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Final Technical Report

Testing mechanisms of how mycorrhizal associations affect forest soil carbon and nitrogen cycling

Awarded to Dartmouth College

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This work was supported as part of the Terrestrial Ecosystem Science Program by the Office of Science, Office of Biological and Environmental Research, of the U.S. Department of Energy under Contract DE-SC0020228.

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Abstract

Trees are in a symbiotic partnership with mycorrhizal fungi in which they provide the fungi with carbon from photosynthesis and the fungi provide the trees with nutrients and water. In temperate forests, the vast majority of trees form symbioses with one of two types of mycorrhizal fungi—arbuscular mycorrhizal (AM) fungi or ectomycorrhizal (EcM) fungi. These fungi differ in their morphology, hyphal length, and nutrient acquisition strategies. Many studies have found systematic differences in soil organic matter and nitrogen availability between forest stands dominated by AM-associating trees versus EcM-associating trees. For instance, there is a larger proportion of organic matter that is mineral-associated, more available nitrogen, and lower soil carbon to nitrogen ratios in AM forest stands relative to EcM forests stands. However, the mechanisms driving these patterns are not known, which complicates our ability to model soil organic matter dynamics in forested ecosystems.

The main objective of this research was to understand the degree to which the observed differences in soil C and N dynamics between AM and EcM dominated forests are driven by tree traits like litter decomposability and root exudation versus mycorrhizal fungal nutrient acquisition strategies. We investigated these mechanisms using observations and targeted experiments and incorporated this knowledge into a process-based soil organic matter model. The observational studies compared the importance of leaf litter decomposability versus fungal identity on soil organic matter processes. We found that often fungal identity and traits were more important drivers of soil organic matter patterns than leaf litter decomposability. We ran two novel experiments: 1) a growth chamber experiment across four EcM and four AM tree species using a ^{13}C-labeled atmosphere to trace seedling-derived C into hyphae, the rhizosphere, and soil; and 2) an *in situ* decomposition experiment of six different ^{13}C and ^{15}N labeled litters that ranged in decomposability incubated across a gradient of EcM dominance at three sites that capture important variation in climate, soils, and forest species composition. In the first experiment, we found no significant differences of seedling mycorrhizal association on soil carbon sequestration over a growing season, but we did find that mycorrhizal association affected rhizodeposition with EcM-associating seedlings depositing more carbon in response to increased nitrogen availability. The decomposition experiment is still ongoing, but thus far, we have found slower litter decomposition in only one of three EcM-dominated forests which suggests that differences between AM- and EcM-dominated forests depend on the environmental context and identity of the EcM fungi. Lastly, we explicitly incorporated mycorrhizal processes into the Carbon, Organisms, Rhizosphere, and Protection in the Soil Environment (CORPSE) model creating Myco-CORPSE. By including the different nutrient acquisition strategies of AM and EcM fungi, we explored the conditions under which EcM fungi can slow decomposition rates and lead to greater soil organic carbon accumulation compared to AM fungi. We found that the effect of EcM fungi was highly context dependent and that EcM fungi decreased decomposition in colder forests with recalcitrant litter inputs and when they produced oxidases and necromass-degrading enzymes. Our research highlights the importance of fungal nutrient acquisition in driving soil organic matter patterns and the need to move beyond the AM-EcM dichotomy to consider the identity and traits of the specific fungi participating in the symbiosis.

Overall, this research has resulted in six, peer-reviewed published papers in journals such as *Global Change Biology*, *Ecology* (2), *Soil Biology and Biochemistry,* and *Ecosystems* (2). There are at least two more papers in progress on this research including one that was recently submitted to *Global Change Biology*.

Background

Seventy-five percent of global soil carbon is stored in forest soils (Jackson et al., 2017). To predict future forest soil carbon storage, we need a better understanding of how tree species affect the quality and quantity of soil organic matter (SOM) and soil nutrient availability. Mycorrhizal associations have been suggested as a major driver of soil organic matter processes (Phillips et al., 2013). Generally, the proportion of particulate organic matter (POM) and mineral-asscociated organic matter (MAOM) in SOM differs with the dominant mycorrhizal association of an ecosystem (Cotrufo et al., 2019; Craig et al., 2019; Wu et al., 2022). EcM-dominated forests tend to have a greater proportion of their SOM stored in POM pools relative to AM-dominated forests.

There are several proposed mechanisms for why SOM differs between forests dominated by AM- or EcM-associated tree species. In one of the first papers from this project (Hicks Pries et al., 2022) (https://www.osti.gov/pages/biblio/1916523), we laid out our conceptual model (reproduced below; Fig 1) highlighting how the traits of trees and the mycorrhizal fungi they associate with may affect SOM. These traits include tree litter quality and tree root rhizodeposition rates and the nutrient acquisition strategies and necromass quality and quantity of mycorrhizal fungi. It is important to note that EcM fungi are more phylogenetically diverse than AM fungi and thus, have a wider range of these traits. For example, only some EcM fungi produce highly melanized litter that decomposes slowly (Fernandez et al., 2016; Siletti et al., 2017) and only some can produce peroxidases to liberate nitrogen from organic matter (Bödeker et al., 2009).

Through observational studies, experiments, and modeling, we investigated the extent to which these tree and fungal traits affected SOM. We will now briefly summarize each of these myriad research efforts.

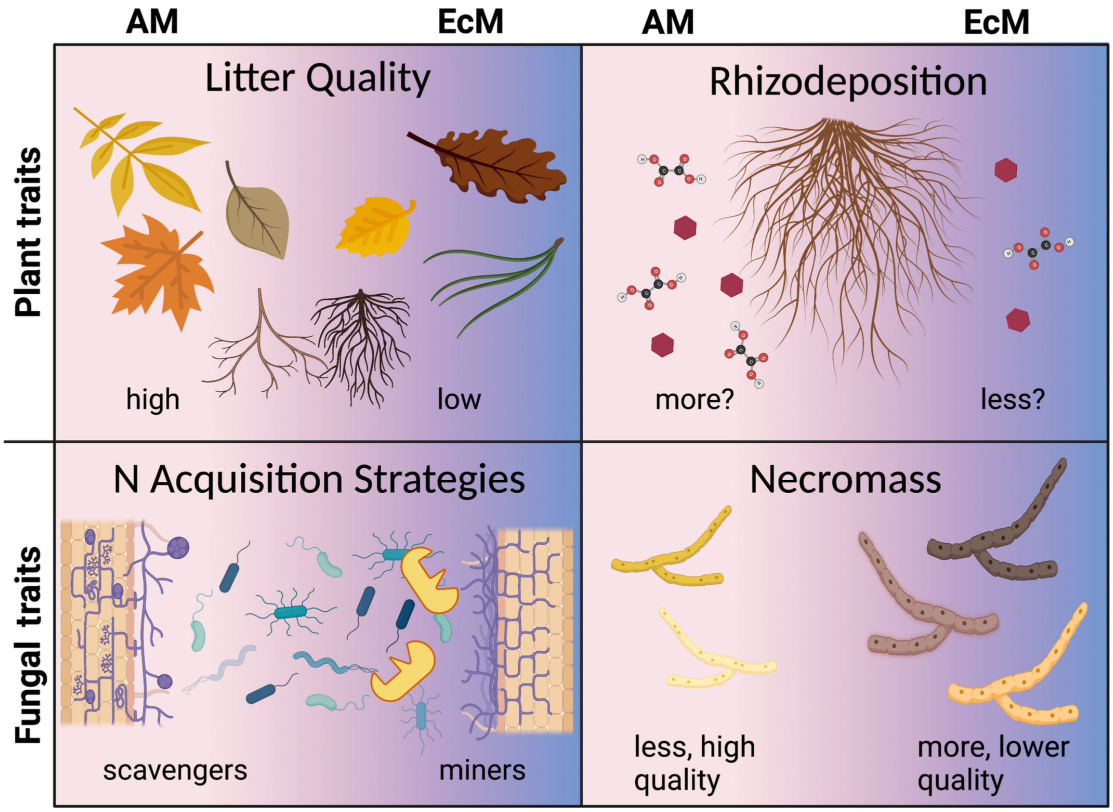

Figure 1. Mechanisms by which plant (top) and fungal (bottom) traits associated with arbuscular mycorrhizae (AM) and ectomycorrhizae (EcM) can affect soil C:N ratios and the partitioning of organic matter among mineral-associated (MAOM) and particulate (POM) pools. For plant traits, EcM-associating trees tend to have low-quality leaf (and sometimes root) litter that can lead to high soil C:N ratios and more organic matter being stored as POM. Recent evidence suggests that AM-associating trees may have higher rhizodeposition rates, which can encourage MAOM formation; however, rhizodeposition comparisons between AM and EcM trees are often idiosyncratic. For fungal traits, AM fungi acquire nitrogen by scavenging it from the environment, whereas some EcM fungi can actively mine nitrogen from organic matter, which can induce competition with saprotrophs that may decrease decomposition and lead to more organic matter remaining as POM. Lastly, EcM fungi tend to produce more hyphal biomass and lower-quality fungal necromass than AM fungi, which may also lead to reduced decomposition and more POM. The extent to which EcM mycorrhizae display the typical EcM traits listed here are taxon dependent. The pink background represents arbuscular mycorrhizal traits, whereas the purple to blue color gradient represents the range of these traits found within EcM trees and fungi. Created with BioRender.com and reprinted from Hicks Pries et al. (2022).

Observational Studies

In the first observational study (Hicks Pries et al. 2022), we quantified how the proportion of soil carbon and nitrogen in MAOM and soil C:N changed with the proportion of tree basal area occupied by trees associating with EcM fungi across four sites throughout the Eastern US. This study was meant to be preliminary data for our labeled litter experiment (see below) to confirm SOM patterns we expected based on meta-analyses. However, we were surprised to find the expected patterns of less C and N in MAOM and higher soil C:N with increasing EcM basal area in only two of our four sites—Georgia and New Hampshire but not Wisconsin or Illinois (Fig. 2). Digging deeper into the data, we found that Georgia and New Hampshire had similar tree and EcM fungal communities that were significantly different from those of Wisconsin or Illinois. In fact, the second principal component of the tree communities, based on tree family, was a better predictor of the soil properties across all sites than EcM basal area. This second principal component was driven by trees in the oak and pine families. Another significant predictor of SOM was the percentage of EcM fungi that can produce peroxidases. As they increased, a smaller proportion of carbon was found in the mineral-associated fraction. These results indicated that the identity of the tree and fungal species involved in the symbiosis were better predictors of SOM patterns than the traditional AM v. EcM dichotomy. Potential mechanisms explaining these patterns included the recalcitrant litter produced by pines and oaks reducing the amount of C and N becoming sorbed to soil minerals and the potential suppressive effect of peroxidase production on saprotrophic communities, but more studies were needed to tease apart these mechanisms.

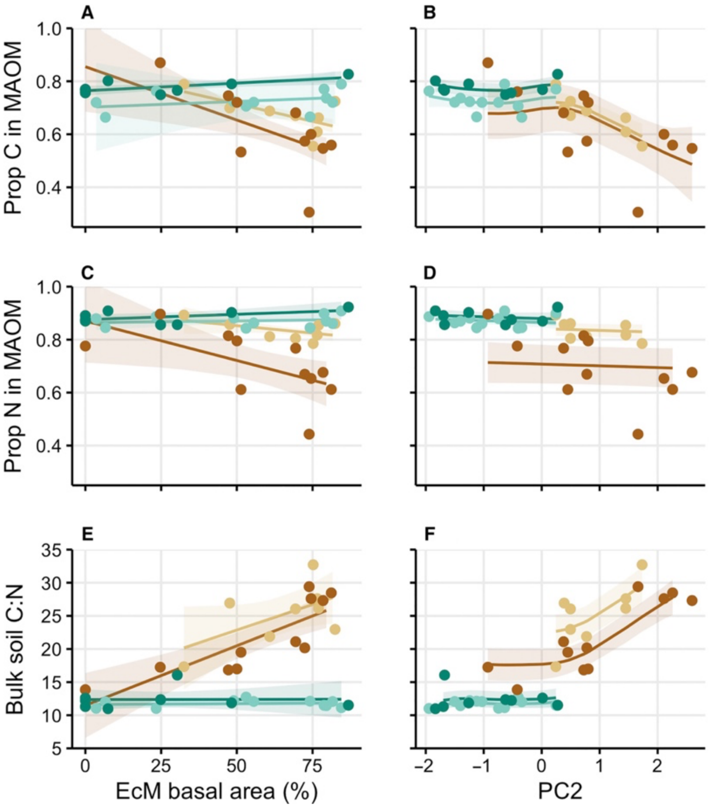

Figure 2. Only two sites (in Georgia [GA] and New Hampshire [NH]) demonstrated the expected relationship between soil organic matter characteristics and ectomycorrhizal (EcM) basal area where the proportion of C and N in mineral-associated organic matter (MAOM) decreased (A, C) and the overall soil C:N increased (E) as EcM-associated trees became more dominant in the forest stand. In contrast, the second principal component (PC2) of the dominant plant family PCA was significantly related to soil organic matter characteristics. The proportion of C and N in MAOM decreased (B, D) and the bulk soil C:N increased (F) as the basal area of trees in the Pinaceae and Fagaceae became more dominant. Brown points represent forest stands in NH, tan in GA, dark green in Wisconsin (WI), and light green in Illinois (IL). The lines show the predictions from significant regressions ($\alpha < 0.05$) and the ribbons show the 95% confidence intervals. Reprinted from Hicks Pries et al. (2022).

A set of observational studies then followed that used a unique design to disentangle the relative importances of leaf litter versus mycorrhizal associations on driving SOM patterns (Fitch et al., 2023; Lang et al., 2025). These studies used a factorial design whereby leaf habit (evergreen versus deciduous) was crossed with mycorrhizal association (AM versus EcM). These studies collected soil under plots dominated (>50%) by the following trees: ash and sugar maple as AM deciduous trees, northern white cedar as an AM evergreen tree, yellow birch and beech as EcM deciduous trees, and hemlock as an EcM evergreen tree. The evergreen trees have the most recalcitrant litter. Overall, 60 soils were collected across eight sites, so that multiple species were sampled from at each site and each species was sampled at multiple sites. For MAOM carbon and nitrogen, there was a significant interaction whereby concentrations were higher under deciduous rather than evergreen AM trees but there was no difference under deciduous and evergreen EcM trees (Lang et al. 2025; OSTI ID 2524098). The C:N ratio of all soil fractions was higher beneath evergreen than deciduous trees, and MAOM C:N was higher beneath EcM than AM trees regardless of leaf habit (Lang et al. 2025). These results show that while leaf litter quality (for which leaf habit is a proxy) is an important determinant of SOM patterns, there are also significant interactions with mycorrhizal association. Looking more deeply into microbial communities and function using this same experimental design, we found that mycorrhizal associations better predicted the composition of microbial communities than leaf habit (Fig. 3; Fitch et al. 2023; https://www.osti.gov/pages/biblio/1971371). Furthermore, oxidative enzyme activities were higher under EcM-associating trees regardless of leaf habit. Thus, patterns in SOM between AM and EcM-dominated forests cannot be explained solely by the fact that AM trees tend to have more easily decomposed litter. Mycorrhizal associations are also affecting the structure and function of microbial communities in ways that affect SOM decomposition.

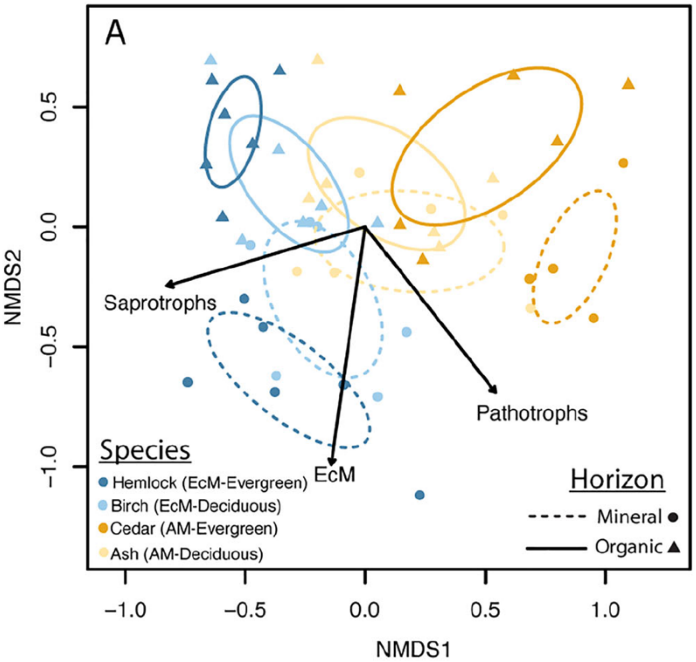

Figure 3. Non-metric multidimensional scaled representation of fungal community composition. Each color represents plots from a tree species of one mycorrhizal type (blue for EcM and yellow for AM), and the shade of the color represents leaf habit (darker for evergreen and lighter for deciduous). Circles represent the mineral soil, while triangles represent the organic horizon. Ellipses show the standard error of plots within one species and horizon, where dashed lines are the mineral soil and solid lines are the organic horizon. Arrows indicate significant correlations ($p < 0.05$) between the relative abundances of fungal guilds (saprotroph, EcM, and pathotroph) and differences in fungal community composition. Reprinted from Fitch et al. 2023.

Experiments

Litter Mesocosms

Our first experiment was an *in situ* incubation of six different ^{13}C and ^{15}N labeled litters across a gradient of EcM tree dominance in forests in three states—New Hampshire, Georgia (different site from observational study above), and Illinois. Our objective, similar to those of the observational studies, was to experimentally determine the relative importance of leaf litter quality versus fungal traits in driving decomposition differences between AM and EcM dominated forests. We hypothesized that the total recovery of litter N and the partitioning of litter C and N among SOM pools will differ according to mycorrhizal function so that, for the same litter type, less litter N will remain in the soil and less litter C and N will be mineral-associated when litter decomposes in EcM-dominated rather than AM-dominated forest stands.

Figure 4. A PVC mesocosm used to incubate labeled litter in situ after harvesting. There are many roots that have grown into it via the mesh screen. Each PVC had two mesh screens.

We created six different dual ^{13}C and ^{15}N labeled substrates by cultivating seedlings in our growing chamber in 2020 (see below). These substrates include oak leaf, maple leaf, tulip leaf, pine needles, pine roots, and oak roots. These substrates were incubated individually under the Oi horizon within PVC mesocosms that were pounded into the soil. The mesocosms had mesh screens to allow root ingrowth (Fig. 4). At each forest (one per state), we established 6 5-meter radius plots with EcM basal areas ranging from 1% to 100%. Three timepoints worth of litters were incubated at each plot plus a control no litter mesocosm for a total of 378 mesocosms across the whole experiment (6 litters plus 1 control x 3 timepoints x 6 plots x 3 forest sites). Upon harvesting, the mesocosm were split into 3 depths (0-5, 5-10, and 10-15 cm), the amount of ^{13}C and ^{15}N remaining in the soil was quantified, and a subsample of the 0-5 cm depth was frozen at -80°C for ITS sequencing of DNA to characterize fungal communities and qPCR to estimate fungal biomass. This experiment is ongoing. The amount of litter C and N remaining after one and two years was similar and so we decided not to collect mesocosms in year three and to instead leave them incubating for another year. We summarize the results from years one and two below.

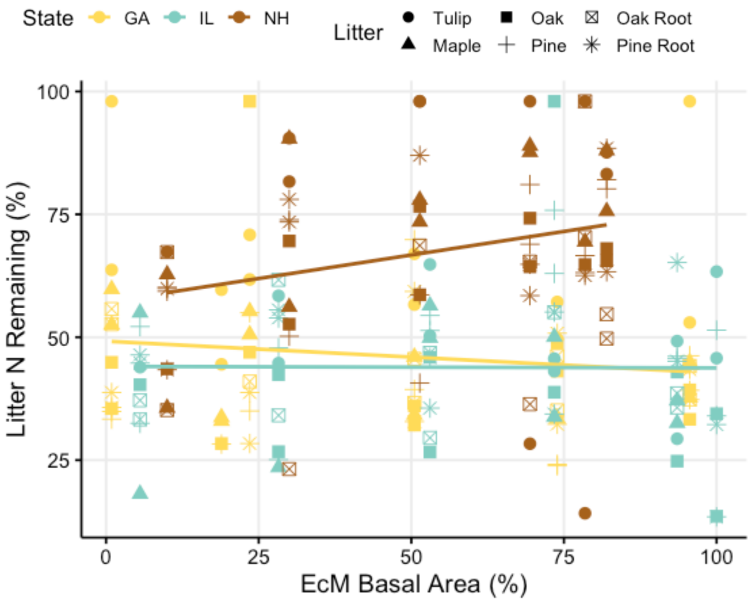

Figure 5. How the percentage of litter nitrogen remaining in the soil after one and two years is affected by EcM basal area across our three sites. The lines are model predictions from a mixed multiple regression. The points are the data with shape determined by litter type.

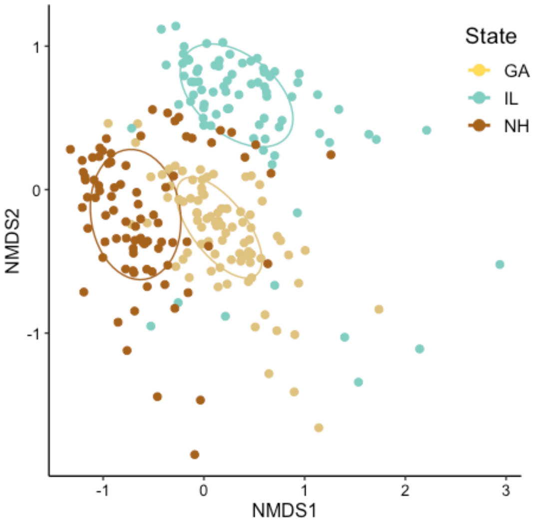

Figure 6. Each forest site harbored a distinct fungal community.

The amount of litter C and N remaining after one and two years increased with EcM dominance (measured as percent basal area) only in New Hampshire but not in Illinois or Georgia (Fig. 5). These different responses may be due to the different fungal communities across the three sites (Fig. 6). Most importantly, the EcM fungal biomass only increased with EcM basal area in New Hampshire but not in Illinois or Georgia implying that EcM tree basal area is an imperfect predictor of the influence of EcM fungi on soils. Furthermore, litter quality (lignin:N) was a significant predictor of the amount of litter C and N remaining, it did not significantly interact with EcM basal area. These preliminary findings indicate that fungal identity and biomass affect the amount mycorrhizae influence SOM, again indicating the AM-EcM dichotomy is too simplistic.

Labeling Chamber

Our labeling chamber experiment (Fig. 7) focused not on leaf litter differences between AM and EcM-associating trees, but instead on another plant trait—rhizodeposition (Fitch et al., 2024)(https://www.osti.gov/pages/biblio/2426976). Our objective was to investigate how rhizodeposition and priming of SOM decomposition differed among AM- and EcM- associated trees. We hypothesized that AM-associated trees, which rely on mycorrhizal fungi with a scavenger-like nitrogen acquisition strategy, would have greater rhizodeposition rates and thus greater priming-induced organic matter losses. We grew eight seedling species over one growing season in a $^{13}CO_2$ labeling chamber so that their photosynthate could be traced into the soil. These species were categorized based on their mycorrhizal associations. The arbuscular mycorrhizal (AM)-associated species included red maple (*Sapindaceae*), black gum (*Cornaceae*), white cedar (*Cupressaceae*), and black cherry (*Rosaceae*). Meanwhile, the ectomycorrhizal (EcM)-associated species consisted of white pine (*Pinaceae*), black birch (*Betulaceae*), red oak (*Fagaceae*), and American basswood (*Malvaceae*). We also aimed to assess how these different tree species respond to varying nitrogen fertilization levels, which was labeled with ^{15}N so we could trace how much nitrogen ended up in plant tissues at the end of the growing season. When planting, pots were inoculated with roots and rhizosphere soil from each of the represented species to ensure that they had access to their own mycorrhizal communities. Each pot contained three 50 g pouches of forest soil, which either included or excluded roots to assess root influence. At the end of the experiment, we quantified seedling biomass and ^{15}N uptake, the amount of 13C-labeled and native soil carbon remaining in the pouches and characterized fungal communities on the seedling roots using amplicon sequencing (ITS) and qPCR.

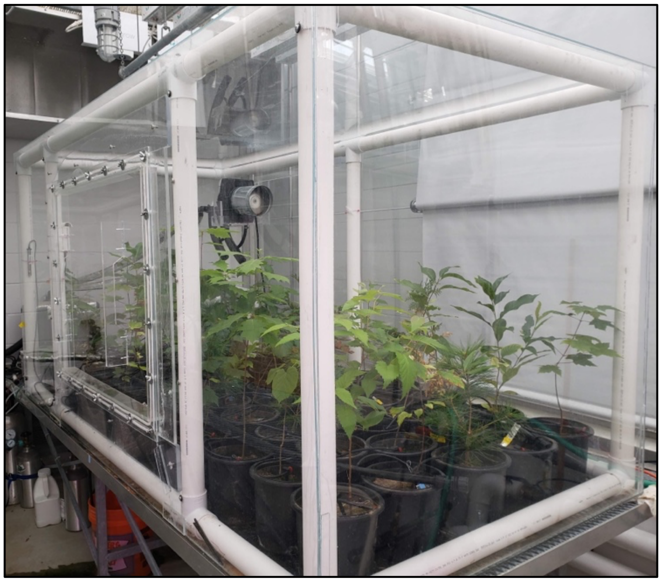

Figure 7. Seedlings growing in the ^{13}C-enriched atmosphere of the labeling chamber.

While we found differences in rhizodeposition between mycorrhizal types, these differences did not lead to a difference in soil carbon at the end of the growing season. In fact, rhizodeposition did not affect the amount of soil carbon remaining in the pouch at all. It seems that the positive priming effects of rhizodeposition are balanced out by the influx of new carbon from rhizodeposits. Furthermore, while C:N changed over the course of the experiment (it increased), these changes were not related to mycorrhizal type. Thus, this experiment rules out rhizodeposition from being a trait that drives differences in SOM beneath AM and EcM-associating trees.

Interestingly, we found a significant difference between AM and EcM-associating trees in how they responded to N fertilization. As the amount of nitrogen taken up from the fertilizer increased, EcM seedlings deposited more C into the soil. This occurred despite there being no differences in root biomass between AM and EcM seedlings. We found this unexpected result interesting because increasing root exudation in response to higher nitrogen availability seems maladaptive—like a waste of photosynthate for EcM seedlings. This trend could explain why EcM trees are often outcompeted by AM trees in forests experiencing high N deposition (Jo et al., 2019).

Myco-CORPSE Model

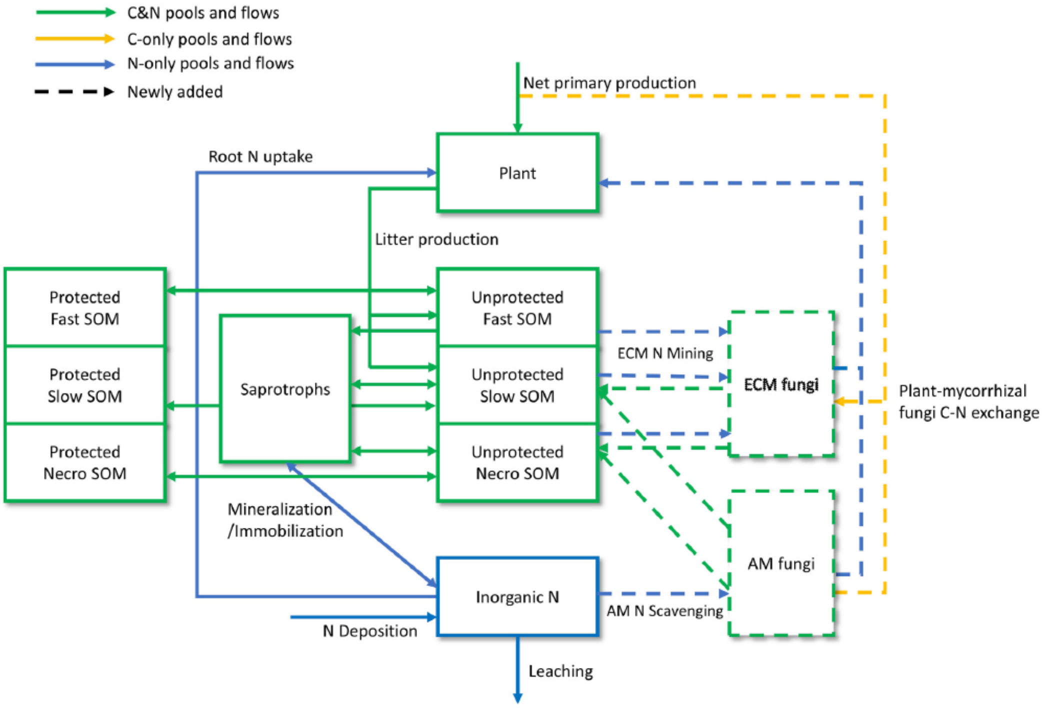

Figure 8. Model structure of myco-CORPSE. Green solid boxes: existing CN pools in CORPSE; blue solid boxes: existing N-only pools in CORPSE; green dotted boxes: newly added CN pools in Myco-CORPSE; green solid arrows: existing CN flows in CORPSE; blue solid arrows: existing N-only flows in CORPSE; green dashed arrows: newly added CN flows in Myco-CORPSE; blue dashed arrows: newly added N-only flows in Myco-CORPSE; yellow dashed arrows: newly added C-only flows in Myco-CORPSE. Reprinted from Shao et al. 2023.

We explicitly incorporated mycorrhizal processes into the Carbon, Organisms, Rhizosphere, and Protection in the Soil Environment (CORPSE) model creating Myco-CORPSE (Shao et al., 2023)(https://www.osti.gov/pages/biblio/1987801). By including the different nutrient acquisition strategies of AM and EcM fungi, we explored the conditions under which EcM fungi can slow decomposition rates and lead to greater soil organic carbon accumulation, a smaller proportion of carbon in mineral-associations, and a higher soil C:N compared to AM fungi. In the model, the EcM fungi could mine organic matter for nitrogen to different degrees depending on their assigned traits (necrominer, miner, or opportunist) while the AM fungi could only scavenge nitrogen already available in the soil solution (Fig. 8). We evaluated our model against the empirical observations of SOM from the original observational study described above (Hicks Pries et al. 2022) and found the model was in good agreement with the measurements. We then set up a series of model experiments to test how litter quality, climate, and EcM fungal nutrient acquisition strategies affected SOC pools and saprotrophic biomass (to investigate when EcM fungi might induce a 'Gadgil' effects whereby they reduce decomposition by outcompeting saprotrophs.

We found that the effect of EcM fungi on soil carbon was highly context dependent and that EcM fungi tended to decrease decomposition relative to AM fungi in colder forests with recalcitrant litter inputs and when they produced oxidases and necromass-degrading enzymes. EcM fungi generally outcompeted saprotrophs for nitrogen and increased the amount of unprotected (POM) carbon but the effect interacted with litter quality and climate. EcM fungi had the strongest effects on saprotrophs and on increasing soil carbon when they were able to mine nitrogen from recalcitrant and necromass organic matter pools. Lastly, EcM fungi had the largest negative effects on saprotrophic biomass and positive effects on soil carbon in cold climates with strong seasonality in litterfall (Fig. 9).

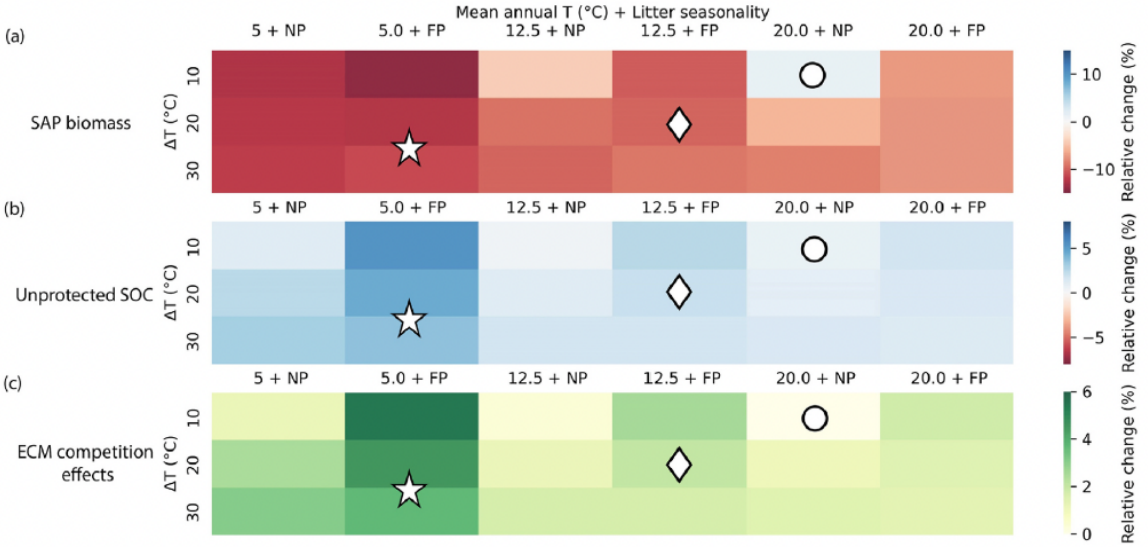

Figure 9. Results of climate and seasonality experiments: Relative changes (%) in SAP biomass (a), unprotected SOC accumulation (b), and ECM competition effects (c) induced by different N acquisition strategies of ectomycorrhizae (100% ECM) relative to arbuscular mycorrhizae (0% ECM) as predicted by Myco-CORPSE across three different mean annual temperatures, seasonal temperature ranges (ΔT), and two scenarios of litter seasonality (NP and FP). NP refers to the scenario where litterfall has no seasonal peak and FP refers to the scenario where litterfall has a fall peak. Colors show the percent difference between 0% ECM and 100% ECM, with positive numbers indicating a higher value at 100% ECM. The star, diamond and round symbols represent climates and litterfall patterns in a typical boreal, temperate, and wet tropical forest, respectively. Reprinted from Shao et al. 2023.

Overall, the Myco-CORPSE model added to the evidence supporting the importance of EcM fungal traits in determining differences between AM and EcM forest soils. The model also indicated another reason that New Hampshire showed the strongest EcM effects in the labeled litter experiment as New Hampshire has the coldest climate of the three sites.

Lastly, we have recently used Myco-CORPSE for a new endeavor—to estimate the amount of photosynthate trees pay to their mycorrhizal partners in temperate forests and to explore how this carbon cost is affected by global change factors (Shao et al. in review). We applied Myco-CORPSE to over 1,800 forest inventory plots across the eastern United States and estimated mycorrhizal carbon costs. Our simulations matched published data, showing higher carbon allocation to EcM fungi (16.0% of net primary production) compared to AM fungi (5.8% of net primary production). We also showed that mixed forests, co-dominated by both AM and ECM trees, allocated less carbon to mycorrhizal fungi compared to forests dominated by either AM or ECM fungi alone, due to complementary nutrient acquisition strategies (see minima in top panels of Fig. 10). Nitrogen deposition and higher temperatures reduced mycorrhizal carbon costs, favoring AM strategies (Fig. 10). These findings underscore the critical role of mycorrhizal functional diversity in plant nutrient acquisition and carbon dynamics, providing new insights into how mycorrhizal symbioses respond to global change.

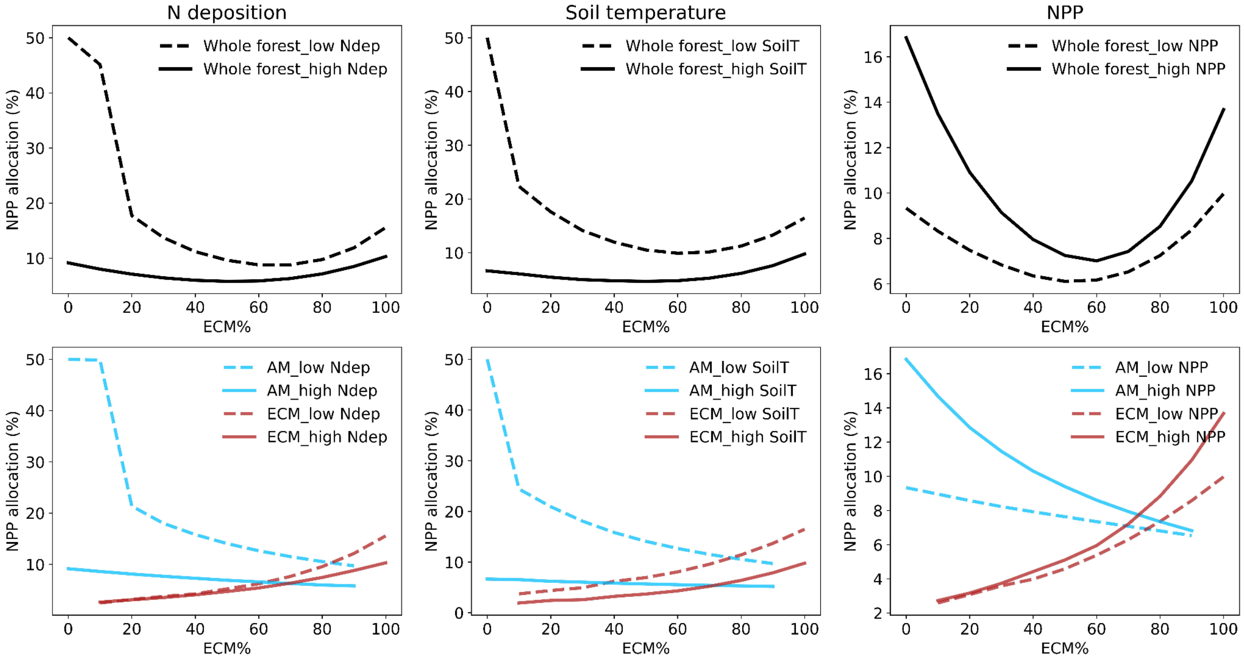

Figure 10. Simulated direct effects of N deposition (Ndep), soil temperature (SoilT), NPP, and ECM dominance (ECM%) on %NPP allocated to mycorrhizal fungi in Myco-CORPSE. The upper panels show %NPP allocated to mycorrhizal fungi for the whole forest, while the lower panels present %NPP allocation to AM and ECM fungi individually. Solid and dashed black lines represent scenarios with low and high global change factors, respectively. In the lower panels, blue and red lines represent AM fungi and ECM fungi, respectively. From Shao et al. in review.

Conclusions

When proposing this research, we had three main questions:

1. How do the nutrient acquisition strategies of AM and EcM roots and fungi affect soil carbon and nitrogen cycling and litter decomposition?
2. To best represent mycorrhizal effects in biogeochemical models and reproduce observed patterns of carbon and nitrogen cycling, should soil microbial communities be explicitly separated into free-living saprotrophs, AM, and EcM fungi?
3. To what extent is the effect of mycorrhizal association on soil carbon and nitrogen driven by differences in litter decomposability?

Through observations, experiments and models, we have discovered that:

1. Mycorrhizal nutrient acquisition strategies can have a large effect on soil organic matter, but the strength of the effect is dependent on the specific fungi involved. Not all EcM fungi have the traits, likely the ability to produce peroxidases to mine nitrogen from organic matter, to affect carbon and nitrogen cycling differently from AM fungi. On the other hand, the root strategy of rhizodeposition does not drive differences in soil organic matter between AM and EcM associations.
2. We were able to reproduce observed patterns in soil carbon fractions, soil C:N, and mycorrhizal carbon costs by explicitly modeling three different microbial groups—saprotrophs, AM fungi, and EcM fungi.
3. There is no doubt that differences in litter decomposability help to drive soil differences (it was an important explanatory factor in the observational studies, litter experiment, and model) beneath AM and EcM-associating trees. However, litter is not the only factor as we have shown that the nutrient acquisition strategies of EcM fungi also affect soil organic matter formation and decomposition.

Key outcomes of this work include a parameterized and tested soil organic matter model incorporating mechanistic differences between major mycorrhizal types that we have used to investigate drivers of AM and EcM differences in soil organic matter and mycorrhizal carbon costs. Our development of Myco-CORPSE sets up the scientific community to make predictions of how soil C and N stocks across the Eastern U.S. will be affected changes to forest community composition brought on by global changes like fire, nitrogen deposition, and a warming climate.

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