Research Article

Site Quality, Disturbance, and Vegetation Effects on Carbon Storage and Accumulation in Old, Mixed-Species Stands in Central Maine, USA

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ABSTRACT

Carbon (C) storage and accumulation in forests is of growing importance as climate change focuses our attention on rising greenhouse gas emissions. In 2012, we measured total ecosystem C pools (including live vegetation, dead wood, and soils) in two unmanaged, mixed-species stands in central Maine, USA. The stands are adjacent to one another and serve as references against which silvicultural treatments can be compared. The soil parent material of the stands was different (marine sediments versus glacial till), which provided an ideal opportunity to compare C stocks between these stands. We used tree ring analysis and repeated forest inventories to estimate tree and dead wood recruitment patterns and past disturbance severity. Site quality influenced C trajectories through its influence on tree species composition, which in turn strongly determined stand susceptibility to insect outbreaks. In 2012, total ecosystem C stocks were 196.3 ± 9.6 Mg ha^{-1} (mean $\pm$ SD) in the stand on soils derived from marine sediments and 247.0 ± 17.7 Mg ha^{-1} in the stand on soils derived from glacial till. Differences in average total ecosystem C stocks were primarily driven by the live tree C pool. Despite the occurrence of several partial disturbance events from 1954 to 2012, live tree C stocks increased over time in both stands. Average C accumulation in recruited dead wood was also positive, indicating that aboveground biomass served as a C sink. Our results can be used to inform decisions related to C objectives in unmanaged stands of similar species composition and soils.

Index terms: forest carbon accounting; soil parent material; tree mortality; tree recruitment; tree ring analysis

INTRODUCTION

Understanding the factors that influence carbon (C) storage and accumulation in forests is important for mitigating climate change. Consequently, it is important to understand the long-term C dynamics associated with currently unmanaged forests that had been previously managed for wood products. As these forests age, stand development and natural disturbances influence C trajectories, which depend on site factors such as soil parent material, soil drainage, topography, and tree species composition (Law et al. 2003; Pregitzer and Euskirchen 2004; Bradford and Kastendick 2010). In older stands over approximately 100 y, overall aboveground C accumulation continues to be positive and sustained due to long-term tree recruitment, high rates of C accumulation on large trees, and large dead wood reserves (Carey et al. 2001; Luyssaert et al. 2008; Stephenson et al. 2014). Studies that contribute to our knowledge of C dynamics on formerly managed lands across a range of sites, particularly in old forests, will be beneficial for planning and policy decisions that include C storage and accumulation.

Site quality strongly influences C storage in forests and soil characteristics are often evaluated to identify reliable indicators of site quality (Wang et al. 2003; Kulmatiski et al. 2004; Keyser 2010). For example, soil drainage and the percentage of coarse fragments in the mineral soil strongly influence ecosystem C pools especially on soils derived from glacial till (Raymond et al. 2013; Puhlick et al. 2016c). Raymond et al. (2013) also found

that soil pH and base saturation increased with increasing soil wetness, reflecting reduced leaching of base cations and the accumulation of base cation leaching from upslope positions (Fernandez et al. 2003). Soil characteristics are also highly dependent on soil parent material, which often varies among and within study sites (Ferwerda et al. 1997). Hence, it can be important to compare ecosystem C storage and accumulation on soils derived from different parent materials. Site quality indices that integrate multiple soil properties into a single value may be particularly useful for evaluating differences in C storage among stands.

Timber harvesting and natural disturbances also influence C storage and accumulation, by altering tree size, age structure, species composition, and deadwood abundance (D'Amato et al. 2011; Powers et al. 2011; Puhlick et al. 2016d). In stands where only a portion of the overstory trees are harvested or killed by natural disturbances, residual overstory trees can benefit from increased resource availability, and advance regeneration of shade-tolerant tree species may be released into the overstory (Westveld 1931; Seymour 1992). In the mixed-species forests of northeastern North America, the prevalent natural disturbance agents are moderate-intensity wind storms and periodic eastern spruce budworm (*Choristoneura fumiferana* Clemens) outbreaks (Seymour et al. 2002; Fraver et al. 2009). Also, eastern white pines (*Pinus strobus* L.) that originated from the abandonment of agricultural lands or timber harvesting during the late 1800s and early 1900s occupy many old, mixed-species stands of the

region. These stands have higher abundance of eastern white pine and many species of intermediate to low shade tolerance compared to the remaining old-growth forests of northeastern North America (D'Amato and Orwig 2008; Fraver et al. 2009).

In the present study, our focus was on how the interacting factors of site quality, disturbance, and vegetation influence C storage and accumulation in stands that were last harvested in the late 1800s. Our overall goal was to evaluate C storage and accumulation in two unmanaged, mixed-species stands on the Penobscot Experimental Forest in central Maine, USA. Because these stands occur on different parent materials yet are adjacent to one another, our study design provides an ideal opportunity to evaluate the influence of parent material on C storage and accumulation. Our research objectives were to (1) compare total ecosystem C stocks between stands, (2) examine the relationship between aboveground C stocks and both site quality and disturbance, (3) assess aboveground C accumulation between stands using repeated inventories of trees on permanent plots, and (4) determine the most influential factors driving the observed trends. A detailed description of forest attributes associated with these stands is needed because they are commonly used to inform local and regional management decisions. Our results are also informative for researchers who might consider using the stands of this study as references to which other management practices are compared, and could be used to guide management decisions where C storage is one of the objectives.

MATERIALS AND METHODS

Study Site and Experimental Design

The 1619 ha Penobscot Experimental Forest (PEF) is located in central Maine, USA (44°52′N, 68°38′W; mean elevation of 43 m), and has a long history and large available data (Kenefic et al. 2015). The PEF is within the Acadian Forest, a transitional zone between the eastern North American broadleaf and boreal forests (Halliday 1937), and Maine is the most northeastern state in the USA. Mean temperatures in February and July are −7.1 °C and 20.0 °C, respectively, and mean annual precipitation is 107 cm. Across the PEF, tree species composition is relatively diverse and includes balsam fir (*Abies balsamea* (L.) Mill), red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* (L.) Carriere), northern white-cedar (*Thuja occidentalis* L.), eastern white pine, red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), and quaking aspen (*Populus tremuloides* Michx.). Since the 1950s, the USDA Forest Service has maintained a study on the PEF to investigate the influence of various silvicultural treatments on stand composition, structure, growth, and yield (Sendak et al. 2003). This long-term study includes a 7.4 ha unmanaged natural area, which was first inventoried in 1954, and is the focus of the present study.

The natural area was not part of the original USDA Forest Service study design, but was later added as a reference. Local records suggest that no harvesting occurred in the stand since the late 1800s (Brissette and Kenefic 2014). In 1993, two stands were delineated in the natural area after it was recognized that there were differences in stand structure, which was partially attributed to stand dynamics following the ca. 1972–1986 spruce budworm outbreak (Sendak et al. 2003). In this study, we used observations of soils extracted with augers along transects to determine that the stands were composed of different soil parent materials. Soils were excavated from the top of the B horizon to a depth of approximately 30 cm; more detailed measurements of soils to a depth of 1 m (see the data collection section) confirmed that the stands were supported by soils composed of different soil parent materials. The soils of the 5.2 ha stand occurring at lower topographic positions were derived from marine sediments, while the soils of the 2.2 ha stand occurring at higher topographic positions were derived from glacial till.

The soils derived from marine sediments included fine, illitic, frigid Aquic Dystric Eutrudepts (Buxton series); fine, illitic, nonacid, frigid Aeric Epiaquepts (Lamoine series); and fine, illitic, nonacid, frigid Typic Epiaquepts (Scantic series). The soils derived from glacial till included loamy-skeletal, isotic, frigid Typic Haplorthods (Danforth series); and coarse-loamy, isotic, frigid Oxyaquic Haplorthods (Plaisted series). Soil series were verified by USDA Natural Resources Conservation Service staff using field measurements and laboratory data. An important distinction between the stands is that the soils derived from marine sediments ranged from poorly to moderately well drained, while the glacial till soils were well drained (Maine Association of Professional Soil Scientists 2015).

In 1954, permanent sampling plots (PSPs) for measuring forest attributes were established in the natural area. Six of these PSPs were in the stand on soils derived from marine sediments (hereafter referred to as the marine sediment stand), and three were in the stand on soils derived from glacial till (hereafter referred to as the glacial till stand). In 1993, four PSPs were added to the marine sediment stand and seven PSPs were added to the glacial till stand, resulting in 10 PSPs per stand. We found that one of these PSPs in the marine sediment stand occurred on glacial till overlying marine sediments within 1 m from the surface of the B horizon, so it was excluded from our analyses. PSPs were measured approximately every 5 y with the exception of the time period between 1999 and 2009 when there was a 10 y span between measurements.

The PSPs consisted of a nested design with 0.08, 0.02, and 0.008 ha circular plots sharing the same plot center. Trees ≥11.4 cm diameter at breast height (dbh; 1.37 m) were measured on the entire 0.08 ha plot; trees ≥6.4 cm dbh were measured on the 0.02 ha plot; and trees ≥1.3 cm dbh were measured on the 0.008 ha plot. Prior to 2000, trees ≥1.3 cm dbh were measured on the 0.02 ha plot. We used measurements from the nine PSPs in the marine sediment stand and the 10 PSPs in the glacial till stand to estimate live tree and dead wood C stocks in 2012. In 2012, we also measured herbaceous, forest floor, and mineral soil C pools on a subset of PSPs: five in the marine sediment stand and four in the glacial till stand.

Data Collection

In 2012, trees ≥1.3 cm dbh were measured on all PSPs in accordance with the USDA Forest Service's nested plot design. In addition to the existing USDA Forest Service sampling, on each PSP, trees <1.3 cm dbh and ≥15.2 cm tall were measured on four new 0.0013 ha subplots (radius = 2.07 m) established 4 m from the PSP center at 0°, 90°, 180°, and 270°. On these subplots,

species and dbh were recorded for trees ≥0.3 cm dbh, and species and height were recorded for trees <0.3 cm dbh. These measurements were used to calculate live tree oven-dry biomass using regional aboveground and belowground allometric regression equations (Young et al. 1980). Biomass was converted to C content using species-specific C concentration estimates (Lamlom and Savidge 2003). These same protocols were used for shrubs, but no shrubs were detected on PSPs or subplots. Herbaceous vegetation C stocks were determined by sampling plants, including trees <15.2 cm tall, on clip plots and from transect measurements of bryophyte cover (Puhlick et al. 2016b, 2016c).

The dead wood C pool was quantified at each PSP and characterized as fine woody debris (FWD), downed coarse woody debris (CWD), or standing dead trees (snags). FWD pieces were tallied by size class along transects, and oven-dry biomass was calculated using formulas developed by Brown (1974) for the Northern Region of the USDA Forest Service (Puhlick et al. 2016c). To derive an estimate of FWD C stocks, the biomass values of individual pieces were then summed and multiplied by a C concentration estimate from samples of FWD buried within the O_i horizon (Puhlick et al. 2016b). Downed CWD and stumps were measured on the 0.02 ha plots. The volume, biomass, and C content of individual downed CWD pieces and stumps were estimated using methods described in Fraver et al. (2007a) and Puhlick et al. (2016c). These C contents were then summed, and expansion factors were used to derive per-ha values for each PSP. Snags were measured on PSPs in accordance with the USDA Forest Service's nested plot design. For broken snags, methods developed by Russell and Weiskittel (2012) were used to determine top diameter. Volume was calculated by (1) dividing the snag into 100 sections of equal length, (2) determining the large- and small-end diameters of each section using taper equations developed by Li et al. (2012), (3) using Smalian's formula to calculate the volume of each section, and (4) summing the section volumes (Husch et al. 2003). Only the volume above the stump was calculated, and biomass and C content were determined using the same methods as for downed CWD (Puhlick et al. 2016c).

Organic (O) horizon and mineral soil C was evaluated using measurements of O horizon depth and soil samples collected on a subset of PSPs. A pedotransfer function developed by Puhlick et al. (2016b) was used to predict O horizon C content from measurements of O horizon depth, producing an average for each PSP. These values were then reduced by the average percentage of coarse root C content in the O horizon for each stand (Puhlick et al. 2016b). This adjustment was made because coarse root C content was already accounted for in the belowground live tree C content estimate. For each PSP, mineral soil was sampled at one location using an impact-driven soil corer with an internal diameter of 5.1 cm (Puhlick et al. 2016a). After the O and E horizons were removed, samples were collected from four depths starting from the top of the B horizon: 0–10, 10–20, 20–43, and 43–100 cm; the 43 cm break corresponded to the average depth of most plant rooting on soils derived from glacial till in a previous study by Puhlick et al. (2016a). Bedrock was not encountered at any of the soil core locations. Total C and N (TC, TN) were measured by

combustion analysis at 1350 °C using a LECO CN-2000 analyzer (LECO, St. Joseph, Michigan, USA). For each sample, the fine fraction oven-dry weight was multiplied by its TC estimate to derive mineral soil fine fraction C mass. For each soil core location, the fine earth fraction (<2 mm) for each depth increment and coarse charcoal, which was manually collected from the fine earth, were summed to derive a total estimate of the mineral soil C stock (Puhlick et al. 2016a). Fine roots were included in this estimate and coarse root C was accounted for in the belowground live tree C stock estimate. The amount of C stored in dead stumps and root systems was estimated using records of tree mortality and a negative exponential function (Puhlick et al. 2016c, 2016d). Also, for each soil sample, organic matter was measured by loss-on-ignition (LOI) analysis at 550 °C.

For each inventory of PSPs established in 1954, we calculated C stocks in live trees ≥1.3 cm dbh and dead wood to evaluate C accumulation over time. Dead wood C stocks were estimated from records of tree mortality combined with downed CWD decay rates (Russell et al. 2014); this methodology assumes that trees were incorporated into the downed CWD pool immediately after death. The estimated dead wood C stocks are conservative, especially for inventories in the more distant past, because they are based on recruited dead wood (i.e., not from trees that died before 1954 or portions of trees that were cut and left on-site before 1954, or from annual and episodic inputs from live trees). For the aboveground live tree and dead wood C pools, we used a stock change approach to calculate the average annual net change in C stocks for time periods between inventories, which were computed as (C stocks in time 2 − C stocks in time 1) / time between inventories in years. From 1954 to 2012, average C accumulation (Mg ha^{-1} yr^{-1}) was derived by summing the net change in C stocks for each inventory period and dividing the sum by the total timespan of measurements for the stand.

To estimate tree recruitment patterns, increment cores were collected from live trees in the marine sediment and glacial till stands in 2016 and 2009, respectively. Cores were collected from trees ≥10 cm dbh on three 0.08 ha circular plots established outside of PSPs within each stand. From each tree, a single core was taken at breast height with a standard 5.2 mm diameter increment borer. Cores were air-dried and secured to wooden mounts, then sanded and polished using increasingly fine sandpaper. Ring-widths were measured to the nearest 0.01 mm using a Velmex sliding stage (Velmex, Bloomfield, New York, USA) with MeasureJ2X software (VoorTech Consulting, Holderness, New Hampshire, USA) and stereomicroscope. Cross-dating was performed using marker years, usually light (narrow band of latewood) or narrow rings, followed by statistical cross-dating using COFECHA software (Holmes 1983). To better understand the disturbance history of the study stands, records of tree mortality were also used to derive dead wood C additions from trees that died between inventory periods for PSPs established in 1954 (Puhlick et al. 2016d).

For each stand, site index was determined using dominant and codominant red spruce trees. The selected trees showed no signs of bole or top damage. Total height was measured for each site tree, and age at breast height was determined from cross-dated

increment cores. Then, methods by Seymour and Fajvan (2001) were used to adjust the ages of spruce trees that endured prolonged growth suppression as saplings in the understory (based on growth pattern evident in tree-ring series). Next, each tree's site index was determined using site index curves developed by Carmean et al. (1989), which are formulations of curves by Meyer (1929) based on total age. As recommended by Carmean et al. (1989), 15 y was added to age at breast height to obtain total age. Site indices from two trees in the marine sediment stand and six trees in the glacial till stand were used to compute average indices for the stands.

In addition to site index, a soil quality index (SQI) developed by Amacher et al. (2007) was used to evaluate site quality. The SQI integrates soil physical and chemical properties into a single number that eliminates the problem of correlations among individual soil properties when multiple soil variables are included in statistical models. For each mineral soil depth increment sampled, we derived SQIs based on the mean percentage of coarse fragments in the mineral soil, soil pH, TC, TN, and 1 M NH_4Cl exchangeable K, Mg, Ca, Al, and 1 M NH_4Cl extractable P, Fe, Mn, and Zn. SQIs based on the same chemical properties were also developed for O horizons sampled at each mineral soil sample location. O horizon samples were collected, processed, and analyzed according to methods by Puhlick et al. (2016b). Briefly, the portion of the O horizon that could be easily removed using a brush with fine bristles was collected as the O_i horizon, and the remaining O horizon was collected as the O_e and O_a horizon. The $O_e + O_a$ samples were sieved through a 6.4 mm screen to separate fine from coarse fractions. Subsamples of the $O_e + O_a$ fine fractions were then ground to 0.85 mm using a Thomas-Wiley laboratory mill (Thomas Scientific, Swedesboro New Jersey, USA) and analyzed for chemical properties. The threshold and index values established by Amacher et al. (2007) were used to determine the relative importance of each soil property. For each stand, the average of these indices was computed for the O horizon and for each mineral soil depth increment.

At each location where mineral soils were sampled, we measured the depth below the surface of the mineral soil to which redoximorphic features were first encountered. The presence of redoximorphic features was determined from the soil profile that was exposed after the extraction of soil samples using the soil corer and the associated removal of soil around the soil corer during sampling. For PSPs where we did not estimate the depth below the surface of the mineral soil to which redoximorphic features were first encountered, we used measurements made by Olson et al. (2011). The relative volume of coarse fragments in the mineral soil was calculated as the estimated volume of coarse fragments within the soil core volume sampled divided by the total volume of the soil core (Puhlick et al. 2016a).

Data Analyses

Descriptive statistics were derived for the C stocks of each stand; analysis of variance (ANOVA) was not used to test for differences between stands because there was only one replicate (i.e., stand) on each parent material within the natural area. The C stocks of six individual pools were evaluated and characterized

as (1) aboveground components of live trees ≥1.3 cm dbh; (2) aboveground components of understory vegetation including saplings (trees <1.3 cm dbh), seedlings, and herbaceous plants; (3) downed CWD as well as the portions of snags and stumps 15.2 cm above the root collar; (4) stump-root systems of live trees, snags, and stumps including components from the root collar to a height of 15.2 cm; (5) forest floor including FWD but not coarse roots; and (6) mineral soil including fine earth fractions and coarse charcoal. We also evaluated the C stocks of three aggregated pools: (1) aboveground (live trees above a 15.2 cm stump, tree regeneration above the root collar, herbaceous plants, and CWD); (2) belowground (stump-root systems, forest floor, and mineral soil); and (3) total ecosystem.

Regression analysis was used to evaluate the influence of several explanatory variables on total ecosystem and aboveground live tree C stocks. These explanatory variables included absolute and relative cumulative disturbance severity indices developed by Puhlick et al. (2016d), depth below the surface of the mineral soil to which redoximorphic features were first encountered, and average mineral soil SQI and pH to a depth of 43 cm. The cumulative severity indices were calculated for PSPs that had tree and mortality records dating back to 1954, and were based on the aboveground portions of trees ≥1.3 cm dbh. The relative disturbance severity indices were calculated as the percentage of live tree biomass prior to disturbance that was then transferred to other C pools during the time between PSP inventories. For each PSP, each disturbance severity index was then downweighted by a time metric, which was related to years since disturbance and the initiation of measurements on PSPs (i.e., 58 y prior to our measurement of total ecosystem C pools). Specifically, the weight for each disturbance severity index was: $(58 - \text{years since disturbance} + 1) / 58$. Year of disturbance was calculated as midpoint between PSP inventories. For each PSP, the sum of the weighted disturbance severity indices was considered to be the cumulative disturbance severity index.

The influence of disturbance severity on average C accumulation in live trees and recruited dead trees was also evaluated using regression analysis. Only PSPs with tree records dating back to 1954 were used to evaluate average C accumulation. Correlated explanatory variables were not used in the same model and collinearity was assessed through bivariate plots, correlation coefficients, and variance inflation factors. The gls and lme functions in the nlme package (Pinheiro et al. 2014) in R (R Development Core Team 2014) were used to fit the models.

RESULTS

Site Quality

For the marine sediment stand and the glacial till stand, site indices (base age = 50 y) were 17.3 ± 0.3 and 15.9 ± 0.4 m (mean SD), respectively. Besides the C/N ratio, there were no major quantitative differences in the measured mineral soil chemical properties between stands for the 0–10 and 10–20 cm depth increments (Table 1). For mineral soils of the marine sediment stand, mean SQIs for the 20–43 and 43–100 cm depth increments were quantitatively greater than those for the glacial till stand. At these depth increments, the pH of soils derived from marine sediments was more basic than for soils derived

Table 1.—Mean (standard deviation) of soil pH, organic matter (measured by loss-on-ignition, LOI) and total C and N, C/N ratio, soil nutrients and Al concentrations, effective cation exchange capacity (CEC_e), and soil quality index (SQI) associated with organic horizon and mineral soil fine fractions (<6.4 mm and <2 mm, respectively) in the marine sediment and glacial till stands.

| Property and stand	O horizon and mineral soil depth increment				
	O horizon	0–10 cm	10–20 cm	20–43 cm	43–100 cm
pH					
marine sediment	4.1 (0.2)	4.3 (0.2)	4.6 (0.1)	5.7 (0.3)	6.6 (0.5)
glacial till	3.9 (0.2)	4.3 (0.3)	4.5 (0.3)	4.7 (0.1)	5.0 (0.2)
LOI (%)					
marine sediment	81.3 (7.5)	7.3 (1.7)	4.5 (2.0)	3.0 (1.0)	2.7 (0.7)
glacial till	89.4 (2.6)	12.0 (8.5)	7.7 (3.0)	5.3 (1.6)	3.2 (0.6)
TC (%)					
marine sediment	41.8 (3.3)	2.81 (0.43)	1.20 (0.66)	0.27 (0.11)	0.12 (0.03)
glacial till	45.4 (2.5)	5.51 (5.28)	2.69 (1.63)	1.58 (1.32)	0.53 (0.35)
TN (%)					
marine sediment	1.5 (0.2)	0.19 (0.06)	0.09 (0.05)	0.04 (0.02)	0.03 (0.01)
glacial till	1.4 (0.2)	0.19 (0.16)	0.11 (0.06)	0.08 (0.05)	0.04 (0.02)
C/N					
marine sediment	27.5 (4.0)	15.7 (2.7)	13.2 (3.5)	6.7 (0.5)	4.0 (0.4)
glacial till	31.8 (2.6)	27.3 (4.0)	23.1 (4.0)	17.6 (5.0)	12.2 (4.2)
P (mg kg^{-1})					
marine sediment	96.0 (43.6)	3.1 (0.8)	1.5 (0.4)	0.7 (0.3)	0.5 (0.2)
glacial till	150.0 (27.4)	3.4 (2.6)	2.1 (1.9)	2.7 (2.4)	1.4 (0.4)
Ca (mg kg^{-1})					
marine sediment	3363 (1750)	166 (96)	113 (67)	923 (228)	1623 (488)
glacial till	4610 (720)	214 (268)	66 (53)	72 (91)	196 (259)
K (mg kg^{-1})					
marine sediment	767.0 (174.5)	85.4 (33.7)	62.8 (27.0)	67.8 (27.9)	75.6 (26.7)
glacial till	709.5 (154.8)	49.3 (12.0)	35.2 (5.0)	41.0 (17.9)	36.7 (17.0)
Mg (mg kg^{-1})					
marine sediment	498.6 (105.3)	50.8 (29.7)	41.0 (22.0)	330.4 (119.8)	542.4 (213.4)
glacial till	510.2 (58.6)	33.7 (28.9)	18.5 (14.4)	17.0 (15.9)	62.5 (89.1)
Al (mg kg^{-1})					
marine sediment	795 (695)	373 (77)	223 (53)	53 (25)	8 (4)
glacial till	199 (70)	502 (235)	376 (244)	221 (92)	104 (17)
Fe (mg kg^{-1})					
marine sediment	164.6 (134.4)	33.8 (16.7)	11.6 (7.5)	1.4 (0.9)	1.2 (1.1)
glacial till	59.0 (32.9)	66.0 (48.5)	26.1 (23.9)	11.0 (8.1)	4.1 (2.8)
CEC_e (cmol kg^{-1})					
marine sediment	39.0 (1.2)	7.8 (0.7)	5.1 (1.4)	8.8 (2.2)	13.1 (4.1)
glacial till	37.2 (3.9)	10.5 (5.5)	6.8 (4.1)	4.5 (2.1)	3.7 (2.2)
SQI					
marine sediment	114.5 (13.8)	70.0 (9.5)	51.7 (19.9)	71.7 (7.5)	90.0 (9.1)
glacial till	111.4 (8.7)	64.6 (14.2)	54.2 (10.8)	43.8 (15.8)	37.5 (14.4)

from glacial till. At these same depth increments, mean Ca and Mg concentrations were quantitatively greatest in the marine sediment stand. P showed an opposite trend and was quantitatively lower on soils derived from marine sediments compared to soils derived from glacial till, while Al and Fe concentrations were quantitatively higher in the acidic subsoils derived from glacial till. For the 20–43 cm depth increment, the glacial till stand contained more organic matter than the marine sediment stand.

Stand Structure

In 2012, the dominant species in the marine sediment stand were eastern white pine, balsam fir, and red maple (Figure 1). The percentage of the total aboveground live tree C composed of various species changed markedly between 1954 and 2012. This was mainly due to growth of large pines and maples, which were recruited into the overstory in the early 1900s (Figure 2). In contrast, the percentage of the total aboveground live tree C composed of balsam fir and red spruce declined from 1954 to 2012. While this was partially due to tree mortality from the ca. 1972–1986 spruce budworm outbreak, noticeable balsam fir mortality was occurring before the outbreak (Figure 3). In the marine sediment stand, mortality of overstory firs and spruces led to substantial recruitment of fir beginning in the late 1970s (Figure 2). In 2012, the age structure of the marine sediment stand included at least two cohorts (Figure 2) with mostly large-sized pines and maples representing an older cohort and mostly small-sized firs representing a younger cohort.

In 2012, the dominant species in the glacial till stand were eastern white pine and eastern hemlock (Figure 1). Between 1954 and 2012, eastern hemlock represented a significant percentage of the total aboveground live tree C, and hemlocks occupied multiple diameter classes. Recruitment of hemlocks into the
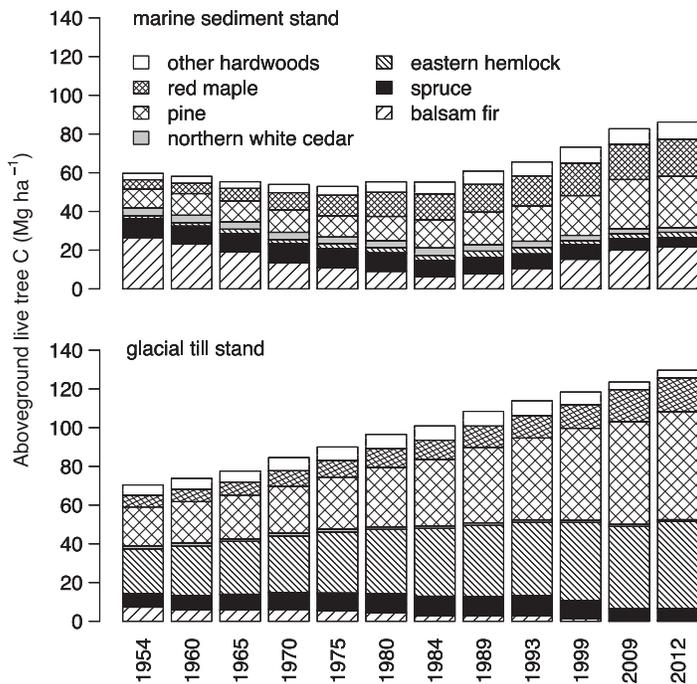
Figure 1.—Mean aboveground live tree C in trees ≥1.3 cm diameter at breast height by year of inventory of permanent plots.

overstory was fairly continuous from the early 1800s to at least 1940 (Figure 2). In 2012, the stand was composed of multiple cohorts of hemlock, with one cohort also including red spruce and eastern white pine as a result of a disturbance in the late 1800s. Mortality of red spruce during the 1990s and 2000s (Figure 3) was partially the result of trees never fully recovering from budworm defoliation, which was inferred from tree cores with consistently narrow growth rings since the last outbreak. Growth of large pines and hemlocks was mainly responsible for the net increase in total aboveground live tree C over time, despite the decline in balsam fir C (Figure 1).

Carbon Stocks

In 2012, total ecosystem C stocks were 196.3 ± 9.6 and 247.0 ± 17.7 Mg ha^{-1} in the marine sediment stand and the glacial till stand, respectively (Table 2). Quantitative differences in total ecosystem C stocks between the stands were primarily driven by the live tree C pool. The forest floor C pool was the only individual or aggregated pool where C stocks were noticeably greater for the marine sediment stand compared to the glacial till stand. Mineral soil C stocks were quantitatively similar between stands. Variability in C stocks among pedons was partially driven by the percentage of coarse fragments in the mineral soil. For the marine sediment stand and the glacial till stand, the percentages of coarse fragments in the mineral soil to a depth of 1 m were 5.8 ± 7.1% and 40.6 ± 14.3%, respectively. The C concentrations of the fine earth fractions of the mineral soil were quantitatively lower in the marine sediment stand (Table 1), which resulted in similar mineral soil C stocks between stands despite the greater fine earth fraction mineral soil masses in the marine sediment stand.

Total ecosystem and aboveground live tree C stocks in 2012 showed a relatively normal distribution and were significantly influenced by the depth below the surface of the mineral soil to which redoximorphic features were first encountered. Specifically, these C pools were positively correlated with the depth to redoximorphic features ($P < 0.05$; Table 3). Therefore, PSPs with better soil drainage tended to have greater total ecosystem and live tree C stocks in 2012. Across all PSPs, the depth to redoximorphic features for the marine sediment stand and the glacial till stand were 9.0 ± 11.9 and 41.9 ± 15.7 cm, respectively. For PSPs with soil chemical data, live tree C stocks were negatively correlated with the average pH of mineral soil to a depth of 43 cm ($P < 0.05$; Table 3). The average pH values for the marine sediment stand and the glacial till stand were 4.9 ± 0.1 and 4.5 ± 0.2, respectively.

For PSPs with forest inventories since 1954, aboveground live tree C stocks in 2012 were significantly influenced by past natural disturbances. Specifically, live tree C stocks were negatively correlated with relative and absolute cumulative disturbance severity indices ($P < 0.05$; Table 3). Therefore, PSPs that had high cumulative disturbance severity indices tended to have less live tree C stocks in 2012. The cumulative disturbance severity indices (unitless) for the marine sediment stand and the glacial till stand were 42.1 ± 14.8 and 17.3 ± 3.7, respectively. The absolute cumulative disturbance severity for the marine sediment stand and the glacial till stand were 52.9 ± 18.5 and 38.8 ± 14.5 Mg ha^{-1}, respectively. The cumulative disturbance severity indices were not significantly correlated with 2012 C stocks of downed CWD and the portions of snags and stumps 15.2 cm above the root collar. The influence of past natural disturbances on total ecosystem C stocks was not evaluated because of the low number of PSPs with estimates of all C pools as well as forest inventories dating back to 1954.

Carbon Accumulation

C accumulation in live trees and recruited dead wood for the marine sediment stand and the glacial till stand was 51.2 ± 15.0 and 76.0 ± 6.9 Mg ha^{-1}, respectively (Figure 4). Average C accumulation in live trees and dead wood for the marine sediment stand and the glacial till stand was 0.89 ± 0.26 and 1.31 ± 0.12 Mg ha^{-1} yr^{-1}, respectively. From 1954 to 2012, mean average C accumulation was negatively correlated with the relative cumulative disturbance severity index ($P < 0.05$; Table 3). Therefore, PSPs with high cumulative disturbance severity indices tended to have lower C accumulation over the length of the long-term study. The influence of individual soil chemical properties and indices on average C accumulation were not modeled because soil samples were only collected on four PSPs that had records of tree inventories dating back to 1954.

DISCUSSION

Average total ecosystem C stocks in 2012 and mean average C accumulation in live trees and recruited dead wood from 1954 to 2012 differed between the two unmanaged reference stands on the PEF. Differences were due to the interacting effects of site quality, disturbance, and tree species composition. While the soil parent material of the stands was different, it is important to

marine sediment stand   **glacial till stand**
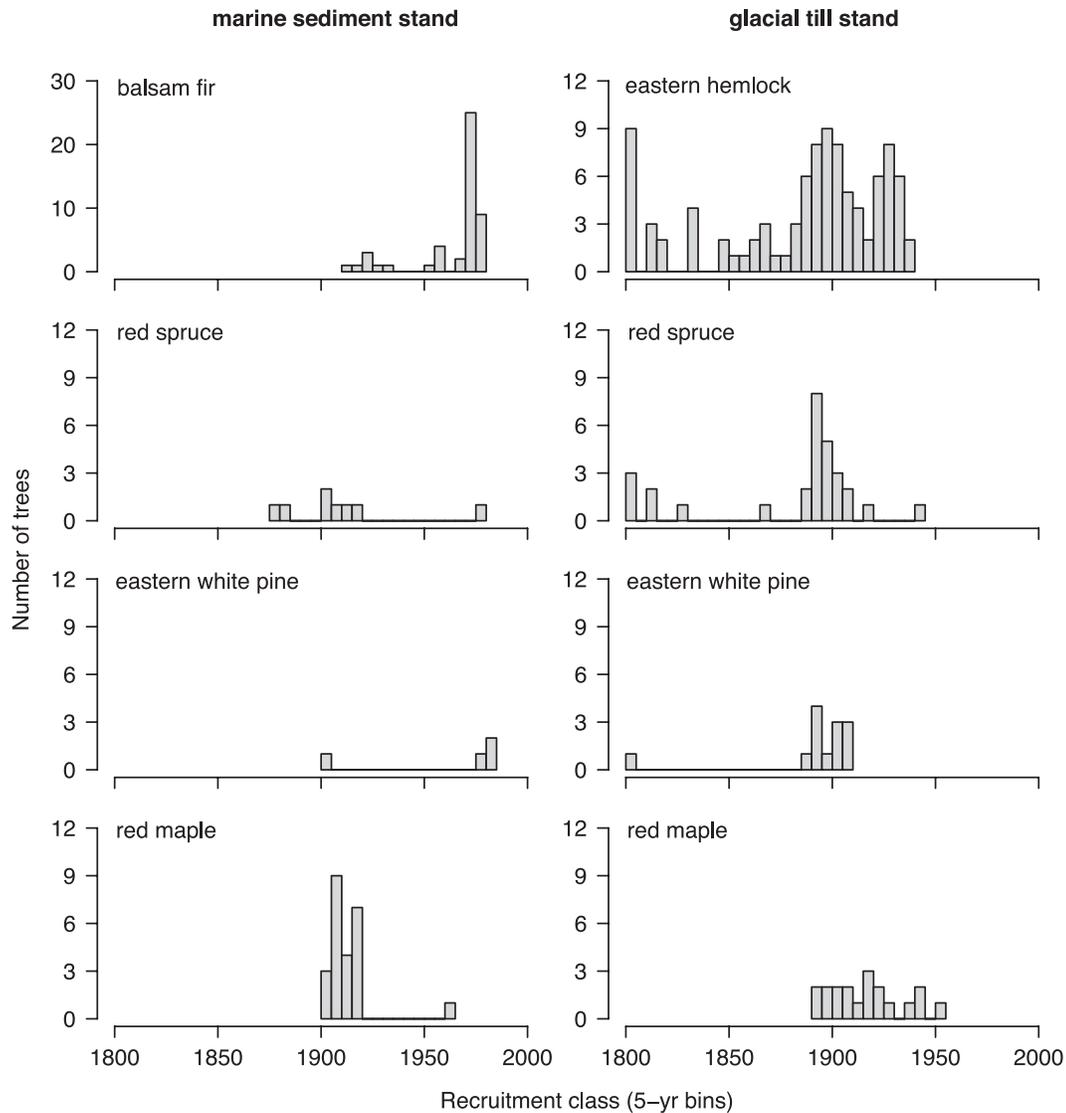
Figure 2.—Distributions of year of recruitment (inferred from tree age at breast height) for common species across all plots where trees were cored. Data were derived from complete cores only; balsam fir and red maple are underrepresented because of heart rot.

consider that our inference was limited to specific soil series derived from marine sediments or glacial till. Other soil series, even those derived from the same parent material, could influence C storage and dynamics differently due to variation in soil physical and chemical properties. An important finding was that the aboveground C pools of both unmanaged reference stands were generally C sinks during each remeasurement period of PSPs. Our results reinforce the findings of other studies that C accumulation in old stands can be positive and sustained (Carey et al. 2001; Luyssaert et al. 2008). Estimates of C accumulation in old stands on specific types of soils can inform decisions about the strategic selection of unmanaged reserves across landscapes when maximizing C storage is an objective. For example, many states in the northeastern USA have implemented ecological reserve systems where C storage is a major objective (Kuehne et al. 2018). This study also adds empirical data to the body of knowledge upon which forest carbon offset projects are structured and measured.

In 2012, the difference in total ecosystem C stocks between the reference stands was driven by the live tree C pool. Other studies have shown that the live tree C pool is primarily responsible for differences in total ecosystem C stocks among varying disturbance severities (Powers et al. 2011). In this study, PSPs with lower cumulative disturbance severity indices had greater C stocks; many of these PSPs were located in the glacial till stand. The glacial till stand also contained large eastern white pines and eastern hemlocks, which can accumulate biomass at rates significantly higher than co-occurring species (Kelty 1989; Teets et al. 2018). In contrast, the marine sediment stand had higher tree mortality rates due to a higher abundance of balsam fir—a species that was severely impacted from defoliation by the spruce budworm and an unknown disturbance agent or natural senescence of a late 1800s cohort prior to the budworm outbreak. Also, our finding that live tree C stocks were negatively correlated with the average pH of mineral soil likely reflected differences in soil drainage rather than a direct pH effect. On
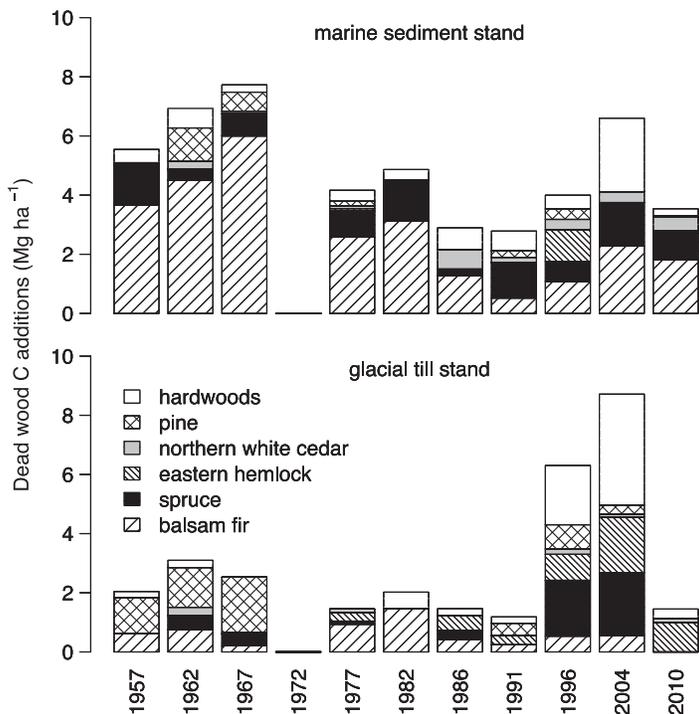
Figure 3.—Mean dead wood C additions (above a 15.2 cm stump) resulting from mortality of trees ≥1.3 cm diameter at breast height. Year of C additions represents the midpoint between inventories of permanent plots. While inventories were usually conducted every 5 y, the longer time period between the 1999 and 2009 inventories corresponds to the 2004 bar. No mortality data exist for the time period 1970–1975, which corresponds to the 1972 bar.

Table 2.—Mean (standard deviation) and range of C stocks (Mg ha^{-1}) in 2012.

C pool	Stand	
	marine sediment	glacial till
Individual C pools		
Live trees (above the stump or root collar)	81.7 (21.7)	129.7 (13.5)
	50.4–114.7	111.1–148.5
Understory vegetation (aboveground)	0.17 (0.15)	0.20 (0.15)
	0.03–0.39	0.02–0.36
Standing dead wood and downed CWD (aboveground)	12.9 (9.7)	15.2 (4.3)
	3.3–28.6	6.8–20.2
Stump-root systems (live and dead)	22.9 (4.7)	36.6 (4.6)
	15.0–30.5	30.7–43.6
Forest floor	22.9 (2.9)	16.9 (3.7)
	19.7–27.4	12.4–20.3
Mineral soil	49.5 (11.9)	45.3 (12.9)
	31.2–61.0	36.8–64.3
Aggregated C pools		
Aboveground	100.1 (14.1)	146.5 (20.2)
	87.6–122.6	128.7–168.7
Belowground	96.3 (7.6)	100.4 (6.6)
	86.8–105.7	96.2–110.3
Total ecosystem	196.3 (9.6)	247.0 (17.7)
	185.6–209.4	226.8–267.3

average, the more basic and wetter soils of the marine sediment stand had lower live tree C stocks than did the glacial till stand. Future studies designed to compare C storage among stands on different parent materials with the same drainage classes would further improve our understanding of C dynamics and ecosystem resilience following disturbances.

Site index and SQIs indicated that the potential for C accumulation in live trees was greater on soils derived from marine sediments than those on glacial till, but contrary to our expectation, the glacial till stand had quantitatively greater C accumulation from 1954 to 2012. Despite having a higher site quality, the marine sediment stand had quantitatively less C accumulation because of the effect of site quality on tree species composition, which, in turn, influenced stand susceptibility to spruce budworm outbreaks. Specifically, tree ring analysis and measurements of trees on PSPs revealed that balsam fir was the dominant species recruited on soils derived from marine sediments, while mostly eastern hemlock was recruited on soils derived from glacial till. Balsam fir can occur across a range of parent materials (Demers et al. 1998), but is often prevalent in softwood stands with fertile soils (Galipeau et al. 1997). In a mixed-species forest in Connecticut, Finzi et al. (1998) found that exchangeable Al and Fe were highest and pH was lowest beneath eastern hemlock canopies. The productive soils of the marine sediment stand included poorly, somewhat poorly, and moderately well drained soils that could also have favored the recruitment of balsam fir. In contrast, the soils of the glacial till

stand were well drained, likely giving eastern hemlock a competitive advantage over balsam fir. These relationships explain the counterintuitive finding that the stand with the lower site quality had the highest live tree C accumulation through the interaction of species composition and hence disturbance susceptibility.

The quantitatively lower forest floor C stocks of the glacial till stand could be due to the observed loose habit of pine litter that can provide more aeration and may accelerate decomposition in comparison to other types of litter. This can partially explain the lower forest floor C stocks in the glacial till stand, which had a higher pine component than the marine sediment stand. In regard to the mineral soil, the mass of C stored in the mineral soil was a function of the percentage of coarse fragments in the mineral soil and the C concentration of the mineral soil. Soils derived from marine sediments typically had lower percentages of coarse fragments in the mineral soil and lower mineral soil C concentrations than soils derived from glacial till. It is possible that the lower C concentrations in the wetter soils of the marine sediment stand resulted from less belowground inputs from roots, coupled with less illuvial accumulations of C because of the higher pH. Our results also show that the ratio of TC (or C concentration) of the mineral soil to the percentage of organic matter in the mineral soil (assessed by LOI) varies by depth increment (Figure 5). The C/N ratio also decreased with depth (Table 1) indicating a relative accumulation of N with depth. While LOI is a commonly used estimate of total organic matter, other volatile constituents can be oxidized at 550 °C besides organic matter (e.g., lattice water in clays), which could partially explain the TC/LOI ratio decrease with depth. The observed TC/LOI and C/N relationships with depth are also likely to be attributed to the proportion of organic matter that is of microbial origin, which has been shown to increase with depth reflecting the low C/N ratio of microbial biomass (Kaiser and

Table 3.—Parameter estimates (standard errors in parentheses) and fit statistics for models of total ecosystem and aboveground live tree C stocks (Mg ha^{-1}) in 2012, and average C accumulation (Mg ha^{-1} yr^{-1}) in live trees and recruited dead wood from 1954 to 2012. Explanatory variables include the depth below the surface of the mineral soil to which redoximorphic features were first encountered (RF; cm), the average pH of mineral soil to a depth of 43 cm (pH), aboveground live tree C stocks in 1954 (IC; Mg ha^{-1}), and the relative and absolute cumulative disturbance severity indices (RD and AD, respectively; % and Mg ha^{-1}, respectively).

| Response variable	Model	Intercept SE	Slope 1 SE	Slope 2 SE	R^2	Residual SE
Total ecosystem C	194.2 + 1.135(RF)	5.6	0.179	NA	0.852	12.059
Live tree C	80.5 + 1.037(RF)	7.7	0.157	NA	0.649	27.898
Live tree C	507.5 − 84.923(pH)	137.5	29.201	NA	0.547	19.874
Live tree C	40.4 + 1.762(IC) − 1.062(AD)	29.9	0.436	0.274	0.828	13.745
Live tree C	151.6 − 1.504(RD)	10.4	0.276	NA	0.809	13.402
C accumulation	1.531 − 0.015(RD)	0.135	0.004	NA	0.710	0.668

SE = standard error.

Kalbitz 2012; Mouginot et al. 2014). A lower C/N ratio with depth is the result of microbial processing leaving more recalcitrant forms and C and N in subsoil organic matter, which is often also protected by mineral particles, and is much less bioavailable than would be low C/N ratio fresh leaf or root litter. Hence, the common practice of simply multiplying the percentage of soil organic matter in a given soil by its total fine-earth fraction mass and then by a constant to estimate C mass may be inappropriate. For C accounting programs, these findings suggest that appropriate multipliers based on soil depth are needed when only the percentage of soil organic matter and soil mass is known.

Despite the occurrence of several partial disturbances from 1954 to 2012, live tree C stocks increased over time in both stands. This was partially due to the release of shade-tolerant species such as balsam fir and red spruce in the understories and lower canopy positions of the stands. Other studies have documented recovery of stand-level biomass and rapid accumulation of biomass on shade-tolerant trees that were suppressed in lower canopy positions following low-severity

Figure 4.—Cumulative sums of net changes in aboveground C stocks over time, which are plotted at the midpoint between inventories of permanent plots.

disturbance (Trotsiuk et al. 2016). Trees in the upper canopy positions that survived disturbances also benefited from increased resource availability and higher resistance to drought (D'Amato et al. 2013), which resulted in increased stand-level C stocks over time. In the glacial till stand, eastern white pine was often in the dominant canopy position, while hemlocks were in partially shaded intermediate canopy positions. In mixed-species, stratified stands, the basal area of eastern hemlock in such canopy positions can be substantial, making these stands more productive than stands of pure hemlock or pure hardwood (Kelty 1986, 1989).

The high proportion of balsam fir in the marine sediment stand made it susceptible to the eastern spruce budworm and unknown disturbance agents before the 1980s. Quantitatively less C accumulation in the aboveground portions of live trees and more recruited dead wood in the marine sediment stand compared to the glacial till stand was partially related to greater mortality of overstory fir in the marine sediment stand following the ca. 1972–1986 spruce budworm outbreak. Furthermore, surviving spruce and fir showed pronounced growth reductions, which is common during defoliation by budworm (Fraver et al. 2007b; Chen et al. 2017a, 2017b), thereby influencing stand-level C accumulation. Even before the outbreak there was noticeable fir mortality in the marine sediment stand. This may have been due to competition, the balsam wooly adelgid (*Adelges piceae* Ratzeburg), internal heart rot, or a combination of these factors. Quantitatively less C accumulation in the marine sediment stand compared to the glacial till stand may have also been related to suboptimal growth of hardwoods, many of which had internal rot, which was detected during tree coring.

The quantitatively greater C accumulation in the aboveground portions of live trees in the glacial till stand can be attributed to growth on large eastern white pines and hemlocks as well as the timing of disturbances. At the nearby Howland Research Forest, Teets et al. (2018) also found that large eastern white pines (and to a lesser extent eastern hemlock) accumulated large amounts of C in unmanaged mixed-species conifer stands. Although spruces were a minor component of the glacial till stand from 1954 to 2012, tree ring analysis revealed that some spruces had growth reductions from ca. 1965 to 1968. This time period corresponds to a regional drought (Leathers et al. 2000; Barlow et al. 2001) and could have predisposed spruce to budworm attack and defoliation. In the glacial till stand, recent mortality across species shifted C to the dead wood pool. Because these materials have only recently begun to decompose, stand-level C
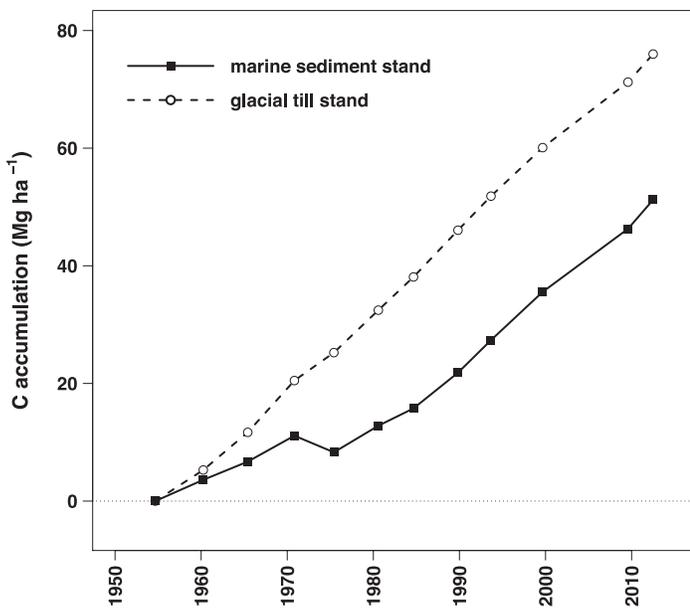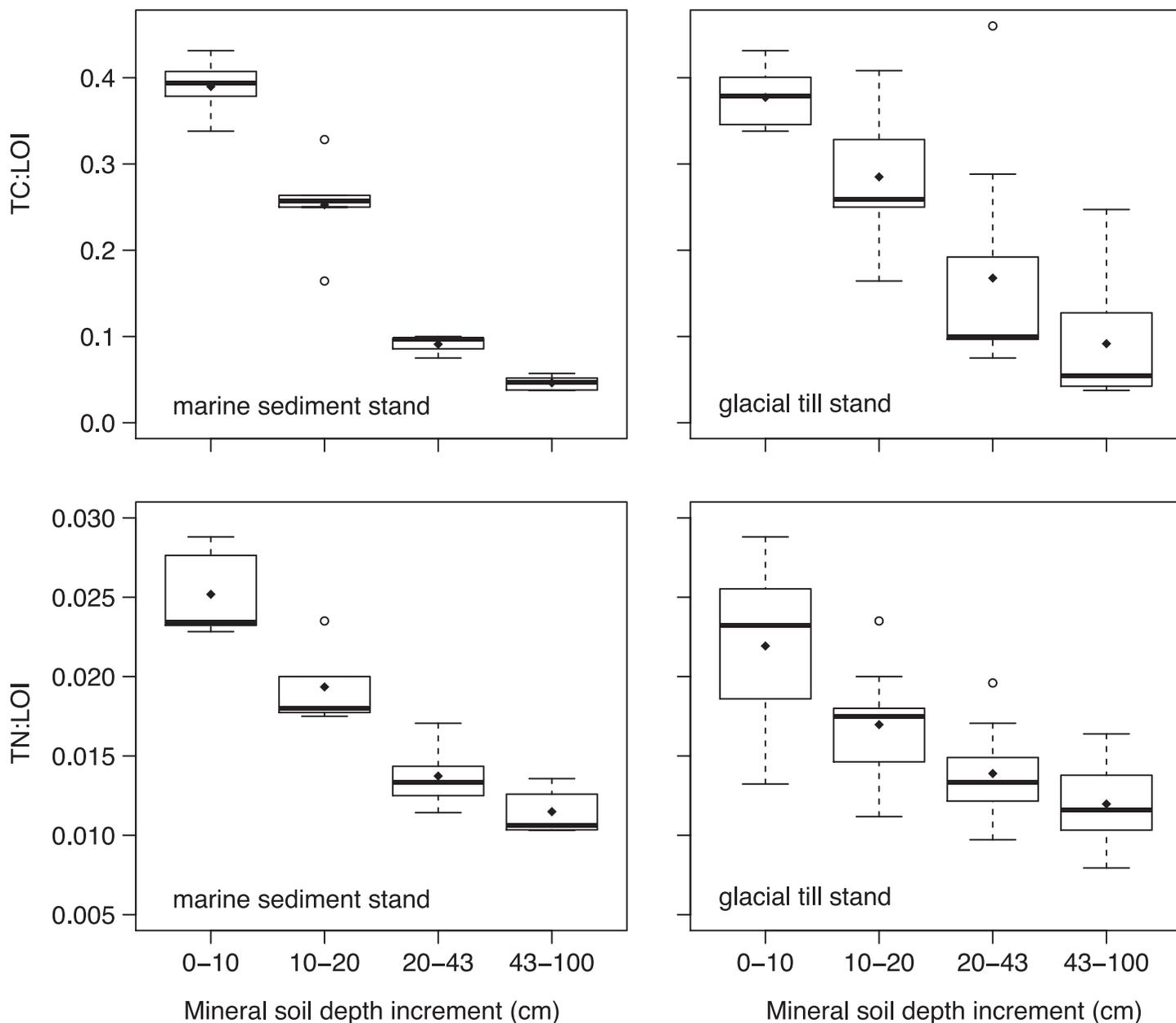
Figure 5.—The ratio of total C (TC) to organic matter (measured by loss-on-ignition, LOI) as well as the ratio of total N (TN) to organic matter by stand and mineral soil depth increment starting from the surface of the B horizon. The horizontal line and black dot in each box are the median and mean, respectively. The boxes define the hinge (25–75% quartile, and the line is 1.5 times the hinge), and points outside the hinge are represented as dots.

accumulation in live trees and dead wood remained positive during the latter part of the study. While the frequency and severity of forest fires on the forest is not known (Kenefic and Brissette 2014), coarse charcoal was detected in O horizon samples from both stands. Fire can consume surface fuels and O horizon materials, and it likely influenced C pools in these stands before the PEF was established in 1950. The angular shape of the charcoal indicates that the charcoal resulted from a relatively recent fire or series of fires, likely around the time of European settlement; charcoal buried in the soil would be more fragmented and rounded if exposed to intense frost–thaw and

rooting activities for longer periods of time (Carcaillet and Talon 1996).

Conclusion

This study demonstrates that relatively old, mixed-species stands without recent timber harvesting can be important sinks of atmospheric C. In the natural area on the PEF, average C accumulation from 1954 to 2012 was positive for stands on soils derived from both marine sediments and from glacial till. The counterintuitive finding that the stand with the lower site quality had the highest live tree C accumulation was partially because of interaction of species composition and hence disturbance

susceptibility. Notable disturbance agents included the eastern spruce budworm, which influenced C and stand dynamics over time. These results can inform decisions related to C objectives in unmanaged stands of similar species composition and soils.

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