



Plant functional type shapes nitrogen availability in a regenerating forest

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Abstract

Background and aims In mature forests, tree and shrub mycorrhizal associations integrate plant and fungal functional traits, making these relationships important controls on soil nitrogen availability. Whether these plant-fungal effects are observed in forests during early succession following disturbances is largely unexplored. We quantify differences in soil nitrogen availability under an ectomycorrhizal tree (*Betula lenta*) and an ericoid mycorrhizal shrub (*Kalmia latifolia*) and explore the potential for known mechanisms, such as the availability of soil carbon, to explain the patterns observed.

Methods We analyze variables indicative of soil nitrogen and carbon availability for incubated soil samples collected from under ecto- or ericoid mycorrhizal plants within a recently harvested temperate forest. Specific measures include net nitrogen mineralization, nitrification, and carbon mineralization rates; active microbial biomass; particulate and mineral-associated soil organic carbon and nitrogen concentrations; and carbon and nitrogen concentrations in plant tissues.

Results Net nitrogen mineralization and nitrification rates were lower under ericoid shrubs than ectomycorrhizal trees. Soil carbon availabilities were similar, suggesting that mechanisms other than carbon accumulation likely create nitrogen limitation under the ericoid shrub in early successional forests. Ectomycorrhizal plant tissues also had higher nitrogen contents and lower carbon-to-nitrogen ratios than ericoid shrubs, providing further support for greater soil nitrogen limitation in the ericoid plots.

Conclusion Our findings suggest local heterogeneity of plant mycorrhizal associations, or at least plant functional types, will be important for understanding differences in soil nitrogen availability in early versus mid- to late-successional forests and hence forest ecosystem responses to intensifying disturbance regimes.

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Introduction

Plant productivity in terrestrial ecosystems is often limited by the availability of nitrogen (N) (Ågren et al. 2012). To improve their capabilities to acquire N, approximately 90% of vascular plant species form symbiotic relationships with mycorrhizal fungi by exchanging carbon (C) for greater access to soil N (Brundrett and Tedersoo 2018). In temperate forests, the vast majority of overstory tree species associate with arbuscular mycorrhizal (AM) and/or ectomycorrhizal (ECM) fungi, while most understory shrubs in the plant family Ericaceae associate with ericoid mycorrhizal (ERM) fungi (Vohník 2020, Smith and Read 2008). The traits of AM trees and fungi typically accelerate soil inorganic N turnover and availability, whereas those of ECM and ERM woody plants and fungi can reduce inorganic N availability (Lin et al. 2017, Martino et al. 2018, Leopold 2016, Phillips et al. 2013). Mycorrhizal associations therefore integrate plant and fungal traits that strongly control soil N availability and could help explain within-stand variation in N limitation that contributes to plant community development following forest disturbances.

Whereas considerable research focuses on the effects of ECM versus AM tree dominance on forest soil C and N cycling (Saifuddin et al. 2021), limited research has examined the effects of understory ERM plants (Ward et al. 2022). Albeit considered more functionally similar than AM associations in terms of their effects on forest soil biogeochemistry, ECM and ERM plants can have functionally distinct effects. For instance, ERM shrubs and fungi are often associated with greater surface accumulation of soil organic matter (Ward et al. 2021, 2023), whereas ECM trees and fungi can reduce soil organic matter content through, for instance, the extensive extracellular enzyme production of some taxa of ECM fungi (Clemmensen et al. 2021). However, such effects of ECM and ERM fungi appear context dependent, with their ability to outcompete free-living saprotrophs and potentially limit decomposition rates (the Gadgil effect) and enhance soil organic matter accrual being dependent on soil fertility, fungal community composition, and climate (Fernandez et al. 2020, Mayer et al. 2023, Fanin et al. 2022, Shao et al. 2023). Further, ERM plants tend to reduce litter and organic matter decomposition rates through lower quality leaf, fine root,

and fungal inputs compared to ECM plants and fungi (Clemmensen et al. 2021; See et al. 2019). For example, many ERM shrubs have high concentrations of condensed tannins in their leaf and root litters, which can form recalcitrant protein-tannin complexes in the soil that “lock-up” N compared to understory areas without ERM shrubs (Wurzburger and Hendrick 2007). At least some ERM fungi can mobilize this organic N, whereas free-living saprotrophs appear less effective at doing so. Such mechanisms may help explain the accretion of organic C under ERM shrubs as well as the reduced efficiency of microbial processing of surface soil organic matter (Ward et al. 2023).

Most research on tree and shrub mycorrhizal effects on soil N cycling in temperate forests has been carried out in mid- to late-successional, closed-canopy forests (but see Bloom and Mallik 2006, Clemmensen et al. 2015, Fanin et al. 2022 for relevant work from boreal forests). Yet numerous disturbances create early successional forests, including windstorms, timber harvesting, fire, and non-native pests and pathogens. Many of these forest disturbances are intensifying in eastern U.S. temperate forests due to climate change (Swanston et al. 2018, Seidl et al. 2017), species invasions (Lovett et al. 2016), and/or human land use changes (Brown et al. 2018), which could increase the area of early-successional forests in this region. These intensifying disturbances also shape the plant species composition of regenerating landscapes, highlighting a need to understand how shifts in the functional composition of plants associated with different types of mycorrhizal fungi might influence soil N availability in early successional forests. Common shrubs in the eastern U.S. that associate with ERM fungi (e.g., *Rhododendron maximum*, *Kalmia latifolia*; Dudley et al. 2020, Monk et al. 1985), for instance, often respond positively to canopy disturbances (Mallik 1995; Royo and Carson 2006) and can suppress tree regeneration by limiting understory light availability (Brose 2016). The clonal growth of ERM shrub species, as well as the capability of ERM fungi to survive and grow in the temporary absence of their plant hosts (Bergero et al. 2003), may help to explain the rapid expansion of ERM shrubs following canopy disturbances. The proliferation of ERM shrubs in early successional forests could therefore reduce the relative abundance of regenerating AM and ECM trees, thereby creating conditions that exacerbate inorganic N limitation (Nilsen et al. 1999).

Indeed, ERM shrubs in eastern temperate forests have been associated with a reduction in the foliar N of nearby regenerating trees (Yamasaki et al. 1998).

Whether the proliferation of ERM shrubs in early successional forests exacerbates soil N limitation is, however, unclear and may be counteracted by the fact that forest disturbances, such as logging, typically accelerate inorganic soil N cycling. For example, net nitrification rates typically increase following canopy disturbances such as timber harvests (Binkley 1984), including harvests that only remove a small portion of the canopy (Kim et al. 1995). Among the mechanisms that might explain this increase, disturbance-induced reductions in soil C concentrations appear to shift competitive outcomes between heterotrophic microbes and the chemoautotrophic nitrifiers that catalyze the conversion of NH_4^+ to NO_3^- ions. Specifically, the nitrifiers appear to be much more competitive for acquiring NH_4^+ when soil C concentrations are low, which positively couples net N mineralization (which supplies NH_4^+) and net nitrification rates (Keiser et al. 2016; Gill et al. 2023). Conversely, as forest stands recover toward mature, closed-canopy forests, the accumulation of surface soil C decouples these soil N cycling processes. Whereas net N mineralization rates can remain high, net nitrification rates remain consistently low (Keiser et al. 2016; Gill et al. 2023). Yet how lower surface soil C concentrations in early successional forest stands interact with different plant mycorrhizal associations to shape soil N cycling appears largely unknown.

To address this knowledge gap, we use an observational study to examine relationships of a regenerating ERM shrub species (*Kalmia latifolia* L.) and ECM tree species (*Betula lenta* L.) with soil N and C cycling in a recently harvested, early successional forest stand. Use of plant species to denote a mycorrhizal relationship is common (Phillips et al. 2013; DeForest and Snell 2020; Soudzilovskaia et al. 2020) but does not quantify the extent of colonization of the plant roots with mycorrhizal fungi. As such, our design cannot disentangle the relative contribution of plant versus fungal influences on soil C and N cycling but instead focuses on the collective effects of plant and fungal traits that distinguish these two plant mycorrhizal types. The timber harvest at our study site followed an irregular shelterwood prescription, which is a common management practice in eastern North America designed to simulate natural disturbance

regimes, such as hurricanes, to facilitate the regeneration of relatively shade-intolerant ECM tree species, such as oaks (*Quercus* spp.). This type of harvest tends to reduce surface soil organic matter that accumulates as stands mature, thereby creating a less heterogeneous, fine-scale mosaic of soil C and N availability compared to closed-canopy, mid- and late-successional forest stands (Carpenter et al. 2021).

Due to the early successional stage of the stand where we conducted this work, we expect there to be comparable levels of surface soil C availability under the ERM and ECM plants, given that soil organic matter has not had time to accumulate under the ERM shrub (H1). If this hypothesis holds, we have two competing hypotheses for how ERM and ECM plants will affect N availability. First, if the accumulation of soil organic C in surface soils as forests mature is a primary mechanism by which ECM trees and ERM shrubs reduce net nitrification rates, then both plant mycorrhizal types should have similar effects on the rate of inorganic N cycling processes in early successional forests (H2a). In this scenario, we would expect no differences in either net potential nitrification or nitrogen mineralization rates under the two plant mycorrhizal types on account of their comparable surface soil C availability. Alternatively, if the suppression of net nitrification rates by ERM shrubs primarily stems from other mechanisms, such as the creation of recalcitrant protein-tannin complexes that sequester organic N (Wurzburger and Hendrick 2007), inhibition of microbial activity (Ward et al. 2023), and/or lower decomposition rates of fine roots and leaves (See et al. 2019), we expect the two plant mycorrhizal types to have different effects on inorganic N cycling (H2b). Under this scenario, we would expect both potential net N mineralization and net nitrification rates to be lower under the regenerating ERM shrub than under the ECM tree species despite comparable surface soil C availability.

Methods

Study site and sampling design

We conducted our study in 2021 in a regenerating 9.6-ha forest stand at Yale-Myers Forest (41°57' N, 41°57' W), a privately owned 3,213-ha mixed hardwood temperate forest in northeastern Connecticut, USA.

Between 1990 and 2020, mean annual precipitation was 127 cm, mean January temperature was -1.9°C , and mean July temperature was 20.9°C (NOAA 2023). In June through August 2021, mean volumetric soil moisture (VWC) was 25.71% (± 1.34 SE). Mean soil pH was 4.93 within our site and ranged from 4.55 to 5.45. The predominant soil type mapped within the stand (83%) is an extremely stoney, moderately well-drained, Woodbridge fine sandy loam with a slope between 3 and 15% (Soil Survey Staff 2021). Other mapped soil types at this site include the Paxton (9%), Ridgebury (5%), Sutton (2%), and Whitman (1%) series, which occur on some hills and depressions (Soil Survey Staff 2021).

To assess the influence of fine-scale differences in the functional composition of plant communities on soil N and C cycling within the recently harvested stand, we focused on the two dominant plant species in the understory of the site and characterized their mycorrhizal associations based on Soudzilovskaia et al. (2020). Specifically, the dominant understory plant species included dense patches of the ERM shrub mountain laurel (*K. latifolia*; Gorman and Starrett 2003) and regenerating saplings of the ECM tree black birch (*B. lenta*; Cortese and Horton 2023). A species within the same genus as *K. latifolia* (*K. angustifolia*) has been shown to exhibit varying percentages of ERM fungal colonization depending on season and habitat (Griffin and Kernaghan 2022). We note, however, that the focus of our study was not to measure root colonization by ERM or ECM fungi, nor to characterize fungal community composition. Instead, we use mycorrhizal associations as a plant functional type to explore links between the aboveground composition of the plant community and soil N and C cycling. This approach for characterizing plant functional types, based on their mycorrhizal associations, is common in ecosystem ecology because it integrates a broad suite of traits (e.g., root, fungal, litter) that collectively affect ecosystem biogeochemical processes (Beidler et al. 2021; Brzostek et al. 2015; Phillips et al. 2013; Read 1991). As a consequence of this approach, the extent to which each of these plant species was colonized by mycorrhizal fungi or how heavily they invested in a mycorrhizal partnership following stand disturbance is unknown. However, given the capability of ERM (Bergero et al. 2003) fungi to persist in the soil following disturbance, as well as the retention of mature ECM legacy

and seed trees (which supply mycorrhizal inoculum) (Jones et al. 2008) under the shelterwood management plan, and the robust growth of regeneration (Liang et al. 2020), it is very likely that mycorrhizal associations were well-developed.

The stand was harvested in 2016, five years before our sampling, using an irregular shelterwood system designed to promote oak regeneration. Shelterwood systems retain existing mature trees for shade and as a seed source for the next crop of trees while preventing plants that dominate in full sun (e.g., *Rubus* spp.) from outcompeting tree regeneration. As such, mature oak (*Quercus rubra* L. and *Q. alba* L.) and maple (*Acer rubrum* L.) trees that were retained as a part of the management strategy were interspersed across the site. Irregular shelterwoods are distinguished from uniform shelterwoods by having an uneven distribution of multiple age classes that are retained in the long term (Raymond et al. 2009; Ashton and Kelty 2018). This retention of standing mature trees and snags (standing dead trees) can mitigate the negative effects of timber harvesting on wildlife (Duguid et al. 2016; Mossman et al. 2019; Hanle et al. 2020) and topsoil health (Carpenter et al. 2021). As part of the management prescription, mountain laurel—the dominant ERM plant species in the forest (Ward et al. 2021)—is systematically crushed to promote tree regeneration and to attempt to limit root sprouting. We therefore anticipate that observed differences in organic matter build-up and nutrient cycling at our site will arise through plant-soil interactions following the harvest.

The study design consisted of 30 50-cm \times 50-cm plots split evenly between 5 areas in the stand. Each area was greater than 100 m apart and included 6 independent plots, half of which were dominated by regenerating black birch and the other half by mountain laurel. The locations of the plots were selected to capture spatial heterogeneity of the distribution of the plant species within the forest stand. Each plot included at least one stem of the designated study species, and no plots had stems of both species. We situated each plot at least 6 m from overstory trees (> 10 cm diameter at breast height (DBH)) to reduce the local influence of mature trees, and all plots in an area were ~ 6 m apart. As a result of their recent shared management history and proximity we anticipated that variables such as earthworm abundance and litter layer accumulation would be similar among

plots, which was consistent with visual inspection of features such as earthworm castings and leaf litter depth and composition. Subsequent measurements of organic layer depth within the stand showed no significant relationship between cover of *K. latifolia* and the depth of the organic layer (Fig. S2).

Soil and vegetation sampling

We sampled soil and vegetation in June 2021 to coincide with full canopy leaf out. To account for potentially confounding environmental variables, we measured soil moisture (i.e., VWC) at three locations in the plot to a depth of 12 cm using a HS2 HydroSense Soil Moisture Probe (Campbell Scientific, Logan, Utah, USA) and calculated the mean for a single June plot value. We likewise measured soil temperature using a digital thermometer. We collected and pooled three 15-cm deep soil cores from within each plot using a 2-cm diameter soil corer. We harvested multiple stems and leaves (at least two) from the study species present within each plot, avoiding leaves that appeared damaged or diseased. The stem sections that we collected from both plant species were from previous years' growth, of similar diameter and all approximately 10 cm in length. We obtained coarse and fine roots from each plot during the process of sieving soils for bulk density analysis (see below).

Most plots received a nutrient amendment after our sampling (see Ferraro et al. 2023), but ten did not receive any treatment. We therefore resampled the soil and vegetation from these sites in August 2021 to account for possible seasonal variation in the soil N and C cycle process rates.

Laboratory analyses

Freshly collected soils used for measuring N and C process rates were homogenized on a plastic tray, passed through a 4-mm sieve, and stored at 4°C in gallon-sized airtight Ziplock bags before analysis. Gravimetric moisture content was calculated for each sample through mass loss after oven-drying at 105 °C to constant mass. Water holding capacity was also calculated by inundating samples of soil with DI-water and allowing the sample to drain for 2 h, then finding the mass of the soil before drying, desiccating, and reweighing. We compared the initial values of extractable inorganic N to values of extractable N

after a 24-d incubation to determine rates of potential net N mineralization and potential net nitrification (Hart et al. 1994; Robertson et al. 1999). For each extraction, we added 25 mL 2 M KCl to each soil subsample (6-g dry weight equivalent), shook vigorously for 30 s, refrigerated for 12 h, and then filtered the subsamples through Whatman grade #42 filters. We colorimetrically analyzed NH_4^+ and NO_3^- concentrations using a flow analyzer (Astoria 2, Astoria-Pacific, Clackamas, Oregon, USA). Net potential nitrification was calculated as the difference in NO_3^- in the incubated and initial samples, and net potential N mineralization as the difference between the initial and final sum of NH_4^+ and NO_3^- . For all these assays, soils were incubated at 20 °C under a moist atmosphere with a Parafilm cover to allow air diffusion with a minimum of moisture loss. Incubated samples received weekly moisture adjustments to 65% of their water holding capacity, which is regarded as being within the optimal moisture range for microbial activity (Robertson et al. 1999). While soil coring and lab analyses disrupt the mycorrhizal symbioses, we chose to use these methods as they allowed for soil temperature and moisture to be standardized and enabled the measurement of free-living microbial biomass under each plant mycorrhizal type.

For C cycle processes, we first measured cumulative C mineralization (labile C) over the course of a 24-day incubation period. At set intervals (days 1, 4, 10, 16, and 24), the CO_2 production rate was estimated as the area under the curve ('AUC') function (Bradford et al. 2008) in the DescTools package (Signorell 2023). We used the cumulative value of C produced over this time series as an indicator of the microbially available C. Free-living active microbial biomass was estimated using the substrate-induced respiration (SIR) method (Anderson and Domsch 1978), modified following West and Sparling (1986) and further following Fierer and Schime (2003) to use autolyzed yeast as substrate. For both C mineralization and microbial biomass, we measured CO_2 concentrations of headspaces over time using an Infra-Red Gas Analyzer (Li-COR model Li-7000, Lincoln, Nebraska, USA).

We complemented the C mineralization and microbial biomass data with measurements of C and N concentrations in the total soil and in different soil organic matter pools. We obtained particulate organic matter (POM; >53 μm fraction)

and mineral-associated organic matter (MAOM; <53 μm fraction) pools from an air-dried soil subsample using chemical dispersal and physical separation (Paul et al. 2001). We used a Costech ECS 4010 Elemental Analyzer with Conflo III interface to analyze the concentrations of C and N in samples from each pool. Measurement of these two soil pools, as well as the total soil, permitted us to test the extent to which organic matter was rebuilding under the ECM and ERM plants. High spatial variability in total soil C concentrations is expected at local spatial scales, making it notoriously difficult to detect treatment differences (see Strickland et al. 2010). To increase the ability to detect differences in soil carbon, fractionation approaches are used (e.g., resolving POM and MAOM pools), as is measurement of fast-cycling and hence early responding pools, such as active microbial biomass and C mineralization rates.

We also collected measurements of C and N concentrations in four different plant tissue pools: leaf, stem, coarse roots, and fine roots. Leaves and stems were collected in the field, while roots were recovered in the process of sieving soil samples. Given the similar stature of the vegetation, we did not directly measure root order. Instead, we separated roots by a size cut-off, separated coarse roots (>2 mm dia.) from fine roots (<2 mm dia.) (McCormack et al. 2015). We assumed coarse roots were primary roots and those below the fine root threshold were secondary and tertiary. Samples of vegetative material were oven dried at 60 °C and homogenized using a ball-mill. We used a Costech ECS 4010 Elemental Analyzer with Conflo III interface to analyze the concentrations of C and N in samples from each tissue pool.

Statistical analysis

We used hierarchical, linear mixed-effects models for all analyses to account for potential spatial autocorrelation associated with how we grouped our plots into five areas across the forest stand. Specifically, we assumed a common slope for the random effects and included ‘area’ to represent different intercepts. All models included plant mycorrhizal association (0=ECM and 1=ERM) as a binary predictor, and we tested the necessity of including continuous environmental predictors, such as soil temperature and moisture. Such predictors were

only tested if they were unlikely to be mediated by the mycorrhizal association and, when tested, were retained only if they had a marked effect on the response variable and/or had an interactive effect with the plant mycorrhizal association. Based on these criteria, VWC was retained in our final statistical models, and we also investigated temperature. One plot had a particularly high nitrification value after incubation, and we tested the sensitivity of our coefficient estimates to inclusion versus exclusion of this datapoint. We ultimately retained this value in the models because the effects of plant mycorrhizal association were unaltered. When residuals strongly contravened assumptions of normality, they were \log_e or square-root transformed. Residuals were then checked for fit, and we checked the coefficient estimates to ensure that our results remained consistent with the underlying, non-transformed data. To permit comparison of the effect sizes of the predictor terms in each model, predictor variables were standardized by centering (the binary predictor) and by dividing by two standard deviations (the continuous predictor), following Gelman (2008). All analyses were conducted using the lmer package in the statistical freeware R (version 3.6.3; Bates et al. 2017; R Core Development Team 2022).

Note that we did not use model selection nor rely on statistical significance and multivariate analyses for our causal inference. Instead, we relied primarily on evaluating standardized coefficient estimates (i.e., conditional effect sizes) considering published evidence of ECM and ERM plants and disturbance effects on soil N cycling. Our approach follows calls in ecology (e.g., Addicott et al. 2022) to reduce over-reliance on indicators of statistical significance (such as p , AIC and r^2 values) for causative science. The calls in ecology reflect a broader shift (e.g., Bradford et al. 2021) advocated by entities such as the American Statistical Association to improve causative statistical inference (Wasserstein et al. 2019). We report p and R^2 values in our tables, given their value in indicating the precision of effect size estimates, but in the text focus on coefficient estimates. Further, we follow emerging best practices in data communication and interpretation by presenting the underlying data observations in all our figures (Weissgerber et al. 2015).

Results

To assess whether the effects of ERM versus ECM plants on N cycle processes might be associated with the accumulation of soil organic C, we measured multiple soil C variables that ranged from faster to slower responding variables to change. For the fastest responding variables, neither active microbial biomass nor C mineralization had a strong relationship with plant mycorrhizal type (Table 1; Fig. 1). Instead, soil moisture (and not temperature, see Table S4) was the only variable that had a strong effect on these two C variables, where the coefficient for soil moisture was an order of magnitude greater for active microbial biomass than the plant mycorrhizal predictor and twice as large for C mineralization (Table 2). The lack of a strong plant mycorrhizal effect on microbial biomass and C mineralization suggested that soil organic matter concentrations were not different under ECM and ERM plants. Indeed, and contrary to what would be expected under mountain laurel in mature temperate forests (Ward et al. 2023), POM, MAOM and total soil C concentrations were, on average, lower in ERM than in ECM plots, but the range of values in each plant mycorrhizal plot type were overlapping (Table 2; Fig. 2). Our results therefore provide no evidence for differences in soil organic C accumulation or C cycle processes under the ECM tree versus ERM shrub (H1).

Despite no evidence for more rapid soil C accumulation under the ERM shrub, rates of potential net N mineralization and nitrification were lower under the ERM shrub than under the ECM tree species (H2b; Fig. 1). Mean reductions in potential net N mineralization and nitrification rates under the ERM shrub compared to the ECM tree were -0.73 ± 0.20 (mean \pm SE) and -0.10 ± 0.04 mg N g soil⁻¹ 24 d⁻¹, respectively (Table 1). Specifically, mean potential net N mineralization rates in ERM plots were less than half that of ECM plots (0.45 vs. 1.34 mg N g soil⁻¹ 24 d⁻¹) (Fig. 1). On excluding a single, high nitrification rate in an ECM plot from the analyses, model residual fits improved, but the negative association of ERM versus ECM plants on nitrification rates was only slightly smaller (-0.06 ± 0.02 mg N g soil⁻¹ 24 d⁻¹). Both the main and interaction effects of soil moisture (measured as VWC) on potential net nitrification were of similar magnitude to mycorrhizal

Table 1 Relationships between plant mycorrhizal association, soil moisture, and soil N and C processes

	Intercept			ERM			Soil Moisture			ERM * Soil Moisture			Fixed Effect R ² / Fixed + Random Effect R ²
	Coeff.	SE	p	Coeff.	SE	p	Coeff.	SE	p	Coeff.	SE	p	
	Microbial Biomass	8.60	0.86	0.000	-0.13	1.19	0.913	-1.13	1.60	0.485	-0.01	2.46	
C Mineralization	525.11	68.78	<0.001*	-87.92	82.54	0.298	-192.71	115.07	0.106	160.68	171.89	0.359	0.1 / 0.22
Potential Net N Mineralization	1.23	0.14	<0.001	-0.73	0.20	0.001	-0.22	0.27	0.420	0.18	0.42	0.679	0.32 / 0.32
Potential Net Nitrification	0.14	0.03	0.001	-0.10	0.04	0.023	-0.09	0.06	0.136	0.08	0.09	0.349	0.2 / 0.23

Standardized coefficients (\pm SE) for the linear mixed models using “area” as a random effect are presented along with *p* - and R² values. Each model is based on a total of 30 observations, with *n* = 15 for the ECM versus ERM vegetation treatments

**p*-values below 0.001 are shown as <0.001

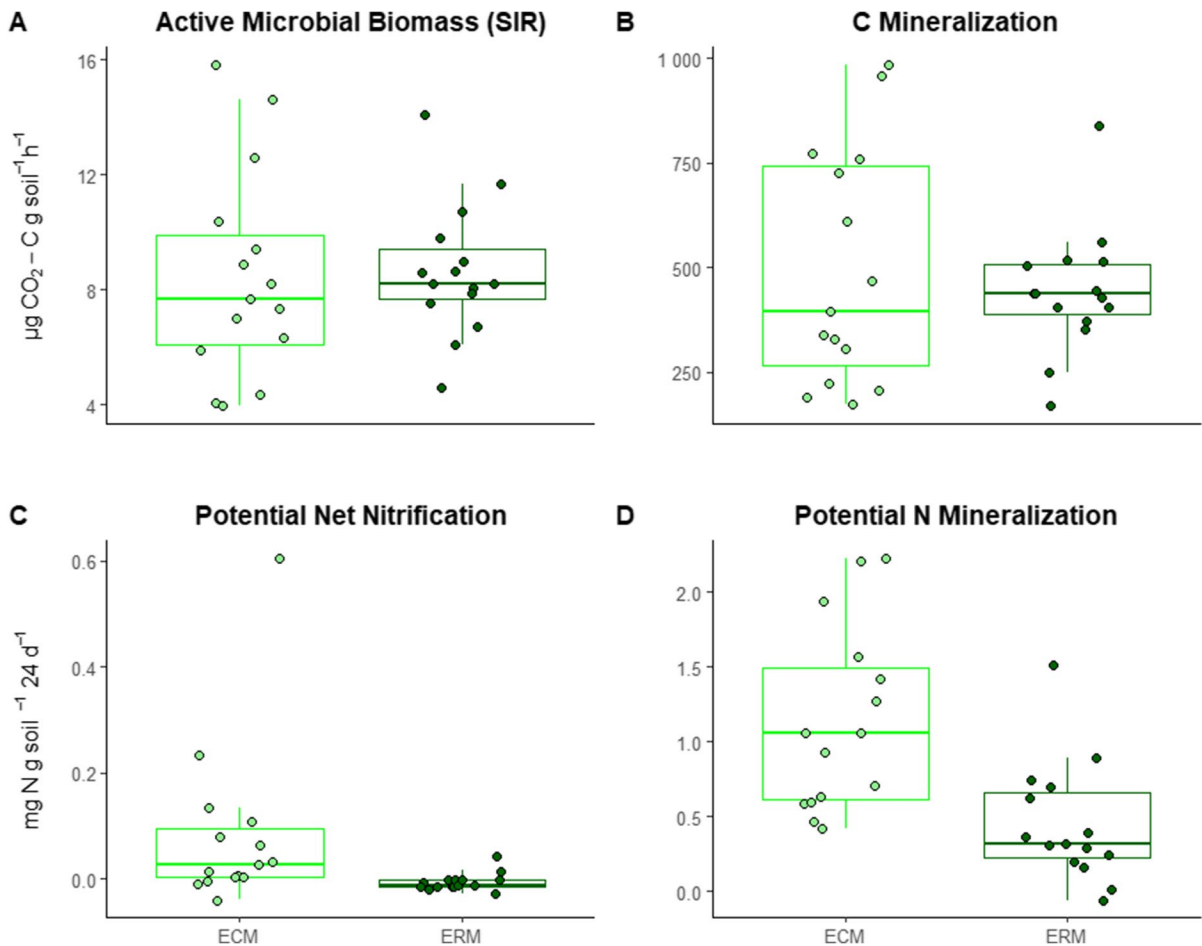


Fig. 1 Boxplots of (A) active microbial biomass, (B) carbon (C) mineralization, (C) potential net nitrification, and (D) potential nitrogen (N) mineralization under ECM and ERM vegetation. Horizontal lines are median values, and the boxes represent the 25th and 75th percentiles. Vertical lines extend to

the first observation closest to, but not exceeding, the 1.5 interquartile range, providing a roughly 95% confidence interval. Each point represents a plot, with 30 plot-level observations per figure plate ($n=15$ under ECM and 15 under ERM)

type, but the latter was the dominant influence on potential net N mineralization rates (Table 1).

The relative effect of temperature on potential net nitrification, on the other hand, varied with inclusion/exclusion of the high nitrification value. When the outlying nitrification point was omitted, temperature appeared unimportant relative to plant mycorrhizal type. Inclusion of the point showed a strong positive effect of temperature on potential net nitrification rates (0.12 ± 0.06 mg N g soil⁻¹ 24 d⁻¹; Table S4). Yet the effect of plant mycorrhizal type was similar in both models: -0.07 ± 0.04 mg N g soil⁻¹ 24 d⁻¹ (with outlier; Table S4) and 0.06 ± 0.02 mg N g soil⁻¹ 24 d⁻¹ (without outlier). The strongest effect in these two

models was the interaction between plant mycorrhizal type and temperature when the outlier was retained (-0.15 ± 0.09 mg N g soil⁻¹ 24 d⁻¹), but this interaction was negligible when the outlier was excluded (-0.01 ± 0.005 mg N g soil⁻¹ 24 d⁻¹). Overall, there was little evidence that lower rates of net N mineralization and nitrification in the ERM plots were associated with build-up of soil organic C nor that the lower rates under the ERM plant were mediated through soil temperature, moisture, available C or microbial biomass. We observed similar patterns in the C and N cycle process rates for the ten plots that we resampled in late August, where net N mineralization and nitrification rates were lower in the ERM plots, whereas

Table 2 Relationships between plant mycorrhizal association and soil moisture on different soil C and N pools and their C:N ratios

	Intercept			ERM			Soil moisture			ERM*Soil Moisture			Fixed effect R ² / Fixed + Random Effect R ²
	Coeff.	SE	p	Coeff.	SE	p	Coeff.	SE	p	Coeff.	SE	p	
POM N (Logged)	0.05	0.01	0.001	-0.01	0.02	0.731	-0.01	0.01	0.21	0	0.02	0.905	0.05 / 0.21
MAOM N	0.24	0.02	<0.001*	0.03	0.04	0.528	-0.08	0.03	0.014	0.01	0.06	0.885	0.24 / 0.36
Total Soil N	0.38	0.05	<0.001	0	0.08	0.951	-0.12	0.05	0.042	0.02	0.11	0.853	0.14 / 0.3
POM C (Logged)	0.6	0.06	<0.001	-0.03	0.11	0.796	-0.08	0.08	0.31	0.02	0.16	0.918	0.03 / 0.16
MAOM C	4.8	0.48	<0.001	0.44	0.81	0.592	-1.3	0.58	0.037	0.43	1.22	0.729	0.21 / 0.31
Total Soil C	8.26	1.04	<0.001	-0.04	1.69	0.981	-2.09	1.21	0.097	0.67	2.51	0.791	0.1 / 0.24
POM CN (Logged)	1.44	0.02	<0.001	0.01	0.03	0.706	0.04	0.02	0.027	0.01	0.04	0.824	0.11 / 0.46
MAOM CN	19.79	0.52	<0.001	-0.17	0.76	0.824	1.35	0.53	0.019	0.93	1.12	0.415	0.15 / 0.37
Total Soil CN	21.94	0.49	<0.001	-0.37	0.83	0.657	1.59	0.6	0.014	0.97	1.25	0.443	0.2 / 0.29

Standardized coefficients (\pm SE) for the linear mixed models using “area” as a random effect are presented along with p - and R^2 values. Each model is based on a total of 30 observations, with $n = 15$ for the ECM versus ERM vegetation treatments. *POM* particulate organic matter and *MAOM* mineral-associated organic matter

* p -values below 0.001 are shown as <0.001

available C and active microbial biomass values were similar to those in the ECM plots (Fig. S1).

When evaluating the relationships between the mycorrhizal associations of the dominant plant species of each plot and the %N and C:N of the plant (leaf, stem, fine root, and coarse root) and soil (total, POM, and MAOM) pools, we found further support for greater N limitation in ERM plots than in ECM plots. Indicative of greater N than C limitation, the N concentrations in the soil pools were consistently lower under ERM shrubs, and the C:N ratios were wider (Fig. 2; Table 2). Similarly, for each of the plant pools, %N was consistently higher in the ECM plants, and the C:N ratios were narrower, compared to the ERM plant tissue values (Table S1, Fig. 3).

Discussion

Research into tree and shrub mycorrhizal effects on soil N cycling has predominantly focused on mid- to late-successional, closed-canopy forests. In these forests, both ERM shrubs and ECM trees, along with their associated mycorrhizal fungi, possess traits that can reduce inorganic N availability compared to AM trees and fungi (Phillips et al. 2013; Ward et al. 2022). However, ECM and ERM plants and fungi can also have functionally distinct effects on soil biogeochemistry (Ward et al. 2021; Clemmensen et al. 2021;

Wurzburger and Hendrick 2007). In closed canopy, mid- to later-successional temperate forests, ERM shrubs may limit soil N availability to a greater extent than mature ECM canopy trees (Wurzburger and Hendrick 2007). This suppressive effect is likely due, in part, to greater surface accumulation of soil organic matter under ERM shrubs (Ward et al. 2023). However, additional mechanisms also likely operate that, for example, make the N in organic compounds less accessible to microbes by slowing the decomposition rates of those compounds (Wurzburger and Hendrick 2007; Clemmensen et al. 2021; See et al. 2019). What remains unclear is how these mechanisms resulting from fine-scale variation in the mycorrhizal associations of regenerating plant communities interact with the effects of forest disturbances, such as timber harvesting, on N and C cycling in early-successional temperate forest stands that have elevated inorganic N availability.

Using an observational study design, we examined whether differences in soil N availability under plants with different mycorrhizal associations, or at least different plant functional traits, were linked to changes in soil organic C accumulation in an early-successional forest stand where the dominant regenerating woody vegetation consisted of an ERM shrub (*K. latifolia*) and an ECM tree (*B. lenta*) species. We expected (H1) that the recent timber harvesting disturbance to the stand would reduce surface soil

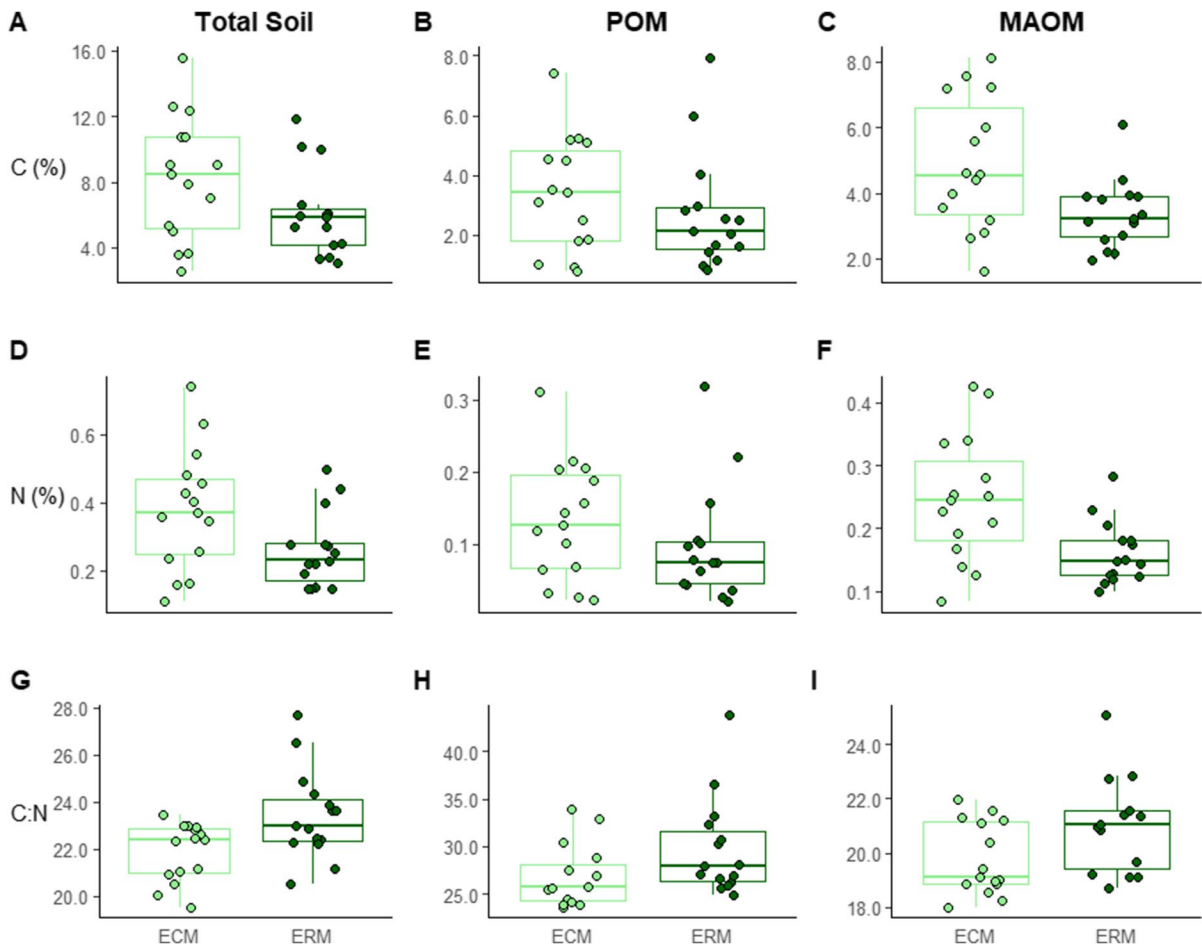


Fig. 2 Boxplots of soil carbon (C; top row) and nitrogen (N; middle row) concentrations, and C:N ratios (bottom row) for the total soil (first column), POM (particulate organic matter, second column) and MAOM (mineral-associated organic matter; third column) pools under ECM and ERM vegetation. Horizontal lines are median values, and the boxes represent

the 25th and 75th percentiles. Vertical lines extend to the first observation closest to, but not exceeding, the 1.5 interquartile range, providing a roughly 95% confidence interval. Each point represents a plot, with 30 plot-level observations ($n=15$ under ECM and 15 under ERM)

organic matter (Carpenter et al. 2021), resulting in no differences in C availability under the two plant mycorrhizal types. In line with this hypothesis, we found that both the faster (C mineralization and active microbial biomass) and slower (POM and MAOM C pools) cycling soil C measures were of similar magnitude under the ERM and ECM plants. Together, these results suggest that there were no pronounced differences in C availability under the different plant mycorrhizal types (Tables 1 and 2; Figs. 1 and 2).

This lack of difference in C concentrations and cycle processes, however, did not result in functionally similar effects of the two plant functional

types on soil N cycling, contrary to what we had proposed in Hypothesis 2a. Instead, and consistent with Hypothesis 2b, potential net N mineralization and nitrification were both lower under the ERM shrub than the regenerating ECM tree. These findings suggest that suppression of N cycling under the ERM shrub was driven by mechanisms independent of surface soil organic matter accumulation. In mature forest systems, the accumulation of organic C and associated increases in microbial biomass and microbially available C can suppress nitrification but not N mineralization (Keiser et al. 2016; Gill et al. 2023). Yet we found that both N cycle

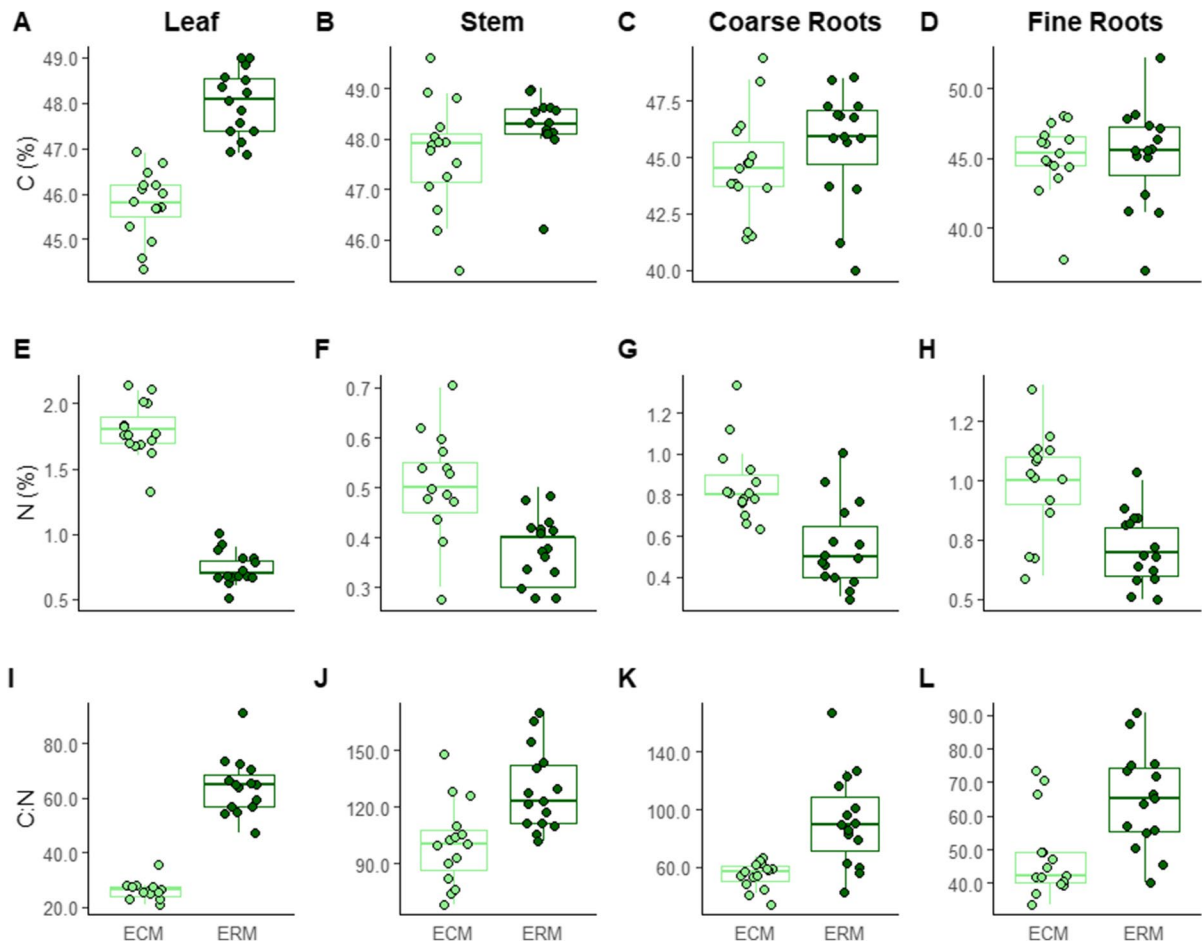


Fig. 3 Boxplots of plant tissue carbon (C; top row) and nitrogen (N; middle row) concentrations, and C:N ratios (bottom row) for the leaves (first column), stems (second column), coarse roots (third column), and fine roots (fourth column), of ECM and ERM plants. Horizontal lines are median values, and

the boxes represent the 25th and 75th percentiles. Vertical lines extend to the first observation closest to, but not exceeding, the 1.5 interquartile range, providing a roughly 95% confidence interval. Each point represents a plot, with 30 plot-level observations ($n = 15$ under ECM and 15 under ERM)

processes were lower under ERM shrubs compared to the ECM tree in our early successional stand despite no differences in organic C and microbial biomass. A different mechanism or mechanisms therefore must limit net N mineralization and nitrification rates in the early successional stand in which we worked. One such mechanism could be the suppression of free-living saprotrophic activity—independent of microbial biomass—under ERM shrubs by the mycorrhizal fungi (Joanisse et al. 2009). Notably, ERM shrubs have been shown to more strongly inhibit leaf litter decomposition rates than ECM trees in a boreal forest through this Gadgil effect (Fanin et al. 2022).

Recalcitrant organic inputs could also reduce N availability under ERM plants even in the absence of contemporary soil C accumulation, and this could enhance the Gadgil effect since mycorrhizal fungi are superior competitors for recalcitrant forms of N compared to free-living saprotrophs (Smith and Wan 2019; Fernandez et al. 2020; Shao et al. 2023). When evaluating the %N and C:N ratios of the above- and belowground ERM versus ECM plant pools, we found much lower N concentrations and wider C:N ratios in the ERM plant tissues (Table S1, Fig. 3). The lower availability of N in these tissues was reflected in the soil pools, where the N concentrations were consistently lower under the ERM shrub and the

C:N ratios were wider (Fig. 2; Table 2). It is then conceivable that the lower net N mineralization and nitrification rates under the ERM shrub in our early-successional stand were, at least in part, a product of the lower quality plant and/or fungal inputs to the soil (Scott and Binkley 1997; Fernandez and Koide 2014) and the resulting differences in rates of decomposition of the fine roots and leaves (See et al. 2019). High concentrations of condensed tannins in ERM plant litter inputs can also “lock-up” N through the formation of protein-tannin complexes (Wurzburger and Hendrick 2007), and this process could outpace soil C accumulation. Finally, the two plant species in our study also differ in leaf habit and hence leaf traits, with the ECM tree being deciduous and the ERM shrub being evergreen. Past work has found leaf habit to be less important than mycorrhizal association as a functional trait in comparisons of AM and ECM tree effects on soil N pools and cycling (Midgley and Sims 2020; Fitch et al. 2020, 2023). Whether this finding holds for the effects of deciduous ECM trees versus evergreen ERM shrubs in early successional temperate forests remains an open question.

Given the observational design of our study, we cannot definitively identify the mechanisms driving the differences in N cycling rates we observed under the ECM tree versus ERM shrub. Future experimental work is therefore needed to resolve these mechanisms in early successional stands. Moreover, in boreal forest systems, N availability can often be higher under ERM shrubs than ECM trees (Mielke et al. 2022; Clemmensen et al. 2021), emphasizing the need to test these effects in a broader range of forest types. Yet regardless of the exact mechanism(s), our findings highlight how N cycling rates in forests can be contingent on both the successional stage of the stand and the functional traits of regenerating plants. In particular, our finding that ERM shrubs have functionally distinct effects from ECM trees on soil N cycling has important implications for how plant functional types are considered in the context of ecosystem ecology. Even within 5 years of forest disturbance, differences in ERM and ECM plant effects were beginning to affect forest soil biogeochemistry in a manner similar to those observed in mid-successional temperate forests (Wurzburger and Hendrick 2009) (Fig. 4).

These results are also important for understanding the role that ERM shrubs play in shaping forest nutrient cycling and successional trajectories as forests

are increasingly exposed to major disturbance events (Seidl et al. 2017, Brown et al. 2018). Under such disturbances, ERM shrubs such as *K. latifolia* and *R. maximum* appear to be able to rapidly expand (Mallik 1995; Royo and Carson 2006; Bergero et al. 2003), changing the relative and absolute abundance of mycorrhizal functional types in forested landscapes. For example, the inhibitory effects of ERM-associated *R. maximum* on stand regeneration in southeastern U.S. forests is well documented (Nilsen et al. 2001), as is its landscape-altering potential through influences on shade, water, and leaf litter accumulation and decomposition rates (Dudley et al. 2020). Similarly, in the northeastern U.S., ERM shrubs like *K. latifolia* can inhibit oak regeneration. Although such observations have been linked to light limitation caused by *K. latifolia* cover (Brose 2016), our results suggest that expansion of ERM shrubs in regenerating forest stands may further limit tree re-establishment by exacerbating N limitation. If the underlying mechanisms include the rapid transformation of soil organic matter chemistry or the formation of recalcitrant organic complexes, then the competitive dominance of ERM shrubs could be further promoted because what N is present may be more accessible to ERM than ECM fungi (Joanisse et al. 2009; Read and Perez-Moreno 2003). However, the extent to which ECM fungi can access recalcitrant forms of organic N varies widely by taxa (Bödeker et al. 2009, 2014; Hasby 2022), necessitating the need to test this plant-soil feedback under a broader range of ECM plant hosts and associated fungal taxa.

It is also important to investigate how the effects of plant mycorrhizal associations on N and C cycling vary spatially and temporally. For instance, seasonality could modulate ECM and ERM plant impacts on soil biogeochemical cycling in young temperate forests. However, we found the same general pattern in N and C cycling under ERM and ECM plants in late August as we did in June (Table S3, Fig. S1), suggesting that our results may hold for at least part of the annual seasonal cycle. Additionally, the extent to which mycorrhizal status or percentage root colonization of ECM or ERM plants translates to a functional symbiosis within and among different plant taxa could plausibly alter ECM and ERM effects on N and C cycling. For instance, colonization rates of ericaceous shrubs can vary across environmental gradients (Griffin and Kernaghan 2022), suggesting

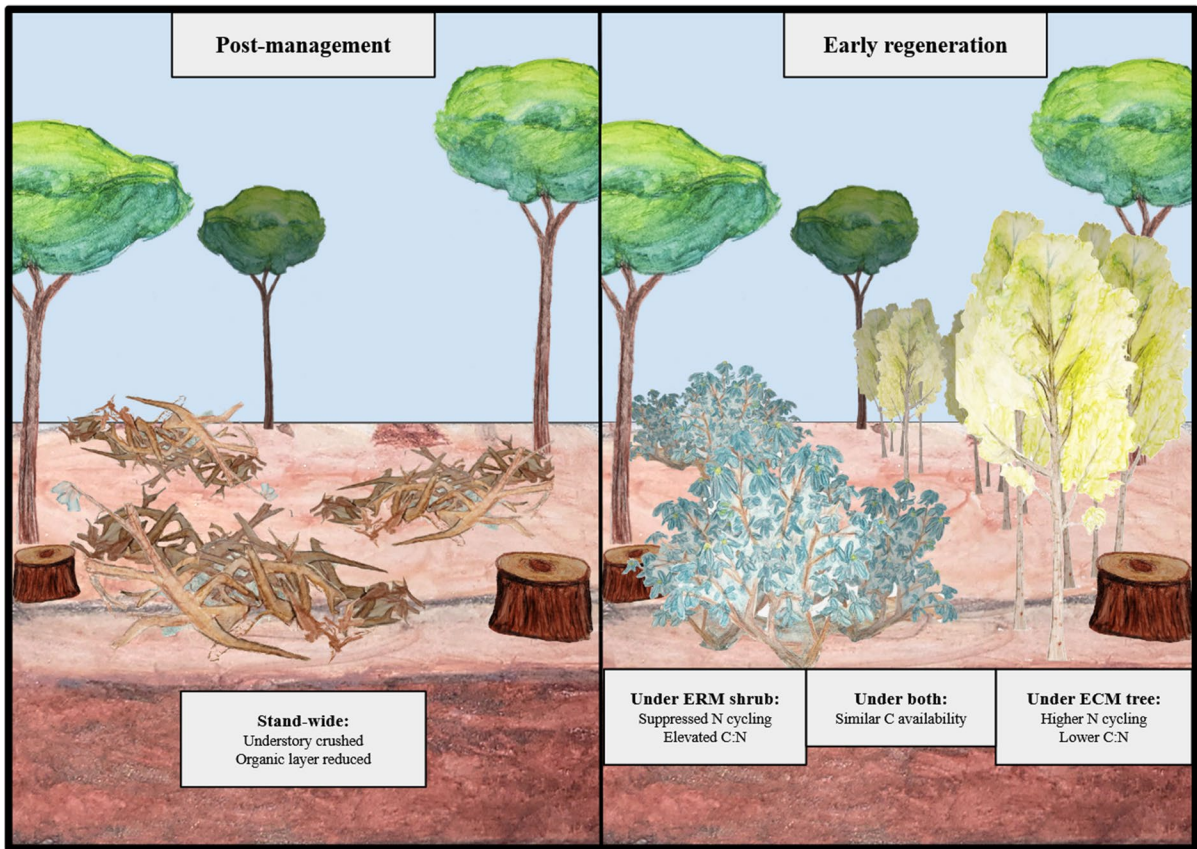


Fig. 4 Conceptual figure showing the differences in soil C and N cycling that we observed under ERM versus ECM plants as the early-successional stand recovers following timber harvesting. In the foreground of the regeneration image are resprouting ERM shrubs and regenerating ECM tree saplings, and in

the background are the much taller, mature canopy trees that were retained in the irregular shelterwood management, which is designed to simulate natural, high intensity disturbances, such as hurricanes, in eastern North American temperate forests

that differences in ERM colonization rates within the same species of ERM shrub could reflect or directly contribute to soil C and N cycling at fine scales. Although we used a plant mycorrhizal functional type framing similar to that used in other ecosystem work on mycorrhizal dominance (e.g., Phillips et al. 2013), it is feasible that effects that we report are attributable in whole or in part to plant traits beyond mycorrhizal status and degree of colonization, such as leaf habit. There is a need for observational studies which build a broader, integrated understanding of how a larger suite of plant traits and mycorrhizal associations together influence N cycling rates in forest soils. Such data would help resolve whether the abundance of plants that associate with different types of mycorrhizal fungi provides enough granularity to infer

relationships between plant community composition and forest biogeochemical processes at multiple spatial scales.

Understanding how local heterogeneity in plant mycorrhizal associations may affect biogeochemical cycling can improve our ability to manage forests in a changing environment. The tree mycorrhizal dominance framework has been used to make broad-scale predictions and inferences about forest soil biogeochemistry (Averill et al. 2014; Carteron et al. 2021; Barceló et al. 2022) but has lacked the finer-scale incorporation of understory plant mycorrhizal associations, such as ERM shrubs and their associated microbial communities (Ward et al. 2022). This lack of data is particularly important for understanding the effects of plant mycorrhizal associations in

early successional forest stands, where understory plant communities and regenerating trees make up a much larger proportion of aboveground biomass in forests. Our study begins to fill this knowledge gap by showing how differences in the effects of ERM and ECM plants on soil C and N cycling can rapidly influence soil biogeochemical cycling at fine scales within forest stands—effects that could also shape regional-scale processes (see Bradford et al. 2021). Our results add to a growing body of literature on ERM shrub effects within temperate forests (Nilsen et al. 2001, Wurzburger and Hendrick 2009, Brose 2016, Ward et al. 2021, 2023) that highlight the need to consider the functional group diversity of mycorrhizal associations, or at least plant functional types, beyond those of only the canopy trees.

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Author contributions All authors conceived the ideas and designed the methodology; KMF, EBW and LW secured funding; KMF, EBW, and LW collected the data; LW led data analysis and manuscript writing with input from all authors on statistical and ecological interpretation.

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Data availability Data, metadata and code will be made available in the Dryad Digital Repository after paper publication.

Supplemental information contains four tables (Tables S1–S4) and two figures (Figs. S1–S2).

Declarations

Competing interests The authors declare no financial or non-financial interests related to this work.

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