



Soil nutrient recovery after shelterwood timber harvesting in a temperate oak hardwood forest: Insights using a twenty-five-year chronosequence

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ABSTRACT

Understanding the effects of forest timber harvests on soil chemistry is essential to manage for a sustainable yield of timber from forests. Yet few studies have examined the long-term effects of timber harvesting on the soils of temperate hardwood forests. We use a 25-year chronosequence of post-regeneration irregular shelterwood harvests in an oak-hardwood forest in Connecticut, USA to examine the impacts of timber harvesting and subsequent forest regeneration on soil and leaf litter chemistry. Soil and leaf litter samples were collected across 34 stands ranging in age from one year to 25 years since harvest. Using hierarchical, linear mixed effects models, we analyzed trends in soil and leaf litter properties over time in the harvested stands and compared these values to undisturbed reference sites. Soil chemistry from two depths (0–10 and 10–20 cm) revealed that surface and sub-surface soils respond differently through time, with the shallow soils being more responsive to harvest and regeneration, but both increasing in fertility with increasing time since harvest. In shelterwood soils, time since harvest had a positive effect on macronutrient concentrations and a negative effect on the carbon (C) stable isotope ratio ($\delta^{13}\text{C}$), with the latter indicative of recovery of faster-cycling soil C pools. In leaf litter, time since harvest had a positive effect on nitrogen (N) concentrations and a negative effect on $\delta^{13}\text{C}$, with the latter again suggesting build-up of more recent litter inputs. Relative to eight unmanaged reference sites, harvested stands were lower in some soil nutrients (magnesium, phosphorus, percent C, as well as cation exchange capacity), but these differences were recovered over time within the 25-year chronosequence. Post-hoc *t*-tests ($\alpha = 0.10$) showed no significant difference in percent nitrogen by 11–15 years post-timber harvest as compared to the undisturbed sites. Likewise, potassium, phosphorus and percent carbon showed no difference by 16–20 years, and magnesium showed no difference by 21–25 years. Calcium never varied significantly between shelterwood and uncut reference sites. Overall, our results suggest that decomposing organic matter acts quickly to promote macronutrient recovery in surface soils following irregular shelterwood harvests.

1. Introduction

Shelterwoods are silvicultural treatments that are designed to leave parent trees as a seed source and maintain canopy shade to foster regeneration after a timber harvest (Ashton and Kelty 2018). As compared to standard shelterwood treatments, irregular shelterwood treatments permanently leave more legacy trees standing to mimic intense natural wind-derived canopy disturbances such as tornadoes, hurricanes, and microstorms that create big openings but retain remnants of an older age-class structure (Ashton and Kelty 2018). The partial canopy of older reserve trees in irregular shelterwood harvests

allows enough sunlight for regeneration of ecologically and economically valuable shade mid-tolerant species like red oak (*Quercus rubra* L.) and hickory (*Carya* spp. Nutt.) in the presence of more tolerant species such as red maple (*Acer rubrum* L.) and black birch (*Betula lenta* L.) (Raymond et al. 2009; Wikle et al. 2019). Irregular shelterwood harvests offer some of the light conditions normally found in even-aged treatments like clear-cuts, while providing benefits afforded by tree retentions, like moderated regeneration conditions and continuity of ecological processes (Gustafsson et al. 2012). Maintaining a degree of canopy cover and leaving much of both coarse and fine woody debris well distributed across the soil surface may reduce the ecological

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impacts of logging by providing partial cover for shade-tolerant species (Duguid and Ashton 2013) as well as structure for breeding birds, amphibians, and mammals (Duguid et al. 2016; Mossman et al. 2019; Hanle et al. 2020). Furthermore, shelterwoods may reduce cation losses via leaching and carbon loss via lower rates of decomposition relative to more intensive regeneration harvesting methods such as true clear-cutting and seed tree that both rely upon surface soil scarification, more open conditions, and removal of woody debris to facilitate regeneration on exposed mineral soil (Ashton and Kelty, 2018; Bormann et al., 1968; Dahlgren and Driscoll, 1994; Jerabkova et al., 2011; Nasiri and Parsakhoo, 2012). However, we are not aware of any studies that have examined long-term changes in soil chemistry following shelterwood harvests with legacy tree retention, particularly for second-growth forests that originated after agricultural abandonment and are widespread throughout much of temperate eastern North America and Western Europe.

Previous research examining changes in soil nutrients after timber harvests has primarily focused on sites and regions where treatments are more intensive and where plantation forestry is dominant, such as short rotations for timber and pulpwood in the southeastern U.S. (Vitousek et al. 1992; Munson et al. 1993; Fox et al. 2007; Achat et al. 2015). These plantations are on weathered clay soils of the coastal plains and require fertilization to overcome deficiencies in nitrogen (N) and phosphorus (P) (Fox et al. 2007). Intensive forestry practices that remove all organic residues through whole tree harvesting can also create nutrient-limiting soil conditions because of reduced microbial activity and poorer quality organic matter (Achat et al. 2015). However, the impact on soil nutrients of shelterwood harvesting to extract timber in native forests has not been fully investigated.

Similar to regular shelterwood harvests, irregular shelterwood harvests reduce tree biomass, decrease long-term inputs of nutrients from leaf litter, increase variability in surface soil temperature and moisture through loss of canopy shade and thermal cover, and increase surface heterogeneity from an influx of coarse woody debris (Ballard 2000; Raymond et al. 2009). Most shelterwood regeneration harvests leave woody debris that may reduce nutrient losses because the high carbon (C) to N ratio of coarse woody debris can immobilize soil nutrients, until the N in the debris is made available for plant uptake (Zimmerman et al. 1995). Nevertheless, a study comparing a clear-cut and a partial-cut, similar to a shelterwood harvest, in a western temperate coniferous forest in British Columbia, Canada found differences in soil N content and forest floor depth but other changes in soil chemistry were negligible (Kranabetter and Coates 2004). In a study evaluating whole tree harvest and conventional harvest effects on soils in Quebec, calcium (Ca) and pH were higher in conventionally harvested areas than the unharvested control one year after harvest because of the nutrient pulse from the debris of the harvest itself, but no differences were detected in amounts of soil organic matter or mineral soil C (Hendrickson et al., 1989). Whether such impacts are also observed following shelterwood harvests in mixed oak-hardwood forests is largely unknown given the limited research attention they have received.

In the United States, mixed oak-hardwood forest types make up 51% of all forests (Smith et al. 2009; Dey 2014). For these forest types, shelterwood regeneration harvests are common and known to be successful in regenerating oak, hickory and other heavy-seeded shade-tolerant to shade mid-tolerant tree species, while uneven-aged management techniques such as those often practiced in northern hardwoods may fail to regenerate the less shade-tolerant species in these systems (Loftis 1990; Brose 2011; Raymond and Bédard 2017; Ashton and Kelty 2018). Soil studies on shelterwoods in these forest types are, however, few and far between and have yielded mixed results. For instance, Scott et al. (2004) studied soil respiration and carbon pools of total biomass but found no major loss in soil C post-harvest over the short-term. In contrast, Warren and Ashton (2014) found that in the twenty years following shelterwood harvests in oak-hardwood sites within our study region (the northeastern U.S.), C in litter and in the

surface (<10 cm depth) horizons of the soil declined in the short term (<5 years post harvest) by about 25%, but the loss was compensated for by the large C pool in woody debris left after logging. This initial input of woody debris declined from 4.5 kg m² to 0.40 kg m² over the twenty-year period but was compensated for by the incremental re-accumulation of biomass in the forest floor. With soil, litter, and woody debris C combined, Warren and Ashton (2014) found no difference in C between harvested and unharvested stands. Such studies provide preliminary evidence on soil C dynamics, but the long-term impacts of timber harvest on soil chemistry in general remain poorly understood. This information gap demands further understanding of how working forests interact with C, soil chemistry, and nutrient cycling (Jurgensen et al. 1997). However, no work, as far as we are aware, has reported long-term trends in soil chemistry post-irregular shelterwood harvest in mixed oak-hardwood forest types.

The purpose of our study is to analyze a twenty-five-year chronosequence of irregular shelterwood harvests to characterize trends in soil nutrient concentrations during second-growth forest succession as related to time since harvest and soil depth. To do so, we collected soil and leaf litter samples from shelterwood harvests and compared them to adjacent undisturbed reference sites where no timber harvest occurred. We quantified changes in soil C, cation exchange capacity (CEC), macronutrient concentrations (N, P, potassium (K), Ca, magnesium (Mg)) and soil pH. Additionally, to better understand C and N cycling within the harvest sites, we characterized stable C and N isotopes because they offer insight into nutrient cycle pathways. Our study is both robust and novel because of the large number of harvests that we sampled spanning a long period of time. These factors allowed us to investigate surface soil development and re-building post-harvest in much more detail than previously reported. The chronosequence approach also enabled us to identify patterns in C and nutrient pools that are notoriously difficult to detect given the slow rate of change and high fine-scale spatial variation in the pool size.

2. Materials & methods

2.1. Site description

The study was conducted at Yale-Myers Forest in northeastern Connecticut (Latitude 41.95 N, Longitude 72.12 W; Fig. 1a). The local climate is temperate and humid with a 21 °C mean annual summer temperature, -2°C mean annual winter temperature, and 123 cm mean annual precipitation (NOAA 1981–2010 Climate Normals). The 3180-ha research forest sits on top of gneissic and schistose bedrock (Meyer and Plusnin 1945; Rodgers 1985). The surficial geology is heavily influenced by glaciation that left behind a network of drumlins, ablation till, kettle holes, and outwash, which define drainage patterns and influence the topography of this region (Hill et al. 1980). In the 20,000 years since the last glacial maximum, soils have redeveloped through plant and microbial activity into acidic, primarily mesic inceptisols (USDA 1975). The forest has variable topography but is not montane, with the highest elevations being about 320 m, and the lowest elevation being 160 m (Meyer and Plusnin 1945).

Like most of New England, the forest grows on what was once farm- and pasture-land. Originally stewarded by Algonquin peoples and more recently by the Nipmuc, the region was subjected to intermittent swidden agriculture and controlled fires for at least 10,000 years (Thomas 1976; Russell 1983). In the early 1700s, the land was settled by European colonizers who cleared the forest in favor of open land until agricultural abandonment in the mid-nineteenth century. Gifted to Yale Forest School in 1930 as a cut-over young second-growth hardwood forest, the area has since developed into a mature, predominately mixed-hardwood forest (Meyer and Plusnin 1945).

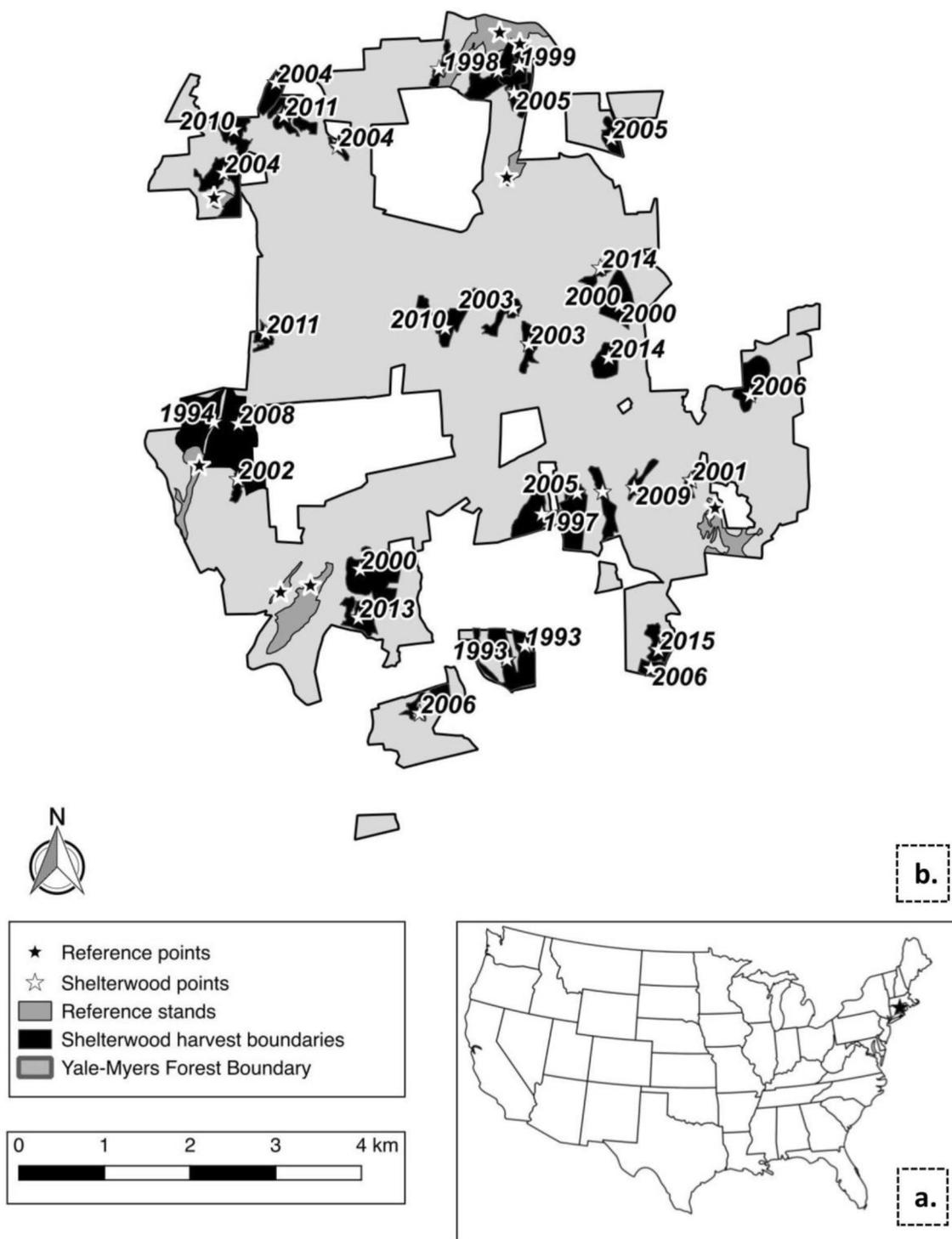


Fig. 1. Map of study site showing (A) Yale Myers Forest in northeast Connecticut, USA and (B) locations of the 34 shelterwood cuts and 8 reference sites throughout Yale Myers Forest, with the former labeled by harvest year.

2.2. Site selection

We used a chronosequence of 34 irregular shelterwood harvests that ranged in age from one to 25 years since the last cut, which spans 1992–2016 for the harvest years. Without replacing the role of long-term studies and modeling efforts (Dean et al. 2017), chronosequences, such as this, offer a snapshot of environmental changes through time (Johnson and Miyanishi 2008; Walker et al. 2010). In addition to the 34 irregular shelterwood stands, we also included eight

undisturbed reference stands that served as controls for comparison. The control stands, like the shelterwood stands prior to harvest, were all second-growth that originated after agricultural abandonment over 100 years ago, but have been little affected by any kind of disturbance; though three had received an intermediate crown thinning over sixty years ago. In the shelterwood stands, the retained overstory basal area for trees ≥ 40 cm DBH ranged from 1.3 to 16.1 $m^2 ha^{-1}$ (Wikle et al. 2019). The post-harvest slash and organic debris are purposefully well-distributed throughout the site (Ashton and Keltly 2018). Harvest sites

vary only modestly in soil type and topography (See Fig. 1b; Supplemental Table S1). The sites were located on mesic Woodbridge, Paxton-Montauk, Charlton-Chatfield, Canton-Charlton and Brookfield-Brimfield soils and soil complexes and drier Gloucester soil (NRCS 2008). Most of the soils are ablation till loams of varying stoniness, texture and depth on top of bedrock. The exceptions are Woodbridge and Paxton-Montauk, which are drumlin soils comprising ablation till loams one-to-two meters in depth, under which there is a perched water table that lies on top of hills of basal till (NRCS 2008). Dominant species include red maple (*A. rubrum*), sugar maple (*Acer saccharum* Marsh.), red oak (*Q. rubra*), white oak (*Quercus alba* L.), black birch (*B. lenta*), eastern hemlock (*Tsuga canadensis* L.), white pine (*Pinus strobus* L.), and hickories (*Carya* spp.) in the overstory and mountain laurel (*Kalmia latifolia* L.) in the shrub layer.

2.3. Sampling design

Plots at each harvest and reference site were oriented around a randomly-placed plot center, at least 50 m from the harvest's boundary (Goodale et al. 2009; Fig. 2). We used three transects radiating out north, southwest, and southeast from plot center. Each transect contained four 0.75-m radius circular sub-plots located 15, 25, 35, and 45 m from plot center. We took one 1.9-cm dia., 20-cm deep core of the mineral soil from the center of each of the sub-plots with a stainless-steel soil corer. We separated the top 10 cm (0–10 cm) of the core from the bottom 10 cm (10–20 cm) (hereafter referred to as surface and sub-surface cores, respectively). We placed the cores into brown paper bags as composite samples of four cores, which yielded approximately 100 g of soil per composite sample. As such, each shelterwood site included six samples—one for each depth bracket on each transect. We sampled at the soil surface because the impacts of disturbances on soil nutrients affect the most mobile and most sensitive part of the soil first. Being further away from the site of impact, deeper horizons are more insulated from its effects (Johnson et al., 1991).

Additionally, we collected one leaf litter sample, which included

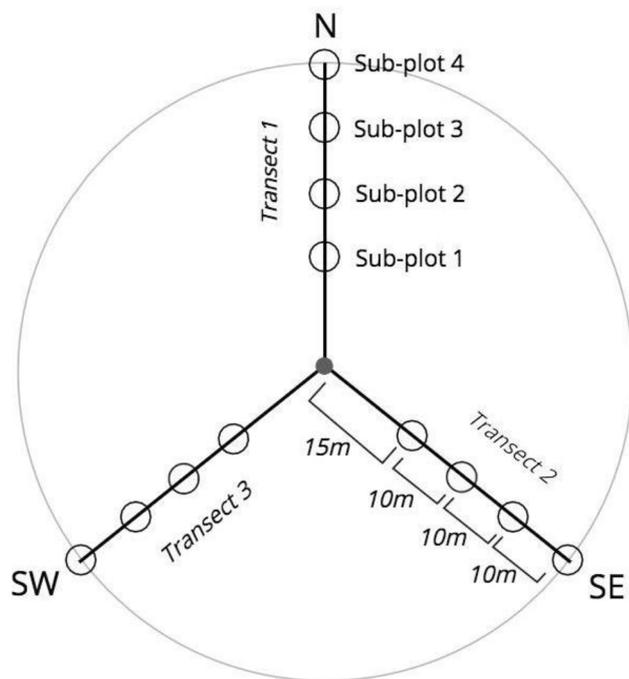


Fig. 2. The sampling design of three transects centered around a randomly-placed plot center in each of the 34 shelterwoods and 8 reference sites. Soil samples were taken at each of the 4 subplots on each of the transects. Leaf litter samples were taken at the 1st and 3rd subplots on each transect.

loose litter and the organic horizon that stopped at the surface of the mineral soil, at each shelterwood site. We cut leaf litter samples from the forest floor using a knife and a 15 by 15-cm square template at a randomly selected spot within every other subplot (i.e., 15-m and 35-m from plot center, see Fig. 2). We placed all six 15 by 15-cm samples into brown paper bags, which yielded one composite sample per harvest site. We collected all harvest leaf litter and soil samples in June and July 2017. We collected leaf litter during the growing season when there is minimal fresh litter input, to reflect nutrient availability at that time.

Using the same sampling design and plot protocol, reference soil and litter samples were collected from the eight oak-hardwood sites that have been undisturbed since at least 1960.

2.4. Soil, organic matter and litter analysis

To prepare the soils for analysis, we passed the air-dried cores through a 2-mm mesh sieve, and discarded all material larger than 2-mm. We then ground the <2-mm fraction with a ceramic mortar and pestle until all particles passed through a 0.420-mm mesh sieve. For the leaf litter preparation, we dried each sample at 70 °C to constant mass, weighed it, then milled it in a Wiley Mill to homogenize, and ball-milled it to a fine powder for nutrient analysis.

Soil nutrients were assessed following standard soil protocols, with the choice to measure total versus extractable pools for any single nutrient made in light of empirical knowledge of their turnover times. So, for example, we expected total N to respond in our system in a meaningful way for N availability given the timescale of our study, whereas the much slower cycles of total P led to us using extractable P as an indicator of its availability.

For the surface soil samples, we conducted %C, %N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis at the Yale Analytical and Stable Isotope Facility, New Haven, Connecticut, USA using an elemental analyzer (Costech ESC 4010, Valencia, California, USA) and a continuous-flow isotope-ratio mass spectrometer (precision $\pm 0.2\%$; Thermo Delta Plus Advantage, San Jose, California, USA).

We sent samples from both depths (0–10 cm, 10–20 cm) to the Soil, Plant and Water Lab at the University of Georgia for cation analysis, cation exchange capacity, and pH. Phosphorus, K, Ca, and Mg were determined using an Inductively Coupled Plasma Spectrograph, and pH was determined by a LabFit AS-3000 pH Analyzer in calcium chloride. The Mehlich-1 extract from this cation analysis and the milliequivalents of exchangeable hydrogen, as determined by direct titration with 0.023 M $\text{Ca}(\text{OH})_2$, were used to determine CEC and percent base saturation (Kissel and Sonon 2008).

2.5. Statistical analyses

We used linear mixed models (LMMs) to analyze changes in soil nutrient concentrations during forest development following shelterwood harvests because LMMs accommodate the hierarchical structure of our data through nested random effects. We calculated R^2 values for the LMMs using the method described by Nakagawa and Schielzeth (2013), which distinguishes between variance explained by fixed effects (marginal R^2) and variance explained by both fixed and random effects (conditional R^2). We considered coefficients with $p < 0.05$ to be significant and coefficients with $p < 0.10$ to be marginally significant. We fit the models using a Gaussian error distribution and ran all analyses with the 'lme4' package in the statistical freeware R (version 3.4.2; R Core Team 2017; Bates et al. 2015).

For the purposes of understanding how timber harvesting affects soil fertility through time, we focused on a core suite of well-recognized soil chemistry measures of nutrients: pH, CEC, percent base saturation, and macronutrients (C, N, Mg, Ca, P, and K) (see Supplemental Table S2 for complete nutrient analysis results).

To examine the impacts of timber harvesting and subsequent regeneration on C and N concentrations, we used %C, %N, $\delta^{13}\text{C}$, and

$\delta^{15}\text{N}$ as response variables. Carbon and N concentrations were natural log-transformed to meet assumptions of normality and homoscedasticity. No transformations were required to meet the assumptions for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. We included time since harvest as a fixed effect and stand as a random effect to account for potential spatial associations between samples collected from the three transects within each site.

For the analysis of soil pH, CEC, and macronutrient—Ca, Mg, K, and P—concentrations we used hydrogen ion concentration ($[\text{H}^+]$) rather than pH since it is on a linear scale and therefore allows for more direct interpretation of the model output. However, we natural log-transformed all six soil response variables, including $[\text{H}^+]$, to meet assumptions of normal residual distributions and homoscedasticity. For these models, we included time since harvest, depth, and the interaction between depth and time as fixed effects and transect nested within stand as random effects.

For the reference models, we used LMMs to compare data from all shelterwood sites to data collected from the eight undisturbed forest stands. For the C and N models, we included management (i.e., shelterwood versus reference site) as a fixed effect and stand as a random effect. For the pH, CEC, and macronutrient models, we included management, depth, and the management by depth interaction as fixed effects and transect nested within stand as random effects. We natural log-transformed all response variables with the exception of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. We treated management and depth as binary indicator variables in the models, where shelterwood sites and subsurface (i.e., 10–20 cm) samples were each coded as “1” and reference sites and surface (i.e., 0–10 cm) samples each coded as “0.” Therefore, the coefficients can be interpreted as the effect of forest management on soil conditions relative to undisturbed sites and the effect of increasing soil depth on nutrient concentrations. As a post-hoc analysis to query if and when nutrient levels in the shelterwood soils returned to pre-harvest levels, we compared means between the reference sites and 5-year age brackets of the shelterwood sites using Welch’s two-sample *t*-tests in R. The two-sample *t*-tests account for variability between data points to determine if the difference in means between reference and harvest sites is significant or non-significant.

For the leaf litter models, we used simple linear regression to analyze trends in %C, %N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ over time since we pooled all leaf litter samples by stand (see Supplemental Table S3 for complete litter analysis results). We also used simple linear regression to compare litter chemistry in shelterwood and reference sites. For the management variable in these models, we coded shelterwood sites as “1” and reference sites as “0.” For dry litter mass, we used a simple linear regression to analyze the trend over time. We checked all model residual distributions for normality and homoscedasticity using the plot function in R.

3. Results

3.1. Difference in soil nutrient concentrations between shelterwood sites and reference sites

Soils in the harvested shelterwood stands consistently had lower concentrations of macronutrients than the undisturbed reference sites. Specifically, we found lower average nutrient concentrations for harvest sites as compared to reference sites for C, Mg, P and CEC, but we also observed an increase in mean pH (Table 1). Mean %C was lower by 1.45 percentage points in the shelterwood sites than in undisturbed reference sites. For P, soil responses to forest harvesting were similar for both the surface and subsurface samples (Table 3). However, significant interactive effects between soil depth and harvesting for Mg, pH, CEC, and K indicated that for some soil variables, surface and subsurface soil horizons responded differently to timber harvesting. In particular, surface soils responded more strongly to harvesting than subsurface soils for Mg, CEC, and pH (Table 3). Mean surface Mg and CEC were 63.88 mg kg⁻¹ and 4.97 meq 100 g⁻¹ lower in the shelterwood sites than in the reference sites, respectively, and mean surface pH increased from 4.49 to

Table 1

Surficial (0–10 cm) soil properties for shelterwood (*n* = 101) and reference sites (*n* = 24).

Variable	Shelterwoods		Reference sites		P value
	Mean	SE	Mean	SE	
C[%]	6.01	0.22	7.46	0.59	<0.05
$\delta^{13}\text{C}$	-27.16	0.038	-27.28	0.084	n.s.
N[%]	0.28	0.011	0.33	0.034	n.s.
$\delta^{15}\text{N}$	3.38	0.094	3.69	0.25	n.s.
Ca (mg/kg)	254.4	22.62	380.5	138.8	n.s.
Mg (mg/kg)	51.22	3.00	115.1	30.29	<0.01
K (mg/kg)	75.88	2.74	88.80	11.02	n.s.
P (mg/kg)	6.46	0.30	12.84	2.70	<0.001
pH*	4.68	0.026	4.49	0.064	<0.001
CEC (meq 100 g ⁻¹)	18.66	0.47	23.63	1.97	<0.01

P values derived from the linear mixed models used to analyze differences between shelterwood and reference sites (see Tables 2 and 3).

* Analyzed as hydrogen ion concentration.

4.68 with management (Table 1). In contrast, for K we found that subsurface samples responded more strongly to harvesting than surface samples and that subsurface K concentrations were higher in the shelterwood stands than in the reference sites. We found no differences in the remaining soil chemistry variables (N, Ca, and $\delta^{13}\text{C}$) between the shelterwood and undisturbed stands for both soil depths.

3.2. Post-harvest soil nutrient recovery trends

We found strong temporal recovery trends for the soil variables across the shelterwood chronosequence. Time since harvest was a significant predictor of changes in Ca, Mg, K and P (Table 3, Fig. 3), as well as for $\delta^{13}\text{C}$ (Table 2, Supplemental Fig. S1). Calcium, Mg, K and P measurements showed the surface soil recovered quickly above the relatively nutrient-stable sub-surface depth. This is corroborated by depth by time interactions which were significant for C and P, and marginally significant for CEC, indicating that the surface soil responded more strongly to time since harvest than the sub-surface soil (Table 3). All macronutrient measures increased through time since harvest, approaching the nutrient levels observed in unharvested reference sites (Fig. 3). Similarly, $\delta^{13}\text{C}$ decreased and approached the reference isotope ratio (Supplemental Fig. S1).

For leaf litter, time since harvest was a significant predictor of changes in $\delta^{13}\text{C}$, which decreased with time, and %N, which increased (Table 2, Supplemental Fig. S2). Stands younger than 10 years averaged 0.97 higher in litter $\delta^{13}\text{C}$ than stands older than 15 years. For %N, stands younger than 10 years averaged 0.34 percentage points lower than stands older than 15 years. The harvest litter C and N concentrations were slightly lower than those of the reference site litter. Time since harvest was not a significant predictor of leaf litter dry mass ($R^2 = 0.014$).

We used two-sample *t*-tests ($\alpha = 0.10$) to examine the responsiveness of the 0–10 cm soil depth and found no significant difference in %N by 11–15 years ($p = 0.031$); K ($p = 0.056$), P ($p = 0.012$) and C ($p = 0.032$) by 16–20 years; Mg ($p = 0.045$) by 21–25 years, and there was never any significant difference in Ca between the shelterwood and reference sites. This indicates that N recovered to pre-harvest levels at 11–15 years, K, P, and C between 16 and 20 years, and Mg between 21 and 25 years.

4. Discussion

The effects of traditional forest timber harvests on ecological processes can be substantial and broad-reaching. Large volumes of plant biomass are removed, harvesting equipment can compact the soil, the microclimate changes under reduced canopy cover, and ecological interactions shift as regeneration proceeds (Startsev and McNabb 2001; Bartels et al. 2016). Although these effects hold for any timber harvest in

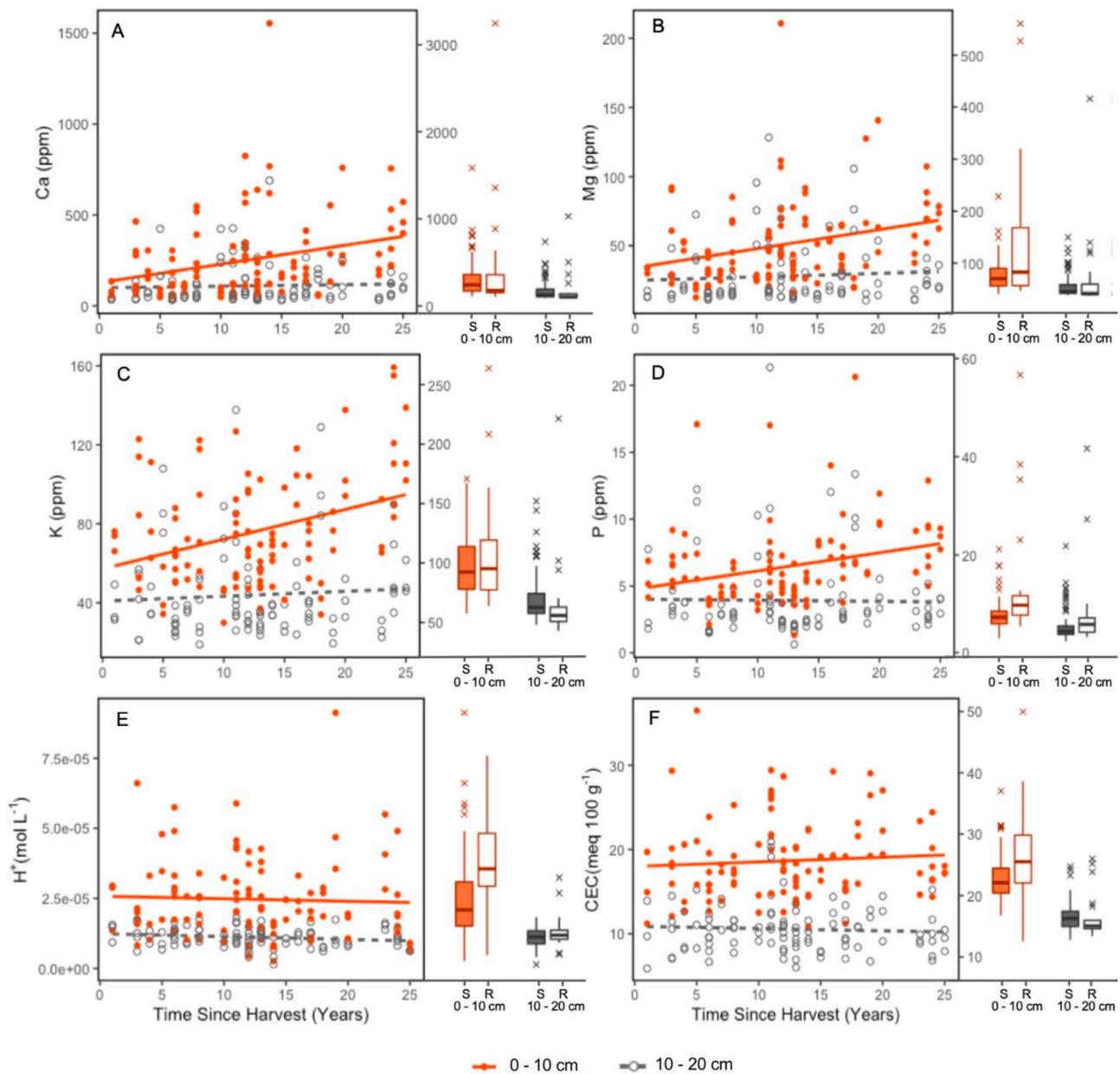


Fig. 3. Effects of shelterwood harvests on pH, analyzed as hydrogen ion concentrations (E), CEC (F) and macronutrients for surficial (0–10 cm) and deeper (10–20 cm) soils (A–D). Scatterplots show trends over time following timber harvest for surficial (closed points, solid line) and deeper (open points, dashed line) soils. Boxplots show differences between shelterwood (S) and reference (R) sites for the two depths. Points show 3 transect-level observations for each of two depth brackets, giving a total n of 204 (102 per depth; the 8 reference sites are additional).

a forest, they can be more pronounced in intensive whole-tree harvesting and short rotation plantations (Fox et al. 2007; Achat et al. 2015). In our study, we found that surface soil nutrients generally recovered over the course of 25 years following an irregular shelterwood harvest. This recovery period is just a fraction of the rotation time for red oaks (*Q. rubra*) and hickories (*Carya* spp.), which is typically 60–80 years with release cuts (Frieswyk and Widmann 2000; Leak et al., 2017). Our results therefore show that the effects of irregular shelterwood harvests, which minimize site treatments to soil while promoting the release of advance regeneration, can be very different from the effects of more intensive harvest treatments on soil nutrient recovery.

The conclusions from our study are drawn from a twenty-five-year shelterwood chronosequence, which enabled us to study post-harvest trends in soil nutrients in regenerating forest stands over a length of time that is logistically difficult to sample with longitudinal observations. However, one limitation of this space-for-time substitution

approach is that variation in environmental factors between sites could obscure trends caused by time since harvest. Like most environmental questions, the effects of shelterwood management are best investigated using multiple, complementary studies that employ different approaches. As such, additional work focusing on temporal trends following shelterwood harvests within the same forest stand are necessary to strengthen and further resolve the trends observed in our study.

4.1. Soil chemistry changes after irregular shelterwood timber harvest

Our results show that in the first few years after harvest, there can be a pulse of nutrient availability due to increased decomposition from large organic matter inputs as well as reduced plant nutrient uptake (Prescott 2002; Lovett and Lindberg 1993; Ballard 2000). In irregular shelterwoods, harvesting leaves behind a large amount of coarse woody branch debris, a layer of twigs and leaf litter, and an intact organic forest

Table 2

Regression coefficients (mean \pm SE) for the linear mixed models used to evaluate the effects of shelterwood harvests on soil (0–10 cm) and litter carbon and nitrogen concentrations. The shelterwood models evaluate changes over time since harvest, and the reference models compare values in the shelterwood and reference sites. Litter numbers were analyzed with simple linear regression instead of linear mixed models.

Response Variable	Substrate	Shelterwood Models			Reference Models		
		R ² Fixed (Full)	Coefficients (\pm SE)		R ² Fixed (Full)	Coefficients (\pm SE)	
			Intercept	Time Since Harvest (Years)		Intercept	Management Effect (Shelterwood/Reference)
% C	Soil	0.52 (33)	1.69 \pm 0.094	0.0038 \pm 0.0067	6.1 (35)	1.95 \pm 0.088	-0.22 \pm 0.098
$\delta^{13}\text{C}$	Litter	4.3	45.96 \pm 0.95	-0.085 \pm 0.068	8.3	46.69 \pm 0.85	-1.79 \pm 0.94
	Soil	9.7 (58)	-26.93 \pm 0.11	-0.019 \pm 0.0082	0.96 (54)	-27.26 \pm 0.098	0.098 \pm 0.13
	Litter	20	-28.22 \pm 0.22	-0.044 \pm 0.016	0.022	-28.79 \pm 0.21	0.022 \pm 0.24
% N	Soil	3.0 (49)	-1.48 \pm 0.11	0.0097 \pm 0.0076	2.0 (48)	-1.22 \pm 0.11	-0.14 \pm 0.12
$\delta^{15}\text{N}$	Litter	12	1.13 \pm 0.099	0.015 \pm 0.0071	5.7	1.48 \pm 0.092	-0.16 \pm 0.10
	Soil	3.0 (60)	3.71 \pm 0.30	-0.026 \pm 0.022	1.2 (53)	3.68 \pm 0.29	-0.29 \pm 0.33
	Litter	1.2	-2.81 \pm 0.27	0.012 \pm 0.019	3.8	-2.99 \pm 0.24	0.33 \pm 0.26

Significant ($p < 0.05$) and marginally significant ($p < 0.1$) coefficients are shown in bold and italic fonts, respectively

Table 3

Regression coefficients (mean \pm SE) for the linear mixed models used to evaluate the effects of shelterwood harvests on pH (analyzed as H⁺), CEC, and cation macronutrients for two soil depths (0–10 cm and 10–20 cm). The shelterwood models evaluate changes over time since harvest, and the reference models compare values in the shelterwood and reference sites.

Soil Response Variable	Shelterwood Models					Reference Models				
	R ² Fixed (Full)	Coefficients \pm SE				R ² Fixed (Full)	Coefficients \pm SE			
		Intercept	Depth	Time Since Harvest (Years)	Depth \times Time Since Harvest		Intercept	Depth	Management Effect	Depth \times Management Effect
Ca	29 (50)	4.68 \pm 0.16	-0.49 \pm 0.19	0.044 \pm 0.012	-0.49 \pm 0.014	22 (58)	5.20 \pm 0.17	-0.95 \pm 0.18	0.026 \pm 0.19	0.10 \pm 0.20
Mg	30 (40)	3.45 \pm 0.12	-0.46 \pm 0.16	0.028 \pm 0.0086	-0.017 \pm 0.011	25 (59)	4.20 \pm 0.14	-1.01 \pm 0.15	-0.40 \pm 0.15	0.34 \pm 0.16
K	39 (39)	4.04 \pm 0.084	-0.43 \pm 0.12	0.018 \pm 0.0060	-0.012 \pm 0.0085	37 (47)	4.35 \pm 0.087	-0.90 \pm 0.12	-0.085 \pm 0.097	0.32 \pm 0.13
P	29 (70)	1.52 \pm 0.11	-0.38 \pm 0.10	0.021 \pm 0.0078	-0.018 \pm 0.0072	29 (73)	2.26 \pm 0.11	-0.63 \pm 0.10	-0.48 \pm 0.13	0.021 \pm 0.11
H ⁺	32 (75)	-10.68 \pm 0.11	-0.67 \pm 0.096	-0.0080 \pm 0.0080	-0.0020 \pm 0.0068	36 (72)	-10.34 \pm 0.11	-1.02 \pm 0.10	-0.44 \pm 0.12	0.33 \pm 0.12
CEC	57 (82)	2.85 \pm 0.054	-0.50 \pm 0.049	0.0039 \pm 0.0039	-0.0061 \pm 0.0035	55 (68)	3.08 \pm 0.057	-0.79 \pm 0.071	-0.18 \pm 0.064	0.22 \pm 0.078

Significant ($p < 0.05$) and marginally significant ($p < 0.1$) coefficients are shown in bold and italic fonts, respectively.

floor protected by the debris on top (Ashton and Kelty 2018). As regeneration proceeds, soil nutrients are lost through nutrient mobilization and reduced leaf litter inputs. With fewer canopy trees, leaf litter volume generally decreases after a traditional harvest (Covington 1981; Nave et al. 2010; Lutz and Chandler 1945; Pastor and Post 1986).

In our study, however, we found that surficial forest soils steadily recovered to pre-harvest nutrient levels. For instance, N concentrations in harvested stands were comparable to unharvested controls after 11–15 years post-timber harvest. Because total soil N is co-regulated by plant uptake and litter biomass return (Xia et al., 2021), continuing litter inputs from reserve trees in shelterwoods could help explain soil N recovery. Indeed, we observed minimal changes in leaf litter mass and quality over time in the twenty-five-year chronosequence, indicating that gradual accumulation of high-quality leaf litter could help replenish soil N. Phosphorus is another limiting nutrient for plant growth, and Wu et al. (2019) suggested that extending rotation periods in managed forests could increase P supply. In our study, we found no differences in P in surficial soil between harvested and unharvested stands by 16–20 years, suggesting that legacy tree retention in irregular shelterwood harvests can also potentially increase P supply in working forests. Similar to N and P, we consistently observed recovery of other soil nutrients. Specifically, we found no differences in surface soil K between harvested and unharvested stands by 16–20 years, no difference in Mg by 21–25 years, and Ca never varied significantly between shelterwood

stands and unharvested controls.

4.2. Leaf litter chemistry changes after irregular shelterwood timber harvest

Many studies have demonstrated a flush of nutrients after a wide range of natural (e.g., tornados) and anthropogenic disturbances to forests (Likens et al. 1970; Marks and Bormann 1972; Bormann and Likens, 1979; Martin et al. 1986). Our results are no different, we demonstrate that N in litter increased through time since harvest but there was no difference in nutrients between harvested and undisturbed controls. The increase in litter N is suggestive of successional changes in species from herbaceous and ericaceous species to mixed-hardwood trees (Aber and Melillo 1982; Finzi and Canham 1998). Furthermore, there was no significant change in litter dry mass over the course of the chronosequence. In a more intensive harvest, we would initially expect a substantial loss of litter nutrients caused by accelerated decomposition of the organic layer (Covington 1981; Hughes and Fahey 1994). Our results suggest that the preserved tree cover in irregular shelterwoods continues to provide substantial leaf litter inputs and canopy shade to the soils, which could shield them from potential increases in temperature and desiccation.

4.3. Soil $\delta^{13}\text{C}$ changes after irregular shelterwood timber harvest

Soil $\delta^{13}\text{C}$ is directly related to organic matter turnover (Balesdent et al. 1993). We demonstrate that mineral soil $\delta^{13}\text{C}$ decreased through time since harvest. This trend reflects the recovery of faster-cycling, particulate pools of soil organic C derived mostly from greater amounts of litter and residual woody debris inputs left from the harvest that are in earlier stages of processing by microbial decomposition (Grandy and Neff 2008, Bradford et al. 2008). Given the high local-scale variation in total soil C values (Bradford et al. 2019), it is often difficult to detect change in total soil C concentrations. Isotopes offer a more sensitive indicator of change (Grandy and Neff 2008, Bradford et al. 2008), an expectation supported by the fact the isotopic values of $\delta^{13}\text{C}$ returned to the undisturbed average within 10 years of harvest, whereas total soil %C rebounded at 16–20 years. Supporting this interpretation is the gradual decrease in $\delta^{13}\text{C}$ in both surface soil and leaf litter, accompanied by the positive coefficient in soil %C, which all point toward recovery of particulate organic C pools. Our results support findings by both Scott et al. (2004) and Warren and Ashton (2014) who found no major loss in soil C in shelterwood harvests. In a global meta-analysis of soil C recovery in temperate second-growth forests after timber harvests, Nave et al. (2010) revealed that in inceptisols, such as those at our study site, C stocks are observed to recover between 6 and 20 years after harvest. This is consistent with our study's estimate of the time scale of recovery.

Contrary to these results, another meta-analysis by Dean et al. (2017) found an overall decrease in soil organic C. However, this meta-analysis synthesized research investigating the effects on soil C from conversion of primary forest to intensive rotations of timber harvests. These findings are relevant to such circumstances as in the U.S. Pacific Northwest and Canada. Our study, like those in Nave et al., (2010), has been conducted in second-growth forests that have regrown back on forestland that was originally cleared for agriculture. Our baseline measure of soil organic C is therefore different from those in primary forests because agricultural conversion dramatically depleted soil C stocks (Guggenberger and Zech 1999). Reforestation increased soil C but to a lower baseline than that of the historical baseline for undisturbed primary forest, which might help explain why irregular shelterwood effects on soil C concentrations are fairly minimal and recoverable within 20 years (Nave et al. 2010).

5. Management implications

Understanding the dynamics of nutrient cycling for irregular shelterwood harvests considerably adds to the literature summarized in a meta-analysis by Jerabkova et al. (2011), in support of creating more complex age-classes and structures within second-growth oak-hardwood forests. Our results demonstrate the beneficial effects of partial overstory retention, retaining coarse woody debris and protecting the forest floor as a strategy for mitigating nutrient and C losses from soil as a result of timber harvesting. Given that harvesting has been reported to cause losses in forest floor and mineral soil C in some settings (Bradley et al. 2001; Nave et al. 2010), mitigating C losses and maximizing potential C sequestration is of interest. Our results support the idea that irregular shelterwood harvests offer a practical, minimally-invasive, soil C-stable harvesting alternative. In this way, irregular shelterwood harvests allow selection for ecologically and economically valuable regeneration of timber species, such as red oak (*Q. rubra*) and hickory (*Carya* spp.) alongside species that are more tolerant to exposure such as red maple (*A. rubrum*) and black birch (*B. lenta*) (Wikle et al. 2019). These species can maintain partial cover for shade-tolerant herbaceous forest plant species (Duguid and Ashton 2013), as well as provide greater structure for breeding birds, amphibians, and mammals (Duguid et al. 2016; Mossman et al. 2019; Hanle et al. 2020).

CRediT authorship contribution statement

Romy Carpenter: Conceptualization, Methodology, Writing – original draft, Investigation. **Elisabeth B. Ward:** Formal analysis, Visualization, Writing – review & editing. **Jessica Wikle:** Visualization, Writing – review & editing. **Marlyse C. Duguid:** Supervision, Writing – review & editing. **Mark A. Bradford:** Writing – review & editing. **Mark S. Ashton:** Supervision, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119604>.

References

- Aber, J.D., Melillo, J.M., 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. *Can. J. Bot.* 60 (11), 2263–2269.
- Achat, D.L., Deleuze, C., Landmann, G., Pousse, N., Ranger, J., Augusto, L., 2015. Quantifying consequences of removing harvesting residues on forest soils and tree growth—A meta-analysis. *For. Ecol. Manage.* 348, 124–141.
- Ashton, M.S., Kelty, M.J., 2018. *The Practice of Silviculture: Applied Forest Ecology*. John Wiley & Sons.
- Balesdent, J., Girardin, C., Mariotti, A., 1993. Site-related (13) C of tree leaves and soil organic matter in a temperate forest. *Ecology* 74 (6), 1713–1721.
- Ballard, T.M., 2000. Impacts of forest management on northern forest soils. *For. Ecol. Manage.* 133 (1–2), 37–42.
- Bartels, S.F., Chen, H.Y.H., Wulder, M.A., White, J.C., 2016. Trends in post-disturbance recovery rates of Canada's forests following wildfire and harvest. *For. Ecol. Manage.* 361, 194–207.
- Bates, D., Machler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48.
- Bormann, F.H., Likens, G.E., 1979. Catastrophic disturbance and the steady state in northern hardwood forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. *AM. J. SCI.* 67 (6), 660–669.
- Bormann, F.H., Likens, G.E., Fisher, D.W., Pierce, R.S., 1968. Nutrient loss accelerated by clear-cutting of a forest ecosystem. *Science* 159 (3817), 882–884.
- Bradford, M.A., Fierer, N., Reynolds, J.F., 2008. Soil carbon stocks in experimental mesocosms are dependent on the rate of labile carbon, nitrogen and phosphorus inputs to soils. *Funct. Ecol.* 22 (6), 964–974.
- Bradford, M.A., Carey, C.J., Atwood, L., Bossio, D., Fenichel, E.P., Gennet, S., Fargione, J., Fisher, J.R.B., Fuller, E., Kane, D.A., Lehmann, J., Oldfield, E.E., Ordway, E.M., Rudek, J., Sanderman, J., Wood, S.A., 2019. Soil carbon science for policy and practice. *Nat. Sustainability* 2 (12), 1070–1072.
- Bradley, R., Titus, B., Hogg, K., 2001. Does shelterwood harvesting have less impact on forest floor nutrient availability and microbial properties than clearcutting? *Biol. Fertil. Soils* 34 (3), 162–169.
- Brose, P.H., 2011. A comparison of the effects of different shelterwood harvest methods on the survival and growth of acorn-origin oak seedlings. *Can. J. For. Res.* 41 (12), 2359–2374.
- Covington, W.W., 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology* 62 (1), 41–48.
- Dahlgren, R.A., Driscoll, C.T., 1994. The effects of whole-tree clear-cutting on soil processes at the Hubbard Brook Experimental Forest, New Hampshire, USA. *Plant Soil* 158 (2), 239–262.
- Dean, C., Kirkpatrick, J.B., Friedland, A.J., 2017. Conventional intensive logging promotes loss of organic carbon from the mineral soil. *Glob. Change Biol.* 23 (1), 1–11.
- Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *For. Sci.* 60 (5), 926–942.

- Duguid, M.C., Ashton, M.S., 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. *For. Ecol. Manage.* 303, 81–90.
- Duguid, M.C., Morrell, E.H., Goodale, E., Ashton, M.S., 2016. Changes in breeding bird abundance and species composition over a 20 year chronosequence following shelterwood harvests in oak-hardwood forests. *For. Ecol. Manage.* 376, 221–230.
- Finzi, A.C., Canham, C.D., 1998. Non-additive effects of litter mixtures on net N mineralization in a southern New England forest. *For. Ecol. Manage.* 105 (1–3), 129–136.
- Fox, T.R., Jokela, E.J., Allen, H.L., 2007. The Development of Pine Plantation Silviculture in the Southern United States. *J. Forest.* 105 (7), 337–347.
- Frieswyk, T.S., Widmann, R.H., 2000. *Forest statistics for New Hampshire; 1983 and 1997*. Resour. Bull. NE-146. Newtown Square, PA; U.S. Department of Agriculture, Forest Service, Northeastern Research Station. p. 130.
- Goodale, E., Lalbhai, P., Goodale, U.M., Ashton, P.M.S., 2009. The relationship between shelterwood cuts and crown thinning and the abundance and distribution of birds in a southern New England forest. *For. Ecol. Manage.* 258 (3), 314–322.
- Grandy, A.S., Neff, J.C., 2008. Molecular C dynamics downstream: the biochemical decomposition sequence and its impact on soil organic matter structure and function. *Sci. Total Environ.* 404 (2–3), 297–307.
- Guggenberger, G., Zech, W., 1999. Soil organic matter composition under primary forest, pasture, and secondary forest succession, Region Huetar Norte, Costa Rica. *For. Ecol. Manage.* 124 (1), 93–104.
- Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D. B., Löhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygesen, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention forestry to maintain multifunctional forests: a world perspective. *BioScience* 62, 633–645.
- Hanle, J., Duguid, M.C., Ashton, M.S., 2020. Legacy forest structure increases bird diversity and abundance in aging young forests. *Ecol. Evol.* 10 (3), 1193–1208.
- Hendrickson, O.Q., Chatarpaul, L., Burgess, D., 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. *Can. J. For. Res.* 19 (6), 725–735.
- Hill, D.E., Sautter, E.H., Gonick, W.N., 1980. *Soils of Connecticut*. Soils of Connecticut (787).
- Hughes, J.W., Fahey, T.J., 1994. Litterfall dynamics and ecosystem recovery during forest development. *For. Ecol. Manage.* 63 (2–3), 181–198.
- Jerabkova, L., Prescott, C.E., Titus, B.D., Hope, G.D., Walters, M.B., 2011. A meta-analysis of the effects of clearcut and variable-retention harvesting on soil nitrogen fluxes in boreal and temperate forests. *Can. J. For. Res.* 41 (9), 1852–1870.
- Johnson, C.E., Johnson, A.H., Huntington, T.G., Sicama, T.G., 1991. Whole-tree clear-cutting effects on soil horizons and organic-matter pools. *Soil Sci. Soc. Am. J.* 55 (2), 497–502.
- Johnson, E.A., Miyaniishi, K., 2008. Testing the assumptions of chronosequences in succession. *Ecol. Lett.* 11 (5), 419–431.
- Jurgensen, M.F., Harvey, A.E., Graham, R.T., Page-Dumroese, D.S., Tonn, J.R., Larsen, M.J., Jain, T.B., 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. *For. Sci.* 43 (2), 234–251.
- Kissel, D.E., Sonon, L.S., 2008. *Soil test handbook for Georgia*.
- Kranabetter, J.M., Coates, K.D., 2004. Ten-year postharvest effects of silviculture systems on soil-resource availability and conifer nutrition in a northern temperate forest. *Can. J. For. Res.* 34 (4), 800–809.
- Leak, W.B., Yamasaki, M., Ward, J., Desmarais, K., Bennett, K.P., 2017. *Ecology and Management of Northern Red Oak in New England*. University of New Hampshire Cooperative Extension.
- Likens, G.E., Bormann, F.H., Johnson, N.M., Fisher, D.W., Pierce, R.S., 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecol. Monogr.* 40 (1), 23–47.
- Loftis, D.L., 1990. A shelterwood method for regenerating red oak in the southern Appalachians. *For. Sci.* 36 (4), 917–929.
- Lovett, G.M., Lindberg, S.E., 1993. Atmospheric deposition and canopy interactions of nitrogen in forests. *Can. J. For. Res.* 23 (8), 1603–1616.
- Lutz, H.J., Chandler, R.F., 1945. *Forest Soils*. John Wiley and Sons, Inc., New York.
- Marks, P.L., Bormann, F.H., 1972. Revegetation following forest cutting: mechanisms for return to steady-state nutrient cycling. *Science* 176 (4037), 914–915.
- Martin, C.W., Pierce, R.S., Likens, G.E., Bormann, F.H., 1986. Clearcutting affects stream chemistry in the White Mountains of New Hampshire. *Res. Pap. NE-579*. Broomall, PA: US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 12, 579.
- Meyer, W.H., Plusnin, B.A., 1945. *The Yale Forest in Tolland and Windham Counties, Connecticut*.
- Mossman, A., Lambert, M.R., Ashton, M.S., Wikle, J., Duguid, M.C., 2019. Two salamander species respond differently to regeneration timber harvest across time. *Peer J* e7604.
- Munson, A.D., Margolis, H.A., Brand, D.G., 1993. Intensive silvicultural treatment: impacts on soil fertility and planted conifer response. *Soil Sci. Soc. Am. J.* 57 (1), 246–255.
- Nakagawa, S., Schielzeth, H., O'Hara, R.B., 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4 (2), 133–142.
- Nasiri, M., Parsakho, A., 2012. Shelterwood cutting system for forest management. *J. Appl. Biol. Sci.* 6 (3).
- Nave, L.E., Vance, E.D., Swanston, C.W., Curtis, P.S., 2010. Harvest impacts on soil carbon storage in temperate forests. *For. Ecol. Manage.* 259 (5), 857–866.
- NRCS, 2008. *Soil Survey of the State of Connecticut*. In Cooperation with the Connecticut Agricultural Experiment Station, The Storrs Agricultural Experiment Station, and Connecticut Department of Environmental Protection.
- Pastor, J., Post, W.M., 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2 (1), 3–27.
- Prescott, C.E., 2002. The influence of the forest canopy on nutrient cycling. *Tree Physiol.* 22 (15–16), 1193–1200.
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org>. Vienna, Austria.
- Raymond, P., Bédard, S., Roy, V., Larouche, C., Tremblay, S., 2009. The irregular shelterwood system: review, classification, and potential application to forests affected by partial disturbances. *J. Forest.* 107 (8), 405–413.
- Raymond, P., Bédard, S., 2017. The irregular shelterwood system as an alternative to clearcutting to achieve compositional and structural objectives in temperate mixedwood stands. *For. Ecol. Manage.* 398, 91–100.
- Rodgers, J., 1985. *Bedrock Geological Map of Connecticut*. Connecticut Geological and Natural History Survey in cooperation with U.S. Geological Survey.
- Russell, H.S., 1983. *Indian New England before the Mayflower*. University Press of New England.
- Scott, N.A., Rodrigues, C.A., Hughes, H., Lee, J.T., Davidson, E.A., Dail, D.B., Malerba, P., Hollinger, D.Y., 2004. Changes in carbon storage and net carbon exchange one year after an initial shelterwood harvest at Howland Forest, ME. *Environ. Manage.* 33 (1), S9–S22.
- Smith, W.B., Miles, P.D., Perry, C.H., Pugh, S.A., 2009. *Forest resources of the United States, 2007: A technical document supporting the forest service 2010 RPA Assessment*. General Technical Report-USDA Forest Service, (WO-78).
- Startsev, A.D., McNabb, D.H., 2001. Skidder traffic effects on water retention, pore-size distribution, and van Genuchten parameters of boreal forest soils. *Soil Sci. Soc. Am. J.* 65 (1), 224–231.
- Thomas, P.A., 1976. Contrastive subsistence strategies and land use as factors for understanding Indian-White relations in New England. *Ethnohistory* 23 (1), 1. <https://doi.org/10.2307/481048>.
- USDA. *Web Site for Official Soil Series Descriptions and Series Classification*. USDA Natural Resources Conservation Service. [Online]. Available at: <https://soilseries.sc.egov.usda.gov>.
- Vitousek, P.M., Andariese, S.W., Matson, P.A., Morris, L., Sanford, R.L., 1992. Effects of harvest intensity, site preparation, and herbicide use on soil nitrogen transformations in a young loblolly pine plantation. *For. Ecol. Manage.* 49 (3–4), 277–292.
- Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. *J. Ecol.* 98 (4), 725–736.
- Warren, K.L., Ashton, M.S., 2014. Change in soil and forest floor carbon after shelterwood harvests in a New England Oak-Hardwood Forest, USA. *Int. J. For. Res.*
- Wikle, J., Duguid, M., Ashton, M.S., 2019. Legacy forest structures in irregular shelterwoods differentially affect regeneration in a temperate hardwood forest. *For. Ecol. Manage.* 454, 117650. <https://doi.org/10.1016/j.foreco.2019.117650>.
- Wu, H., Xiang, W., Chen, L., Ouyang, S., Xiao, W., Li, S., Forrester, D.I., Lei, P., Zeng, Y., Deng, X., Zeng, L., Kuzyakov, Y., 2019. Soil phosphorus bioavailability and recycling increased with stand age in Chinese fir plantations. *Ecosystems* 23 (5), 973–988.
- Xia, Q.I., Chen, L., Xiang, W., Ouyang, S., Wu, H., Lei, P., Xiao, W., Li, S., Zeng, L., Kuzyakov, Y., 2021. Increase of soil nitrogen availability and recycling with stand age of Chinese-fir plantations. *For. Ecol. Manage.* 480, 118643. <https://doi.org/10.1016/j.foreco.2020.118643>.
- Zimmerman, J.K., Pulliam, W.M., Lodge, D.J., Quiñones-Orfila, V., Fetcher, N., Guzmán-Grajales, S., Parrotta, J.A., Asbury, C.E., Walker, L.R., Waide, R.B., Quinones-Orfila, V., Guzman-Grajales, S., 1995. Nitrogen immobilization by decomposing woody debris and the recovery of tropical wet forest from hurricane damage. *Oikos* 72 (3), 314. <https://doi.org/10.2307/3546116>.