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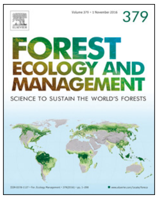

Tree basal area and conifer abundance predict soil carbon stocks and concentrations in an actively managed forest of northern New Hampshire, USA

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ABSTRACT

Although northern temperate forests account for a substantial portion of global soil carbon stocks, the relationship between soil carbon and management remains unclear. As the active management of forests and associated forest product industries is often cited as a tactic to offset global greenhouse gas emissions, quantifying the effect of management activities on soil carbon pools is paramount to mitigating future climate change. Hence, our goal was to identify commonalities among the spatial variability, potential drivers, and total soil carbon stocks and concentrations at two locations with different management histories in an actively managed northern U.S. mixed wood forest. We measured the carbon pools of two soil profiles, separated into three layers, within 98 0.04-hectare plots in each of the two management areas. We scaled soil and aboveground carbon to estimate total carbon stocks in each area and examined plot-level soil carbon data in relation to landscape and vegetation factors to evaluate potential drivers of soil carbon. Soil carbon represented approximately 40% of the total carbon in both areas. Total soil carbon was similar between the two areas, but the vertical distribution of carbon differed, with more mineral soil carbon in the area with greater coniferous basal area and fewer harvests in the last 80 years. Soil carbon was moderately variable at small spatial scales (< 10 m) and showed little or no spatial structure at the scale of hundreds of meters. Aboveground basal area and the proportion of coniferous vegetation were positively related to soil carbon, matching our expectations. Our best models to predict variation in soil carbon among plots also included elevation, composite topographic index, and pH, but not all relationships matched theoretical expectations. Topography and elevation influenced soil horizon depths and bulk density, and therefore had greater importance for total soil carbon than for carbon concentrations. Although many questions remain, the management activities in northern temperate forests appear to be a slow-moving driver of the relatively large but stable soil carbon pool – especially through management influences on site productivity and tree species composition.

1. Introduction

1.1. Forest soil carbon and global change

Globally, there is twice as much carbon stored in soil than in vegetation (Scharlemann et al., 2014). Approximately two thirds of soil carbon is soil organic carbon (SOC), which is the carbon in soils that ultimately originated from vegetation (Scharlemann et al., 2014). As 70% of global SOC is found in forests (Jobbagy and Jackson, 2000), forest systems in particular have the potential to help mitigate climate change by storing carbon dioxide fixed by plants in biomass and soil (Canadell and Raupach, 2008; Mckinley et al., 2011; Pan et al., 2011). Indeed forests often store more than half of their total carbon in soils rather than vegetation, although these estimates contain large uncertainty due to difficulties in standardizing the methods for quantifying SOC and in some cases from poor data resolution (Domke et al.,

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2017). Additionally, quantifying SOC stocks and detecting temporal change can be challenging due to spatial variability created by disturbance and land-use legacies, microtopography, and differences in microbial metabolic rates and community composition (Conen et al., 2004). These drivers of SOC spatial variability can impact processes that influence rates of carbon flux into and out of soils, including heterotrophic respiration, decomposition, leaching and overland transport, so forests with high soil carbon content often exhibit large spatial variability at the landscape scale (Conen et al., 2004; Domke et al., 2017). Increasingly, forest management practices in the United States include carbon storage or sequestration objectives (Mckinley et al., 2011). Therefore, it is important that we improve our understanding of the drivers of stocks of SOC and the influence of forest composition and demographics and the associated management regimes on SOC stocks and concentrations in actively managed forests.

1.2. Drivers of variation in soil carbon

Stocks of SOC are the net result of carbon inputs to and losses from the soil pool. Inputs of organic carbon to soil are dominated by autotrophic vegetation, which contribute aboveground and belowground litter as well as root exudates to the soil pool. The primary pathway by which SOC is lost from soil is the respiration of CO_2 by soil fungi, microorganisms and fauna, often as they decompose the litter inputs (Kuzyakov, 2006). Soil heterotroph biomass and necromass represents a major internal recycling pathway of SOC, but represents well under 5% of the total SOC pool (Piao et al., 2001). Relative to these dominant pathways, inputs and losses of SOC due to overland transport of organic carbon (Seibert et al., 2007) and losses due to leaching of dissolved organic carbon (Neff and Asner, 2001) both tend to be small.

Microorganisms can influence carbon input rates through the production of microbial products, including the hyphae of mycorrhizal fungi (Godbold et al., 2006), which are a major component of SOC and can vary at both the landscape and sub-meter scale (Paul, 2016). More importantly, soil decomposers represent the primary pathway by which carbon leaves the soil (i.e. during the respiration of CO_2). Metabolic rates of heterotrophs are sensitive to soil temperature, moisture, and nutrient conditions, which can vary at the microtopographic scale of meters (e.g., hummocks and hollows), causing differences in decomposition rates (Gessler et al., 2000). Differences in decomposition rates can also be driven by differences in soil microbial communities and community dynamics (Schimel and Schaeffer, 2012), mycorrhizal fungi (Leifheit et al., 2015), and invertebrate communities (Ulyshen, 2016), which all can vary on the scale of meters.

Vegetation controls on SOC can influence input and output rates, both directly and indirectly through interactions with the heterotrophic soil community. Evidence that trees can directly influence carbon stocks – versus the alternative that carbon stocks influence trees – comes from common garden experiments (Hansson et al., 2011; Vesterdal et al., 2012) and mesocosm studies (Wurzburger and Brookshire, 2017). Higher total tree basal area and biomass (Li et al., 2010) and productivity (Lal, 2005) result in greater above- and belowground litter, both of which directly increase the carbon inputs to the SOC pool (Paul, 2016). Root production can contribute both directly to SOC as an input (e.g. belowground litter and exudation) and to the stabilization of that carbon in the soil, such that roots can contribute at least half of the plant-derived carbon to soil (Rasse et al., 2005).

Indirect effects of vegetation may also influence SOC. For example, recent evidence suggests that litter quality feedbacks are complex, and that while chemically recalcitrant litter may accumulate in upper soil, labile litter containing higher proportions of carbohydrates, proteins and lipids may also contribute significantly to SOC (Cotrufo et al., 2013; Laganière et al., 2017; Schmidt et al., 2011). The rate at which microbial stabilization occurs may differ depending upon litter quality (Cotrufo et al., 2013) and the type of mycorrhizal fungi associated with the dominant vegetation (Craig et al., 2018). Additionally the soil microbial communities themselves may covary with the dominant vegetation (Burns et al., 2015; Myers et al., 2001).

Effects of tree species on SOC are generally greatest in the forest floor and upper soil horizons, as above- and below-ground litter inputs dominate this SOC pool (Kurth et al., 2014; Vesterdal et al., 2013) and fine root biomass tends to be concentrated in the upper soil (Yanai et al., 2008). Coniferous trees tend to be associated with more SOC than deciduous trees (Boča et al., 2014; Finzi et al., 1998b; Laganière et al., 2015; Schulp et al., 2008; Vesterdal et al., 2013; Waring et al., 2015). This may be explained by differences in foliar chemistry: conifer litter typically has higher lignin:nitrogen ratios and more complex carbon molecules, and decomposes more slowly (Hobbie et al., 2006; Laganière et al., 2015). In addition, conifers typically decrease soil pH (Berthrong et al., 2009; Finzi et al., 1998a). The resulting acidification tends to slow decomposition (Averill and Waring, 2017), as increasing acidity increases how strongly organic material is bound to clay particles (Newcomb et al., 2017). Additionally, soil pH affects microbial community composition, resulting in differences in mineralization and immobilization rates (Rousk et al., 2009). Therefore, regardless of whether soil pH is a consequence of the vegetative community, it can be an important control on SOC dynamics.

Soil organic carbon also varies with topography (Domke et al., 2017; Thompson and Kolka, 2005). Elevation may indirectly influence inputs to SOC via the effects on vegetation productivity, which tends to be lower at higher elevation (Stephenson and Van Mantgem, 2005). Elevation also influences rates of decomposition, which happens faster at higher temperatures, although this effect is highly context dependent (Bradford et al., 2017; Kirschbaum, 2006; Oldfield et al., 2018). Topography may also influence soil moisture, which can similarly influences SOC indirectly through effects on productivity or by influencing decomposition rates; at low or very high soil moisture, decomposition is slowed, which can lead to a buildup of SOC (Garten et al., 2009).

Clay content has often been used as a predictor of SOC (Rasmussen et al., 2018), as carbon sorbed to clay particles are chemically stabilized in the soil and protected from further mineralization (Six et al., 2002). Mineralogy also interacts with the microbial community to influence the rate at which microbial products (i.e. microbial biomass and necromass) become physico-chemically protected (Cotrufo et al., 2013). These stabilization processes decreases the rate of loss of carbon from the soil, as the SOC will turn over more slowly when chemically bound to clay particles (von Lützow et al., 2007). Therefore parent material and mineralogy are also considered important predictors of SOC (Angst et al., 2018; Six et al., 2000; Torn et al., 1997).

Each of the drivers discussed above can cause changes in either the rate of inputs or outputs of SOC. The spatial scale at which each driver operates may range from less than millimeters (e.g. microbial community composition) to kilometers (e.g. elevation). This results in high levels of heterogeneity at both large (Domke et al., 2017) and small (Conen et al., 2004; Muukkonen et al., 2009; Schöning et al., 2006) spatial scales. To better understand landscape scale controls on SOC at a scale relevant to actively managed mixed forests, we considered controls that operate at that spatial scale, namely elevation, soil moisture, soil pH and vegetation.

1.3. Forest management and soil carbon

Human management of forest systems can influence SOC (Davis et al., 2009; Jandl et al., 2007; Mckinley et al., 2011; Noormets et al., 2014). Direct effects of management, such as physical soil scarification from harvesting equipment (Picchio et al., 2012), can decrease SOC, and harvesting method and intensity can alter the response of SOC to management (Achat et al., 2015; Thiffault et al., 2011). Harvesting also reduces or removes carbon inputs from aboveground pools such as downed dead wood (Woodall et al., 2015), slowing the potential accumulation of SOC. Harvesting can increase nutrient availability, which causes higher decomposition rates of leaf litter (Bird and Chatarpaul,

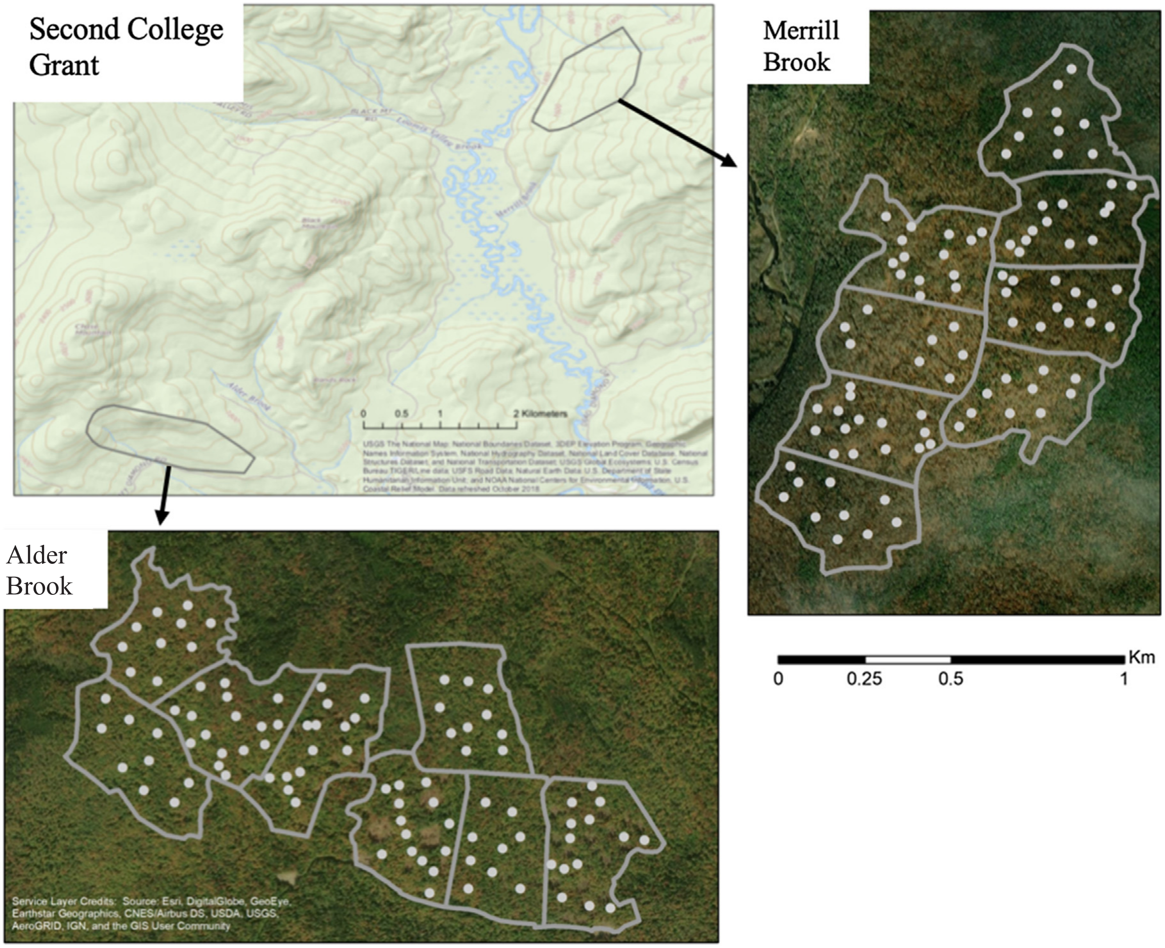

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Fig. 1. Relative location of Alder Brook and Merrill Brook within Dartmouth's Second College Grant in Carroll County, NH. Gray points represent 11.4 m radius sampling plots.

1988) and therefore lower carbon inputs to SOC pools. SOC loss with management tends to be nonlinear, with moderate harvests resulting in minimal SOC losses (Strukelj et al., 2015; Thornley and Cannell, 2000), and in some cases, particularly in conifer forests, harvesting may result in increases in SOC (Johnson and Curtis, 2001). Forest management may also influence SOC indirectly, primarily through effects on vegetation. Management tends to alter productivity, biomass, and species composition of the forest, all of which can cascade to effects on SOC (see discussion of vegetation effects on SOC above).

Forest floor carbon pools typically decline following harvest (Yanai et al., 2000). Spodosols, which contain relatively large forest floor carbon pools, seem particularly vulnerable to forest floor carbon loss following harvest (Nave et al., 2010). However, changes to the forest floor carbon pool are also very difficult to detect (Yanai et al., 2000). In the forest floor, the direct effects of management via soil scarification and mixing into the mineral layer can result in apparent SOC loss, as well as the decrease in inputs from vegetation (Yanai et al., 2003). Indirect effects can also influence forest floor carbon, as forest management frequently influences tree species composition through regeneration harvests and intermediate treatments. This manipulation may influence subsequent SOC accumulation via the quantity and quality of organic inputs to soil (Poirier et al., 2016) and resulting effects on soil biota (Schulp et al., 2008). The increased water and nutrient availability in managed forests may decrease allocation to fine roots, exudation and rhizosymbionts, such that increasing productivity in managed forests may be associated with lower belowground carbon pools (Noormets et al., 2014).

Effects of forest management on SOC have been most evident in the upper horizons, but deeper soil pools are less studied. Petrenko and Friedland (2015), working across New England and including at our study site, found a signal of reduced SOC in mineral layers more than a century after the last harvest. The inputs of carbon to the mineral soil pool come from the upper soil layers, and therefore the mechanisms that influence the forest floor are likely to cascade down to mineral soil. Additionally, management can cause increased weathering, releasing nutrients that can have consequences for SOC stocks in the mineral soil (Vadeboncoeur et al., 2014). Mineral soil in different soil orders seem to respond differently to harvests, suggesting that minerology and soil texture influence the stabilization of those inputs and play a role in how mineral soil responds to management. However, the specific mechanisms (i.e., direct vs indirect) that drive differences in both the forest floor and mineral SOC pools following harvest remain poorly investigated, and considerable uncertainty remains regarding the magnitude of the effects of forest management on SOC stocks (Nave et al., 2010).

1.4. Objective

The goal of this project was to assess local drivers of SOC stocks and concentrations in two areas with different management histories in an actively managed forest in the northeastern U.S. We tested whether the management area with a more intensive harvesting history had less SOC. We went on to evaluate relationships with the drivers of SOC stock dynamics by testing the following hypotheses: SOC is spatially variable at the scale of meters but with patterns that emerge at larger spatial scales; total SOC and SOC concentrations are positively related to elevation, soil moisture, and total tree basal area, and negatively related to soil pH. Furthermore, we tested whether the local abundance of conifers was positively associated with carbon concentrations in the upper soil but negatively related to concentrations in the mineral soil.

2. Methods

2.1. Site description

We conducted our studies within the Second College Grant, which is a township of 10,800 ha in northern New Hampshire, USA, and a property of Dartmouth College (Fig. 1). The mean annual temperature is 3.2 °C, the mean annual precipitation is 1179 mm (30-year climatology 1981–2010) and the soils are spodosols (Petrenko and Friedland, 2015). The forest is in the temperate-boreal transition zone, and is approximately 50% northern hardwood forests, dominated by *Acer saccharum*, *Fagus grandifolia*, and *Betula alleghaniensis*, 20% softwood forests dominated primarily *Picea rubens*, *Abies balsamea*, and *Pinus strobus*, and 30% mixed hardwood-softwood stands (Evans, 2011).

2.2. Site history

The Second College Grant has been actively managed for timber production since the New Hampshire State legislature granted it to Dartmouth College in 1808. Until the 1940s, conifers were harvested almost exclusively, shifting species composition towards deciduous hardwood trees in areas historically dominated by mixed hardwood-softwood stands. Hardwoods began to be included in the harvests after road infrastructure was improved in the mid 1900s (Daniell and Noon, 2007). Our study was conducted in two areas, Alder Brook and Merrill Brook (Fig. 1). We were able to characterize the history of these management areas from a combination of harvesting records and cover maps, as Dartmouth College has archived maps of all harvests since 1947. We used a combination of a forest type and stand-size map that was part of a project of the Charles Lathrop Pack Forestry Foundation in 1947, a forest type and land use map prepared by Cooperative Extension Service, University of New Hampshire in cooperation with the New Hampshire Division of Resources and Economic Development, United States Forest Service, and the North Country RC&D Project in 1972, and more records of more recent harvests recorded in (Evans, 2011).

2.2.1. Alder Brook

A 1947 cover type map shows Alder Brook as northern hardwood light sawtimber. During 1955–1967 there were saw log cuts that were probably aimed at the removal of *Betula alleghaniensis*. Typical of the time, it was likely cut in winter on snow over frozen ground using horses, which would tend to produce relatively little soil disturbance. A 1972 cover map shows it as H2B type, meaning that it was dominated by hardwoods 13–25 cm in diameter with crown closure of 30–60%. A cut map shows a harvest in 1975 that would have removed larger diameter hardwoods and softwoods. This was a summer harvest with skidders, which presumably resulted in some soil scarification. Records from other cuttings by similar prescription around the same time resulted in stands with remaining basal area of 9–18 m^2/ha. The most recent harvest was an improvement cut in 1996 that aimed to reduce basal area to 17–19.5 m^2/ha by thinning across diameter size classes. This was a summer/fall harvest using a Feller Buncher and cable skidders, which resulted in soil scarification.

2.2.2. Merrill Brook

The management history of Merrill Brook was similar to Alder Brook but differs in that there was no harvest in the 1970s. The 1947 cover map shows Merrill Brook as heavy sawtimber of mostly hardwoods, suggesting slightly higher stocking in Merrill Brook than Alder Brook at that time. As with Alder Brook, there was likely a winter harvest with horses between 1955 and 67, which would have resulted in minimal direct soil disturbance. The 1955–67 harvest of Merrill Brook may have been more intensive than Alder Brook, given that both sites are categorized as forest type H2B in the 1972 cover map. The most recent cut was in 2000, with similar in goals and methods to that conducted in 1996 in Alder Brook. The result of this harvest was an average basal area of 18.5 m^2/ha with a heterogeneous diameter distribution including, and it was accomplished in the summer using a Feller Buncher and cable skidders resulting in soil scarification.

2.3. Field sampling

During the summer of 2017, field crews sampled within 98 plots with 11.4-meter radii (plot area of 0.04 ha) in both Alder Brook and Merrill Brook. Plots were established as part of the Adaptive Silviculture for Climate Change experiment (Nagel et al., 2017) with sampling intensity designed to capture anticipated variability in overstory canopy within eight 10-ha study blocks in each study area. Between 10 and 16 plots were randomly located within each block, with the restriction that there be at least one plot per hectare, and they be at least 30 m apart. Subsequent to our study, two blocks each, within both Alder and Merrill Brook, were assigned to one of four silvicultural treatments representing a gradient of adaptation options: control (no management), resistance, resilience, and transition (Nagel et al., 2017). Treatments were not applied until the autumn after we conducted our sampling and so our analyses here did not incorporate blocks, but our data are well suited by design to provide baseline measurements for studies of treatment effects in subsequent years. Within each of our 196 0.04-ha study plots, we recorded the species and diameter of all trees with DBH > 10 cm, and estimated the corresponding biomass following Woodall et al. (2011).

Within each plot we collected two soil samples (5 m east and west of the plot center). At both locations, we placed a 15 × 15 cm template, recorded the depth of the Oi/Oe layer in each corner, and collected the Oi/Oe material for analyses. Within the same template, we similarly measured and collected the remainder of the organic layer and the A layer of the mineral soil, if present, as an Oa/A sample (Yanai et al., 2000). Finally, we extracted two cores per template (2.54 cm in diameter) of the mineral soil to 30 cm or to a lesser measured depth that went as deep as possible given the presence of large rocks or bedrock outcroppings. The cores of mineral soil usually included an E and a B horizon, and occasionally a C horizon.

2.4. Lab processing

Oi/Oe samples were immediately air-dried. Woody and non-woody portions were separated and weighed. The non-woody portion was ground to a powder in a coffee grinder and analyzed for carbon content on Thermo Flash EA 1112 Series CN Soil Analyzer. Oa/A and mineral layer samples were stored at 4 °C until processing when they were sieved to 2 mm; rocks (> 2 mm diameter) and roots were separated, weighed, and their volume measured by displacement. The soil portion of each sample was homogenized before extracting a 5-g subsample that was dried at 60 °C for at least 48 h before being ground in a mortar and pestle and analyzed for carbon content on Thermo Flash EA 1112 Series CN Soil Analyzer. An additional 5-g subsample was mixed with 10 mL of deionized water before measurement of pH (Orion model 410 pH meter with an Orion Sureflow electrode).

For subsequent analyses, percent carbon of each soil layer was multiplied by the total dry mass of soil (excluding the mass of roots and rocks > 2 mm) and scaled to estimate total carbon mass per square meter in each layer. The sum of the three layers was taken as total SOC per square meter. Because not all samples reached the same 30-cm depth (due to rocks and bedrock), we analyzed both total carbon pools (which account for different soil depths) and carbon concentrations (which were not directly affected by soil depth).

2.5. Landscape topography and soils

We used geographic information systems (GIS) analysis to extract topographic data that corresponded to our plot locations (ArcMap version 10.2.1, Redlands, CA). The elevation of each plot was estimated from 7.5-minute digital elevation models (DEMs) of the Second College Grant produced by USGS and acquired through NH GRANIT (Complex Systems Research Center, University of New Hampshire. Digital Elevation Model - Quad 14. 1999; Complex Systems Research Center, University of New Hampshire. Digital Elevation Model - Quad 15. 1999). We used the Geomorphometry & Gradient Metrics Toolbox to estimate slope, aspect, and compound topographic index (CTI) for each plot. CTI, which was derived to approximate a steady-state wetness index, was calculated as:

$$\mathrm{CTI} = \ln\left(\frac{\alpha}{\tan(\theta)}\right)$$

where α = Catchment area · [(flow accumulation + 1) · (pixel area in m^2)] and θ = slope angle in radians.

To facilitate comparison of SOC between the two areas based on management, rather than underlaying soil properties, we used the Soil Survey Geographic (SSURGO), a soil mapping database for New Hampshire (acquired through GRANIT, produced by USGS) to identify the putative soil series present at each of our plot locations. Using these we identified the dominant soil series at each management area, which provides us information about the soil texture and depth of each horizon.

2.6. Comparison of SOC between management areas

We used t-tests to compare the three soil strata (Oi/Oe, Oa/A, and mineral) in the two study areas with respect to: C concentration, layer depth, and total SOC per layer per m^2. We also scaled the carbon pools to Mg C per hectare in order to facilitate comparisons between the two study areas with respect to the total amount of C in above-ground tree biomass relative to total C in each of the three soil layers; this was done by taking plot-level averages of soil carbon in each sampled layer, then scaling these values to Mg C per hectare.

2.7. Spatial analyses

We evaluated spatial autocorrelation patterns within our two study areas by calculating Moran's I using the R package *ape*, (Paradis et al., 2004) and testing for departures from spatial randomness that would indicate either positive or negative autocorrelations. We also fit semivariograms models to the total carbon pool and carbon concentration for each layer in both study areas using the R package *gstat;* (Gräler et al., 2016; Pebesma, 2004).

2.8. Predictors of soil carbon pools and concentrations

We used linear regression analyses to evaluate the contributions of five putative drivers of plot-to-plot variation in SOC: elevation, CTI (an approximation of steady-state soil moisture), soil pH, total basal area of trees, and the proportion of basal area from conifers. We used total basal area as a representation of productivity, as we do not have productivity measurements at the plot level, although we will in the future. As only 4 species contributed > 90% of the tree biomass, we used proportion conifers as our vegetative community metric. All 4 species are correlated with one or both aggregated vegetation metrics (Supplementary materials, Table S1).

We evaluated all 32 possible models that included 1, 2, 3, 4 or 5 of these independent variables, employed multimodel inference to identify the inclusion set of top models (ΔAIC < 2 relative to top model), and then used model averaging of regression coefficients to estimate the contributions from each independent variable toward explaining SOC (Burnham and Anderson, 2002). We also allowed for the possibility of non-additive effects between proportion conifers and basal area by including their interaction in the candidate set of models. We initially tested the theoretical possibility of a nonlinear relationship between soil moisture and SOC by including both CTI and CTI^2 in candidate models but found no evidence of nonlinearity (no support for models that included CTI^2) and therefore only included CTI in our final set of models. Analyses were performed using each plot in both study areas as an observation and we included study area (Alder Brook or Merrill Brook) as a categorical effect in all models. Estimates of individual regression coefficients were standardized based on partial standard deviations for each coefficient (Cade, 2015). Models were fit and averaged using the R package MuMIn (Bartoń, 2018). We used graphical analyses based on the averaged model coefficients to evaluate the relative strength and direction of contributions from each variable that was represented in the set of top models. This process was repeated for each of four response variables: total SOC (kg C/m^2) and %C in each of the Oi/Oe, Oa/A, and mineral layers.

3. Results and discussion

3.1. Physiography and vegetation of management areas

The two areas of varying management histories were dominated by different soil groups, with Alder Brook dominated by 1A soils, while Merrill Brook was split nearly evenly between 1B and 2A soils, which are considered somewhat less fertile (Table 1). The soils in both areas are considered coarse-loamy, isotic, frigid haplorthods. Approximately 70% of Alder Brook is dominated by Peru complexes, which typically have an organic horizon of 0–2.5 cm followed by an A horizon of 2.5–13 cm and an E horizon. The mineral soils beneath are fine sandy loams. The remaining 30% of Alder Brook is Tunbridge complexes, which typically have an organic horizon of 0–13 cm including an Oa horizon followed by an E horizon. The mineral soils beneath are also fine sandy loams. Merrill Brook is dominated entirely by Tunbridge complexes. Alder Brook was about 40 m higher in elevation on average and includes some steeper areas than Merrill Brook, but had generally

Table 1
Physiography and vegetation attributes of each of the two management areas. Standard deviations in parentheses.

Attributes	Alder Brook	Merrill Brook
Soil attributes		
Dominant soil group(s)[a]	1A	1B, IIA
Soil series[b]	73% Peru, 27% Tunbridge	97% Tunbridge, 3% other
Physiography		
Elevation (m)	563 (45.1)	524 (42.3)
Slope (%)	13.7 (7.9)	11.0 (3.7)
CTI	6.6 (1.5)	6.3 (1.3)
pH	4.5 (0.4)	4.3 (0.4)
Vegetation		
Acer saccharum (m^2/ha)	15.2 (6.5)	12.2 (6.6)
Fagus grandifolia (m^2/ha)	4.5 (4.4)	7.7 (6.4)
Betula alleghaniensis (m^2/ha)	4.1 (3.6)	2.7 (3.3)
Picea rubens (m^2/ha)	0.5 (1.2)	1.4 (2.6)
Total basal area (m^2/ha)	27.0 (7.5)	25.7 (5.6)
% basal area conifers	2.1 (4.3)	5.4 (10.2)

[a] Group IA. Deeper, loamy textured, moderately well, and well-drained soils. Group IB. Sandy or loamy over sandy textures and slightly less fertile than those in Group IA. Group IIA. Similar to groups IA and IB, except physically limited due to steep slopes, bedrock outcrops, etc. Definitions from New Hampshire Soil Attribute Data Dictionary (Natural Resources Conservation Service and USDA, 2013).

[b] See Section 3.1 for descriptions of soil series attributes.

similar CTI values. Average basal area was similar between areas (26–27 m^2/ha), but Alder Brook contained more *Acer saccharum* and *Betula alleghaniensis* and less *Fagus grandifolia* and *Picea rubens* (Table 1). The percentage of basal area from coniferous trees was about twice as high in Merrill Brook vs. Alder Brook (5.4 vs. 2.1%).

The landscape factors were similar between the two management areas in this study, including the soil types. The current basal area of the two management areas is also very similar, which is unsurprising since similar management methods and goals were enacted in the two management areas during the most recent harvests in 1996 and 2000 respectively (Section 2.2). However, the composition of the tree community was different between the two places, which is likely due to a combination of habitat suitability of the different tree species and the somewhat different past management that has occurred on the two areas. Alder Brook, which has the more fertile soil, had fewer conifers and more *Acer saccharum,* as well as some *Fraxinus americana* (which was absent at Merrill Brook). The pH at Alder Brook was slightly higher, which is compatible with the dominant soil group and the lower coniferous basal area.

3.2. Soil carbon across management areas

Percent C was significantly lower in all three soil layers at Alder Brook (Fig. 2 left; Oi/Oe: p = 0.02; Oa/A: $p < 0.01$; Mineral: $p < 0.01$). The depths of the soil horizons were similar in the two study areas, although the sampled mineral layer was deeper in Alder Brook than in Merrill Brook (Fig. 2 middle; p = 0.02). Note that this does not necessarily indicate deeper soil, as our maximum sampling depth was 30 cm. Rather, this indicated a greater frequency of samples in Merrill Brook that were less than the 30-cm maximum. Despite this, total SOC in the mineral layer was higher in Merrill Brook (Fig. 2 right; p = 0.014), but in the Oa/A layer was higher in Alder Brook (p = 0.015). Total carbon summed across the three horizons was very similar between the two areas (Fig. 2 right; p = 0.98). These patterns remained when scaled up to the entire management areas, with similar carbon pools in vegetation and Oi/Oe but higher total carbon in Alder Brook Oa/A and Merrill Brook mineral soil (Table 2). In both study areas, soil carbon comprised about 40% of the total carbon in soil plus aboveground biomass. This fraction is similar to the 48% of carbon stored in soils at the reference watershed in the Hubbard Brook Experimental Forest in New Hampshire (Fahey et al., 2005) for SOM to 20 cm, which was our average sampling depth, and is somewhat lower than estimates from a range of North American forests that include SOC to depths up to 1 m (Marty et al., 2015). Carbon pools in tree biomass and soil at Merrill Brook and Alder Brook were 34–35% lower than that estimated for forest stands of similar tree species and climate in Watershed 6 of Hubbard Brook (Fahey et al., 2005) that have not been cut since some salvage logging following the 1938 hurricane (Campbell et al., 2007). Watershed 6 at Hubbard Brook provides a reasonable point of comparison for our site given the similar climate (the difference in latitude compensated by elevation) and correspondingly similar tree species.

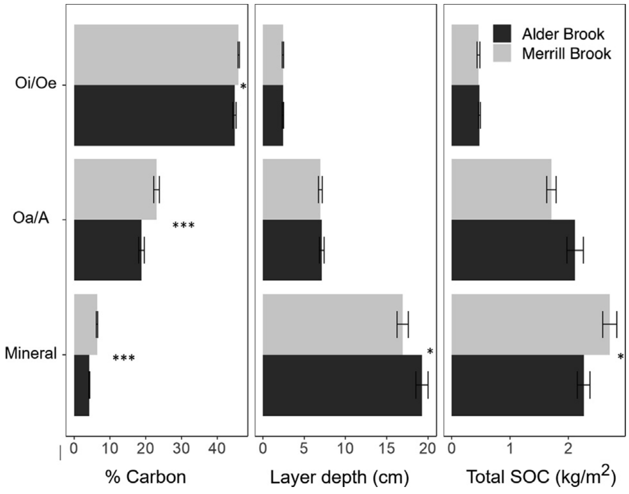

Fig. 2. Mean carbon concentration, layer depth, and total SOC for each sampled soil layer in the two management areas (black bars: Alder Brook, gray bars: Merrill Brook). Statistical differences between the study areas, where they exist, are indicated: *$P < 0.05$, ***$P < 0.001$.

Table 2
Estimated carbon by pool in each of the two management areas.[a]

Carbon pool	Mg C/hectare ± SE	
	Alder Brook	Merrill Brook
Tree biomass	73.5 (2.0)	69.7 (1.6)
Oi/Oe	4.7 (0.2)	4.5 (0.2)
Oa/A	21.1 (1.5)	17.0 (0.9)
Mineral	22.9 (1.2)	27.0 (1.4)

[a] The average sampling depth of the mineral layer was 19.4 cm in Alder Brook and 16.8 cm in Merrill Brook.

Although the two management areas had similar SOC pools when considering the entire sampled soil profile, the relative amounts of carbon within soil layers was different. In Alder Brook, which has historically been a productive hardwood forest (Kevin Evans, personal communication), a larger proportion of the total soil C is in the Oa/A layer. This may be important for long term dynamics of soil carbon because SOC in mineral soil tends to form organomineral complexes that are relatively protected from loss, compared to the more labile SOC in the forest floor (Garten et al., 1999; Kaiser et al., 2002). Merrill Brook, which has a higher proportion of conifers and one fewer harvest in the last 80 years, contains relatively more carbon in the mineral layer; this was because of higher carbon concentrations, as the average depth of the sampled mineral soil was less in Merrill Brook than in Alder Brook (Table 1). Increasing abundance of conifers is often associated with increased carbon belowground, particularly in the upper, organic layers (Dawud et al., 2016; Finzi et al., 1998b; Laganière et al., 2013; Marty et al., 2015). However, conifers were relatively rare overall in our study sites (5% of basal area at Merrill Brook vs. 2% at Alder Brook). Additionally, our study areas have been managed such that species composition now does not reflect the distribution of conifers prior to their selective removal during the 1900s. As conifers likely composed a broader distribution in this forest in the past (Daniell and Noon, 2007), the patterns of SOC in the mineral soil could reflect a history of conifer abundance at this site, and the resultant legacy of low pH and nutrient availability. Finally, there is a possibility that the difference in mineral SOC between the two site may be due to some difference mineralogy or texture which can influence SOC (Six et al., 2000; Torn et al., 1997). However, given that both sites are dominated by coarse-loamy, isotic, frigid haplorthods this possibility seems unlikely.

3.3. Spatial patterns in soil carbon pools

There was no evidence for positive spatial correlations with SOC within the two study areas. Moran's I was indistinguishable from the null model of random spatial variation in 7 of 8 comparisons, with the only exception being in the mineral soil at Alder Brook, where the tendency was for a negative rather than a positive autocorrelation (Supplementary materials, Table S2). Similarly, semivariograms for SOC (Fig. 3) showed that most of the variation was captured by the nugget, again indicating a general lack of spatial structure to total SOC at the scale of tens of hectares. In only one case did the nugget account for < 50% of the semivariance (%C in Oa/A layer and in mineral soil at Merrill Brook), and even there the suggested range of the spatial correlation was < 200 m (Table 3). Apart from elevation, there was a

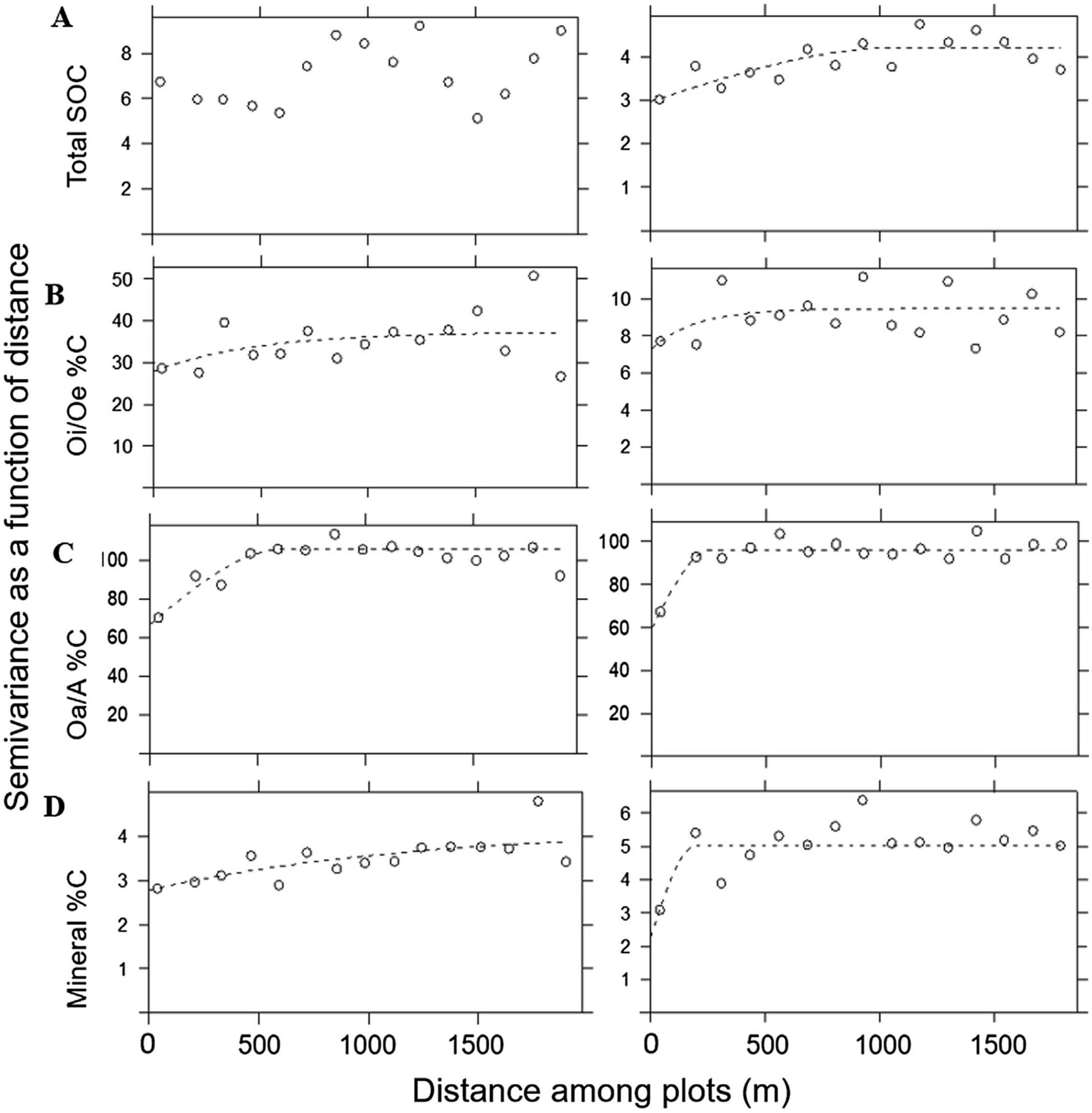

Fig. 3. Semivariograms of total SOC (panel A), Oi/Oe %C (panel B), Oa/A %C (panel C), Mineral %C (panel D) in each of the two study areas.

similar lack of spatial patterns in the independent variables that were evaluated as potential predictors of soil carbon (Supplementary materials, Fig. S1).

Our results refute the hypothesis that soil carbon in this managed forest is patchy at the scale of tens to hundreds of meters. Lack of spatial correlation in soil carbon could arise if SOC is quite uniform across the studied landscape. Indeed, the coefficients of variation in total SOC (SD/mean) were on the low side of what has been reported in comparable studies of forest soils: 41 and 54% at Alder Brook and Merrill Brook, respectively, (Table 3) vs. 10–132% (Conen et al., 2004), 64% (Jobbagy and Jackson, 2000) and 27–49% (Schöning et al., 2006). Still, there was substantial variation in our system, but the patchiness is apparently at the scale of < 10 m. This is consistent with studies reporting that the range of spatial continuity of SOC may be as small as 2 m (Muukkonen et al., 2009) or 6 m (Schöning et al., 2006). Possible sources for patchiness at this scale include microtopography (Chaplot et al., 2001), preferential flow paths caused by roots (Bundt et al., 2001), and heterogeneity in soil microbial communities on the scale of < 10 m (Saetre and Baath, 2000; Štursova et al., 2016). Finally, it is possible that some of this variation in our systems is due to soil scarification from previous summer harvests (Picchio et al., 2012). Importantly, this study tested the spatial patterning in SOC from 10 to

Table 3
Geostatistical parameters of soil carbon pool and concentrations in each layer in the two study areas. [CV = coefficient of variation = (SD/mean) · 100. Models: No fit, exponential, or spherical. Nugget variance = Co/(Co + C). Sill = Co + C. Range is in meters.]).

Measurement	Alder Brook						Merrill Brook					
	Mean	CV	Model	Nugget	Sill	Range	Mean	CV	Model	Nugget	Sill	Range
Total SOC (kg/m^2)	4.9	54	No fit				4.9	41	Exp	0.69	4	431
Oi/Oe SOC (%C)	44.8	13	Exp	0.75	37	473	45.9	7	Exp	0.77	10	197
Oa/A SOC (%C)	18.8	53	Sph	0.63	106	619	23.0	42	Sph	0.62	96	261
Mineral SOC (%C)	4.2	44	Exp	0.67	4	1200	6.4	36	Sph	0.46	5	193

Table 4

Standardized coefficient estimates from models predicting four measures of soil carbon. Coefficients are the weighted averages from 4 to 9 models with dAIC < 2 relative to the model with the lowest AIC. Independent variables were study area (Merrill Brook or Alder Brook, elevation (m asl), compound topographic index (CTI), pH, total basal area (m^2/ha), and the proportion of total basal made up by conifers.

Response variable	Number of models	Averaged standardized regression coefficients					
		Study area	Elevation	CTI	pH	Total BA	Prop. conif.
Total SOC (kg/m^2)	6	−0.06	−0.26	0.27	−0.18	0.30	−0.11
Oi/Oe SOC (%C)	4	0.27	0.06	0.03	−1.16	0.67	0.06
Oa/A SOC (%C)	9	1.36	0.22	0.37	−1.04	0.29	1.80
Mineral SOC (%C)	7	1.11	0.38	0.23	−0.19	0.12	0.32

1500 m, a scale that is currently underrepresented in the literature, which mostly includes cases of smaller (Conen et al., 2004; Muukkonen et al., 2009; Schöning et al., 2006) or broader (Domke et al., 2017; Köchy et al., 2015) spatial scales.

3.4. Predictors of soil carbon pools and concentrations

Regression modeling indicated contributions from all five putative drivers of soil carbon: elevation, CTI (an approximation for steady-state soil moisture), pH, total basal area of trees, and the proportion of total basal area from conifers (Table 4). The number of candidate models in the inclusion set ranged from 4 to 9 depending on the response variable, but never included the null model (intercept only, or intercept and area only). Correlations among individual drivers were low (Supplementary material, Table S2).

The strongest predictors of total SOC (kg/m^2, Fig. 4A) were basal area and CTI. Total SOC increased by more than 20% across the range of observed basal areas and by more than 10% across the range of observed CTI scores. The positive relationship between SOC and basal area was consistent with theoretical expectations, but still somewhat surprising due to the regular harvests at this site. The weak positive relationship with CTI was contrary to theoretical expectations that greater soil moisture would increase decomposition and therefore be associated with lower SOC. It seems unlikely that soils in our system are regularly so wet that decomposition is suppressed by low oxygen. It seems more likely that the positive association between CTI and total SOC is because landscape positions with high CTI values tend to be more productive areas for tree growth, and therefore have higher carbon inputs and greater total SOC. A weakness of this explanation is that our modeling included direct measurements of basal area, but a static measurement of basal area might not readily capture local variation in productivity – especially in a managed forest. Another possible explanation for the positive relationship is that the CTI index was reflecting other factors in addition to steady-state soil moisture as we intended. The CTI index uses landscape characteristics to predict water flows and pools. However, organic matter may also be subject to transport on the landscape and therefore CTI can be positively correlated with the depth of the organic layer (Seibert et al., 2007). This was true in our case: a weak but positive correlation between CTI and depth of the Oa/A layer (Supplementary materials, Fig. S2). Thus, the positive relationship between CTI total SOC may in part be because the CTI index reflects increased organic input more strongly than increased steady state moisture. This is consistent with the result that CTI was a relatively strong positive predictor of total SOC, but a very weak predictor of C concentrations (more below). As it is, we have a limited understanding of how soil moisture influences soil carbon in our study system. There would be value in further studies that employ more direct measurements of soil moisture than CTI.

The negative relationship between total SOC and elevation was opposite to expectations based on the model of cooler soils having lower decomposition rates. However, lower productivity at higher elevations may help to explain this pattern; a hypothesis that we do not yet have the data to explore. Additionally, while the measured soil was shallower at higher elevations (Supplementary materials, Fig. S3); the percent C in soil, especially mineral soil, increased with elevation as predicted if soils at cooler, higher elevations have lower carbon mineralization rates (Chaplot et al., 2001; Domke et al., 2017; Wiesmeier et al., 2013). Both pH and the proportion of conifers also entered into the model for total SOC (Table 4), and both were in the hypothesized direction, but neither made more than a minor contribution to predictions of total soil C/m^2 (Fig. 4, upper panel).

The predictive model for percent C in the Oi/Oe layer (Fig. 4B) was dominated by a negative relationship with pH and a positive relationship with basal area. The relationship with pH matched theoretical and empirical expectations of lower C mineralization rates at lower pH (Finzi et al., 1998b). Higher input of low pH litter from conifers is a candidate cause for low pH (Hornung, 1985), but empirically the proportion of conifers was only weakly related to percent C in the Oi/Oe layer (Fig. 4B). One possibility is that soil pH in our system is a relatively slow-moving variable that reflects the integrated effects of tree species composition over a longer time than is reflected by the current tree species. In this case, plots having relatively low pH soil – with high percent C – may be legacies of historical patterns in conifer abundance. This may be reflected in the fact that the strength of the contribution of conifer abundance to percent C increased with soil depth (Fig. 4: right-hand column). However, without more specific information about the historic vegetation composition we cannot be sure what legacy effects be influencing the patterns we see today.

The predictive model for percent C in the Oa/A layer (Fig. 4C) included a negative relationship with pH and a positive relationship with basal area, as in the Oi/Oe layer. In contrast to the model for the Oi/Oa, there was a relatively strong effect of increasing percent C with increasing percent conifers. This is consistent with many previous reports of higher SOC in coniferous stands than in deciduous stands (Boča et al., 2014; Finzi et al., 1998b; Gartzia-Bengoetxea et al., 2009; Laganière et al., 2013; Schulp et al., 2008). There was a modest positive relationship of percent C in the Oa/A layer with CTI, which is consistent with the stronger positive association of CTI with total SOC.

The predictive model for percent C in the mineral soil (Fig. 4D) was dominated by a positive relationship with elevation. This was consistent with the expectation of reduced C mineralization rates in cooler soils at higher elevations. There was also a positive relationship with percent conifers. This matched the pattern in the Oa/A layer and is consistent with the hypothesis of lasting effects from the input of recalcitrant conifer litter.

4. Conclusions

Understanding whether and how management influences SOC is of critical importance as forests continue to be central to strategies to offset global CO_2 emissions. Not only do we see lower SOC in our study's managed forest than in other, less disturbed forests, but we also find evidence of a legacy of previous management decisions in the vertical distribution of SOC. Some of the strongest drivers of SOC stocks and concentrations, namely the type and amount of vegetation, are also those that are manipulated by management. The spatial variability of

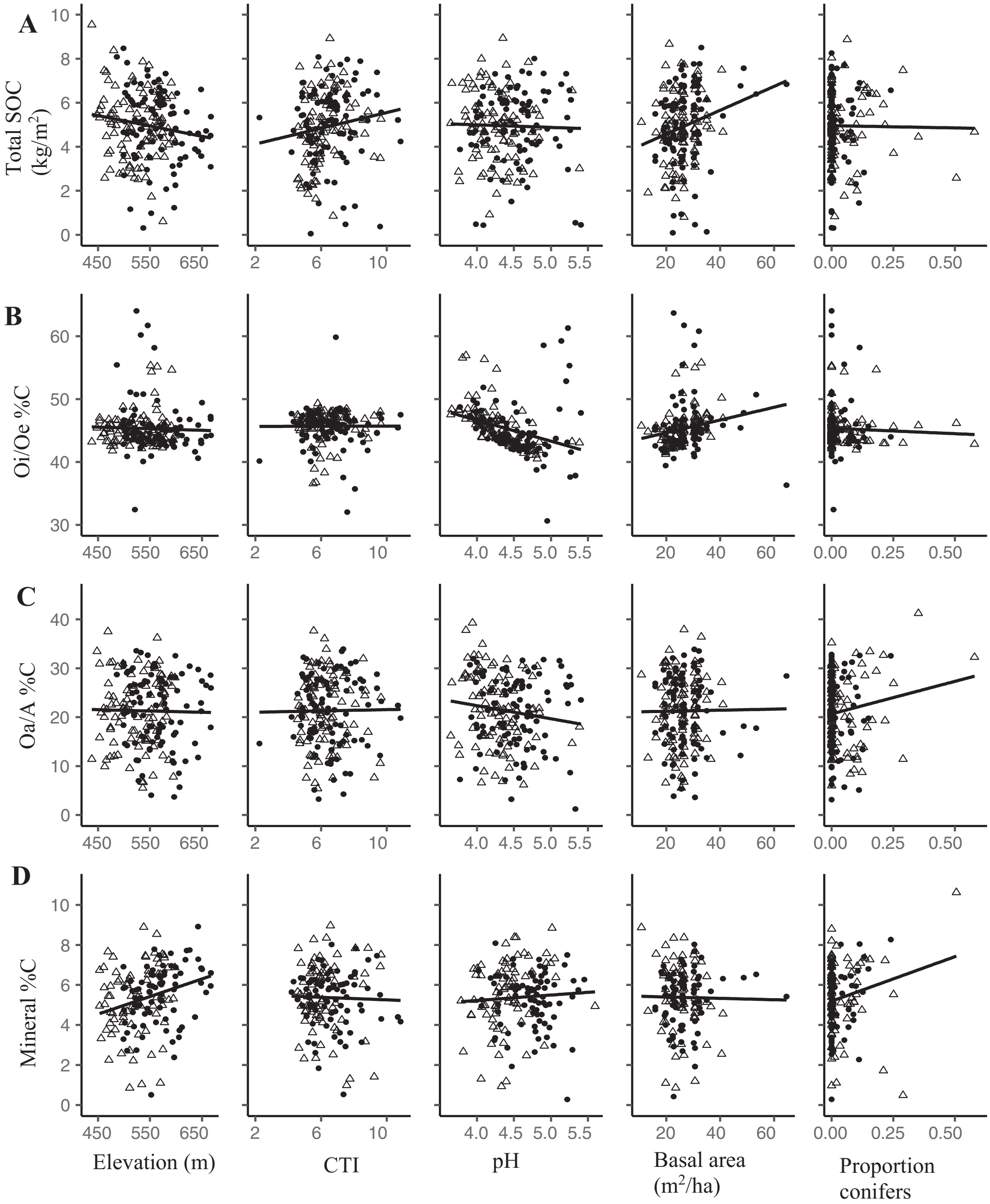

Fig. 4. Carbon pools (panel A) and concentrations (panels B-D) as a function of five independent predictors. Each point represents one plot. Y-values in each panel are adjusted for the effects of the other independent variables (Table 4). Alder Brook (circles) and Merrill Brook (triangles).

SOC stocks and concentrations remains a challenge for studying the short- and long-term effects of forest management. Our study contributes by providing a spatially explicit baseline of SOC within the experimental units of the Adaptive Silviculture for Climate Change project. This will allow assessment of subsequent changes in SOC and permit tests of the interpretations developed here that SOC change will differ across the four experimental treatments, with changes initially mirroring the direct effects of harvest intensity, but eventually being driven by subsequent changes in vegetation composition.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117534.

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