Received: 6 December 2017 | Accepted: 8 February 2018

DOI: 10.1111/gcb.14132

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter

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Funding information
Biological and Environmental Research, Grant/Award Number: DE-SC0016188; National Natural Science Foundation of China, Grant/Award Number: 41471218; Smithsonian Tropical Research Institute; Division of Environmental Biology, Grant/Award Number: 1153401; U.S. Department of Energy

Abstract

Forest soils store large amounts of carbon (C) and nitrogen (N), yet how predicted shifts in forest composition will impact long-term C and N persistence remains poorly understood. A recent hypothesis predicts that soils under trees associated with arbuscular mycorrhizas (AM) store less C than soils dominated by trees associated with ectomycorrhizas (ECM), due to slower decomposition in ECM-dominated forests. However, an incipient hypothesis predicts that systems with rapid decomposition—e.g. most AM-dominated forests—enhance soil organic matter (SOM) stabilization by accelerating the production of microbial residues. To address these contrasting predictions, we quantified soil C and N to 1 m depth across gradients of ECM-dominance in three temperate forests. By focusing on sites where AM- and ECM-plants co-occur, our analysis controls for climatic factors that covary with mycorrhizal dominance across broad scales. We found that while ECM stands contain more SOM in topsoil, AM stands contain more SOM when subsoil to 1 m depth is included. Biomarkers and soil fractionations reveal that these patterns are driven by an accumulation of microbial residues in AM-dominated soils. Collectively, our results support emerging theory on SOM formation, demonstrate the importance of subsurface soils in mediating plant effects on soil C and N, and indicate that shifts in the mycorrhizal composition of temperate forests may alter the stabilization of SOM.

KEYWORDS
amino sugars, decomposition, MEMs hypothesis, mineral-associated, mycorrhizal fungi, soil carbon, soil depth, soil nitrogen, temperate forest

1 | INTRODUCTION

Soil organic matter (SOM) accounts for more than 70% of terrestrial organic carbon (C) stocks (Jobbágy & Jackson, 2000) and can comprise more than 95% of soil nitrogen (N: Bingham & Cotrufo, 2016). Yet changes in SOM remain difficult to forecast (Todd-Brown et al., 2014), due in part to our incomplete understanding of the myriad processes that control SOM dynamics (Bradford et al., 2016; Schimel, 2013; Treseder et al., 2012). Plant species and their associated microbes differ in their effects on SOM formation and decomposition, making it difficult to generalize about biotic effects on SOM dynamics in biodiverse systems. Moreover, soil minerals play a critical role in mediating biotic effects on SOM, especially in subsurface soils (Rumpel & Kögel-Knabner, 2011). Accordingly, predicting spatial patterns in SOM stocks requires a conceptual framework that integrates both biotic and abiotic factors (Cotrufo, Wallenstein, Boot, Denef, & Paul, 2013; Liang, Schimel, & Jastro, 2017), and can be scaled based on easily quantifiable predictors (Phillips, Brzostek, & Midgley, 2013).

In temperate forests, nearly all tree species associate with either arbuscular mycorrhizal (AM) or ectomycorrhizal (ECM) fungi, and

abundant research suggests that the dominance of ECM- vs. AM-associated trees can predict plant and microbial effects on soil C and N dynamics in surface soils (Brzostek, Fisher, & Phillips, 2014; Chapman, Langley, Hart, & Koch, 2006; Lin, Mccormack, Ma, & Guo, 2016; Phillips et al., 2013; Read & Perez-Moreno, 2003; Soudzilovskaia et al., 2015). ECM-associated plants and fungi are thought to reduce decomposition rates by producing recalcitrant tissues (Clemmensen et al., 2013; Cornelissen, Aerts, Cerabolini, Werger, & van der Heijden, 2001; Fernandez, McCormack, Hill, Pritchard, & Koide, 2013; Midgley, Brzostek, & Phillips, 2015) and by inhibiting the activities of saprotrophic decomposers by depleting nitrogen directly from soil organic matter (Averill & Hawkes, 2016; Fernandez & Kennedy, 2016; Gadgil & Gadgil, 1971; Orwin, Kirschbaum, St John, & Dickie, 2011). This "Slow Decay Hypothesis" leads to the prediction that ECM-dominated forests should store more soil C (Averill, 2016; Averill, Turner, & Finzi, 2014) than AM-dominated forests, an effect that could be amplified given greater belowground carbon inputs in ECM-dominated forests (Gill & Finzi, 2016).

Yet, the premise that slow decomposition necessarily leads to long-term SOM persistence is increasingly contested by emerging theories of SOM formation and stabilization (Cotrufo et al., 2013). Undecomposed plant inputs have conventionally been viewed as the primary source of stable SOM (Berg & McClaugherty, 2008). However, while recalcitrant compounds can undoubtedly lead to SOM buildup in surface organic soils (Clemmensen et al., 2013), accumulating evidence shows that the oldest SOM is primarily composed of labile microbial products that become protected through their association with reactive silts and clays in mineral soil horizons (Bradford, Keiser, Davies, Mersmann, & Strickland, 2013; Gleixner, 2013; Grandy & Neff, 2008; Kallenbach, Grandy, & Frey, 2016; Liang, Cheng, Wixon, & Balser, 2011; Schmidt et al., 2011). Consequently, mineral-stabilized SOM formation should be promoted under fast decay conditions which can enhance the rate and efficiency of microbial biomass production (Cotrufo et al., 2013; Cotrufo et al., 2015)—more commonly known as the "Microbial Efficiency-Matrix Stabilization or 'MEMS' Hypothesis". AM-dominated forests are typically characterized by higher nutrient availability and higher quality leaf litter than ECM-dominated forests (Lin et al., 2016; Midgley et al., 2015; Phillips et al., 2013; Waring, Adams, Branco, & Powers, 2016), and recent evidence suggests that AM-associated roots, which can account of a majority of SOM at depth (Rasse, Rumpel, & Dignac, 2005), also decay faster (e.g. Jacobs, Sulman, Brzostek, Feighery, & Phillips, 2018; but see McCormack, Adams, Smithwick, & Eissenstat, 2014). Given that these conditions may enhance microbial growth efficiency and growth rate (Frey, Lee, Melillo, & Six, 2013; Lee & Schmidt, 2014; Manzoni, Taylor, Richter, Porporato, & Agren, 2012), the MEMS Hypothesis leads to the prediction that soil C storage should be greatest in AM forests.

Of course, these two hypotheses are not mutually exclusive. Soils with slow decay rates (e.g. ECM-dominated) may store greater amounts of SOM in surface organic horizons, while soils with fast decay (e.g. AM-dominated) rates may store greater amounts of SOM in deeper mineral horizons. Similarly, soils receiving inputs of fast decay litter (e.g. AM-dominated forests) may store more SOM in low- to mid-latitude forests where mineral-stabilized SOM accounts for a majority of soil C and N, but store less SOM in high latitude forests where climatic constraints on decomposition (Koven, Gustaf, Lawrence, & Weider, 2017) lead to a greater importance of accumulated plant detritus for SOM stocks.

These considerations may explain the lack of consensus on the relationship between mycorrhizal associations and SOM stocks in temperate forests. Averill et al. (2014) compiled a dataset of 1 m deep soil C and N stocks from spatially independent AM- and ECM-dominated plots, which showed that temperate ECM soils store more C than temperate AM soils. In contrast, Zhu, McCormack, Lankau, Egan, and Wurzburger (2018) found no differences in soil C when analyzing upper surface soils from an even larger dataset of spatially independent temperate plots. In both studies, the use of spatially independent plots meant that climate and underlying soil factors could only be accounted for statistically using coarse-scale data (e.g. MAT, MAP). Thus, there is a critical need to hold constant climate and other state factors by examining SOM in areas where both mycorrhizal types co-occur at the same site or across the same landscape (Lin et al., 2016). In addition, there is a need to look beyond "ECM-dominated" and "AM-dominated" systems, as most plots in temperate forests contain mixtures of AM- and ECM-associated tree species (Phillips et al., 2013), and to observe SOM stocks at a higher resolution (i.e. different depths and pools), as SOM storage mechanisms may differ between AM- and ECM-systems.

To evaluate the relationship between mycorrhizal associations and SOM, while holding constant the potentially confounding effects of climate, we quantified 1 m deep soil C and N stocks along "mycorrhizal gradients" (plots varying in the relative abundance of AM vs. ECM trees) nested within three mid-latitude, ca. 100-year-old temperate broadleaf forests varying in their biotic, climatic, and edaphic properties. Because SOM changes on decadal time scales (Smith, 2004), and because of the long lifespan of trees, these forests provide an opportunity to investigate relationships between plant traits and SOM. Moreover, by focusing on broadleaf forests we avoid confounding ECM dominance with leaf habit (i.e. most needle-leaf trees associate with ECM-fungi). In addition to our SOM inventory, we assessed soil C and N in size fractions, microbial residues, and leaf litter quality at one site to assess the relative importance of slow decay vs. fast decay (i.e. MEMS) mechanisms in our study. Given previous evidence of fast decay conditions in AM-dominated temperate broadleaf forests (e.g. Cornelissen et al., 2001; Midgley et al., 2015; Phillips et al., 2013; Taylor, Lankau, & Wurzburger, 2016), we hypothesized that more SOM would be stored in microbe-derived, mineral-associated, and deep pools with increasing AM dominance and decreasing ECM dominance.

2 | MATERIALS AND METHODS

2.1 | Site description

We conducted this research within the Smithsonian's Forest Global Earth Observatory (ForestGEO) network (Anderson-Teixeira et al., 2015) in three temperate broadleaf forests of the Eastern and Midwestern US that vary in their climatic, edaphic properties, and tree species composition, but all contain co-occurring AM and ECM trees (Tables 1 and 2; Figure S1). The sites include Lilly-Dickey Woods (LDW), the Smithsonian Conservation Biology Institute (SCBI; Bourg, McShea, Thompson, McGarvey, & Shen, 2013) and the Smithsonian Environmental Research Center (SERC). These sites are typical of mature secondary forests in Eastern US with most dominant trees having established 85–150 years ago. The forest at LDW has not been disturbed since at least 1900, prior to which it was likely subject to some logging and light pasturing (Lindsey, 1969). Similarly, the majority of trees at SCBI established around 1900 (Bourg et al., 2013). Before then, this area was likely used for cropland or pasture. The majority of land at SERC was pasture that was abandoned in the late 1800s, with a small portion remaining under pasture until the 1930s.

Soils differ among the three sites. At LDW, soils are silt loams on moderate to steep slopes. In Soil Taxonomy (Soil Survey Staff, 1999), these soils are classified as Typic Dystrudepts and Typic Hapludults. Soils at SCBI occur on moderate slopes and are classified predominately as Typic Hapludalfs with gravelly silt loam epipedons over silty clay loam subsoils. Soils at SERC are on gentle slopes with sandy loam epipedons over sandy clay loam subsoil, and are classified as Typic or Aquic Hapludults. Small areas of all three plots occur in footslopes and narrow floodplains that undergo periodic saturation to relatively shallow depth. These soils are Aquic Fragiudalfs, Aquic Hapludalfs, and Fluventic Endoaquepts, at the three sites, respectively.

2.2 | Soil sampling

Each site was divided into 100 × 100 m cells. As the center of each cell, we established a 20 × 20 m plot, though two plots were relocated when sampling was infeasible due to topography or potential interference with ongoing studies. This sampling scheme allowed for a total of 25, 24, and 16 plots at LDW, SCBI, and SERC, respectively (65 total plots). Within each plot, we collected mineral soils in depth increments to 100 cm in June 2010 (SCBI), November 2014 (SERC), and May–July 2015 (LDW). Shallow samples (0–10, 10–20 cm) were collected, in a 3 × 3 grid pattern (i.e. eight evenly spaced points along the plot boundary and one in the plot center), using a 6.35-cm diameter constant-volume corer at LDW and SERC, or by hand excavating within a 0.25 × 0.25 m quadrat and filling with sand to determine volume at SCBI where surface soils were too stony to obtain a core. At LDW, but not SERC or SCBI, the forest floor contains a discontinuous shallow Oe and Oa layer, which we sampled separately from a 0.25 × 0.25 m square. The litter layer (Oi layer) was not assessed at any site due to its potentially high variability across sample dates at the different sites. Thus, throughout we refer to the "O horizon" as the sum of the Oe and Oa layers. The remaining samples (20–50, 50–100 cm) were collected from the corners and middle of the plot (i.e. five locations) using a 5.08-cm diameter auger. At LDW and SCBI, sampling was sometimes impeded by bedrock or a water table before reaching 100 cm depth. The average soil depth was therefore 89 cm at LDW and 77 cm at SCBI, but was unrelated to the dominance of ECM- vs. AM-associated trees ($r = -.16$). Samples from the same depth and plot were composited, returned to the laboratory, and processed immediately (SCBI and SERC) or stored at 4°C for <1 week (LDW).

2.3 | Sample processing and C and N analysis

After recording the total fresh weight of each sample, fine roots (<2 mm) and coarse roots (≥2 mm) were removed from soil samples —by two observers for a period of 30 min—dried (60°C), and weighed, and soil subsamples were dried (105°C) to determine gravimetric moisture. Soil samples were then air-dried and sieved (2 mm), and the mass of all stones (>2 mm) was recorded. Bulk density was calculated as the dry mass of soil (i.e. <2 mm particles) divided by the total sample volume (i.e. the volume of the core before the roots and stones were removed). For deeper soils, where we did not collect intact soil samples, bulk density was estimated in soil profile pits excavated to 1.5–2.0 m at each site using values obtained by the compliant cavity method (Grossman & Reinsch, 2002), which involves a precise determination of the excavated sample volume. Three to six pits were excavated at each site and qualitatively matched to plots based on topographic similarity. On average, bulk densities were 0.85, 0.82, and 1.04 in upper surface soils at LDW, SCBI, and SERC, respectively, and 1.16, 1.33, and 1.46 at ca. 75 cm. Soils were ground to a powder and analyzed for total C and N on an

TABLE 1 General properties of the three study sites

Site	Latitude	Longitude	MAT (°C)	MAP (mm/year)	Plot size (Ha)	% Ectomycorrhizal trees[a]
LDW	39°14′N	86°13′W	11.6	1,203	25	72
SCBI	38°54′N	78°9′W	12.9	1,001	25.6	44
SERC	38°53′N	76°34′W	13.2	1,068	16	32

Climate data for Lilly-Dickey Woods, Indiana, USA (LDW), Smithsonian Conservation Biology Institute, Virginia, USA (SCBI), and Smithsonian Environmental Research Center, Maryland, USA (SERC) obtained from Anderson-Teixeira et al. (2015).
[a]Calculated as percent of total basal area in plot.

TABLE 2 Percentage of total basal area (% BA) for most common (>1% BA) arbuscular mycorrhizal-associated trees (AM species) and ectomycorrhizal-associated trees ([ECM] species) at Lilly-Dickey Woods, Indiana, USA (LDW), Smithsonian Conservation Biology Institute, Virginia, USA (SCBI), and Smithsonian Environmental Research Center, Maryland, USA (SERC)

	LDW		SCBI		SERC	
	Species	% BA	Species	% BA	Species	% BA
AM species	*Acer saccharum*	20.3	*Liriodendron tulipifera*	41.4	*Liriodendron tulipifera*	33.3
	Acer rubrum	2.0	*Fraxinus americana*	5.1	*Liquidambar styraciflua*	16.0
	Nyssa sylvatica	1.6	*Nyssa sylvatica*	2.1	*Fraxinus pennsylvanica*	5.4
	Liriodendron tulipifera	1.4	*Juglans nigra*	2.1	*Acer rubrum*	4.8
	Fraxinus americana	1.2	*Acer rubrum*	1.0	*Platanus occidentalis*	3.5
					Ulmus rubra	1.1
					Nyssa sylvatica	1.1
ECM species	*Quercus prinus*	38.8	*Quercus alba*	8.8	*Fagus grandifolia*	11.2
	Quercus rubra	8.7	*Quercus rubra*	8.4	*Quercus alba*	5.6
	Quercus velutina	7.8	*Quercus velutina*	8.1	*Carya alba*	5.4
	Quercus alba	5.2	*Carya glabra*	4.8	*Quercus rubra*	1.9
	Fagus grandifolia	4.7	*Quercus prinus*	3.4	*Quercus falcata*	1.8
	Carya glabra	3.8	*Carya tomentosa*	3.1	*Carpinus caroliniana*	1.8
			Carya ovalis	1.8	*Carya glabra*	1.6
			Carya cordiformis	1.8	*Quercus velutina*	1.6
			Fagus grandifolia	1.2		

elemental combustion system (LDW: Costech ECS 4010, Costech Analytical Technologies, Valencia, CA, USA; SCBI and SERC: Thermo Flash 1112 Elemental Analyzer, Bremen, Germany). At LDW, we additionally analyzed all soils for soil pH (8:1 ml 0.01 M $CaCl_2$:g soil) using a bench-top pH meter. To calculate soil C and N stocks, concentrations were multiplied by the bulk density and sample depth increment.

2.4 | Soil organic matter characterization

To assess the stability and origin of SOM, we conducted an additional suite of measurements on surface soils (0–10 cm) at LDW. First, we separated SOM into mineral-associated organic matter (MAOM) and particulate organic matter (POM) using the size fractionation procedure (Cambardella & Elliott, 1992) as modified by Bradford, Fierer, and Reynolds (2008). Given that organic matter in the clay and silt fraction has a longer residence time and a higher abundance of microbial-derived compounds (Anderson & Paul, 1984; Grandy & Neff, 2008), this method separates the slow-cycling, microbe-derived, silt- and clay-associated SOM (i.e. MAOM) from the fast-cycling, plant-derived, sand-associated and free particulate SOM (i.e. POM). Briefly, we dispersed soil samples in 5% (w/v) sodium hexametaphosphate for 20 hr on a reciprocal shaker and washed each sample through a 53-μm sieve. The fraction retained on the sieve was considered POM while the finer fraction that passed through the sieve was considered MAOM. POM and MAOM samples were dried, ground, and analyzed for total C and N. We additionally determined soil texture using a standard hydrometer procedure (Ulmer, Knuteson, & Patterson, 1994).

Second, we quantified amino sugars. Because amino sugars are important components of microbial cell walls, but are not significantly produced by higher plants and soil animals (Amelung, 2001), these compounds are reliable molecular biomarkers for determining contribution of microbial-derived compounds to SOM pools (Amelung, 2001; Guggenberger, Frey, Six, Paustian, & Elliott, 1999). Amino sugars were extracted, purified, converted to aldononitrile acetates, and then quantified with internal standard myo-inositol (Liang, Read, & Balser, 2012; Zhang & Amelung, 1996). We quantified the abundance of three amino sugars: glucosamine (GluN), galactosamine (GalN), and muramic acid (MurA). Because of the predominant fungal origin of GluN in soils and the unique bacterial origin of MurA (Amelung, 2001; Guggenberger et al., 1999), we used the ratio of GluN-to-MurA as an index of the fungal vs. bacterial residues of SOM. GalN is generally considered to have a predominant bacterial origin (Glaser, Turrión, & Alef, 2004; Guggenberger et al., 1999), but this interpretation is currently disputed (Engelking, Flessa, & Joergensen, 2007). Thus, we use the ratio of GluN-to-GalN to describe overall amino sugar accumulation patterns rather than differences in fungal vs. bacterial residues (sensu Liang, Gutknecht, & Balser, 2015).

2.5 | Leaf litter quality

We collected litter from the nineteen most dominant species (by basal area) at LDW in October and November 2015. We visited the site once per week, before major rain events, for the duration of senescence and leaf-fall to collect litter. We targeted species with litter baskets and supplemented with freshly senesced litter from the

ground where appropriate. For each species, litter was collected from at least three different locations in the site, homogenized, air-dried ground in triplicate subsamples, and analyzed for C and N on an elemental combustion system (Costech ECS 4010, Costech Analytical Technologies, Valencia, CA, USA). We used a sequential extraction as in Moorhead and Reynolds (1993) to estimate lignin content. Specifically, we removed ethanol- and water-soluble compounds in a sonicating water bath at 60°C. The remaining residue was, dried (60°C), weighed, treated with 72% H_2SO_4 at 30°C for 1 hr, diluted to 4.5% H_2SO_4, and autoclaved (121°C) for 1 hr. The mass of the remaining residue minus the ash remaining after 24 in a muffle furnace at 500°C was considered lignin. Thus, our definition of "lignin" refers to insoluble material that resisted degradation by a strong acid.

2.6 | Plot characterization

The total basal area of all trees and all ECM-associated tree stems was determined within a 30 m radius of each plot center. We considered this radius large enough to avoid edge effects around our 20 × 20 m plot, given that leaf litter can fall far from the tree crown and roots can extend up to 22 m from a parent stem (Jones et al., 2011). Mycorrhizal associations were determined based on published records (Phillips et al., 2013). ECM dominance was calculated as the percentage of ECM-associated basal area relative to the total basal area. Tree species known to associate with both AM- and ECM-fungi and tree species with unknown mycorrhizal associations accounted for 1% or less of the basal area. Thus, low values of ECM dominance indicate AM-dominated plots. To determine whether ECM dominance is related to topographic factors and to understand the extent to which topography relates to SOM properties, we quantified the slope, aspect, and elevation of each plot, using a digital elevation model (National Elevation Dataset; Gesch, 2007) with a 1/9 arcsec (~3 m) horizontal resolution. Spatial analyses were performed using ESRI's ArcGIS Desktop 10.4 software.

2.7 | Data analysis

By sampling mycorrhizal gradients nested within three sites, our study design uniquely allowed us to isolate the relationship between ECM dominance and SOM properties without the potentially confounding effects of climate or parent material. However, other factors such as topography, productivity, or soil texture could still covary with ECM dominance at the plot-scale. For example across our three sites, we noted a weak correlation between ECM dominance and total basal area, and between total basal area and slope (Table S1). To account for the effects of topography and total basal area, we evaluated the relationship between ECM dominance and SOM properties by fitting linear mixed models with ECM dominance, total basal area, and slope as fixed factors. Additionally, we included site and the interaction between site and ECM dominance as random factors. However, the interaction term was dropped in every case but one, as it was nonsignificant and, often, its inclusion resulted in model estimation errors. We chose to include slope, rather than other topographic variables, because previous research suggests it is an important controller of soil C and N stocks (Weintraub, Porder, Cleveland, Asner, & Townsend, 2015), and because preliminary correlations confirmed a slight relationship between SOM properties and slope in our study (Table S1). Soil texture was not included as it was not available for the full dataset and, at LDW, we found no evidence that ECM dominance was related to % clay, % silt or % sand ($-.13 < r < .12$). As response variables, we modeled soil C stock, N stock, and C:N integrated across both the mineral soil profile and the whole soil profile (including the O horizon). To investigate how ECM dominance relates to the depth distribution, we modeled the proportion of C and N stored in the O horizon + the top 10 cm of the soil profile. Additionally, we quantified the Pearson's correlation coefficient for the relationship between ECM dominance and soil C or N stock for each cumulative sample depth (i.e. O horizon, O horizon – 10 cm, O horizon – 20 cm, etc.). For all models, we tested whether residuals met assumptions of normality (Shapiro-Wilk test) and homoscedasticity (visual assessment of residual plots) and ln-transformed data when it was required to meet these assumptions. We discarded data from one low elevation plot at SERC where a potentially high water table may override our independent variables. This plot, which had an ECM dominance of 12%, had a C (31.2 kg C/m^2) and N stock (2.5 kg N/m^2) that were 83% and 69% higher, respectively, than the next highest value at the site and, therefore, caused severe violations of the test assumptions. We report mixed model coefficients, type 3 tests of significance, and partial R^2 values (Edwards, Muller, Wolfinger, Qaqish, & Schabenberger, 2008) to examine the variation explained by ECM dominance after accounting for covarying factors. However, to intuitively visualize patterns, we plotted site-specific bivariate relationships between ECM dominance and untransformed soil variables.

For factors measured only at LDW—organic horizon stocks, soil fractions, amino sugars, and soil pH—we fit a general linear model with ECM dominance, total basal area, and slope as predictor variables. For soil fraction, amino sugar, and pH analyses, we also included sand content (1 – % silt and clay). We used sand instead of clay content as a metric of soil texture because sand (CV = 36%) contributed more than clay (CV = 10%) to the variation in soil texture. We report type 3 tests of significance and squared partial correlations to examine the variation explained by ECM dominance after accounting for covarying factors. O horizon C and N stocks were square-root transformed to meet assumptions of homoscedasticity. All analyses were performed using SAS v. 9.4 (Proc Mixed, Proc GLM, and Proc Reg; SAS Institute, Cary, NC, USA).

3 | RESULTS

3.1 | Soil carbon and nitrogen stocks across a mycorrhizal gradient

Integrated across the 1 m soil profile—including the organic horizon—soil C and N stocks were strongly associated with the dominance

of ECM-associated trees (Figure 1; Table S2). Soil C:N ranged from 9 to 21 and was positively associated with ECM dominance ($R^2_{partial}$ = .38, p < .001). However, this relationship was not driven by greater C in ECM- compared to AM-dominated soils; ECM dominance was negatively related to the amount of total C stored to 1 m depth ($R^2_{partial}$ = .12, p = .01). Instead, the positive relationship between ECM dominance and soil C:N was driven by a strong negative association between ECM dominance and soil N stocks ($R^2_{partial}$ = .50, p < .001). The relationship between ECM dominance and soil C stocks exhibited some site dependence, as it was less negative at LDW than at SERC and SCBI. Soil C and N patterns were qualitatively similar when analyzing only mineral soil profiles—i.e. omitting the O horizon at LDW from the analysis—although the slopes relating ECM dominance to soil C stocks appeared more consistent among the sites (Figure S2; Table S2).

Fine root biomass was positively related to ECM dominance ($F_{1,56}$ = 13.8, p < .001) and this effect persisted at each sample depth (Figure S3). In addition, this effect was strongest at SCBI and weakest at SERC (site × ECM dominance: $F_{2,56}$ = 4.9, p = .01). Topography and total basal area were less important for explaining SOM properties. Slope was significantly negatively related to soil N (p = .03), marginally related to soil C (p = .06), and unrelated to soil C:N (p = .97) and fine root stocks ($F_{1,56}$ = 1.6, p = .21). Total basal area was marginally negatively related to soil C (p = .06) and N (p = .09), and unrelated to soil C:N or root stocks (p > .62).

3.2 | SOM patterns with depth

On average, 41% of soil C and 35% of soil N was stored in the top 10 cm of soil—including the O horizon where present. However, the depth distribution of SOM depended on mycorrhizal dominance. Specifically, ECM dominance was positively associated with the proportion of soil C ($R^2_{partial}$ = .24, p < .001; Figure 2a) and N ($R^2_{partial}$ = .10, p = .01; Figure S4a) stored in the top 10 cm. Moreover, despite the general negative relationship between ECM dominance and total mineral soil C and N, there was a strong positive association between ECM dominance and O horizon C ($F_{1,21}$ = 34.2, p < .001; Figure S5a) and N stocks ($F_{1,21}$ = 34.7, p < .001; Figure S5b) at the site with an O horizon. No other factor significantly related to O horizon C or N stocks at LDW, or the proportion of C and N stored in the top 10 cm (p > .12) across all sites. The relationship between ECM dominance and SOM stocks depended on sample depth. The correlation coefficients relating ECM dominance to soil C and N stocks decreased, switching from positive to negative, as sample depth increased (Figures 2b and S4b), and this switch occurred at shallower depths for N than for C.

3.3 | Soil and leaf litter properties at LDW

The concentrations of all measured amino sugars in the top 10 cm of mineral soils were negatively related to ECM dominance (p < .001; Figure 3a; Table S3). ECM dominance was significantly, negatively related to GluN (p < .001), GalN (p < .001), and MurA

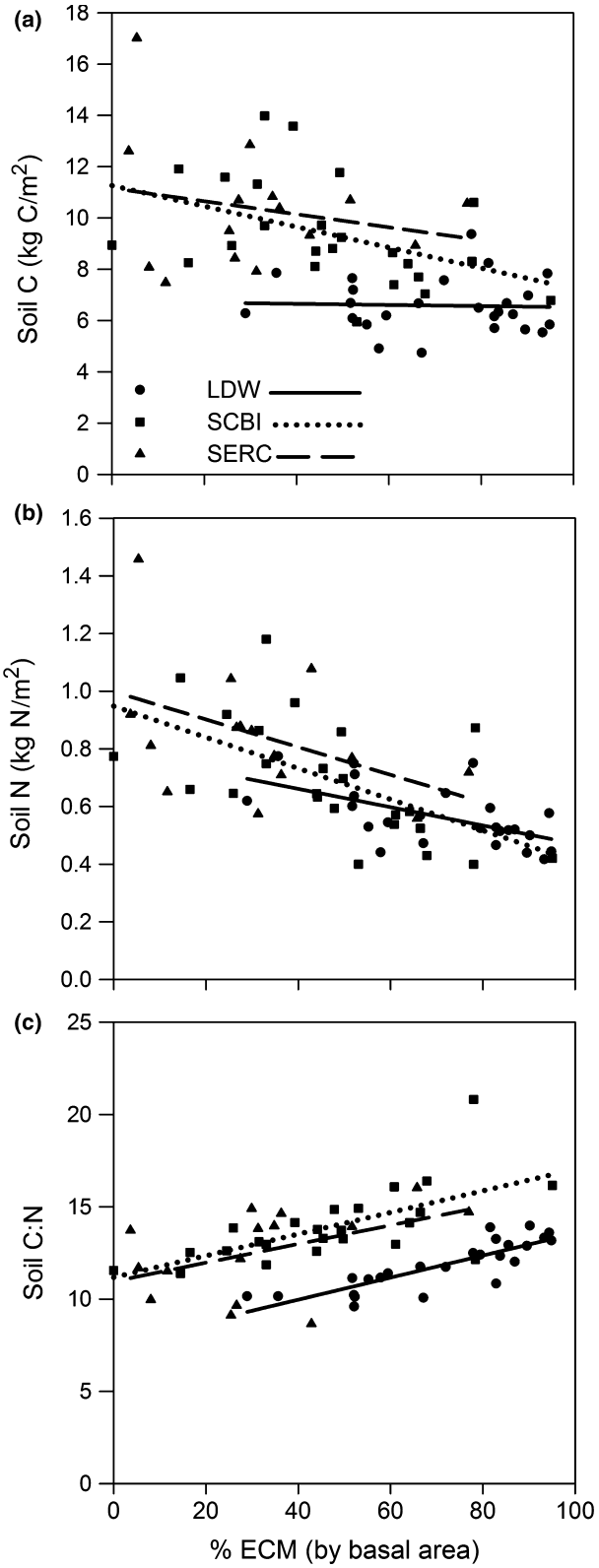

FIGURE 1 Soil carbon stock (a), nitrogen stock (b), and carbon-to-nitrogen ratio (c) to 1 m depth, including the organic horizon, along a gradient of ectomycorrhizal-associated tree dominance at Lilly-Dickey Woods, Indiana, USA (LDW; n = 25), Smithsonian Conservation Biology Institute, Virginia, USA (SCBI; n = 24), and Smithsonian Environmental Research Center, Maryland, USA (SERC; n = 15)

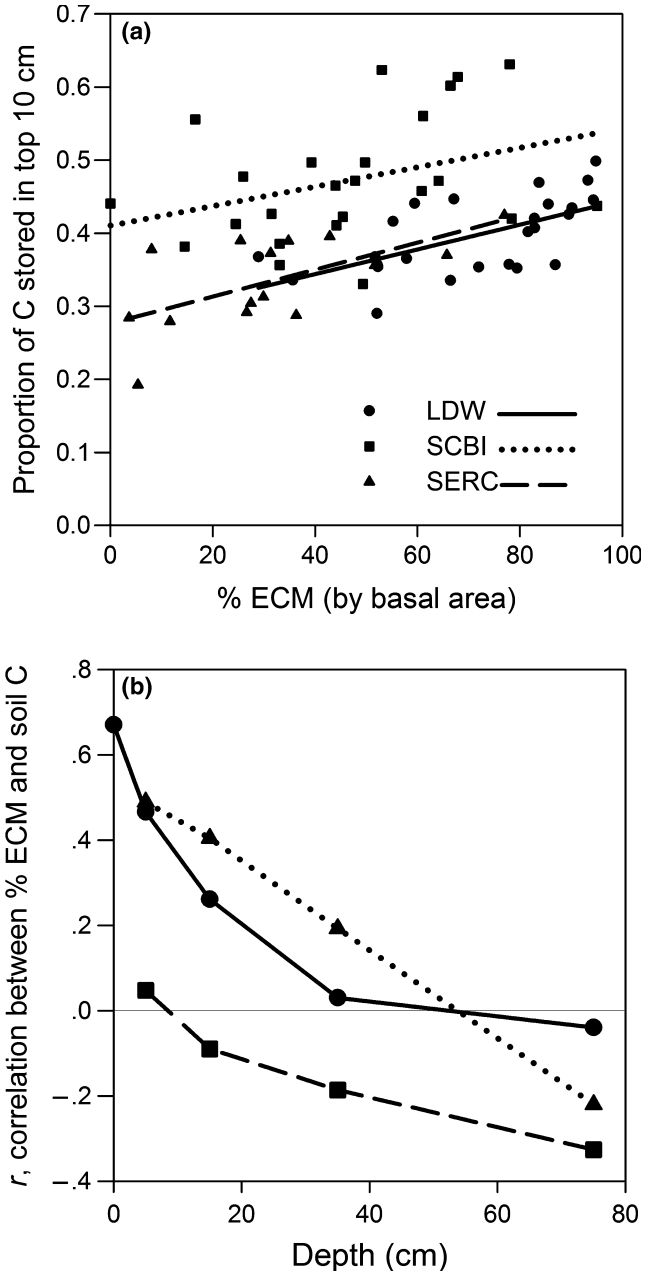

FIGURE 2 Proportion of carbon, relative to the 1 m carbon stock, stored in the top 10 cm of mineral soil plus the organic horizon along a gradient of ectomycorrhizal-associated tree dominance (a) and the Pearson's correlation coefficients relating ectomycorrhizal tree dominance to soil carbon stocks as sample depth increases (b) at Lilly-Dickey Woods, Indiana, USA (LDW; $n = 25$), Smithsonian Conservation Biology Institute, Virginia, USA (SCBI; $n = 24$), and Smithsonian Environmental Research Center, Maryland, USA (SERC; $n = 15$). Depth refers to the mid-point of each sample increment (0–10, 10–20, 20–50, and 50–100 cm), except for Depth = 0 which refers to the O horizon

($p < .001$). Amino sugars were unrelated to other factors ($p > .11$) with the exception of GluN which tended to increase with total basal area ($p = .08$), and MurA which tended to increase with silt and clay content ($p = .09$).

Ectomycorrhizal tree dominance was also related to the composition of microbial biomarkers. While the ratio of GluN-to-MurA was not predicted by ECM dominance ($p = .13$; Table S3), the ratio of GluN-to-GalN was strongly positively related to ECM dominance ($p < .001$; Figure 3b). Total basal area, topography, and silt + clay were all unrelated to these variables ($p > .20$).

Soil organic matter fractions were also related to mycorrhizal associations. ECM dominance was strongly negatively related to the amount of N stored in the MAOM pool ($p < .001$; Figure 3c; Table S3), but was not significantly related to MAOM-C ($p = .20$), POM-N ($p = .42$), or POM-C ($p = .53$). Mineral-associated N and C concentrations were positively related to amino sugar concentrations (Figures 4 and S6). Total basal area and slope were not significant predictors of any soil fraction ($p > .31$). Silt and clay content were positively related to MAOM-N ($p = .08$) and negatively related to POM-C ($p = .06$).

The mycorrhizal association of dominant trees found at all three sites was associated with leaf litter chemistry at LDW (Figure S7). Specifically, leaf litter from AM-associated trees tended to have lower lignin:N ratios than ECM-associated trees ($p = .001$), driven by higher lignin content ($p < .001$) and nonsignificantly lower N content ($p = .36$) in leaf litter from ECM-associated trees ($p < .001$). In addition, AM-associated litters tended to have a higher concentration of soluble compounds ($p = .03$).

Lastly, soils at LDW reflected a soil pH gradient. Soil pH ranged from 3.6 to 5.4 in surface soils (0–10 cm), from 3.8 to 4.7 in subsoils (50–100 cm) and was always lower in ECM- compared to AM plots ($p < .01$).

4 | DISCUSSION

Shifts in the relative abundance of AM and ECM trees owing to climate change, invasive species, and altered disturbance regimes, among other factors, are hypothesized to impact ecosystem C and nutrient cycling, resulting in important global change feedbacks (Phillips et al., 2013; Sulman et al., 2017). Previous investigations of mycorrhizal effects on SOM stocks have focused on upper surface soils, have looked across broadly distributed sites where climate factors potentially covary with mycorrhizal associations, or have compared "ECM-dominated" and "AM-dominated" forests (e.g. Averill et al., 2014; Phillips et al., 2013; Taylor et al., 2016; Zhu et al., 2018). Here, we examined how SOM properties vary across a mycorrhizal gradient both within sites where AM and ECM trees co-occur, and vertically within the soil profile. While our results agree with previous studies suggesting that ECM dominance is positively related to soil C:N (e.g. Averill et al., 2014; Lin et al., 2016; Zhu et al., 2018), we find no evidence that this pattern is driven by greater C storage in ECM-dominated soils when considering 1 m deep soil profiles in a temperate broadleaf study system. Our results indicate that AM, not ECM, soils store greater amounts of C and N overall in temperate broadleaf forests and, importantly, greater SOM in the putatively most stable pools—e.g. greater C and N in subsoils and greater N in

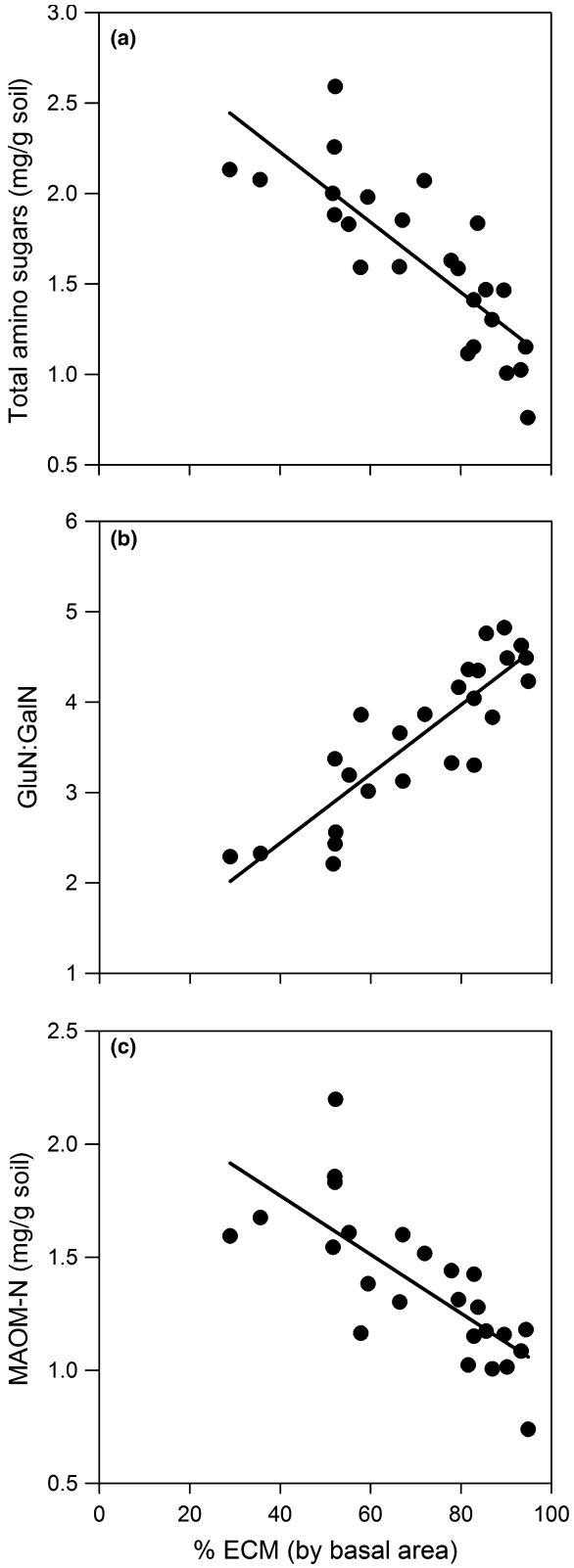

FIGURE 3 Total amino sugar concentrations (a; $R^2_{partial}$ = .63), the ratio of glucosamine (GluN)-to-galactosamine (GalN) (b; $R^2_{partial}$ = .54) and the concentration of mineral-associated organic matter nitrogen (MAOM-N) (c; $R^2_{partial}$ = .52) along a gradient of ectomycorrhizal-associated tree dominance at Lilly-Dickey Woods, Indiana, USA (LDW; n = 25)

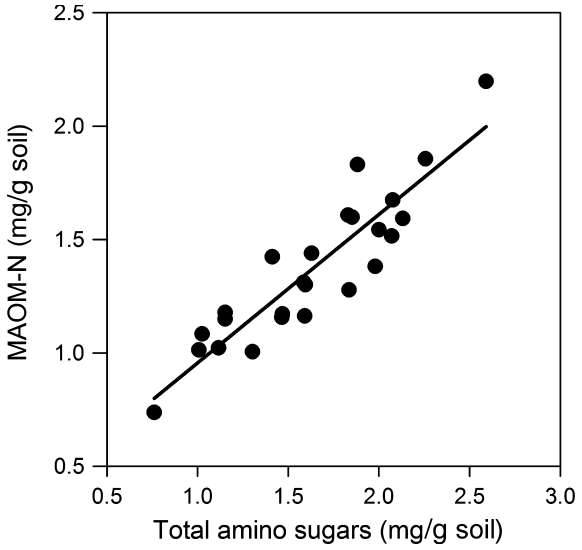

FIGURE 4 The relationship between total amino sugars and mineral-associated organic matter nitrogen (MAOM-N; R^2 = .82) at Lilly-Dickey Woods, Indiana, USA (LDW; n = 25)

mineral-associated SOM. In addition, amino sugar patterns—i.e. GluN, GalN, and MurA—suggest a greater contribution of microbial residues to SOM in AM-dominated soils. Taken together with our observation of higher quality leaf litter—i.e. lower lignin:N—for AM-associated trees, and with previous observations of faster organic matter decay in AM-dominated Eastern US temperate forests (Averill & Hawkes, 2016; Midgley et al., 2015), our results support the hypothesis that systems with rapid decomposition lead to stable SOM formation by promoting microbial production (Cotrufo et al., 2013). To the extent that the vertical distribution and mineral association of SOM affect turnover times and modulate responses to environmental perturbations (Schmidt et al., 2011), AM vs. ECM dominance may importantly determine the sensitivity of soil C and N stocks to global change.

4.1 | Soil carbon and nitrogen stocks

One of the most striking patterns from our gradient analysis is the consistent, positive relationship between ECM dominance and soil C:N, a pattern that has been reported for AM- vs. ECM-dominated areas (e.g. Averill et al., 2014; Lin et al., 2016) and for gradients of ECM dominance (Cheeke et al., 2016). In agreement with a recent broad-scale analysis of SOM in surface soils of the US Forest Service's Forest Inventory and Analysis plots (Zhu et al., 2018), our analysis of site-level mycorrhizal gradients and deeper soil profiles reveals that this soil C:N pattern is explained by differences in N, rather than C. This result is critical, as the finding of greater C:N in ECM-systems (Averill et al., 2014) has been commonly interpreted as evidence of greater soil C storage overall (e.g. Averill, 2016; Averill & Hawkes, 2016; Averill et al., 2014; Kotowska, Leuschner, Tridiati, Meriem, & Dietrich, 2015; Peay, 2016; Pringle, 2016).

Lower N stocks in ECM stands confirm the long-held view that AM- and ECM-plants and associated microbes differ in their acquisition, use of, and effects on soil nutrients (Brzostek et al., 2014; Chapman et al., 2006; Lin et al., 2016; Phillips et al., 2013; Read & Perez-Moreno, 2003). Differences in N outputs or inputs likely do not account for differences in soil N stocks given that N outputs (via leaching) are typically greater, not less, in AM forests (Lovett, Weathers, & Arthur, 2002; Midgley & Phillips, 2014; but see Christiansen et al., 2010), and the fine scale of our analysis (i.e. within-site) should preclude differences in N inputs via N deposition. We did note higher pH in AM-dominated soils, which could favor non-symbiotic N-fixation (Limmer & Drake, 1996), but AM soils have high inorganic N availability compared to ECM soils (Phillips et al., 2013), which should constrain N-fixation (Vitousek, Menge, Reed, & Cleveland, 2013). Instead, our results support previous evidence that ECM-associated trees are able to take up and retain greater amounts of N (Goodale, 2017) by mining N directly from soil organic matter (Courty et al., 2010; Phillips, Finzi, & Bernhardt, 2011; but see Pellitier & Zak, 2017), resulting in a redistribution of N from mineral soils to plant biomass and organic soil horizons.

4.2 | Patterns across depth

We find that AM soils store a greater proportion of C and N at depth while ECM plots contain a greater proportion of C and N in upper soil layers. Because of this, we observe greater soil C and N in ECM plots when analyzing only upper surface soils—a finding which agrees with the Slow Decay Hypothesis, as well as previous studies (Averill et al., 2014; Soudzilovskaia et al., 2015)—but we observe less C and N in ECM soils when analyzing the 1 m soil profile. This finding supports the hypothesis of a tradeoff between C storage in shallow organic vs. deeper mineral horizons (Vesterdal, Elberling, Christiansen, Callesen, & Schmidt, 2012), and demonstrates that sampling depth can dramatically alter the observed relationship between vegetation and SOM properties. We therefore caution against the common approach of inferring plant-driven differences in total SOM stocks from shallow soil samples alone.

We propose three hypotheses that may explain differences in SOM depth between AM- and ECM-dominated plots. (i) Researchers have hypothesized that either ECM-saprotroph competition or recalcitrant inputs should suppress decomposition in ECM soils, leading to a buildup of organic matter (Averill, 2016; Gadgil & Gadgil, 1971; Orwin et al., 2011; Phillips et al., 2013). Given that ECM-fungi and plant inputs mostly exert influence near the soil surface (Lindahl et al., 2007), these mechanisms may explain SOM accumulation in topsoil, but not subsoil in ECM-dominated plots. (ii) Differences in root or hyphal traits could influence the formation and decomposition of deep SOM. Although we observed greater root biomass across the 1 m profile in ECM-dominated plots, AM roots and hyphae often have higher N content and turnover rates (Lin et al., 2016; Read & Perez-Moreno, 2003; Veresoglou, Chen, & Rillig, 2012), which could promote greater N inputs and microbial growth in deep AM-dominated soils. Alternatively, ECM dominance may lead to deep SOM losses if root-induced decay exceeds root inputs to deep soils (Fontaine et al., 2007; Mobley et al., 2015; but see De Graaff, Jastrow, Gillette, Johns, & Wullschleger, 2014). (iii) Differences in organic matter transport may underlie differences in the vertical distribution of SOM. For example, higher quality organic inputs in AM soils could facilitate the production of microbial compounds, which are more mobile in the soil profile due to their small size and high solubility compared to plant compounds (Kleber et al., 2015). Alternatively, high-quality inputs or less acidic soils in AM plots could favor anecic earthworms or other meso-fauna capable of mixing the soil profile (Bohlen et al., 2004). More research is needed to discern these potential mechanisms.

While the sensitivity of deep SOM pools to global change is still a matter of debate (e.g. Bernal et al., 2016), deep soil C typically has a slower turnover time and potentially a greater long-term stability than soil C at the surface (Gaudinski, Trumbore, & Davidson, 2000; Schmidt et al., 2011). Thus, our finding that AM soils store greater SOM at depth implies greater long-term storage and greater SOM stability in AM-dominated systems.

4.3 | Microbial biomarkers and mineral-associated organic matter

We observed a positive association between AM dominance and the concentrations of all measured amino sugars—compounds that represent an integrative measure of microbial contributions to SOM over time (Glaser et al., 2004). This pattern supports that the growth and turnover of the soil microbial biomass is greater in AM-dominated soils. Such effects could be driven by the high soil nutrient availability or high organic input quality often observed in AM-dominated forests (e.g. Lin et al., 2016; Phillips et al., 2013), given that these conditions can enhance microbial growth efficiency and growth rate (Manzoni et al., 2012; Roller & Schmidt, 2015). Alternatively, differences in microbial growth and turnover may reflect differences in the microbial community composition (Kallenbach et al., 2016). In agreement with previous studies on the active soil microbial community (Cheeke et al., 2016), we observed differences in the GluN:GalN ratio indicating differences in the microbial community composition across a gradient of ECM dominance.

We found that the concentration of amino sugars is strongly and positively linked to the amount of N stored in the MAOM. This observation corroborates the ample body of research showing that microbial compounds are particularly susceptible to protection by silt and clay minerals (e.g. Bradford et al., 2013; Grandy & Neff, 2008). Moreover, this pattern along with our observation of greater MAOM-, but not POM-N, in AM-dominated plots supports predictions from the MEMS Hypothesis (Cotrufo et al., 2013) that AM dominance enhances MAOM by facilitating the production and stabilization of microbial residues. Because MAOM has a slower turnover rate (e.g. Anderson & Paul, 1984) and is often protected from microbial degradation, and because AM-fungi have also been shown to enhance the protection of SOM in soil aggregates (Rillig, 2004), we suggest that SOM may be more stable in AM-dominated plots. As

these analyses focused on one site, further work should determine the generality of these patterns across sites differing in their climate, soil properties, and ECM dominance.

4.4 | Research priorities

Our analysis demonstrates a tight within-site correlation between the dominance of AM- vs. ECM-associated trees and SOM properties, independent of topography and total tree biomass. We acknowledge that our study was observational and we cannot rule out that pre-existing differences in soil conditions contributed to the observed patterns—e.g. if AM trees preferentially establish in more fertile soils than ECM trees. However, while plant establishment is undoubtedly influenced by resource availability, there is ample evidence that plants reinforce patterns in nutrient and C cycling via their nutrient use strategies (Hobbie, 2015; Hobbie et al., 2007; van Breemen et al., 2000). Indeed, evidence from plantations and common gardens suggest that AM and ECM trees cause divergent effects on C and N cycling (Lin et al., 2016)—often, but not always, consistent with the upper surface soil patterns reported here (e.g. Hobbie et al., 2007; Mueller et al., 2012, 2015; Vesterdal, Schmidt, Callesen, Nilsson, & Gundersen, 2008). However, the mechanisms underlying patterns observed in common garden studies are varied (Mueller et al., 2015), largely untested, and likely depend on soil depth (Vesterdal et al., 2012). Thus, to validate the hypotheses put forth in this study, there is a need for common gardens and other experiments that investigate relationships between litter quality and decay rates, microbial growth and turnover, and SOM stabilization in surface and subsurface soils.

While our data support recently proposed mechanisms about stable SOM formation, we note that other factors could covary with ECM dominance and, therefore, other mechanisms may also be important. For example at LDW, we find that ECM soils are more acidic, especially at the soil surface suggesting an influence of ECM trees. Differences in soil pH could mediate slow decay in ECM-systems, but could also influence mineral-organic associations, N-fixation, soil microbial communities, or other factors. Thus, we recommend that future studies experimentally manipulate factors to determine the mechanisms underlying our observed differences in SOM stocks and stability. Such studies might also allow researchers to tease apart the relative importance of different factors—e.g. leaf, root or fungal litter, or soil fertility—in facilitating microbe-mediated SOM stabilization. Lastly, comparisons of global change effects between AM- and ECM-systems would enable researchers to assess the stability of our observed patterns, and whether mycorrhizal dominance might mediate ecosystem responses to global change (Terrer, Vicca, Hungate, Phillips, & Prentice, 2016).

Our goal was to provide a high-resolution characterization of SOM variation in temperate broadleaf forests. As such, our study naturally focused on the ECM-associated tree species that dominate such forests—i.e. members of the order Fagales. Future work, motivated to understand the role of ECM trees per se, could look across a wider phylogenetic range of ECM-associated tree species. However, a more important direction for enhancing our understanding of spatial variation in SOM would be to look across a broader climatic gradient to determine whether the direction and magnitude of mycorrhizal effects change with climatic context. For example, we found that ECM dominance was strongly related to C storage in the O horizon, perhaps due to litter recalcitrance (Cornelissen et al., 2001) or N limitation of saprotrophic decomposers (Averill & Hawkes, 2016). Because of this, the site where an O horizon was present (i.e. LDW) exhibited a less negative relationship between ECM dominance and soil C when the O horizon was included in total SOM stock (i.e. mineral soil + O horizon) calculations. Thus, ECM dominance may enhance organic matter storage in systems where the organic horizon accounts for a greater proportion of total SOM storage.

4.5 | Implications for soil organic matter models

Our results have important implications for land surface models, which are faced with the difficulty of representing an intractable amount of biotic factors. In our dataset, it is notable that the relationship between ECM dominance and SOM properties follows a general pattern in three Eastern US temperate broadleaf forests. Given the ability of mycorrhizal associations to integrate across a suite of plant and microbial traits, and provided these patterns hold over wider climatic and edaphic gradients, our results suggest that representing mycorrhizal associations in models is an efficient way to incorporate biotic factors into our predictions of SOM dynamics (Sulman et al., 2017). By using forest inventory data (e.g. US Forest Service's "FIA plots"; Zhu et al., 2018) or remote sensing (Fisher et al., 2016), land surface models can incorporate these effects based on the relative abundance of AM- or ECM-associated trees in a given community (Shi, Fisher, Brzostek, & Phillips, 2016). Given that climatic shifts (Iverson, Schwartz, & Prasad, 2004), invasive pests (Lovett et al., 2016), and failures of oak regeneration (Abrams, 1992), among other factors, are removing dominant AM and ECM tree species from forests, representing mycorrhizal abundances may facilitate broad predictions of how changing plant communities will alter SOM in forest ecosystems.

ACKNOWLEDGEMENTS

This material is based upon work supported by the Smithsonian Tropical Research Institute. The Center for Tropical Forest Science-Forest Global Earth Observatory supported the establishment of these plots and the CTFS-ForestGEO Grants Program funded the soil analyses. LDW is part of Indiana University's Research and Teaching Preserve. We also acknowledge the support of the U.S. Department of Energy Office of Biological and Environmental Research, Terrestrial Ecosystem Science Program (Award# DE-SC0016188), the US National Science Foundation Ecosystem Studies Program (1153401), and the National Natural Science Foundation of China (41471218). We thank D. Agudo, T. Beresky, D. Du, P. Escobar, L. Podzikowski, X. Shen, and the many technicians who

contributed to this project in the field and laboratory, and we thank B. McShea, N. Bourg, and G. Parker for coordinating and sharing data from the forest inventories at SCBI and SERC. Lastly, we thank members of the Phillips lab, M. Bradford, the anonymous reviewers, and the editor, F. Cotrufo, for their helpful comments. The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

MC and RP developed the project. MC, BT, CL, KC, and DJ collected or contributed data. MC analyzed the data. MC wrote the first draft and RP, BT, CL, KC, and DJ edited the manuscript.

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SUPPORTING INFORMATION

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How to cite this article: Craig ME, Turner BL, Liang C, Clay K, Johnson DJ, Phillips RP. Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. *Glob Change Biol*. 2018;00:1–14. https://doi.org/10.1111/gcb.14132