Evaluation of projected carbon accumulation after implementing different forest management treatments in mixed-species stands in northern Maine

Joshua J. Puhlick, Aaron R. Weiskittel, Ivan J. Fernandez, Kevin A. Solarik and Darren J. H. Sleep

The Jones Center at Ichauway, Newton, GA, USA; School of Forest Resources, University of Maine, Orono, ME, USA; Center for Research on Sustainable Forests, University of Maine, Orono, ME, USA; Climate Change Institute, University of Maine, Orono, ME, USA; Forest Research, National Council for Air and Stream Improvement (NCASI), Cary, NC, USA; Conservation Science and Strategies, Sustainable Forestry Initiative (SFI) Inc, Washington, DC, USA

ABSTRACT
Comparing forest and harvested wood product carbon (C) stocks and accumulation among forest management treatments commonly applied in managed forests is needed to inform planning and policy decisions for C objectives. Therefore, pre- and post-harvest C stocks were quantified and C accumulation was projected over a 31-year period (to C242050) among forest management treatments that were applied on a subset (n = 3) of the Maine Adaptive Silviculture Network installations in northern Maine, USA. These installations included mature, second-growth forests composed of northern hardwood and hardwood-dominated mixedwood stands. Before treatments were initiated, average aboveground live tree C stocks ranged from 67.1 to 99.7 Mg ha−1. For the aboveground portions of live trees, dead wood and harvested wood products, the projected average annual net change in C (AAC) was 0.232 ± 1.164 Mg ha−1 year−1 (mean ± standard deviation). Models of projected AAC indicated that less biomass removal during harvests and greater representation of tree species with low tolerance of shade were associated with positive AAC values. The results emphasize the importance of leveraging multiple harvesting strategies to achieve C objectives, including consideration of forest reserves and using targeted yet operationally feasible silvicultural treatments that promote forest resilience relative to climate change.

KEYWORDS
Carbon sequestration; climate change; silviculture; mixedwood; northern hardwood

Introduction
Predictions of carbon (C) stocks and accumulation based on stand structure, species composition and biomass removals for wood products are needed to inform planning and policy decisions related to C management and sequestration as a contribution to mitigating climate change. These factors can be considered in the context of forest management treatments that are commonly used within regions and actions that purposefully focus on adapting forests to the potential negative impacts of climate change (e.g. insect outbreaks, drought, etc.) [1–3]. Current research suggests multi-aged forest management systems, such as irregular shelterwood and selection systems, may enhance C stocks and accumulation in naturally regenerated forests when compared to silvicultural practices that remove most of the standing biomass during single entries with little or no focus on tree regeneration (e.g. commercial clearcutting) [4–6]. Forest reserves (i.e. areas where timber harvesting is restricted) can also accumulate C over time [7], but they may also have a greater predisposition to disturbance depending on species composition, stand structure and stage of stand development [8]. Across both managed forests and reserves, species composition can also influence rates of C accumulation. Early successional stands composed of fast-growing species such as poplar (Populus spp.) may accumulate more C than softwood stands with similar tree densities and in a similar stage of stand development [9–11]. Accounting for C stored in wood products, particularly when comparing managed forests and reserves, is also needed to identify strategies best suited for maximizing C storage [12–14].

Several studies have compared C stocks and accumulation among forest management scenarios [6,15,16] and stands with different species...
composition [7] in the northeastern USA. In mixed-species stands dominated by shade-tolerant coniferous species, Puhlick et al. [6] found that scenarios with selection cutting accumulated more C than those with shelterwood cutting followed by thinning or with diameter-limit cutting on a rotation basis. For example, the scenario with selection cutting on a 20-year cycle accumulated 63% more C than the scenario with fixed diameter-limit cutting. In northern hardwood stands, Schwenk et al. [15] found that scenarios with individual tree selection had greater mean aboveground live tree C stocks than shelterwood and clearcut scenarios over a 100-year period. While selection cutting using the BDq method to specify target residual basal area, maximum diameter, and distribution of trees among size classes [16] can enhance C accumulation when compared with alternative forest management strategies (e.g. diameter-limit cutting), this form of selection cutting in North America has been mostly practiced on experimental forests in the USA and Canada [17–19]. In addition, species composition can also influence C accumulation because of differences in wood densities and growth rates among species [20], where softwood stands tend to have greater tree densities than hardwood stands of similar age or stage of stand development [21].

Disturbances, such as insect and disease complexes that can induce reductions in tree growth and increase mortality, should be accounted for in projections of C stocks and accumulation over time [8,22,23]. Such disturbances can influence C storage and accumulation by altering tree size, age structure, species composition, and dead wood abundance [7,24]. In stands where only a portion of the overstory trees are killed, residual overstory trees and advance regeneration can benefit from increased resource availability (e.g. light, water, and nutrients) [25,26]. In northeastern North America, northern hardwood and mixedwood stands with American beech (Fagus grandifolia Ehrh.) are often subject to beech bark disease, which can influence C dynamics by increasing American beech mortality rates and crown dieback. Residual, diseased American beech may have reduced growth rates due to decreased vigor or increased growth rates due to increased resource availability [27]. In stands infected by the disease, timber harvesting usually perpetuates dense thickets of diseased American beech mainly through root suckering [28]. However, some studies have shown that co-occurring species such as sugar maple (Acer saccharum Marsh.) can gain dominance over time [29]. Another prominent insect known to affect northern hardwoods, the emerald ash borer (Agrilus planipennis), can also have a significant short-term influence on C dynamics by killing nearly all infected ash (Fraxinus spp.) trees within 6 years of invading a forest [23,30,31]. The hemlock woolly adelgid (Adelges tsugae) may also invade forests north of the insect’s current extent under changing climate conditions. Accounting for these disturbances based on current or predicted infestation levels is important when modeling C stocks and accumulation over time.

To better understand the influence of forest management on C dynamics, current (2018–2021) aboveground live tree, dead wood and harvested wood product C stocks were quantified and future C accumulations were projected over a 31-year period (to ~2050) among different forest management treatments that were applied to stands within the northern hardwood and hardwood-dominated mixedwood forests of Maine, USA, in 2018 and 2020. The first objective was to determine pre- and post-harvest C stocks for the aboveground portions of live trees, dead wood and harvested wood products using repeat measurements of forest attributes on permanent plots [32,33]. The second objective was to estimate aboveground forest and product C stocks over a 31-year period starting with stand conditions in 2018 and 2020, and to assess the cumulative sum of net changes in C over the simulation period (2020–2050); this period corresponds to a key timeframe for achieving C policy objectives in the Maine Climate Action Plan [34]. The final objective was to evaluate the influence of pre- and post-harvest stand attributes and amount of biomass removed during harvests on the projected average annual net change in C (AAC as in Moore et al. [35] and Puhlick et al. [6]; Mg ha\(^{-1}\) year\(^{-1}\)) for the aboveground portions of live trees, dead wood and harvested wood products. A direct forest management treatment effect was not tested for because some treatments were not replicated across research sites.

**Methods**

**Study sites and experimental design**

The study was conducted on a subset of the Maine Adaptive Silviculture Network (MASN) installations in northern Maine, USA. The MASN includes forest management treatments that are commonly used to manage forestlands for timber harvesting and harvested wood products while enhancing resource availability and ecosystem health.
used in Maine and actions that focus on adapting forests to predicted changes in climatic and disturbance regimes. Three installations were selected to monitor forest soil C and nutrient stocks over time [34]. These installations were used to evaluate projected C accumulation in live trees, dead wood and harvested wood products for this study (Figure 1). The first of these installations was located west of Eagle Lake near Sauls Brook on the timberlands of J.D. Irving Limited (47°04′N, 68°73′W; hereafter referred to as Sauls Brook). The other installations were located on the timberlands of Seven Islands Land Company near the Seven Islands campsite on the Saint John River (46°79′N, 69°60′W; hereafter referred to as Seven Islands) and along Route 11 in Nashville Plantation (46°72′N, 68°46′W; hereafter referred to as Nashville Plantation). For these installations, the average elevation was 289 m, and the mean annual precipitation and temperature from 1991 to 2020 were 108 cm and 4°C [36], respectively.

Aboveground forest attributes were measured before and after harvesting treatments (listed in Table 1 and described later in this section). The soils of the installations formed in glacial till, and the soil texture of upper mineral soil horizons tended to be silt loam based on feel and soil taxonomic descriptions. The soil series of each installation is described in detail by Puhlick et al. [33]. At each of the installations, tree species included sugar maple, red maple (Acer rubrum L.), yellow birch (Betula alleghaniensis Britt.), red spruce (Picea rubens Sarg.) and balsam fir (Abies balsamea (L.) Mill) (Table 2). The installations also had attributes associated with older forests, such as abundant dead wood and large tree sizes (Table 1). At Sauls Brook and Seven Islands, previous logging occurred between the 1950s and 1970s and was completed using hand crews with cable skidders or small bulldozers and horses. During this time period, partial cutting focused on removing red spruce, possibly balsam fir, and yellow birch for veneer, as evidenced by notches in yellow birches that were not harvested due to heart rot. At Nashville Plantation, partial cutting occurred in the 1990s, which resulted in a forest with at least two cohorts of trees: an older cohort of large eastern hemlocks (Tsuga canadensis (L.) Carrière) and hardwoods (including sugar maple, red maple and yellow birch), and a younger cohort that included poplar and birches (Betula spp.).

For the MASN project, various forest management treatments were randomly assigned to units within installations. Units ranged from 16 to 20 ha in size, and each treatment was applied to one unit within each installation. Treatments varied by installation, partially because of differences in initial stand conditions, particularly species composition. This study evaluated projected C accumulation in three units of each of three installations (Table 1 and Supplementary material). For one unit at Sauls Brook, a shelterwood prescription
included partial removal of overstory trees and cutting poor-quality American beech saplings < 7.6 m in height. In another unit, commercial clearcutting focused on removing all merchantable growing stock with little attention to future tree quality or tree regeneration; this is different than clearcutting as a regeneration method in silviculture, which removes all vegetation and may or may not be followed by tree planting depending on the desired commercial species. A crop tree release prescription for one unit at Seven Islands involved removing trees competing with valuable sawlog- and pole-sized crop trees. In another unit, diameter-limit cutting focused on removing large overstory trees, and retaining pole-sized birches and maples (Acer spp.). At Nashville Plantation, improvement cutting included retaining the seed sources of tree species such as yellow birch, sugar maple and red spruce, which were scattered throughout the unit. Large eastern hemlocks were also retained to meet biodiversity and C storage objectives. Other objectives included maintaining a multi-aged structure, promoting species predicted to be well-adapted to future climate

| Installation/treatment | Pre-harvest BA (m² ha⁻¹) | Pre-harvest TPH (trees ha⁻¹) | Pre-harvest QMD (cm) | Post-harvest BA (m² ha⁻¹) | Post-harvest TPH (trees ha⁻¹) | Post-harvest QMD (cm) |
|------------------------|--------------------------|-----------------------------|---------------------|--------------------------|-----------------------------|---------------------|
| Sauls Brook            |                          |                             |                     |                          |                             |                     |
| Control                | 25.3                     | 2397                        | 11.6                | 25.3                     | 2397                        | 11.6                |
| Shelterwood            | (5.4)                    | (468)                       | (1.4)               | (5.4)                    | (468)                       | (1.4)               |
| Commercial clearcut    | 29.0                     | 2242                        | 13.3                | 5.7                      | 420                         | 16.8                |
| (3.5)                  | (763)                    | (3.0)                       | (1.9)               | (359)                    | (8.9)                       |
| Seven Islands          |                          |                             |                     |                          |                             |                     |
| Control                | 30.8                     | 1117                        | 19.0                | 30.8                     | 1117                        | 19.0                |
| (8.5)                  | (396)                    | (1.2)                       | (8.5)               | (396)                    | (1.2)                       |
| Crop tree release      | 28.8                     | 838                         | 21.4                | 10.1                     | 339                         | 20.0                |
| (5.5)                  | (202)                    | (4.3)                       | (2.2)               | (116)                    | (3.1)                       |
| Diameter-limit cutting | 29.2                     | 1023                        | 19.5                | 7.9                      | 427                         | 15.9                |
| (4.0)                  | (248)                    | (3.4)                       | (3.9)               | (204)                    | (3.9)                       |
| Nashville Plantation   |                          |                             |                     |                          |                             |                     |
| Control                | 36.0                     | 4819                        | 9.9                 | 36.0                     | 4819                        | 9.9                 |
| (4.7)                  | (1065)                   | (1.1)                       | (4.7)               | (1065)                   | (1.1)                       |
| Improvement cut        | 34.4                     | 5977                        | 8.7                 | 21.4                     | 3894                        | 8.6                 |
| (2.9)                  | (1467)                   | (1.3)                       | (4.2)               | (1092)                   | (1.8)                       |
| Overstory removal      | 34.1                     | 7384                        | 7.8                 | 9.6                      | 5379                        | 4.9                 |
| (6.2)                  | (2266)                   | (1.3)                       | (2.3)               | (2146)                   | (0.7)                       |

Post-harvest values were derived from live tree tallies conducted within 1 month after harvest and do not include growth on residual trees (no cutting was done in the controls).

Table 2. Mean pre- and post-harvest species composition (% of the total basal area represented by a given species or species group) by installation and forest management treatment.

| Installation/treatment | Fir | Spruces | Cedar | Hemlock | Sugar maple | Red maple | Ashes | Beech | Yellow birch | Paper birch | Poplar |
|------------------------|-----|---------|-------|---------|-------------|-----------|-------|-------|--------------|-------------|--------|
| Pre-harvest Sauls Brook |     |         |       |         |             |           |       |       |              |             |        |
| Control                | 12.1| 4.1     | 0     | 0       | 32.0        | 4.4       | 0     | 35.9  | 8.1          | 0           | 0      |
| Shelterwood            | 20.9| 22.2    | 0     | 0       | 9.6         | 24.3      | 0     | 15.6  | 6.1          | 0           | 0      |
| Commercial clearcut    | 6.7 | 1.9     | 0     | 0       | 50.3        | 3.4       | 0     | 20.0  | 17.7         | 0           | 0      |
| Seven Islands          |     |         |       |         |             |           |       |       |              |             |        |
| Control                | 7.1 | 7.8     | 0     | 0       | 44.9        | 17.7      | 0     | 16.5  | 0.6          | 3.0         |        |
| Crop tree release      | 6.1 | 0.3     | 0     | 0       | 62.3        | 18.8      | 0     | 12.2  | 0            | 0           | 0      |
| Diameter-limit cutting | 3.4 | 2.6     | 1.1   | 0       | 42.3        | 26.5      | 0     | 21.6  | 0.3          | 1.4         | 0      |
| Nashville Plantation   |     |         |       |         |             |           |       |       |              |             |        |
| Control                | 35.9| 0.3     | 3.9   | 1.4     | 11.5        | 9.5       | 13.9  | 3.6   | 11.0         | 4.1         | 0.5    |
| Improvement cut        | 16.6| 0.3     | 8.0   | 12.3    | 2.0         | 13.0      | 0.3   | 0     | 8.0          | 14.5        | 21.1   |
| Overstory removal      | 19.9| 0.6     | 2.6   | 2.7     | 22.7        | 21.0      | 0.5   | 2.8   | 6.6          | 1.8         | 9.2    |
| Post-harvest Sauls Brook |     |         |       |         |             |           |       |       |              |             |        |
| Shelterwood            | 2.5 | 11.0    | 0     | 0       | 29.3        | 40.6      | 0     | 4.1   | 12.4         | 0           | 0      |
| Commercial clearcut    | 3.1 | 0       | 0     | 0       | 31.0        | 3.0       | 0     | 56.5  | 6.4          | 0           | 0      |
| Seven Islands          |     |         |       |         |             |           |       |       |              |             |        |
| Crop tree release      | 0   | 0       | 0     | 0       | 74.9        | 17.0      | 0     | 8.1   | 0            | 0           | 0      |
| Diameter-limit cutting | 0   | 0       | 0     | 0       | 29.3        | 48.7      | 0     | 21.2  | 0            | 0           | 0      |
| Nashville Plantation   |     |         |       |         |             |           |       |       |              |             |        |
| Improvement cut        | 17.5| 0.4     | 8.8   | 16.4    | 2.5         | 17.1      | 0.5   | 11.2  | 16.7         | 5.0         |        |
| Overstory removal      | 45.0| 0.8     | 9.6   | 3.9     | 8.8         | 1.6       | 0.2   | 2.0   | 4.8          | 11.5        |        |

Post-harvest values were derived from live tree tallies conducted within 1 month after harvest (no cutting was done in the controls).

* Red, black and white spruce.

* White and brown ash.

* Quaking and bigtooth aspen, and balsam poplar.
conditions (e.g. yellow birch, poplar and maples), and regenerating yellow birch in canopy gaps during future harvests. A regional framework and associated resources for adapting forests to predicted changes in climate were used in developing the prescription for this unit [37,38]. At Nashville Plantation, C stocks and accumulation were also assessed in a unit where most overstory trees were removed to release advance regeneration. Logging occurred in 2018 at Sauls Brook and Seven Islands, and in 2020 at Nashville Plantation. The analyses also included controls at each installation with no cutting at the time when other treatments were initiated.

Data collection

Permanent sampling plots consisted of a nested design with 0.08-, 0.02- and 0.008-ha circular plots sharing the same plot center. All trees (living and standing dead (snags)) with a diameter at breast height (DBH, where breast height was 1.37 m) ≥ 11.4 cm were measured on the entire 0.08-ha plot; trees with a DBH ≥ 6.4 cm were measured on the 0.02-ha plot; and trees with a DBH ≥ 1.3 cm were measured on the 0.008-ha plot. Downed woody debris (DWD) was measured on the 0.02-ha plots following the methodology developed by Puhlick et al. [5]. Plot locations were selected using a systematic grid. Criteria for plot selection included plots that occurred on the dominant soil series of an installation and were at least 30 m from the installation boundaries. All trees were measured for DBH, and species were recorded. For standing dead trees, height and decay class was also measured following the methodology developed by Waskiewicz et al. [39]. Distance and azimuth from the plot center to all live trees and snags was recorded, and each tree was assigned a unique tree number, which was painted on the tree. Live tree and dead wood inventories were conducted prior to harvest (in the same year and season as harvest) and 1 year after harvesting.

Aboveground C in live trees was estimated using regional biomass equations [40] and species-specific C concentrations [9]. For snags and DWD, aboveground volume, biomass and C were calculated using methods described in Puhlick et al. [5]. The C stocks of individual live trees and snags, and of DWD pieces, were summed and expansion factors were used to derive per-ha values for each permanent plot. A production approach based on methods by Smith et al. [41] was used to estimate C in harvested wood products and landfills. Trees that were cut from plots were determined from tallies of trees conducted before and after harvest. These tallies occurred within approximately 1 month of harvest. The volume in sawlogs and pulpwod was determined from cut lists associated with growth and modeling (see the section on projecting C stocks). For each harvest, the amount of wood biomass in each product was calculated using equations from Miles and Smith [42], and C concentration estimates by Lamplom and Savidge [9] were used to calculate C stocks. Finally, C in wood products and landfills over time was estimated using residence time data from Smith et al. [41].

Projecting carbon stocks

C dynamics were simulated over a 31-year period beginning with the C stocks that were present before the initiation of treatments on the MASN installations (i.e. in year 0). Pre- and post-harvest DWD inventories were used to calculate the change in DWD C stocks from year 0 to year 1. The post-harvest inventories were then used to project C of individual DWD pieces over time. This involved using equations by Russell et al. [43] to estimate DWD decay class transitions over 5-year periods (i.e. in years 6, 11, 16, 21, 26 and 31). Then, C in each DWD piece was calculated using the methods outlined in the data collection section. Species-specific estimates of the 5-year probability of snags advancing in decay class or falling were also made using transition matrices developed by Russell and Weiskittel [44]. In year 11, snags present in year 1 were prevented from remaining in decay class 1 (in these instances, the snag was reassigned to a decay class of 3). Similar adjustments were made for years 16 and 21, and by year 26, any snags that were present in year 1 were assumed to have fallen. These assumptions were based on decay class transition models and snag survival in Russell and Weiskittel [44]. Snags that were predicted to fall to the ground were added to the DWD pool. For each permanent plot and years 6, 11, 16, 21, 26 and 31 after harvest, the C estimated to be in individual snags and DWD pieces was summed, and expansion factors were used to estimate C stocks on a per-ha basis.

The pre-harvest inventories of live trees ≥ 1.3 cm DBH were used to simulate future growth and mortality using the Northeast variant of the United States Department of Agriculture (USDA)
Forest Service, Forest Vegetation Simulator (FVS-NE) [45]. The FVS keywords used to implement management actions, simulate regeneration and make adjustments to growth and yield calculations are listed in the Supplementary material. For the unit where a partial overwood removal was conducted in year 0 to release advance regeneration, removal of the remaining overwood (i.e. trees ≥ 12.7 cm DBH) was simulated in year 15 except for 1.1 m² ha⁻¹ of live trees ≥ 12.7 cm DBH as reserves. For the unit where the crop tree release was conducted in year 0, a partial overwood removal (to a residual basal area of 6.9 m² ha⁻¹) was simulated in year 15 to release advance regeneration. In other units, no harvesting was simulated after the initial treatments in year 0. Methods for calculating the C in harvested wood products are described in the Supplementary material. A site index of 56 m (base-age 50 years) was used for sugar maple, which was based on Natural Resources Conservation Service Forestland Productivity reports [46].

Increased mortality of American beech trees was simulated at Sauls Brook, where beech bark disease has affected stands for decades, evident from the high occurrence of snags (78 ± 23 (mean ± SD) American beech snags ha⁻¹ with DBH ≥ 11.4 cm) inventoried on permanent plots in 2018. Once a stand is infected, mortality levels can reach 50% within the first decade [27]. In aftermath stands, mortality rates are lower, while many trees remain infested with the scale insect (Cryptococcus fagisuga). Given this information, 1% of American beech trees ≥ 11.4 cm DBH were added to the annual FVS baseline mortality. At Nashville Plantation, it was also observed that large eastern hemlocks showed signs of declining health, such as crown dieback. Given these observations, 1% of eastern hemlock trees ≥ 55.9 cm DBH were added to the annual FVS baseline mortality. Increased mortality of white ash (Fraxinus americana L.) was also specified, due to detecting the emerald ash borer in northern Maine in 2018. It was specified that 5, 5, 25, 25, 25 and 100% of white ash trees ≥ 2.5 cm DBH would die in years 2–7 of the simulation based on mortality rates by Knight et al. [31] and Klooster et al. [30].

For non-harvest related mortality, bole and branch C above the stump was calculated using the annual growth and mortality projections, equations developed by Young et al. [40], and C concentrations by Lamlom and Savidge [9]. For year 15 of the simulations, these methods were also used to estimate C in the tops and branches of trees killed during harvest, plus the portions of boles with a defect. Then, species-specific DWD decay rates for eastern USA forests and the study area’s climate regime [47] were used to estimate dead wood C stocks from non-harvest mortality and harvest residues (from harvests in year 15) for each year of the projection period; this methodology assumes that dead wood was incorporated into the DWD pool immediately after death and that harvest residues were left on the plot. For each 5-year time step of the simulations (i.e. year 1, year 6, etc.), these dead wood C stocks were summed with the C estimated to be remaining in dead wood that was measured during post-harvest inventories in year 1. This represents the total dead wood pool in the cumulative sum of net changes in C over time.

A stock change approach described by Puhlick et al. [7] was then used to calculate the average annual net change in aboveground C stocks plus harvested wood product C for time periods between years 0 and 1, 1 and 6, 6 and 11, etc. The equation was: (C stocks in time 2 – C stocks in time 1)/length of the time period in years. For each permanent plot, AAC was derived by summing the net change in C stocks for each time period and dividing the sum by the total timespan of measurements (i.e. 31 years). Year 0 represents the pre-harvest aboveground C stocks which were calculated from initial inventory data. Hence, the metric of AAC accounts for changes in C associated with cutting mature forests. Such changes include transfers of C from the live tree pool to the harvested wood product and dead wood pools, and C accumulation in residual trees and natural regeneration. Values for AAC were derived using simulations with baseline mortality only and with baseline mortality plus increased mortality due to beech bark disease, emerald ash borer, and senescence of large eastern hemlock trees. These simulations were also used to calculate separate values for AAC in aboveground live tree C stocks only.

Data analyses

Linear mixed effects modeling (LMM) and generalized additive mixed effects modeling (GAMM) were used to evaluate the influence of numerous explanatory variables on AAC in the aboveground components of live trees, dead wood and harvested wood products. The explanatory variables considered for inclusion in models of AAC were:
pre-harvest aboveground C stocks (a covariate to account for differences in pre-harvest C among permanent plots), post-harvest basal area, post-harvest density (i.e. trees ha\(^{-1}\)), post-harvest quadratic mean diameter, percentage biomass removed during harvests in 2018 or 2020, cumulative biomass removed during the initial (in 2018 or 2020) and (if any) future harvests, and species composition indices. For each permanent plot, the percentage biomass removed was calculated by dividing the post-harvest bole biomass by the pre-harvest biomass removed during harvests in 2018 or 2020, cumulative biomass removed during the initial (in 2018 or 2020) and (if any) future harvests, and species composition indices. For each permanent plot, the percentage biomass removed was calculated by dividing the post-harvest bole biomass by the pre-harvest bole biomass and multiplying by 100 [48]. The cumulative biomass removed was calculated by summing the bole biomass removed from a plot over the entire simulation period. The first species composition index was derived by assigning trees to a shade tolerance group (Table 3) and determining each group’s relative basal area (or dominance) by plot and simulation year. These values were then multiplied by the shade tolerance values shown in Table 3. For each plot and simulation year, the resulting (weighted) values were summed, yielding a species composition value ranging from 3 to 1. Finally, species composition values were averaged over all simulation years for each plot. A second species composition index was also derived that involved determining an importance value \([relative \text{ basal area} + relative \text{ density}]/2\) [49] for each shade tolerance group; other calculations were the same as for the first species composition index. Correlated explanatory variables were not used in the same model, and collinearity was assessed through bivariate plots, correlation coefficients, and variance inflation factors (VIFs). If two or more explanatory variables were highly correlated (the threshold was \(r \geq 0.7\), only the explanatory variable most strongly correlated with AAC was included. Additionally, if some of the explanatory variables had VIF values \(> 3\), the variable with the highest VIF was removed, the VIF values were recalculated, and the process was repeated until all variables had VIF values \(< 3\) [50].

The frequency distribution of AAC values was assessed using histograms, and relationships between AAC and explanatory variables were evaluated using bivariate plots and correlation coefficients. The AAC values were normally distributed. Post-harvest basal area and the species composition index based on relative basal area displayed quadratic relationships with AAC. Hence, polynomial terms were added to the LMM. Installation and unit within installation were included in models as random effects. The optimal models in terms of fixed effects were determined based on an evaluation of the t-statistics associated with model parameters and likelihood ratio tests [50]. The lme function in the nlme package [51] in R [52] was used to fit the LMM models. Generalized additive modeling was also performed to allow for non-linear relationships between AAC and multiple explanatory variables, an alternative to extending models with polynomial terms or applying transformations to the explanatory variables. The gam function in the mgcv package was used to fit the GAMM. Smoothers with \(P\) values of \(< .001\) were retained, based on recommendations by Wood [53].

**Results**

Before initiating forest management treatments in 2018 and 2020, average aboveground live tree C stocks across units within installations ranged from 67.1 to 99.7 Mg ha\(^{-1}\) (Table 4). After harvesting, average aboveground live tree C stocks ranged from 14.6 to 96.8 Mg ha\(^{-1}\). In units with harvesting, the average C in harvested wood products accounted for 9 to 44% of the average total C for all of the post-harvest C pools that were evaluated (Table 4). For the control units where no harvesting occurred, the average cumulative sum of net changes in C stocks for the aboveground portions of live trees plus dead wood was positive for the entire 31-year period after treatments were initiated (Figure 2(a,d,g)). For the control unit at Nashville Plantation, the initial loss of C in live trees was mostly because of simulated tree mortality due to the emerald ash borer. For units that were harvested in 2018 or 2020, the initial loss of C in live trees was associated with increases in dead wood and harvested wood product C accumulation. Besides the controls, improvement cutting was the only treatment for which the average

| Species          | Very intolerant | Intolerant | Intermediate | Tolerant | Very tolerant |
|------------------|-----------------|------------|--------------|----------|--------------|
| Pin cherry       | 1.5             | 2          | 2.5          | 3        | 2.5          |
| Quaking aspen    | Paper birch     | 2          | White spruce |          | 3            |
| Balsam poplar   | Balsam fir      | 1.5        | Yellow birch | 3        |              |
| Black willow     |                 |            | White ash    |          |              |

Table 3. Species assigned to shade tolerance groups and their associated shade tolerance values.
total C accumulation was positive by the end of the 31-year period. However, average total C accumulation was near zero for the unit where advance regeneration of conifers and hardwoods were released following overstory removal.

Across all permanent plots, projected AAC in the aboveground portions of live trees, dead wood and harvested wood products was 0.232 ± 1.164 (mean ± standard deviation, SD) and ranged from −1.768 to 1.925. On average, permanent plots in the control and improvement cut units had positive AAC values (Table 5). For the Sauls Brook and Nashville Plantation permanent plots, AAC values derived from results of simulations with increased mortality due to beech bark disease, emerald ash borer and senescence of large eastern hemlock trees were 5.8% less than those derived from results of simulations with baseline mortality only (Table 5). Accounting for expected increases in mortality is important, and all of the AAC values used in the models were derived from simulations with increased mortality. Of the variables considered for inclusion in models of AAC, percentage biomass removed and cumulative biomass

| Installation/treatment          | Pre-harvest C stocks | Post-harvest C stocks |
|--------------------------------|----------------------|-----------------------|
|                                | Live tree | Snag | DWD | Total | Live tree | Snag | DWD | Product | Total |
| **Sauls Brook**                |           |      |     |       |           |      |     |         |       |
| Control                        | 80.2      | 6.0  | 8.1 | 94.2  | 81.2      | 6.0  | 8.1 | NA      | 95.7  |
| (22.3)                         | (0.8)     | (5.7) | (19.2) |       | (22.4)     | (0.8) | (5.7) | NA      | (19.3) |
| Shelterwood                    | 77.0      | 6.1  | 3.2 | 86.4  | 17.5      | 1.7  | 11.3| 16.2     | 47.0  |
| (9.3)                          | (4.8)     | (1.4) | (5.1) |       | (7.3)      | (1.7) | (6.3) | (0.9)   | (6.0)  |
| Commercial clearcut            | 99.7      | 5.4  | 5.7 | 110.8 | 14.6      | 2.8  | 17.7| 27.8     | 62.9  |
| (27.4)                         | (1.0)     | (3.0) | (26.4) |       | (7.1)      | (1.7) | (9.2) | (8.7)   | (19.3) |
| **Seven Islands**              |           |      |     |       |           |      |     |         |       |
| Control                        | 95.6      | 3.2  | 5.0 | 103.8 | 96.8      | 3.2  | 5.0 | NA      | 105.3 |
| (31.2)                         | (1.7)     | (5.3) | (35.3) |       | (31.2)     | (1.7) | (5.3) | NA      | (35.4) |
| Crop tree release              | 96.7      | 2.7  | 3.6 | 102.9 | 34.9      | 1.2  | 9.4 | 20.4     | 66.0  |
| (24.1)                         | (0.9)     | (5.0) | (21.9) |       | (8.5)      | (1.0) | (5.0) | (6.7)   | (11.8) |
| Diameter-limit cutting         | 90.0      | 3.0  | 2.9 | 96.0  | 20.7      | 1.2  | 16.5| 22.9     | 61.3  |
| (23.8)                         | (0.9)     | (2.9) | (23.3) |       | (8.9)      | (1.1) | (8.6) | (9.9)   | (13.7) |
| **Nashville Plantation**       |           |      |     |       |           |      |     |         |       |
| Control                        | 82.5      | 3.2  | 1.5 | 87.1  | 84.3      | 3.2  | 1.5 | NA      | 89.7  |
| (13.5)                         | (2.3)     | (1.1) | (13.3) |       | (13.6)     | (2.3) | (1.1) | NA      | (13.7) |
| Improvement cut                | 67.1      | 1.0  | 2.7 | 70.8  | 42.3      | 0.7  | 5.1 | 5.4      | 62.4  |
| (6.4)                          | (1.4)     | (1.7) | (6.2) |       | (13.7)     | (1.2) | (2.5) | (2.4)   | (9.9)  |
| Overstory removal              | 81.7      | 0.8  | 1.3 | 83.8  | 15.4      | 0.1  | 2.6 | 20.8     | 61.5  |
| (13.3)                         | (0.4)     | (1.5) | (14.4) |       | (1.6)      | (0.2) | (2.2) | (3.5)   | (10.3) |

Post-harvest live tree stocks include 1 year of simulated growth. Dead wood pools were remeasured 1 year after the initial inventories, except in the controls.

DWD: Downed woody debris; NA: Not applicable, i.e. no trees were cut in control units.

Figure 2. Projected cumulative sum of net changes in C stocks (Mg ha⁻¹) over a 31-year period by installation and forest management treatment. Net changes in C stocks between inventories can be positive (C accumulation) or negative (C loss).
Table 5. Mean (standard deviation in parentheses) projected average annual net change in C (AAC) over the 31-year time period investigated, percentage biomass removed (based on removals in year 0), cumulative biomass removed (sum of biomass removals over time), and species composition indices by installation and forest management treatment.

| Installation/treatment | AAC: increased mortality | AAC: base mortality only | Percentage biomass removed (% 0–100) | Cumulative biomass removed (Mg ha⁻¹) | Composition: relative basal area (Scale of 1–3) | Composition: importance value (Scale of 1–3) |
|------------------------|--------------------------|-------------------------|---------------------------------------|--------------------------------------|-----------------------------------------------|---------------------------------------------|
| Sauls Brook Control    | 1.295                    | 1.379                   | 0                                     | 0                                    | 2.89                                          | 2.94                                        |
|                         | (0.107)                  | (0.125)                 | (0)                                   | (0)                                  | (0.09)                                       | (0.05)                                      |
| Shelterwood            | −1.065                   | −1.062                  | 78.4                                  | 117.8³                           | (0.08)                                        | (0.04)                                      |
| Commercial clearcut     | −1.007                   | −0.948                  | 87.9                                  | 124.8                               | 2.94                                          | 2.96                                        |
|                         | (0.462)                  | (0.449)                 | (5.2)                                 | (36.3)                              | (0.04)                                        | (0.02)                                      |
| Seven Islands Control   | 1.350                    | 1.350                   | 0                                     | 0                                    | 2.63                                          | 2.77                                        |
|                         | (0.318)                  | (0.318)                 | (0)                                   | (0)                                  | (0.30)                                       | (0.17)                                      |
| Crop tree release       | −0.982                   | −0.982                  | 60.7                                  | 119.5³                             | 2.85                                          | 2.90                                        |
|                         | (0.500)                  | (0.500)                 | (8.7)                                 | (38.8)                              | (0.13)                                        | (0.07)                                      |
| Diameter-limit cutting  | −0.511                   | −0.511                  | 71.3                                  | 99.7                                | 2.64                                          | 2.76                                        |
|                         | (0.739)                  | (0.739)                 | (14.8)                                | (41.2)                              | (0.21)                                        | (0.15)                                      |
| Nashville Plantation    | 1.536                    | 1.942                   | 0                                     | 0                                    | 2.70                                          | 2.79                                        |
| Control                | (0.550)                  | (0.140)                 | (0)                                   | (0)                                  | (0.11)                                       | (0.08)                                      |
| Improvement cut         | 1.165                    | 1.242                   | 51.1                                  | 35.6                                | 2.32                                          | 2.11                                        |
|                         | (0.098)                  | (0.084)                 | (24.4)                                | (15.9)                              | (0.13)                                        | (0.20)                                      |
| Overstory removal       | −0.078                   | 0.025                   | 95.3                                  | 103.8                               | 2.68                                          | 2.74                                        |
|                         | (0.288)                  | (0.319)                 | (3.7)                                 | (24.2)                              | (0.11)                                        | (0.10)                                      |

For species composition indices, values near 1 indicate dominance (i.e., relative basal area) or importance (dominance and relative tree density) by species with low tolerance of shade. AAC values are shown for simulations with baseline mortality only, as well as baseline mortality plus increased mortality due to beech bark disease, emerald ash borer and senescence of large eastern hemlock trees.

³Includes 26.8 ± 12.6 Mg ha⁻¹ (mean ± standard deviation) of biomass from cutting in year 15.

Table 6. Parameter estimates and model fit statistics for linear mixed effects models (LMM 1 and LMM 2) of the average annual net change in C (Mg ha⁻¹ year⁻¹).

| Model | LMM 1 | LMM 2 |
|-------|-------|-------|
| Intercept SE | 0.333 | 5.156 |
| Slope 1 SE | 0.002 | < 0.001 |
| Slope 2 SE | 0.011 | 0.001 |
| Slope 3 SE | 0.022 | 3.954 |
| Slope 4 SE | 0.001 | 0.754 |
| Marginal R² | 0.910 | 0.950 |
| Conditional R² | 0.967 | 0.950 |
| Residual SE | 0.244 | 0.001 |
| b₀, SE | 0.292 | 0.001 |
| b₁, SE | 0.001 | 0.223 |

Pre-harvest C stock (Mg ha⁻¹), post-harvest quadratic mean diameter (QMD; cm), post-harvest basal area (BA; m² ha⁻¹), density (trees ha⁻¹), cumulative biomass removed (Mg ha⁻¹) and species composition index values are restricted to a range of 1–3, with values near 1 indicating dominance by species with low tolerance of shade) are fixed effects. Unit within installation and installation are random effects (b₀, b₁ respectively).

LMM 1: 0.603 − 0.019(C stock) − 0.026(QMD) + 0.137(BA) − 0.002(BA²) + b₀ + b₁.

LMM 2: 15.1 + 0.0001(density) − 0.171(cumulative biomass removed) − 10.194(composition²) + 1.835(composition) + b₀ + b₁.

SE: Standard error; NA: Not applicable.

Discussion

The projections of C accumulation in the aboveground portions of live trees, dead wood and
harvested wood products over a 31-year period (to ~2050), based on detailed pre- and post-harvest inventories, indicated that unharvested controls and the unit with improvement cutting were net C sinks. These results support the idea of retaining some forests as reserves when objectives prioritize enhancing C accumulation at the landscape scale [34]. Improvement cutting can also be a useful strategy for enhancing C accumulation and accomplishing other ecosystem objectives. More specifically, seed source trees for species that are predicted to be well-adapted to future climate conditions (e.g. yellow birch, poplar and maples) were retained at the study sites [37,38]. Dead wood structure and biomass were also enhanced by retaining large eastern hemlocks (≥ 55.9 cm DBH), many of which died due to senescence during the simulation period, and by retaining live ash trees that were killed by the emerald ash borer. Additionally, structural diversity was promoted by maintaining multiple size classes of live trees and establishing new aspen stems from stump sprouting and root suckering. Elements of the prescription for the unit with improvement cutting were derived from adaptation resources [37,38], providing evidence that adaptation actions can contribute to C management objectives.

In the present study, improvement cutting was associated with lower biomass removal and species composition indices than other forms of harvesting. The lower species composition indices reflect greater relative dominance by species with low and intermediate tolerance of shade. Such species tend to have high growth rates (e.g. paper birch and poplar), especially following harvest, which may partially explain the relatively high amount of C accumulation in the unit with improvement cutting. For the unit with shade-tolerant conifer seedlings and pole-sized hardwoods and conifers released after removing overstory

![Figure 3. Estimated smoothers and 95% confidence bands for two generalized additive mixed effects models (GAMM 1 and GAMM 2) of projected average annual net change in C (Mg ha⁻¹ year⁻¹) for the aboveground portions of live trees, dead wood and harvested wood products over a 31-year period. The smoothers are centered around zero. Fitted values can be obtained by adding the intercept and contributions from random effects. BA: Basal area; Biomass removal: Cumulative biomass removed; Composition: Species composition index (values are restricted to a range of 1–3, with values near 1 indicating dominance by species with low tolerance of shade).](image-url)
trees, the cumulative sum of changes in C stocks was nearly zero (−0.078) by year 31. This unit had greater post-harvest tree densities than other units with harvesting, and post-harvest density was positively correlated with C accumulation over time in models of AAC. Across installations, post-harvest density was negatively correlated with quadratic mean diameter ($r = −0.67$). These findings indicate that stands with adequate stocking of residual trees in the sub-merchantable size classes can rapidly sequester C over a relatively short timeframe as competition for resources (e.g. light, water, nutrients) is reduced. Interestingly, the two units with harvesting that had the greatest mean tree densities and AAC were composed of mixed-wood stands.

While this study shows that biomass removal and post-harvest stand attributes (i.e. basal area, density, quadratic mean diameter and species composition based on relative dominance and shade tolerance) are useful predictors of C accumulation, species-specific influences on C accumulation should also be considered [7,54]. For example, the shelterwood and commercial clear-cutting units at Sauls Brook had similar mean AAC and biomass removals (Table 5), but commercial clearcutting shifted species composition toward American beech and eliminated the overstory red spruce component on permanent plots. In contrast, shelterwood cutting reduced the American beech and balsam fir component, while increasing the relative proportion of maples and yellow birch. The latter species are often preferred and generally more successful for disseminating seed into areas void of advance regeneration, and some overstory trees of these species may be beneficial as reserve trees for accumulating C after the final overwood removal [55]. When implementing shelterwood cutting in stands with a high proportion of American beech with beech bark disease, site preparation may be needed to control American beech root suckering and stump sprouting so that desired species have a higher probability of dominating the new cohort [28,56,57]. At Nashville Plantation, overstory removal shifted species composition toward fast-growing intolerant hardwoods and balsam fir, which rapidly accumulated C over the 31-year simulation period. Hence, residual stand conditions, including species composition, are important to consider when objectives include enhancing C accumulation.

Also, while many treatments had negative AAC values, the results should be considered in the context of conditions across the MASN installations before harvesting in 2018 and 2020. Prior to harvesting, the installations had many attributes of older forests, including large trees (Table S4) and abundant standing and downed dead wood (Table 4). When comparing C accumulation among forest management treatments, initial conditions directly influence estimates of C accumulation and the ranking of treatments with regard to C objectives. For example, estimates of AAC could be different if starting from a well-stocked forest, cutover stand conditions, or clearcutting followed by tree planting. The starting conditions of the two installations with hardwood stands (Sauls Brook and Seven Islands) were similar to those of second-growth northern hardwood stands in the Lake States [58] and at Hubbard Brook in New Hampshire [59]. However, Sauls Brook had greater mean dead wood C stocks than Seven Islands and the Lake States, partly because of the greater proportion of American beech at Sauls Brook and inputs to the dead wood pool from dead and declining American beech with beech bark disease. In fact, American beech accounted for 51% of the coarse downed woody debris C at Sauls Brook (Table S5).

The mean pre-harvest live tree C stocks for mixed-wood stands at Nashville Plantation were similar to those of conifer-dominated mixedwood stands at the Penobscot Experiment Forest before the initiation of forest management treatments on the forest in the 1950s [6].

The controls were relatively resilient to simulated increases in tree mortality due to disturbance agents and natural senescence. At Sauls Brook, aboveground C accumulation was positive despite increased American beech mortality levels due to beech bark disease. This could be partially attributable to increased growth rates of co-occurring species in response to greater resource availability [27]. While the control at Nashville Plantation had a short-term loss of live tree C due to simulated white ash mortality caused by the emerald ash borer, live tree C accumulation rebounded and aboveground C accumulation in live trees and dead wood was positive for the entire simulation period. The relatively small differences in mean AAC for values derived from simulations with increased tree mortality and those derived from simulations with baseline mortality only (Table 5) is partially due to the high diversity of tree species at each of the study sites (Table 2). Albani et al. [22] noted that while insect outbreaks can be locally severe, C fluxes may be minimally affected.
if highly productive tree species replace the lost or reduced ones due to outbreaks. Although FVS simulations indicated increased growth and yield in all of the stands without harvesting, future monitoring of tree growth and C accumulation will be needed to verify these results. For instance, northern hardwood stands at Hubbard Brook accumulated C in aboveground pools and organic horizons to about 70 years after harvesting, but accumulated little C thereafter [59]. In contrast, other studies using empirical data have shown continued C accumulation in old, mixed-species stands in Maine [6,7,54].

Overall, the results show that biomass removal and post-harvest stand attributes are important factors to consider when evaluating C accumulation in forests and harvested wood products. In forestry, biomass removal and residual stand conditions have also been important for determining regeneration outcomes and dead wood biomass over time [48,60,61]. Additionally, specific forest management treatments should be evaluated for their influence on C accumulation, regeneration outcomes and dead wood biomass. In this study, biomass removal and post-harvest stand attributes proved to be useful metrics for evaluating C accumulation because some prescriptions were not replicated across installations, which precluded testing for direct treatment effects. Also, while this study involved assessments of C accumulation to ~2050, longer projections are needed to inform management decisions regarding multiple ecosystem services, including C sequestration. As future treatments are implemented (or other disturbances occur) in these stands and a longer time interval is evaluated, weighting biomass removals by time and date of initiation of treatments on the MASN may be useful for modeling C accumulation [48].

To accomplish C objectives in regions with forests similar to the ones of this study, multiple strategies could be used across forests, including keeping some forests in reserve and using silvicultural treatments that maintain a high proportion of the initial stand biomass in species that are predicted to be better adapted to future disturbances and climate change. The timing and allocation of these strategies at a landscape scale have important consequences for C sequestration and additional ecosystem services that forests provide [62], which deserves greater consideration in future analyses. Additionally, growth and yield models are imperfect tools that include many assumptions and relatively simple relationships built on limited data, which means that projection uncertainty increases exponentially with time, even in rather simple systems or scenarios [63]. Although the simulations began with detailed empirical field data and projections were limited to less than three decades, the consequences and interpretation of projection uncertainty were not quantified in this study. This needs to be considered in the broader implications of this work, and future efforts are needed to both verify the presented findings and continue to explore this topic given its importance.

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Author contributions

All authors contributed substantially to the work reported. Conceptualization, JP, AW and IF; methodology, JP and IF; software, JP and AW; validation, JP, AW and IF; formal analysis, JP, AW and IF; investigation, JP; resources, JP and IF; data curation, JP; writing – original draft preparation, JP; writing – review and editing, JP, AW, IF, KS and DS; visualization, JP, AW and IF; supervision, JP; project administration, JP; funding acquisition, JP, AW and IF. All authors have read and agreed to the published version of the manuscript.

Competing interests

The authors declare there are no competing interests.

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