S3). Regardless of the approach used to determine percent ErM plant cover, we found that ErM plants were most abundant in the shrub layers, in which they made up ~20% of total vegetation cover, though this value varied substantially amongst plots.

3.2 | Relationship between ErM plant cover and EcM relative abundance

Percent ErM plant cover was positively associated with EcM plant dominance in both the CT (Figure S4) and regional (Figure 2) datasets, and this positive relationship held for the percent cover of both deciduous and evergreen EcM trees (Figure S5). The marginal effect (\pm SE) of increasing EcM plant dominance on ErM plant cover was $0.21 \pm 0.07\%$ in the CT forest plots and $0.30 \pm 0.02\%$ in the eastern U.S. forest plots. These trends resulted in a ~2.2- and ~3.7-fold increase in mean (\pm SE) ErM plant cover in EcM-dominated ($\geq 50\%$ EcM plant relative cover) plots ($30.9 \pm 1.7\%$ in CT, $n = 374$ and $22.0 \pm 1.0\%$ in eastern U.S., $n = 1,151$) compared to AM-dominated ($< 50\%$ EcM plant relative cover) plots ($14.1 \pm 3.6\%$ in CT, $n = 40$ and $5.9 \pm 0.4\%$ in eastern U.S., $n = 2,351$) in the CT and regional datasets, respectively. Variation in ErM plant cover explained by EcM plant dominance was,

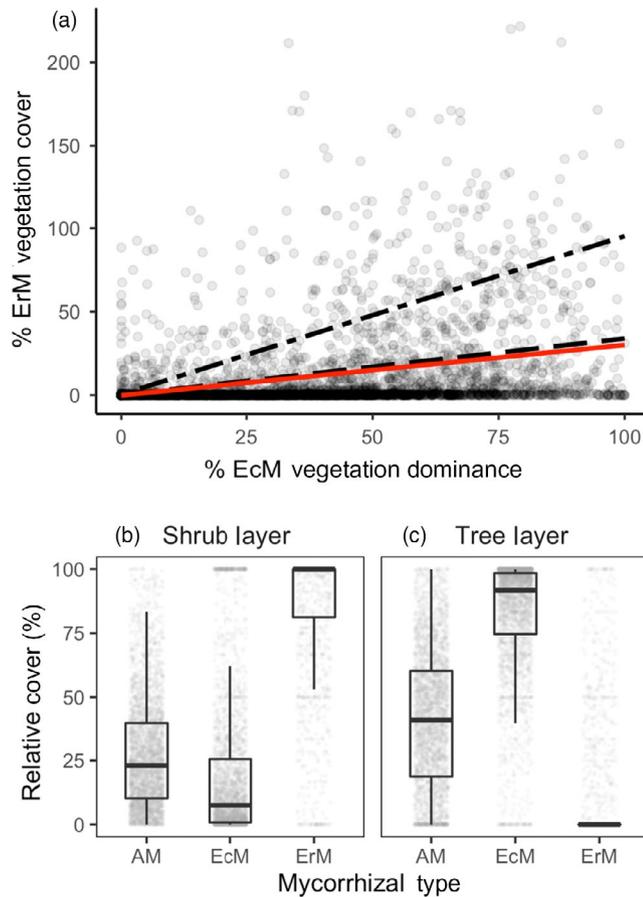


FIGURE 2 Regional vegetation data from eastern U.S. forests showed that ericoid mycorrhizal (ErM) plant cover is (a) positively associated with the relative abundance of ectomycorrhizal (EcM) plants and (b) primarily occurs in the shrub (<5 m) layer. Although ErM plants reach higher percent cover levels in EcM-dominated stands, they occurred across the full AM–EcM plant dominance gradient (a), and by occupying a different vertical niche (sub-canopy versus canopy), ErM plants can coexist with AM and EcM trees. In the scatterplot (a), EcM plant dominance was calculated using the proportion of EcM plant cover out of the sum of AM and EcM plant cover across all vegetation layers in the U.S. National Park Service and U.S. Forest Service plots ($n = 3,502$). Black dashed lines show the 75th (single-dashed) and 90th (double-dashed) quantile regressions and red solid lines show the least squares (mean) regressions. Boxplots (b, c) show the median, first and third quartiles, and whiskers show the upper ($1.5 \times$ interquartile range) and lower ($1.5 \times$ interquartile range) range, excluding outliers. Points show the sum cover of plants in each mycorrhizal group and vegetation layer within each plot divided by the total cover of plants in that mycorrhizal group across all vegetation layers in the plot

however, low ($R^2 = 0.02$ in CT and 0.10 in eastern U.S.). We therefore supplemented the LMMs with quantile regression, which can be used to detect relationships when unexplained variation with least squares regression is high and the response variable is the product of multiple causative variables (Cade & Noon, 2003). Through these analyses, we observed a stronger positive effect of EcM plant dominance on ErM plant cover in both the CT and eastern U.S. datasets. The marginal effect (\pm SE) of EcM plant dominance on the

75th quantile of ErM plant cover was $0.65 \pm 0.12\%$ in the CT plots (Figure S4) and $0.33 \pm 0.02\%$ in the eastern U.S. plots (Figure 2). At the 90th quantile of ErM plant cover, the marginal effect of increasing EcM dominance was $0.54 \pm 0.21\%$ and $0.94 \pm 0.04\%$ in the CT (Figure S4) and regional (Figure 2) datasets, respectively.

3.3 | Relationships between ErM plants, tree mycorrhizal dominance and soil C and N concentrations

We observed strong relationships between plant mycorrhizal types and surface SOM and C and N concentrations at the CT forest site. Plots ranged from 100% AM to 100% EcM tree basal area, and ErM plant cover ranged from 0% to 113% (Figure S4). Overall, however, EcM trees were more dominant than AM trees and made up 84% of total basal area across all plots (Table S3). Although we observed a positive association between ErM plant cover and EcM tree dominance within the forest (Figure S4), ErM plants still occurred across the full tree mycorrhizal dominance gradient, which enabled us to evaluate the extent to which interactions between ErM plant cover and EcM tree dominance were consistent with our different hypotheses (see Figure 1).

Notably, we observed strong ErM plant cover by EcM tree dominance interaction effects on SOM, %C and %N (Table 2; Figure 3), but the form of these relationships departed substantially from our hypotheses (Figure 1). Specifically, we found stronger positive relationships between ErM plant cover and %SOM, %C and %N in plots with higher AM tree relative basal area (Figure 3). Moreover, in the absence of ErM plants, the relationships between tree mycorrhizal dominance and %SOM, %C and %N were weak to negligible (Figure 3). When ErM plants were present, mean %C (\pm SE) was $\sim 25\%$ higher in AM-dominated (<50% EcM tree basal area) plots ($15.6 \pm 1.7\%$, $n = 27$) than in EcM-dominated ($\geq 50\%$ EcM tree basal area) plots ($12.4 \pm 0.3\%$, $n = 298$), but these differences were negligible in the absence of ErM plants ($11.8 \pm 1.2\%$, $n = 13$ in AM-dominated plots versus $12.0 \pm 0.6\%$, $n = 71$ in EcM-dominated plots). Similarly, mean %N (\pm SE) was $\sim 58\%$ higher in AM- ($0.79 \pm 0.079\%$, $n = 27$) than in EcM- ($0.50 \pm 0.013\%$, $n = 299$) dominated stands in the presence of ErM plants but only $\sim 22\%$ higher in AM-dominated stands when ErM plants were absent ($0.70 \pm 0.083\%$, $n = 27$ in AM-dominated plots versus $0.57 \pm 0.026\%$, $n = 71$ in EcM-dominated plots).

Ericoid mycorrhizal plant cover, EcM tree dominance and the EcM by basal area interaction terms were all positively associated with surface soil C:N. However, the ErM plant cover by EcM tree dominance interaction effect on C:N was weak, indicating that the cumulative effect of co-occurring ErM plants and EcM trees was largely additive (Table 2; Figure 3). The magnitudes of the standardized coefficients in the C:N model were also approximately equal for EcM tree dominance and ErM plant cover (Table 2). Yet the patterns between ErM plant cover and EcM tree dominance and soil C and N concentrations were distinct (Table 2; Figure 4). Whereas the relationships between ErM plant cover and %SOM, %C, and %N were all

TABLE 2 Relationships between ectomycorrhizal (EcM) tree dominance, ericoid mycorrhizal (ErM) plant cover and surface soil organic matter, carbon (C) and nitrogen (N) concentrations in a temperate forest in Connecticut, United States. Values are the standardized coefficients (\pm SE) for the linear mixed models. Notably, ErM plant cover was positively associated with all soil response variables and strongly modulated the effect of EcM tree dominance on soil organic matter and C and N concentrations. Significant ($p < 0.05$) coefficients are indicated in bold.

Predictors	Standardized model coefficients ^a \pm SE			
	Soil organic matter ^b (%)	Carbon ^b (%)	Nitrogen ^b (%)	C:N ^{b,c}
Intercept	3.0 \pm 0.046	2.5 \pm 0.039	-0.70 \pm 0.041	3.2 \pm 0.015
ErM plant cover (%)	0.090 \pm 0.019	0.11 \pm 0.020	0.064 \pm 0.019	0.047 \pm 0.0081
EcM tree dominance (%)	-0.052 \pm 0.020	-0.054 \pm 0.021	-0.10 \pm 0.020	0.044 \pm 0.0086
Basal area (m ² /ha)	0.091 \pm 0.019	0.083 \pm 0.020	0.063 \pm 0.019	0.020 \pm 0.0081
Soil moisture (%)	0.15 \pm 0.020	0.121 \pm 0.020	0.161 \pm 0.019	-0.045 \pm 0.0082
Soil pH	-0.12 \pm 0.018	-0.136 \pm 0.019	-0.098 \pm 0.018	-0.035 \pm 0.0078
Soil temperature (°C)	0.0063 \pm 0.028	-0.001 \pm 0.027	0.0020 \pm 0.027	0.00045 \pm 0.011
EcM \times ErM	-0.055 \pm 0.021	-0.063 \pm 0.021	-0.057 \pm 0.020	-0.012 \pm 0.0087
EcM \times Basal area	-0.044 \pm 0.018	-0.038 \pm 0.018	-0.056 \pm 0.017	0.017 \pm 0.007
<i>n</i> ^d	414	409	410	409
Fixed <i>R</i> ² /Full	0.24/0.50	0.26/0.44	0.29/0.50	0.42/0.54

^aUnstandardized coefficients are provided in Table S7.

^bAll response variables were natural log-transformed.

^cWe report coefficient estimates from models for %N with %C as an additional predictor and %C with %N as an additional predictor in Table S8.

^dOne plot had no overstorey trees, four plots were missing %C and %N values and one plot was missing %C only.

positive, we observed negative associations between EcM tree dominance and these variables (Table 2; Figure 4). The EcM dominance by basal area interaction effects were also negative for each of these variables (Table 2). Notably, the magnitude of the effect of ErM plant cover was about twice as high as that of EcM tree dominance for %SOM and %C (compare standardized coefficients in Table 2). For N, however, the magnitude of the effect of EcM tree dominance was larger than that of ErM cover (Table 2). The positive relationships with soil C:N were therefore driven by relatively lower N per unit C for EcM tree dominance but relatively higher C per unit N for ErM plant cover (Table 2; Figure 4). In addition to the mycorrhizal plant effects, basal area and soil moisture both had strong positive relationships and pH had strong negative relationships with %SOM, %C and %N (Table 2). For C:N, we found a strong positive association with basal area and strong negative associations with soil moisture and pH (Table 2).

Given inferential issues with analysing ratios (Isles, 2020; Jasiński & Bazzaz, 1999), we corroborated these relationships by comparing the relative effects of ErM plant cover and EcM tree dominance on soil C and N concentrations when controlling for %N and %C, respectively. For %N, the magnitude of the EcM tree dominance effect was over twice as large as that of ErM plant cover (compare standardized coefficients in Table S8), and both relationships were negative. We also observed a strong negative EcM dominance by basal area interaction effect in the N model (Table S8). In contrast, for the C model, the positive effect size of ErM plant cover was larger than that of EcM tree dominance (Table S8). Notably, the effect sizes of ErM plant cover and EcM tree dominance were within the same

order of magnitude or larger than those of other known soil biogeochemical controls. In the N model, these included positive associations with soil moisture and pH (Table S8), and in the C model, these included strong negative associations with soil moisture and pH and a strong positive association with total basal area. As expected, we also observed strong positive associations between %C and %N in both models (Table S8). Overall, fixed effects in these models explained 86% of variation in %C and 87% of variation in %N (Table S8).

Finally, we examined the relationship between EcM tree dominance and soil moisture in the CT forest plots since we observed a negative correlation between these variables when we evaluated them as predictors ($r = -0.46$; Figure S7), and they were both strongly associated with %SOM, %C, %N and C:N (Table 2). Soil moisture explained 17% of variation in EcM tree dominance at our site, and fixed and random effects explained 32% of variation. The relationship between these variables was strongly negative (Figure S8); for every 1% increase in soil moisture, EcM tree dominance declined by 0.88% (\pm SE, 0.09%).

4 | DISCUSSION

4.1 | Accounting for ErM shrubs in temperate forests

Understanding how local differences in site conditions influence the ecosystem biogeochemical effects of AM versus EcM trees can improve our ability to use the mycorrhizal dominance framework

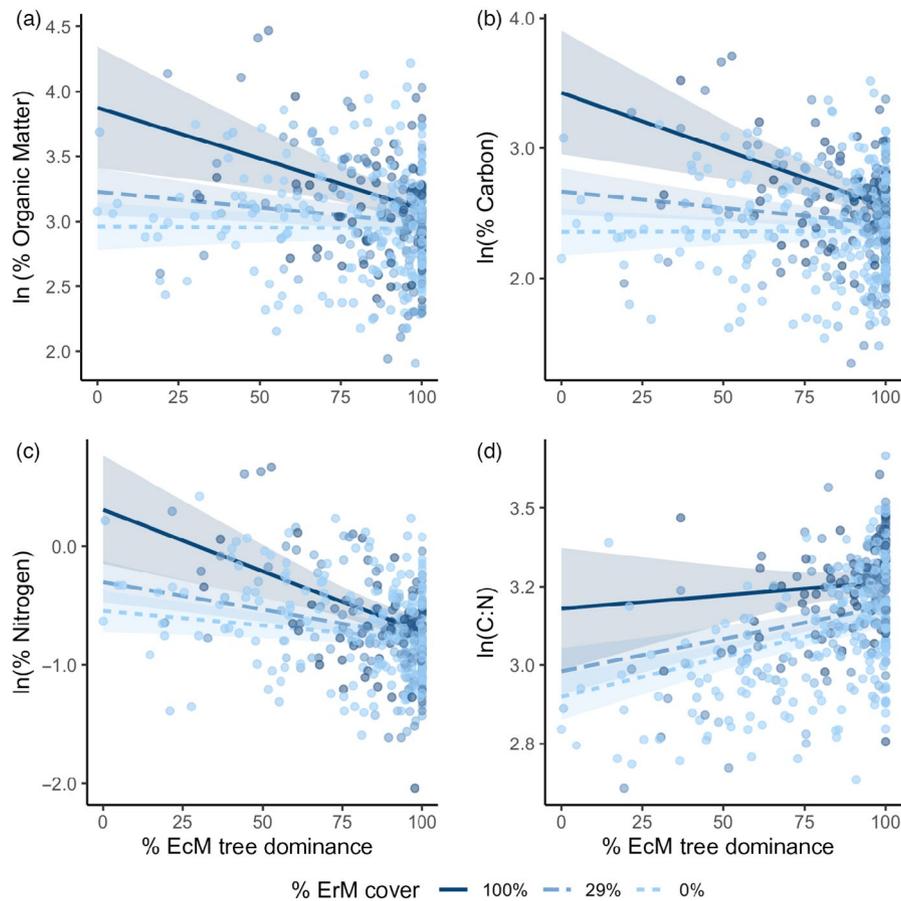


FIGURE 3 The relationships between ectomycorrhizal (EcM) tree dominance and surface (0–7 cm) soil (a) organic matter ($n = 414$), (b) carbon (C; $n = 409$) and (c) nitrogen (N; $n = 410$) were strongly modulated by ericoid mycorrhizal (ErM) plant cover. Ericoid mycorrhizal plants also strengthened the positive relationship between EcM tree dominance and (d) soil C:N ($n = 409$). Vegetation and soil data were collected from mixed-hardwood forest plots in Connecticut, United States. Ectomycorrhizal tree dominance was calculated based on basal area relative to arbuscular mycorrhizal (AM) trees. The regression lines depict the modelled effects of the interaction between EcM tree dominance and ErM plant cover for each soil response variable using the unstandardized coefficients from the statistical models (Table S7), and the shaded areas show the 95% confidence intervals. Solid, dashed and dotted lines show predictions for 100%, 29% (the mean ErM plant cover across the 414 plots) and 0% ErM plant cover, respectively. Points are shaded on a continuous scale with darker blue indicating higher ErM cover (maximum of 113%) and lighter blue indicating lower values (minimum of 0% cover). The scatter in the data reflects the fact that the response variables are controlled by multiple predictors included in the models (soil temperature, soil moisture, pH and basal area). The regression line is plotted while holding these other variables constant at their mean values to isolate the effects of changes in ErM plant cover and EcM tree dominance

to predict terrestrial ecosystem processes and their responses to global change. Incorporating finer-scale biotic and abiotic context dependencies and microbial community interactions has been recognized as the next frontier in research investigating mycorrhizal biogeochemical effects (Bradford et al., 2021; Fernandez & Kennedy, 2016; Fernandez et al., 2020; Smith & Peay, 2020; Zak et al., 2019). Variation in understory ErM plant cover among forest stands is one example of how microsite conditions can shape ecosystem-level predictions of soil C and N (Chastain et al., 2006; Osburn et al., 2018; Wurzbarger & Hendrick, 2009). We found that the vast majority of ErM plant cover in eastern U.S. forests occurs in the shrub layer and is therefore not captured in assessments of mycorrhizal dominance that use the relative basal area of AM versus EcM trees. Indeed, many AM versus EcM dominance comparisons have highlighted the lack of ErM plant data (e.g. Bennett & Classen, 2020;

Soudzilovskaia et al., 2019; Steidinger et al., 2019), particularly in ecosystems other than boreal forests and heathlands (Albornoz et al., 2020; Leopold, 2016). Given the strong associations of ErM plants with surface soil C and N concentrations that we observed in this study, our findings have important implications for how we characterize mycorrhizal functional types in temperate forests and suggest a need to test alternative metrics in stands in which ErM shrubs co-occur with AM and/or EcM trees.

Globally, 85% of known ErM plant species are shrubs compared to only 7% that are trees (Soudzilovskaia et al., 2020), suggesting that our results could generalize to forests in other regions. In boreal forests, for instance, ErM fungi and shrubs can strongly affect C and N cycling and storage through mechanisms distinct from those invoked for EcM trees (Adamczyk et al., 2016; Clemmensen et al., 2013, 2015; Read et al., 2004). For instance, Clemmensen

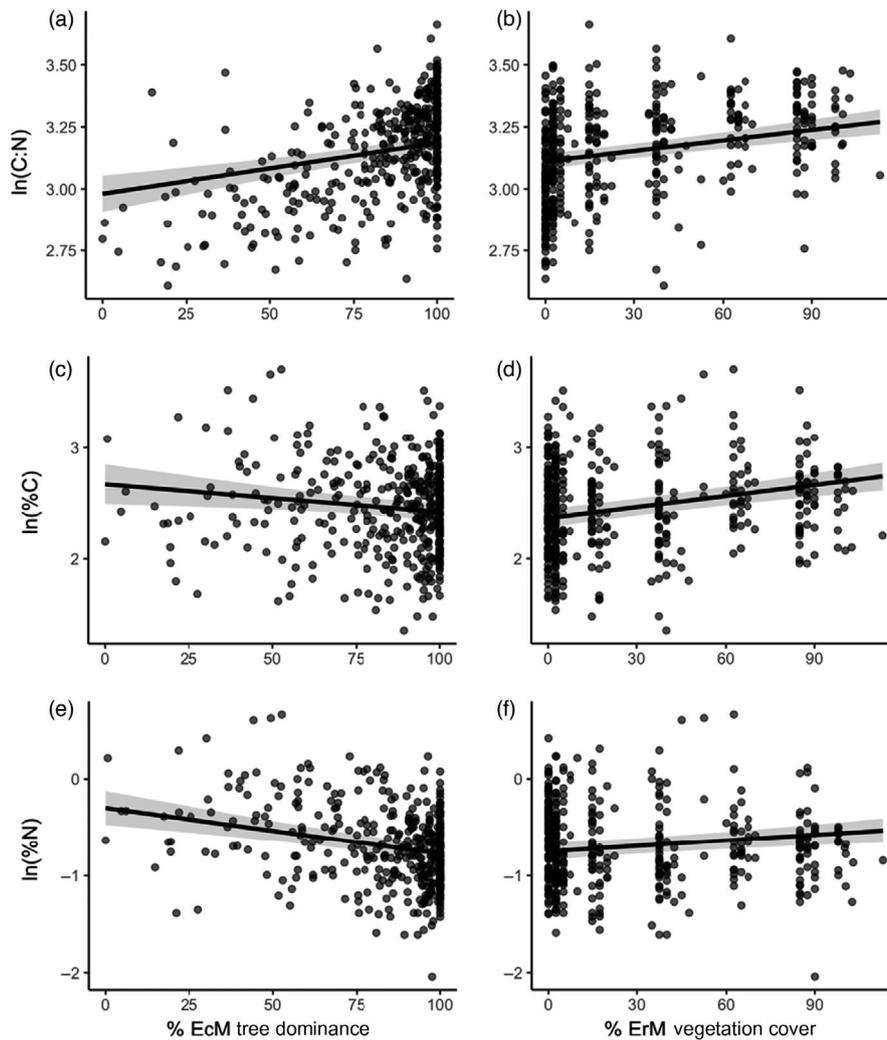


FIGURE 4 Relationships between (a, c, e) ectomycorrhizal (EcM) tree dominance and (b, d, f) ericoid mycorrhizal (ErM) vegetation cover and surface (0–7 cm) soil (a, b) carbon-to-nitrogen ratio (C:N; $n = 409$) and total (c, d) carbon (C; $n = 409$) and (e, f) nitrogen (N; $n = 410$) concentrations. The regression lines depict the modelled effects using the unstandardized coefficients from the statistical models (Table S7), and the shaded areas show the 95% confidence intervals. Although EcM tree dominance and ErM vegetation cover were both positively associated with soil C:N (a, b), these trends were driven by contrasting relationships with C and N concentrations. Ectomycorrhizal tree dominance was negatively associated with both soil C (c) and N (e) concentrations, whereas ErM plant cover was positively associated with %C (d) and %N (f). Higher soil C:N was therefore driven by a stronger negative relationship with %N compared to that of %C for EcM tree dominance but by a stronger positive relationship with %C relative to that of %N for ErM plant cover. These distinct patterns suggest that different mechanisms underpin the relationships between EcM and ErM plants and fungi and soil organic matter dynamics, making the effects of these two mycorrhizal groups functionally distinct

et al. (2021) showed that variation in C and N cycling across a boreal forest heath vegetation gradient were driven by certain genera of EcM fungi that accelerated decomposition but that ErM fungi increased SOM build up across all sites. The authors also found a higher relative abundance of ErM fungi in forests with an ErM shrub layer than in the adjacent ericaceous heathland, illustrating how there can be differences between the dominant plant mycorrhizal type within an ecosystem (e.g. EcM trees in the forest, ErM shrubs in the heathland) and the composition of the fungal community. In this instance, consideration of the mycorrhizal associations of sub-dominant ErM shrubs in the forest site was important for teasing out ErM and EcM plant and fungal effects. Similar trends could emerge in temperate forests with an ErM shrub layer that are commonly classified by the

relative abundance of AM versus EcM trees on the basis that trees account for the majority of above-ground plant biomass.

Accounting for variation in ErM shrub cover in temperate forests is particularly important given their potential to confound interpretation of tree mycorrhizal dominance effects. In both analysed datasets, we observed a positive association between ErM plant cover and EcM vegetation dominance, and this relationship held for both deciduous and evergreen EcM trees. Given that species of EcM and ErM fungi are (a) both generally associated with organic-rich soils with low N availability (Read, 1991; Read & Perez-Moreno, 2003), (b) have some taxonomic overlap (Fehrer et al., 2019), (c) can affiliate with roots of the same plant hosts (Bergero et al., 2000; Villarreal-Ruiz et al., 2004; Vohník et al., 2013) and (d) co-occur in

many ecosystems world-wide (Adamczyk et al., 2016; Clemmensen et al., 2021; Wurzburger et al., 2012; Xu et al., 2020), these findings were unsurprising. They did, however, highlight the potential for the effects of ErM shrubs to be ascribed to EcM trees in studies that do not account for their presence. Variation in ErM shrub cover could also help explain idiosyncratic effects of AM versus EcM plant dominance on soil C (Averill & Hawkes, 2016; Averill et al., 2014; Lin et al., 2017; Taylor et al., 2016; Zhu et al., 2018), though scale and depth dependencies also likely contribute to these differences (Craig et al., 2018; Frey, 2019). In our study, we found that the relationships between tree mycorrhizal dominance and surface SOM and C concentrations were negligible in the absence of ErM plants but strengthened with increasing ErM vegetation cover. Tree mycorrhizal dominance effects on these variables were therefore contingent on the presence of ErM plants, and in the absence of those data, our analysis could have suggested that the tree mycorrhizal dominance gradient had no influence on SOM and soil C concentrations at our site. Our findings therefore suggest that the ability to discern meaningful effect sizes of AM versus EcM tree dominance may be dependent on having data on the abundance of ErM plants in systems where they co-occur.

Although ErM plants were overall less abundant in eastern U.S. forests than AM and EcM vegetation—as would be expected based on their species richness and growth form—variation among plots was high, indicating that ErM plants can make up an important component of vegetation in some stands. Indeed, ErM shrubs can form dense, persistent thickets that suppress tree growth and regeneration (Figure S1; Bolstad et al., 2018; Dudley et al., 2020; Royo & Carson, 2006). Two ErM shrubs in the eastern U.S.—mountain laurel (*K. latifolia*) and rosebay laurel (*Rhododendron maximum* L.)—can account for as much as 32%–42% of all leaf biomass in some forests (Elliot & Vose, 2012; Monk et al., 1985). Other ErM shrub species have similar effects in temperate forests in other regions, including Scotch heather (*Calluna vulgaris* (L.) Hull), rhododendron (*R. ponticum* L.), salal (*Gaultheria shallon* Pursh) and sheep laurel (*K. angustifolia* L.; Mallik, 1995; Esen & Zedaker, 2004). The proliferation of ErM shrubs has been linked to forest disturbances, such as logging and loss of canopy species from invasive pests and pathogens (Ellison et al., 2005; Mallik, 1995; Vandermast & Van Lear, 2002). As the frequency and severity of canopy disturbances from drought, storms and invasive pests are expected to increase with changes in climate (Seidl et al., 2017), ErM shrub cover could continue to expand (Brose, 2016; Dobbs & Parker, 2004). Shifts in the forest canopy that favor AM trees are also expected to occur (Jo et al., 2019), and because we observed strong interactions between ErM plant cover and EcM tree dominance, disturbances that differentially affect the co-occurrence of mycorrhizal functional types within forests could also alter soil C and N dynamics.

4.2 | Distinct relationships between ErM plant cover and EcM tree dominance and soil C and N

Previous work and theory have suggested that the physiological traits of plants and fungi fall along an AM-EcM-ErM continuum and

that vegetation associated with these groups is aligned with gradients of organic matter accumulation and N limitation (Read, 1991; Read & Perez-Moreno, 2003). Differences in leaf, fine root and fungal biomass litter quality and decomposition rates have generally aligned with this conceptual framework (Clemmensen et al., 2015; Cornelissen et al., 2001; See et al., 2019; Xu et al., 2020), as have comparisons of the variety and abundance of genes that regulate the production of organic matter-degrading enzymes (Kohler et al., 2015; Martino et al., 2018; Miyauchi et al., 2020; Tisserant et al., 2013). Given this support for an AM-EcM-ErM trait continuum, we hypothesized that ErM plant effects would functionally extend or be functionally redundant with those of EcM tree dominance (Figure 1). Our data, however, did not support these hypotheses and instead suggested that ErM and EcM plants and fungi are functionally distinct. Specifically, although we observed positive associations between both EcM tree dominance and ErM plant cover and soil C:N, these relationships were driven by contrasting trends. Whereas EcM tree dominance was negatively linked to both C and N concentrations, ErM plant cover was positively associated with these variables. As such, the positive relationship with soil C:N was driven by relatively lower N per unit C for EcM tree dominance but by higher C per unit of N for ErM plant cover.

The positive association between ErM plant cover and soil C and N concentrations observed in our study could be attributed to the biochemical traits of ErM plants and fungi. Ericoid mycorrhizal fungal biomass and necromass can contain high melanin concentrations, which has been shown to slow decomposition and increase SOM accumulation in studies conducted in boreal forests (Clemmensen et al., 2015, 2021; Fernandez et al., 2020; Read et al., 2004). The foliar litters and roots of ErM plants also contain polyphenolic compounds, which can bind with organic N to create protein-tannin complexes that are strongly persistent in the soil (Adamczyk et al., 2016; Wurzburger & Hendrick, 2009). Tannins from ErM shrub litters can, in turn, decrease extracellular enzyme activity in soil (Joanisse et al., 2007), and interactions between litter tannins and fungal necromass can create persistent soil C (Adamczyk et al., 2019). In temperate forests, the presence of recalcitrant protein-tannin complexes has been shown to increase N retention in sites with ErM shrubs (Wurzburger & Hendrick, 2009), and experimental removal of ErM shrubs can increase N availability and microbial C demand (Osburn et al., 2018). Notably, ErM fungi possess the enzymes needed to access these complexed forms of N, which are less available to other co-occurring mycorrhizal plant types (Bending & Read, 1996; Wurzburger & Hendrick, 2007, 2009). Together, these studies suggest that ErM plants and fungi have distinct biochemical traits that contribute to SOM build-up and that C accumulation is likely to exceed that of organic N.

In contrast, we found that EcM tree dominance was associated with lower C and N concentrations and that the reductions in N were greater than those of C. This finding is consistent with past work (Craig et al., 2018; Lin et al., 2017; Zhu et al., 2018) and could be driven by selective mining of N from SOM by EcM fungi (Lindahl & Tunlid, 2015; Nicolás et al., 2019). Rhizosphere priming by EcM

tree roots, which are thought to allocate more C to mycorrhizal fungi than AM trees (Soudzilovskaia et al., 2015), also has the potential to enhance SOM decomposition in stands with a greater relative abundance of EcM trees (Brzostek et al., 2015). In our study, however, increased SOM and C concentrations in stands with a higher relative abundance of AM trees were contingent on the presence of ErM shrubs, which could reflect the reduced capacity of AM fungi to access recalcitrant organic complexes derived from ErM root and litter inputs (Tisserant et al., 2013). Moreover, the negative relationship we observed between EcM tree dominance and SOM and C concentrations counters what we would expect from the Gadgil effect in which suppression of decomposition rates through antagonistic interactions between EcM fungi and free-living saprotrophs would lead to SOM accumulation. The Gadgil effect is, however, thought to depend on organic substrate quality since EcM fungi are superior competitors for recalcitrant forms of N than free-living saprotrophs (Fernandez et al., 2020; Smith & Wan, 2019). Indeed, empirical evidence in support of the Gadgil effect has often been limited to coniferous, rather than deciduous, temperate forest types (Fernandez et al., 2020; Lang et al., 2021). Although our site included a mixture of deciduous and coniferous tree species, hardwood trees were more abundant. Whether the negative relationship between EcM tree dominance and SOM and C and N concentrations observed in our study would extend to sites that have a greater proportion of coniferous EcM trees is an open question.

Our study used an observational approach, which enabled us to capture variation in stand structure, species composition and local site conditions across a heterogeneous forested landscape, making our results more broadly representative of forests in the region. This study design also allowed us to tease out relationships between plant mycorrhizal functional types and soil C and N while accounting for natural variation in other biogeochemical controls. For instance, we observed a strong negative relationship between EcM tree dominance and soil moisture at our site. Different types of mycorrhizal fungi are adapted to different moisture regimes (e.g. through melanin concentrations) and can also vary in their ability to directly absorb water from the soil (Fernandez & Kennedy, 2016; Fernandez & Koide, 2013; Koide & Wu, 2003). Moisture, in turn, influences the build-up and decomposition of SOM (Orchard & Cook, 1983) and is non-randomly associated with tree species composition. As such, moisture has the potential to confound tree mycorrhizal dominance effects. Yet by capturing variation in moisture across a forest, we showed that relationships between EcM tree dominance and ErM plant cover and soil C and N were, at least in part, independent of those of moisture. While observational studies such as ours have high external validity (Bradford & Reynolds, 2006; Bradford et al., 2021), they cannot disentangle correlation from causation. As such, experiments that manipulate the composition and abundance of the mycorrhizal groups are required to investigate causal relationships between co-occurring AM, EcM and ErM plants and soil C and N dynamics. Additionally, because the relationships between soil C

and N and plant mycorrhizal dominance can shift across soil horizons (Craig et al., 2018), future work that explores potential depth dependencies of the relationships observed in our study is warranted. Still, our study demonstrates that the presence of ErM shrubs can plausibly alter relationships between tree mycorrhizal dominance and surface soil C and N concentrations across a range of environmental conditions and therefore bolsters growing calls to consider mycorrhizal functional types as variables that exert strong effects on forest biogeochemistry.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

E.B.W. and M.A.B. conceived of the project idea, with contributions from M.C.D., S.E.K. and J.C.L.; M.C.D. planned and implemented soil and vegetation sampling and laboratory analyses in the CT forest plots; R.J.W. collated data from the USNPS Vegetation Inventory; E.B.W. and M.A.B. analysed and interpreted data; E.B.W. wrote the original manuscript, with contributions from M.C.D., S.E.K., J.C.L. and R.J.W.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13734>.

DATA AVAILABILITY STATEMENT

The USFS data (Project: Carolina Vegetation Survey (67): NatureServe_USDA-NF; Accession Code: urn:lsid:cvs.bio.unc.edu:project:CVS.Pj.CVS-67) are available from Vegbank: http://vegbank.org/vegbank/views/project_detail.jsp?view=detail&wparam=10888&entity=project¶ms=10888.Pj.CVS-67. The USNPS data were collated from the USNPS Vegetation Inventory and Monitoring Program website and are publicly available at <https://www.nps.gov/im/vmi-products.htm>. The subset of the USNPS data used our analysis as well as the Connecticut soil and vegetation data is available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.4b8gthtcn> (Ward et al., 2021).

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SUPPORTING INFORMATION

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