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# Mineral soil carbon pool responses to forest clearing in Northeastern hardwood forests

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## Abstract

Harvesting forests introduces substantial changes to the ecosystem, including physical and chemical alterations to the soil. In the Northeastern United States, soils account for at least 50% of total ecosystem C storage, with mineral soils comprising the majority of that storage. However, mineral soils are sometimes omitted from whole-system C accounting models due to variability, lack of data, and sample collection challenges. This study aimed to provide a better understanding of how forest harvest affects mineral soil C pools over the century following disturbance. We hypothesized that mineral soil C pools would be lower in forests that had been harvested in the last one hundred years vs. forests that were >100 years old. We collected mineral soil cores (to 60 cm depth) from 20 forest stands across the Northeastern United States, representing seven geographic areas and a range of times since last harvest. We compared recently harvested forests to >100-year-old forests and used an information theoretic approach to model C pool dynamics over time after disturbance. We found no significant differences between soil C pools in >100-year-old and harvested forests. However, we found a significant negative relationship between time since forest harvest and the size of mineral soil C pools, which suggested a gradual decline in C pools across the region after harvesting. We found a positive trend between C : N ratio and % SOM in harvested forests, but in >100-year-old forests a weak negative trend was found. Our study suggests that forest harvest does cause biogeochemical changes in mineral soil, but that a small change in a C pool may be difficult to detect when comparing large, variable C pools. Our results are consistent with previous studies that found that soil C pools have a gradual and slow response to disturbance, which may last for several decades following harvest.

*Keywords:* clear-cut, forest harvest, mineral soil, Northeastern United States, soil carbon, spodosol, temperate forest

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## Introduction

In the Northeastern United States, reductions in carbon dioxide ($CO_2$) emissions have been attempted by using local wood as a putative carbon (C) neutral alternative to fossil fuels. Currently, there are over 200 institutional wood energy users and biomass power producers across the northeastern region of the United States (University of Tennessee Center for Renewable Carbon, 2014), and substantial increases in bioenergy production are expected in both developed and developing countries (Schulze *et al.*, 2012). The C neutrality of bioenergy has been called into question for several reasons: fossil fuels are used to harvest and process biomass (Schulze *et al.*, 2012); clearing forests forgoes C-sequestration that would have otherwise occurred in a mature forest (Searchinger, 2010); and $CO_2$ emissions from bioenergy are not immediately compensated for by regenerating forests. Instead, $CO_2$ molecules remain in the atmosphere for decades and contribute to climate change (Cherubini *et al.*, 2011).

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Harvesting forests may introduce substantial changes to the ecosystem, including physical and chemical alterations to the soil (Jandl, 2007; Diochon *et al.*, 2009). Soil is the largest terrestrial C pool on earth, storing an estimated 2300 Pg (Jobbagy & Jackson, 2000), of which forest soils account for 70% (Jandl, 2007). Plants, by comparison, store 1500 Pg C, and the atmosphere 700 Pg C. Because the soil C pool is so large, even relatively small losses from it could have a significant impact on atmospheric $CO_2$ concentrations (Schlesinger, 1991; Trumbore *et al.*, 1996). Soil also plays a key role in forest productivity by maintaining the quality and quantity of organic matter (Nave *et al.*, 2010), which contains macronutrients (i.e. nitrogen, phosphorus, and sulfur) (Dungait *et al.*, 2012).

Despite a growing appreciation for the role that soil plays in the global C cycle, mineral soil C pools, which store up to 50% of total ecosystem C in northern hardwood forests (Fahey *et al*., 2005), have gone largely understudied and unreported in C accounting. For example, USDA Forest Service recommendations for C accounting in the Northeastern United States assume that all soil C pools, including the mineral horizons, do not change after harvest (Smith *et al*., 2005). These statistics inform federal policy and serve as the foundation of economic models (e.g. Gutrich & Howarth, 2007). In rocky northeastern soils, high spatial variability, the difficulty of sampling (Bormann & Likens, 1978; Staddon, 2004; Fahey *et al*., 2010), and the resulting paucity of data are challenges to including mineral soils in C accounting models of harvested forests (Smith *et al*., 2005; Buchholz *et al*., 2014).

Studies that have been conducted in the Northeastern United States and elsewhere have returned differing conclusions as to the response of soil C to forest harvest. Covington (1981) and Federer (1984) reported dramatic C loss and recovery from the organic soil horizon following clear-cutting of northern hardwood forests, but various contemporary studies have not reproduced those findings (as described in Yanai *et al*., 2003). Furthermore, few studies have investigated changes in mineral soil C with forest harvesting. A meta-analysis of soil C pools across the Northeast found significant C loss in deep mineral soils (>40 cm depth) of Spodosols, but found no significant change in the mineral soil profile as a whole (Nave *et al*., 2010). The few published studies that have focused on the *long-term* effect of forest harvest on mineral soils have found that soil C declines over several decades following a clear-cut, and that the effect of cutting may not be apparent in the first 10–15 years after the disturbance (Diochon *et al*., 2009; Vario *et al*., 2014). At present, researchers do not have a full understanding of how and on what timescale soil C responds to forest harvest.

Carbon persists in soil due to physical mechanisms such as aggregate protection and adsorption to minerals, limits to microbial activity (i.e. enzyme production and substrate degradation), and abiotic factors such as temperature and moisture (Von Lutzow *et al*., 2006; Kögel-Knabner *et al*., 2008; Schmidt *et al*., 2011; Dungait *et al*., 2012). Fundamental changes to an ecosystem, which may affect the mechanisms of C storage, can rapidly destabilize soil organic C even in deep, relatively stable pools (Schmidt *et al*., 2011). When a forest is harvested, broad and potentially severe changes do occur in the ecosystem. Carbon inputs to soil decrease, as primary production accounts for the vast majority of C entering temperate forests (Bormann & Likens, 1978). Loss of the forest canopy cover leads to increases in soil temperature and decreases in transpiration (Lal, 2005), both of which stimulate microbial activity. The physical stability of soil may be compromised by compaction (Zummo & Friedland, 2011), which influences C storage via the destruction of soil aggregates (Von Lutzow *et al*., 2006).

This study measured C pools in the mineral soil horizons of harvested and undisturbed forests across the Northeastern United States. We hypothesized that (i) mineral soil C pools are higher in undisturbed forests compared to those that have been harvested in the last century, and (ii) mineral soil C pools gradually decline over time after harvest, with measurable effects of the disturbance occurring and/or continuing several decades after harvest. We measured C pools and concentrations, soil texture, and C : N ratios, as well as collected data on landscape characteristics to test these hypotheses.

## Materials and methods

### *Study sites*

The study utilized research forests, conservation land, and privately owned woodlands across the Northeastern United States to construct a chronosequence of time since clear-cutting (Fig. 1). The study areas included the Bartlett Experimental Forest ('BEF,' Bartlett, NH, USA), Harvard Forest ('HF,' Petersham, MA, USA), the Adirondack Ecological Center ('AEC,' Newcomb, NY, USA), Dartmouth's Second College Grant ('SCG,' near Errol, NH, USA), the Bowl Research Natural Area ('Bowl RNA,' Mount Whiteface, NH, USA), Gifford Woods State Park ('GW,' Killington, VT, USA), and forest privately owned by Lyme Timber Company ('SPEC,' Speculator, NY, USA) (Fig. 1). At each of the study areas, between one and five forest stands of varying ages were selected (Table 1) with assistance from local land managers using harvest records for the area. The Harvard Forest and SPEC study areas offered digitized geographic information systems (GIS) records of land-use history, which were used to select study sites. The Bowl RNA and GW are single, undisturbed forest stands with only one age class at each location. Both forests are located on protected state and national land and have been used as undisturbed comparison plots in previous scientific studies (i.e. Goodale & Aber, 2001; Clark & Johnson, 2011). Study sites at BEF, SCG, and AEC were chosen based on knowledge from land managers and foresters, in addition to historical records of cutting available at each of the respective forest headquarter offices.

We attempted to isolate the treatment effect of forest harvest by selecting only low-elevation hardwood forest stands on well-drained soils. Only hardwood forests were considered in the study and were comprised of *Betula* spp., *Populus* spp., *Fagus grandifolia* Ehrh., *Quercus* spp., and *Acer* spp. In the older forest stands, interspersed eastern hemlock (*Tsuga canadensis*) was common. Edaphic soil characteristics naturally vary across the Northeastern United States, so we did not constrain our study areas based on all soil qualities. All soils were acidic and moderately to well-drained. All study areas except for the Harvard Forest, the most southern site, were of the soil order Spodosol and of a frigid soil temperature regime (Table 1).

**Table 1** Study area characteristics

| Study Areas | Number of stands sampled | Ages of stands sampled | Elevation (m) | Soil order* | Soil temperature regime* | Drainage class* | MAT† (°C) | MAP† (mm) |
|---|---|---|---|---|---|---|---|---|
| BEF | 5 | 5, 12, 25, 55, 120 | 304 | Spodosol | Frigid | Well | 6.2 | 1326 |
| SCG | 3 | 25, 50, 75 | 427 | Spodosol | Frigid | Moderate | 3.2 | 1179 |
| Bowl RNA | 1 | Undisturbed | 600 | Spodosol | Frigid | Well | 4.3 | 1606 |
| GW | 1 | Undisturbed | 490 | Spodosol | Fridid | Moderate | 6.1 | 1308 |
| HF | 4 | 5, 20, 64, 84 | 360 | Inceptisol | Mesic | Well-Excessive | 7.8 | 1197 |
| AEC | 4 | 1, 19, 55, Undisturbed | 550 | Spodosol | Frigid | Well | 5.2 | 1074 |
| SPEC | 2 | 5, Undisturbed | 530 | Spodosol | Frigid | Moderate | 5.0 | 1246 |

Abbreviations for study areas are as follows: Bartlett Experimental Forest (BEF), Harvard Forest (HF), the Adirondack Ecological Center (AEC), Dartmouth's Second College Grant (SCG), the Bowl Research Natural Area (Bowl RNA), Gifford Woods State Park (GW), and property owned by Lyme Timber Company in Speculator, NY (SPEC).
*Soil classification from NRCS Soil Survey (Soil Survey Staff, 2014).
†Climate data retrieved from PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 4 Feb 2004.

Mean annual temperature ranged from 3.2 °C at SCG, the most northern study area, to 7.8 °C at HF, the most southern study area (Table 1). Mean annual precipitation ranged from approximately 1000 to 1600 mm across all study areas (Table 1). Soil pH ranged from 4.6 to 6.9 across all sites (Table 2). Clay content ranged from 4 to 16% across all sites (Table 2). Soil pH and clay content are presented as means of the whole mineral soil profile. In total, the study included 177 (59 pooled) deep mineral soil cores from 20 independent forest stands. The ages of the forest stands ranged from 1 year after harvest to >100 years after harvest (Table 1).

## *Soil collection*

Sampling took place during the summers of 2011 and 2012. Within each forest stand, we selected three 'microsites' for soil core excavation. Microsites were at least 10 m aside from each other and met criterion for ground slope, pit and mound formation, and distance to nearest tree, as described in Vario *et al.* (2014). Soil cores were extracted using a gas powered auger (Earthquake™ 9800B) with a diamond tipped, 9.5 cm diameter drill bit and extension tube (Tools Direct™ Premium Red Diamond Drill Bit) following methods of Rau *et al.* (2011) and Levine *et al.* (2012). The diamond tipped drill bit cut through small rocks and allowed for drilling without compacting soil (Rau *et al.*, 2011). We excavated cores incrementally in the following order: organic soil horizons (Oi, Oe, and Oa together, when present); and mineral soil depth increments 0–10 cm; 10–20 cm; 20–30 cm; 30–45 cm; and 45–60 cm (Zummo & Friedland, 2011).

In isolated cases, the delineation of the organic-mineral boundary was not possible in the field. Organic soil is defined by having >20% C, and mineral soil as having < 20% C (Soil Survey Staff, 2014). In C-rich soils, the point at which C concentration crosses the definitive threshold from organic to mineral soil can be difficult to determine in the field and must be verified by elemental analysis in the laboratory. Therefore, if the 0–10 cm mineral depth increment of a soil core was

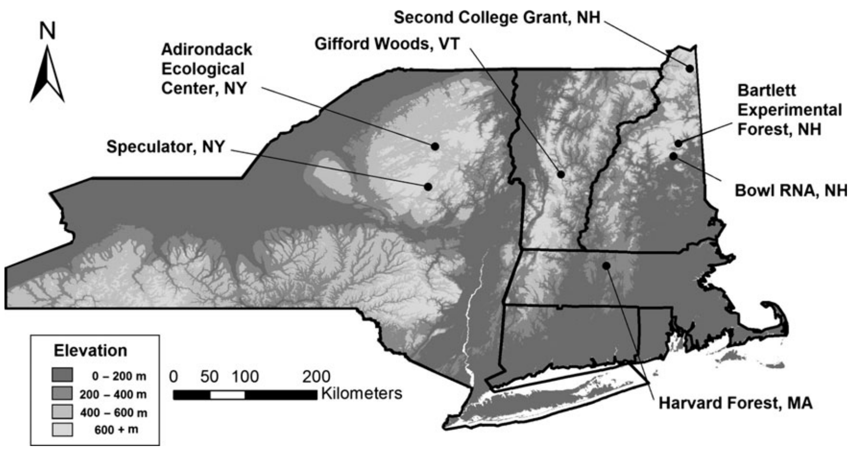


**Fig. 1** Elevation map of the Northeastern United States with study areas indicated. At each study location, between one and five stands were sampled as part of a chronosequence of time since clear-cutting.

**Table 2** Soil particle distribution and pH at each forest stand in the study. Values represent the mean of the mineral soil solum to 60 cm depth

| Study areas | Years since harvest | Percent sand | Percent silt | Percent clay | pH |
|---|---|---|---|---|---|
| BEF | 5 | 67 | 27 | 6 | 5.0 |
| | 12 | 62 | 31 | 7 | 5.2 |
| | 25 | 73 | 20 | 7 | 4.9 |
| | 55 | 70 | 26 | 4 | 5.1 |
| | 120 | 72 | 22 | 7 | 4.7 |
| SCG | 25 | 68 | 25 | 7 | 5.0 |
| | 50 | 43 | 48 | 9 | 5.1 |
| | 75 | 59 | 36 | 5 | 5.1 |
| HF | 5 | 67 | 25 | 8 | 4.9 |
| | 20 | 72 | 23 | 6 | 4.9 |
| | 64 | 67 | 26 | 7 | 4.9 |
| | 84 | 66 | 29 | 6 | 4.8 |
| AEC | 1 | 68 | 24 | 8 | 5.2 |
| | 19 | 66 | 23 | 11 | 4.9 |
| | 55 | 60 | 24 | 16 | 4.7 |
| | Undisturbed | 76 | 14 | 10 | 4.8 |
| SPEC | 5 | 76 | 16 | 8 | 5.5 |
| | Undisturbed | 79 | 17 | 4 | 6.9 |
| Bowl RNA | Undisturbed | 69 | 20 | 11 | 4.9 |
| GW | Undisturbed | 61 | 26 | 13 | 4.6 |

subsequently found to be >20% C by empirical analysis, the soil core was removed from the dataset. The entire core was removed from the dataset, because delineation of all mineral soil depth increments depends on the correct determination of the organic-mineral boundary. In total, five microsites of 59 microsites were omitted due to this phenomenon.

Within each microsite, we extracted three separate cores and bulked the depth increments to achieve a sample mass more similar to quantitative soil pit methods. This approach resulted in nine independent and subsequently three pooled soil cores per forest stand. The data presented here represent 165 deep soil cores, which were pooled to 54 samples per depth interval. We sieved all soil collected from each depth interval to 12.5 mm following the methods of Huntington & Ryan (1990). The >12.5 mm fraction was separated into rock and root fractions, weighed in the field (±2.5 g precision) and discarded. The <12.5 mm fraction from each depth increment was homogenized before taking a weighed subsample for laboratory analyses (Vario *et al.*, 2014).

## *Laboratory analyses*

Samples were kept at 4 °C for no more than 2 weeks before air-drying was initiated. We determined soil moisture gravimetrically and sieved soils to 2 mm then weighed the $\leq$ 2 mm soil fraction and $\geq$2 mm rock fraction (Vario *et al.*, 2014). Total field soil mass from each depth increment was corrected for $\geq$ 2 mm rock content and soil moisture before calculating bulk density. Bulk density was calculated following the hybrid method of Throop *et al.* (2012), which uses $\leq$ 2 mm soil fraction and total core volume to calculate soil mass (g) per unit volume ($cm^3$).

Subsamples from each soil sample were ground to fine powder using a ball mill. The mill was cleaned with isopropyl alcohol between samples. Percent C and nitrogen (N) were measured on the $\leq$2 mm ground subsamples using a Carlo-Erba elemental analyzer. Due to a pH of 6.9 in soils from SPEC, those soils were treated with 6 N hydrochloric acid to remove inorganic C before C analyses were conducted. Mineral soil C pools were calculated according to Huntington & Ryan (1990). Pools were calculated for each depth increment and then summed for the mineral solum total.

Air-dried, <2 mm soil samples were prepared for pH analysis by making a 1 : 1 mixture with deionized water according to the Soil Science Society of America (SSSA) Methods of Soil Analyses No. 5 (1996). pH was measured with a VWR 8015 electroprobe calibrated with pH 4 and pH 7 buffer solutions. Texture analyses were conducted on the 2 mm soil fraction using the hydrometer method with soil dispersion in sodium-hexametaphosphate (50 g $l^{-1}$) as described by the SSSA Methods of Soil Analysis No. 5 (1996). Soils with >15% organic matter were treated with hydrogen peroxide at a 0.3:1 (m/v) ratio of organic matter to hydrogen peroxide and left to stand for 24 h before texture analysis. Hydrometer readings were taken at 30 s, 60 s, 1.5 h, and 24 h after mixing in columns.

## *Statistical analyses*

To test the hypothesis that soil C is greater in undisturbed forests than in harvested forests, we compared C pools of both the total mineral solum and those of each depth increment. We used two-sample *t*-tests, assuming unequal variances, to test the difference between treatments. Tests were performed on stand level means ($n$ = 15 for harvested forests and $n$ = 5 for >100-year-old forests).

We used a least-squares multivariate model to test the relationship between C : N ratio as the response variable and soil depth increment and percent SOM as predictor variables. Insignificant variables were removed from the model. C pool, concentration, SOM, and C : N ratio data were right skewed; data were log-transformed to meet normal distribution assumptions of least-squares methods. Significance was determined at $\alpha = 0.05$. Analyses were performed with JMP11 software (JMP®, Version 11. SAS Institute Inc.,Cary, NC, USA).

We used a mixed-effects statistical model to test the hypothesis that mineral soil C storage gradually decreases over several decades following forest clear-cutting. We constructed a set of candidate statistical models and used corrected Akaike Information Criterion (AICc) to determine the best-fit model in the set. The set of candidate models included predictor variables known to affect soil C storage, such as clay content (Torn *et al.*, 1997), and elevation (Siccama, 1974), in addition to years since forest harvest. Total C in the mineral soil solum (0–60 cm depth) was the response variable for all models. Percent clay, elevation (m), and years since forest harvest were treated as fixed effects in the models. Study area was included as a random effect in all models to account for natural variability across the region. We treated years since harvest as a continuous variable. We tested our models for the harvested forests only, which ranged between 1 and 84 years since harvest. Because the ages of the >100-year-old (or 'old growth') forests were unknown in most cases, we could not include them in a model using time since harvest as a continuous variable. This approach captured variation in soil C over the first century after forest harvest. The best-fit model was selected using AICc with a predetermined delta AICc of two. Models were tested with the lme4 package for R statistical software (Bates *et al.*, 2014). AICc scores were calculated with the AICcmodavg package for R (Mazerolle, 2013), and conditional *r*-squared values for our best-fit models were determined with the MuMIn package for R (Barton, 2014).

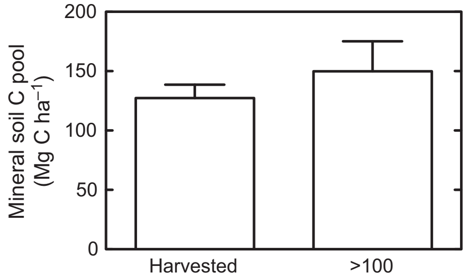


**Fig. 3** Mean mineral soil C pools in harvested and >100-year-old forests. Error bars represent the standard error of the mean. Number of stands varied between harvested ($n$ = 15) and >100-year-old ($n$ = 5) treatments.

## Results

Mineral soil C concentrations were generally higher in >100-year-old forests than in harvested forests, but the differences were not significant for any individual depth layer (Fig. 2). Statistical tests for differences in soil C pools, both total solum and by depth increment, were performed on log-transformed data to meet the normal distribution assumption. In the total mineral solum and in individual depth increments, mean soil C pools were higher in >100-year-old forest stands than in harvested forests, but differences were not statistically significant (Figs 3 and 4, respectively). The difference between harvested and >100-year-old forests increased with soil depth, and harvested forests had between 5% and 31% less mineral soil C than >100-year-old forests (Fig. 4b). Statistics and C pool and concentration values are presented in Figures S1 and S2, respectively.

In both >100-year-old forests and clear-cut forests, soil depth increment was not significant in multivariate regression of C : N vs. SOM and depth ($P$ > 0.05). Depth was removed from the model and the relationship between SOM and C : N ratio was tested in a bivariate linear model. In >100-year-old forests, there was a weak negative relationship between C : N and SOM ($P$ = 0.02, $r$-squared = 0.23, Fig. 5b). However, C : N was strongly positively correlated with SOM in forest stands that had been clear-cut in the last 100 years ($P$ < 0.0001; $r$-squared = 0.38; Fig. 5a).

A model that included only time since harvest outperformed other models in predicting mineral soil C pools across the northeastern region (Table S3). The best-fit linear model included study area as a random effect and showed a significant negative relationship between time since harvest and mineral soil C pools ($P$ = 0.003, $r$-squared = 0.86, Fig. 6). All parameter estimates for the AICc-selected model are presented in Table S4. The graphic presentation of the linear relationship was restricted to the range of time for which we have data (between 0 and 84 years after harvest), assuming that C pools would not plausibly continue to decline to zero.

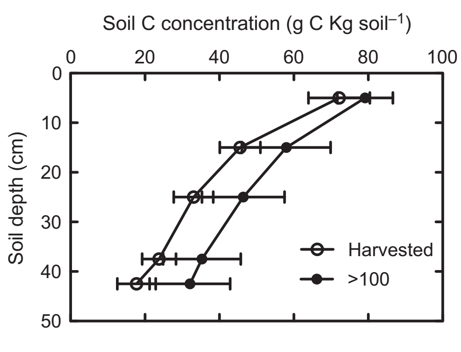


**Fig. 2** Mean mineral soil carbon concentrations by depth increment in a chronosequence of harvested northeastern hardwood forests. Error bars represent the standard error of the mean. Number of stands varied between harvested ($n$ = 15) and >100-year-old ($n$ = 5) treatments.

## Discussion

### *Suitability of study sites*

Edaphic characteristics of forest soils naturally vary across the northeastern region of the United States, which presents a challenge in isolating the effects of disturbance. The geographic range of our study areas precluded the control of all variables that may influence C storage. However, we are confident in the general comparability of the study areas. We provide a dataset that was corrected for MAT to eliminate some of the inherent variation in climate across the northeastern region (Table S1 and Table S2). However, correcting for MAT did not change the results of the study.

The number of stands in the >100-year-old age class throughout the study region were limited due to widespread deforestation that occurred through the late

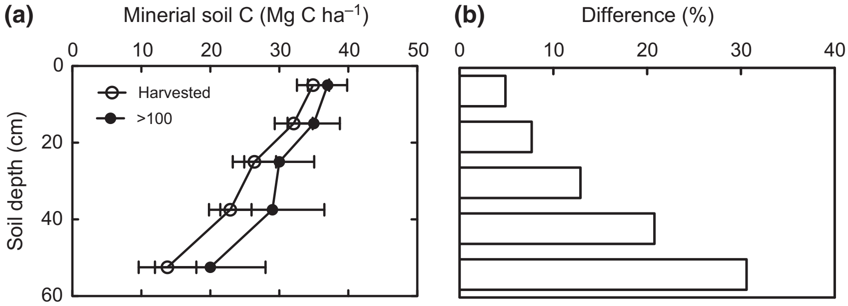


**Fig. 4** (a) Mean soil carbon pools by mineral soil depth increment in forests with different management histories, and (b) percent difference between >100-year-old forests and harvested forests. Number of stands varied between harvested ($n$ = 15) and >100-year-old ($n$ = 5) treatments. Error bars represent the standard error of the mean.

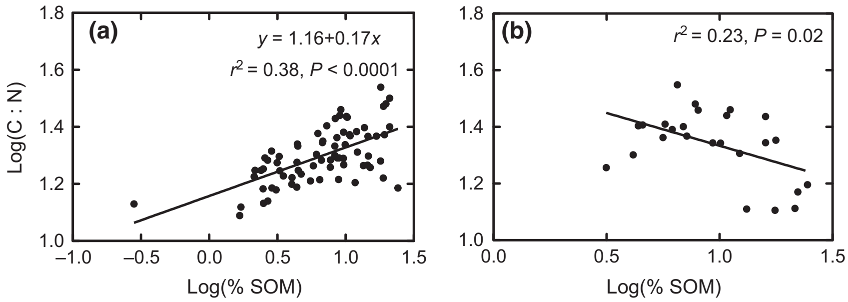


**Fig. 5** Relationship between log-transformed percent SOM and log-transformed C:N ratio in (a) harvested and (b) >100-year-old forests.

1800s in New England (Fahey *et al.*, 2005). At HF and SCG, older forests that met our criteria for soil and forest characteristics either did not exist or were not available for us to sample. Both areas were heavily logged for wood products (SCG) or for pasture (HF) historically.

### *Mineral soil carbon concentrations and pools*

We did not detect significant differences between C pools or C concentrations in harvested and >100-year-old forests. However, mean values of C pools and concentrations for each mineral depth increment and for the mineral solum overall were higher in >100-year-old forests (Figs 2 and 4). The high spatial variability introduced by conducting the study across a wide geographic area increases error of the mean (Yanai *et al.*, 2003), and may therefore increase the possibility of Type II error. Inferential error is typically high for soils due to high spatial variability even on a stand level. Despite not having the statistical power to determine significant differences between undisturbed and harvested forests, pools were between 5% and 31% higher in >100-year-old forests, which suggests a regional trend. Intensive sampling of one geographic location may enable researchers and land managers to better understand the effects of harvest in one location and may improve statistical power.

A *post hoc* power analysis showed that between approximately 60 and 230 forest stands would be required to detect significant differences in C pools in the 20–30, 30–45, and 45–60 cm mineral depth increments. However, this type of study is constrained by the number and suitability of study sites at both local and regional scales. Our study sampled 20 forest stands, and further candidate stands were sparse. Key requirements of our study included having sites with comparable characteristics and known harvest histories, and availability of older forests to serve as 'controls.' Given the high variability in soil C pools in general and the practical constraints on natural experiments such this, it may not be possible to show statistically significant changes in soil C pools after forest harvest when comparing treatments across a broad geographic area.

The effect of forest harvest on both carbon pools (Figs 3 and 4) and concentrations (Table S2) increased with soil depth. For C pools, the percent difference between >100-year-old and harvested forests ranged from approximately 5% in the 0–10 cm mineral depth increment to 31% in the 45–60 cm mineral depth increment. The downward movement of soluble organic acids, which characterizes Spodosols, may explain a mechanism whereby C mobilization may be initiated in deep soils. Nave *et al.* (2010) found significant losses in deep mineral soil C in Spodosols, but did not find the same effect in other soil orders. Ussiri & Johnson (2007) found both redistribution of C and changes in C compounds throughout the mineral soil profile in an experiment comparing a 15-year-old and undisturbed forest. A study on the mechanics of C movement through the podzol soil profiles in Siberian clear-cut vs. undisturbed forests found higher proportions of fulvic acids throughout the mineral soil profile after clear-cutting (Falsone *et al.*, 2012). Aluminum and iron, characteristic leachates in the podzolization process, were also mobilized by clear-cutting (Falsone *et al.*, 2012). The study confirmed the movement of C to deeper layers of the mineral soil and proposed that deposition of C in deep mineral layers may serve to protect C in the short term (Falsone *et al.*, 2012). It is possible, however, for C additions to mineral soil layers to create a priming effect, whereby stable, pre-existing C is degraded when a labile energy source is added to the C-poor system (Fontaine *et al.*, 2007). Furthermore, microbial communities in mineral soils tend to respond more strongly to nutrient additions than those in surface soils (Fierer *et al.*, 2003). The long and gradual response time of soils to harvest could occur because some roots decay for up to 65 years (Ludovici *et al.*, 2002). Easily degradable C inputs to the mineral soil may stimulate the mineralization of pre-existing C, creating a priming effect (Fontaine *et al.*, 2007; Kuzyakov *et al.*, 2000). Our finding that deep mineral soil C pools (45–60 cm depth) of >100-year-old forests were 30% higher than those of harvested forests suggests a potential decline in C pools at depth. This finding is consistent with the downward movement of organics stimulating microbial activity after cutting.

### *Soil carbon dynamics over time after harvest*

Our analysis of mineral soil C storage over time since harvest showed that time since harvest most accurately predicted mineral soil C pools, as compared with other variables that also control soil C storage (Fig. 6, Table S4). We found a significant, negative relationship between time after harvest and mineral soil C pools, with a slope, or loss, equal to −0.46 Mg C ha$^{-1}$ yr$^{-1}$ (Table S4). At Hubbard Brook Experimental Forest, a well-studied, representative hardwood forest near our study areas, annual C flux from soils by heterotrophic respiration is approximately 4 Mg ha$^{-1}$ yr$^{-1}$ (Fahey *et al.*, 2005). Our study found losses from soil to be approximately 10% of this estimate of ambient heterotrophic respiration. Harvest-induced losses equaling 10% of ambient C losses is a liberal estimate, given that all C fluxes from soils, including root respiration and hydrologic fluxes, total more than 600 Mg ha$^{-1}$ yr$^{-1}$ (Fahey *et al.*, 2005). Our estimated magnitude of annual C loss after forest harvest therefore seems plausible. Furthermore, annual losses of <0.5 Mg C – approximately 0.3% of mean C pools in this study – may be difficult to detect even after many years.

Our model included a random effect term (random intercept), which allows for the movement of the y-intercept according to differences between study areas. The high conditional R-squared value (0.86, Fig. 6), which takes into account the random effect in the model, demonstrates the strong influence of geographic area on the function's intercept. Without movement of the y-intercept, the model only explained 10% of the variation in the dataset. MAT may explain the significant shift in the intercept of the model for each of the study areas. Harvard Forest, for example, has the lowest C values overall and thus the lowest y-intercept. Harvard Forest is also the warmest site, in which decomposition should be highest. This result reiterates the importance of investigating changes in mineral soil C pools in distinct locations where heavy harvesting might occur. The same negative relationship between time after clear-cutting and soil C pools applied to all locations, but the starting and ending C pools of each relationship were different. Forest clearing in rotations

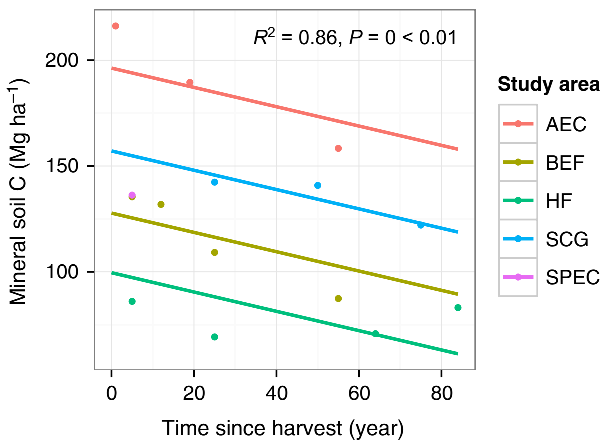


**Fig. 6** Linear mixed-effects statistical model of mineral soil C pools over time since harvest. A model that used a linear function of years since harvest to predict changes in C pools over time had the best (lowest) AICc score in a set of models that included other factors that control C storage, such as elevation and clay. The random intercept model moved the y-intercept of the relationship for each individual study area. The conditional *r*-squared = 0.86, which takes into account the random effect. Time since harvest was a significant predictor of mineral soil C pools ($P$ < 0.01).

may cause differences in the relationship between time after harvest and soil C. For example, a previous study that modeled the response of soil C to forest harvest in the Northeastern United States found that soil C decline was greatest with simulations of 60-year harvest rotations with 90% biomass removal (Johnson *et al.*, 2010).

Our previous findings from a study at only the Bartlett Experimental Forest location showed significant differences in mineral soil C pools of varying-aged forests (Vario *et al.*, 2014). Although the present study did not find significant differences between harvested and older forests across the whole northeastern region, the mixed-effects model suggests that differences among study areas must be taken into account to measure differences in C over time. To gain a better understanding of soil C dynamics with forest harvest, future studies may choose to intensively sample one geographic location, as responses may differ across time and space.

Our dataset did not include forests that were between 84 and 100 years after harvest, so we could not empirically measure the recovery of C during this period. Based on previous studies (Covington, 1981; Federer, 1984; Diochon *et al.*, 2009), we assume that C pools do recover. Furthermore, it is implausible that C pools would continue to decline linearly to zero. However, there is little regional data for the recovery time period in Spodic soils (Nave *et al.*, 2010). As it is unlikely that mineral soil C would continue to decline indefinitely, we proposed three scenarios whereby C pools may recover to preharvest levels, or, levels of >100-year-old forests. Panel (b) in Fig. 7 shows linear, exponential, and sigmoidal functions that capture the recovery of C pools from the model-predicted lowest C pool (106 Mg C $ha^{-1}$) to the mean C pool of >100-year-old forests (150 Mg C $ha^{-1}$). The recovery of C pools according to a sigmoidal function may be the most biologically plausible, given that both aboveground and belowground C accumulation asymptotes after the first century of forest succession (Bormann & Likens, 1978). Because no harvest records existed for many of the >100-year-old-stands, forest age is not known and was varied between 120 and 150 years for the modeling exercise (Fig. 7b).

Although specific rates of C accumulation varied between linear, exponential, and sigmoidal recoveries, overall C reaccumulation rates were between .67 Mg C $ha^{-1}$ $yr^{-1}$ for recovery by 150 years after harvest and 1.22 Mg C $ha^{-1}$ $yr^{-1}$ for recovery by 120 years after harvest. Carbon inputs to mineral soils were estimated to be approximately 1.5 $ha^{-1}$ $yr^{-1}$ at Hubbard Brook (Fahey *et al.*, 2005), although the pool is proposed to be in steady state overall.

Our representation of C reaccumulation serves as a visual model of the potential rates and nature of C pool recovery. However, data for the range of time over which C recovery is likely to occur must be collected for these models to be empirically tested. Understanding not only C pool decline but also C pool recovery will enable researchers to better predict long-term dynamics in C pools – particularly in stands that are harvested in rotations.

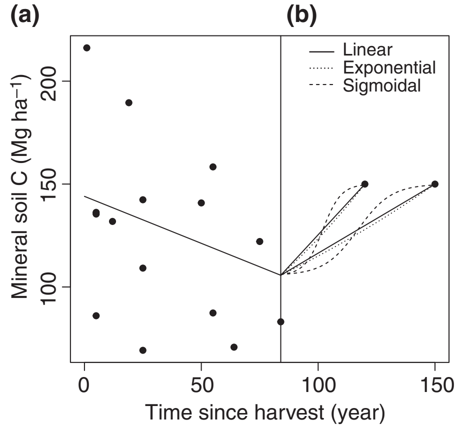


**Fig. 7** Panel (a) shows the overall model of mineral soil C storage over time after harvest, without random effect being taken into account. Panel (b) shows modeled recovery of soil C pools from their predicted lowest point 84 years after harvest to the mean of mineral solum C pools in >100-year-old forests. Recovery was modeled with linear, exponential, and logistic functions, and time to recovery varied between 120–150 years after harvest.

### *Relationship between C : N ratio and percent SOM*

In harvested forests, there was a significant positive relationship between percent SOM and C : N ratio, whereas >100-year-old forests showed a significant, yet poorly fit, negative relationship (Fig. 5). C : N ratios in old growth forests tend to be at steady state (Grand & Lavkulich, 2012) – C inputs and outputs are at or near steady state in the system, while N amounts are relatively constant and tightly cycled. A positive relationship between SOM and C : N ratio may indicate a nutrient dilution effect, in which SOC is being added to the soils faster than N (Grand & Lavkulich, 2012). The varying C : N ratio across levels of SOM may also indicate changes in the nitrogen pool itself. Productive sites that have relatively high SOM concentrations due to high C inputs to the soil may require more nitrogen to maintain photosynthetic rates in aboveground biomass. In a long-term monitoring experiment at the Hubbard Brook Experimental Forest in New Hampshire, second-growth forests accumulated more N than was available in the system via measured pathways. The mineral soil N pool, which accounts for 70% of total ecosystem N at Hubbard Brook was proposed as a likely source of the missing

N supporting the regrowth of forests, although this hypothesis remains untested (Yanai *et al*., 2013). A trend for increasing C : N ratios in the mineral soils of harvested forests may provide some evidence of N uptake from mineral soils by aggrading forests.

### *Future work*

We did not have the resolution to measure MAT, MAP, and net primary production (NPP) on a forest stand level, which precluded these variables from being included in our model. For example, all stands within the AEC study area were assigned the same MAT and MAP based on PRISM Climate Group Data. These variables have been included in other models of soil C storage that utilize robust, global datasets and thus include a wide range of such variables (for example, Averill *et al*., 2014). In order for a study of this type to include such information, MAT, MAP, and NPP should be measured at every stand individually, or a geographically broader dataset representing more levels of each variable could be sampled.

Future efforts should focus on collecting data that would enable mineral soil C to be included in C budgets across the northeastern region. Because of the variability in soil C pools, studies that utilize different strategies to measure changes in soil C often return varying results. For example, in a meta-analysis of the effect of clearing forests on soil C pools, Nave *et al.* (2010) considered any forest that had not been harvested in the past 40 years to be an undisturbed, or control, forest. Based on our study and others (e.g. Diochon *et al*., 2009), this timeframe would not capture declines in soil C pools, or would falsely assign forests that were at a C minimum as undisturbed controls. Strategic or coordinated efforts to measure C pools using consistent timescales and techniques may allow for more consistent findings, and therefore a more sound understanding of soil C dynamics. An example of such an effort is the NRCS Rapid Carbon Assessment, which has collected data from over 30,000 soil profiles across the United States (Soil Survey Staff, 2013). Although this dataset does not currently include detailed information about the management history of forestlands, it may be used as a baseline to understand future changes in mineral soil C pools.

A better understanding of the mechanisms causing C loss in harvested forests would greatly enable the predictive power of C accounting models. To meet the challenges of sampling in a highly heterogeneous system such as soil, process-based models could play an important and informative role to understand how soil C pools change with forest clearing (i.e. Johnson *et al*., 2010). Because it may be impossible to measure small fluxes from a large mineral soil C pool, process-based models that utilize our current understanding of the biogeochemical processes that drive soil C dynamics (for instance, the downward movement of organics and metals after forest clearing) may more efficiently lead to answers and practical management solutions.

## Conclusion

Efforts to reduce C emissions through fuel switching from fossil fuels to biomass will be successful only when there is an accurate understanding of the C balance implications of increased forest harvesting. The most significant ecosystem C pool in temperate forests, the mineral soil, should be studied more closely before the carbon neutrality of bioenergy from local wood in temperate forests is asserted. Given that ecosystem disturbances can influence the mechanisms of C storage and retention in soils, it follows that a severe ecosystem disturbance, such as clear-cutting forests, may cause C release from the soil via heating of the soil, increased water availability, compaction, and reduced C inputs to the system. Our study is the first to provide evidence of a regional trend of lower soil C pools in soils of harvested hardwood forests compared to mature or pristine hardwood forests. However, measuring differences in C pools across a broad geographic area containing forests with a wide range of carbon pools returned statistically insignificant results. We propose that unexplained variation introduced to the dataset due to the geographic scope of the study reduced the power of the analysis, and we suggest intensive sampling in areas of interest may uncover localized trends.

We constructed a mixed-effects statistical model to take into account variation between regional study areas. We offer a statistical model to begin to understand mineral soil C pool changes over time since harvest and conclude that time since harvest is a statistically significant predictor of mineral soil C pools. Time since harvest outperformed other variables that naturally influence soil C retention, such as clay content and elevation, in predicting mineral soil C pools. We measured differences in the chemistry of soils from harvested and >100-year-old forests, specifically in the relationship between C : N ratio and percent SOM. The differences suggest that C and N pools in soils of harvested stands may not be in steady state.

Including more managed and undisturbed forests in our model could broaden its applicability to the discussion of C accounting models with respect to bioenergy. It appears to be possible to overcome some of the traditionally held views about challenges to soil sampling, such as sampling difficulty and sample size, by including random effects in models, which may account for some of the natural variability across the landscape.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Mean soil carbon pools by mineral depth increment, effect sizes, and p-values for differences between pools.
**Table S2.** Mean C concentrations in harvested forests and >100-year-old forests.
**Table S3.** Candidate models ranked by AICc. Each model is represented by the fixed effects included in the model.
**Table S4.** (a) Parameter estimates for a model of mineral soil C pools over time after harvest. (b) The random effect estimates for each study area are deviations from the overall estimate of the intercept.