



Interaction of land use history, earthworms, soil chemistry and tree species on soil carbon distribution in managed forests in Vermont, USA

Donald S. Ross^{a,*}, Meghan E. Knowles^a, Juliette I. Juillerat^a, Josef H. Görres^a, Charles V. Cogbill^b, Sandy Wilmot^c, Kristen D'Agati^a

^a Department of Plant & Soil Science, University of Vermont, Jeffords Hall, Burlington, VT 05405, USA

^b Harvard Forest, Harvard University, Petersham, MA 01366, USA

^c Vermont Department of Forests, Parks and Recreation, 111 West St, Essex Junction, VT 05452, USA

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ABSTRACT

Forest soils store a globally important pool of carbon (C) and reforestation has the potential to increase this pool. Past land use, tree species composition, and current management are known to affect carbon storage rates and amounts. Another important factor, especially in the vertical distribution of soil C, is the presence or absence of earthworms. We investigated these interactions in eighteen managed forest sites in Vermont that have varied land use history (cultivation, pasture, woodlot, continuous woodland) and a range of time since reforestation from 60 to 100+ years. Soils were sampled to about 1 m, or shallower if bedrock was reached, and both C and exchangeable cation pools quantified. Earthworms were enumerated to a depth of 20 cm and identified by species. Basal area by tree species was also measured and aboveground C calculated. Detailed land use history was documented using archival sources. Forest type was primarily northern hardwood, with a few lowland spruce-fir sites included. Eleven different species of earthworms were found, representing all ecotypes, and numbers ranged from 0 (at 8 of the 18 sites) to 319 individuals/m². Carbon pools in the forest floor (1.5–30.1 Mg/ha) were greater with higher site elevation (range of 154–651 masl) and also greater with lower numbers of earthworms. Besides elevation, the best predictor of earthworm presence or absence, and overall numbers, was the soil exchangeable calcium (Ca) pool in the Oa and A horizons (range of 9.4–1288 cmol_c/m²). Because soil exchangeable Ca and aluminum (Al) pools were inversely related, higher exchangeable Al was associated with lower earthworm numbers. In the mineral soil, the C pool (82.1–210.8 Mg/ha) was best explained by the thickness of the B horizons with the exchangeable Al pool as a positive, secondary factor. The thickness of the A horizon (0–16.3 cm), and its contribution to the entire profile C pool (0–54.7 Mg/ha), decreased relative to past land use in the order: cultivated < pasture < woodlot. No earthworm metric was strongly related to the C pool in either the mineral soil or the full soil profile. Dramatic differences in the vertical distribution of carbon were related to past land use and earthworm presence, which in turn was negatively correlated with elevation and the presence of conifers. While it is clear that earthworms and prior land-use have a long-lasting effect on the forest floor C pool, it is less clear whether or not there is an effect on full profile C sequestration over time.

1. Introduction

Understanding the factors controlling soil organic carbon (SOC) stores and distribution in forested soils is essential for proper management (Mayer et al., 2020). Landscapes undergoing afforestation have the potential to accumulate considerable quantities of SOC (Nave et al., 2018; Bossio et al., 2020). A number of recent meta-analyses on the effect of afforestation after different land uses have been performed on

studies from the USA (Nave et al., 2013), Europe (Barcena et al., 2014) and world-wide (Laganière et al., 2010; Li et al., 2012; Shi et al., 2013). The conclusions from these analyses is that afforestation after cultivated agriculture will generally result in SOC accumulation but conversion of pasture or grassland to forests may not. Increases in SOC were clearer in the conversion from cultivation to forest when the forest floor (Oi, Oe and Oa horizons) SOC was included in the calculation (Laganière et al., 2010; Barcena et al., 2014). The depth of sampling of the mineral soil

* Corresponding author.

E-mail address: dross@uvm.edu (D.S. Ross).

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was also important because rates of change vary and including the carbon in deeper sampling, e.g. 0–100 cm vs. 0–20 cm, can increase the overall rate of increase by more than 1.5 (Shi et al., 2013). Also, the stability of carbon in the deeper soil can be affected by land-use change differently than near-surface carbon (Lyu et al., 2021). The rate of change varied in these analyses, with some studies showing initial declines after land-use conversion but most showing the positive effect by 30 years (Li et al., 2012; Nave et al., 2013). Forest management, after afforestation, can also have effects on SOC stores, especially in the forest floor (Jandl et al., 2007; Mayer et al., 2020).

The landscape of New England has undergone significant changes over the past 200–300 years. There was extensive forest clearing for agriculture that peaked in the mid- to late-1800s and extensive reforestation since (Compton and Boone, 2000). Much of the cleared land was used for pasture, although a considerable amount was cultivated. This increase in cultivated soils led to a large regional decrease in SOC and release of CO₂ (Houghton and Hackler, 2000; Templer et al., 2003). A number of studies have looked at the effect of reforestation in this region on SOC stores (Hamburg, 1984; Compton and Boone, 2000; Hooker and Compton, 2003; Clark and Johnson, 2011; Richardson and Stolt, 2013). Most have used chronosequences spanning over 100+ years since reforestation and inferred that the increase in SOC in formerly cultivated soils was either largely or completely in the forest floor. Clark and Johnson (2011), in sites from western New England, found similar rates of SOC accumulation in formerly pastured or hayed fields (grouped together) and formerly cultivated sites. The assumption for all these land uses is that the forest floor, present before clearing, was lost after agricultural conversion. The rate of SOC accumulation varied in these studies and the estimate of time to a new steady-state SOC stock ranged from about 100 yrs (Clark and Johnson, 2011) to up to 200 yrs (Hooker and Compton, 2003).

Earthworms, often termed ‘ecosystem engineers’ can have a profound effect on forest SOC distribution in recently invaded sites that were formerly earthworm-free (Frellich et al., 2006). The most recent glaciation extirpated native earthworms in much of New England and the upper Midwest. Soils in this region probably developed without significant numbers of earthworms and the introduction of North American, European and Asian species has been shown in a number of studies to result in large losses of near-surface SOC (Hale et al., 2005; Frellich et al., 2006; Fahey et al., 2013). The ultimate effect of earthworms on total SOC stocks is not clear because they can also stabilize SOC in the mineral soil through their effect on particle aggregation, and the net result could be positive (Zhang et al., 2013; Knowles et al., 2016). A recent meta-analysis by Ferlian et al. (2020) confirmed this opposite effect of invasive earthworms on SOC changes in the mineral vs. organic soil. Spread of earthworms into forests in the upper Midwest can be observed as invasion fronts (Hale et al., 2005) but the distribution in the forests of New England is not as clear, likely because of a longer history of introduction by European colonists. Although species effects vary, the spread of earthworms appears to be limited by unfavorable soil conditions such as low pH or high C:N ratios (Bernard et al., 2009; Moore et al., 2013; Shartell et al., 2013; De Wandeler et al., 2016; Homan et al., 2016). Stoscheck et al. (2012) found that invasive earthworms did not expand over a decade in a hardwood forest in New York and local abundance was associated with higher pH and wetter soils. The effect of pH is difficult to separate from the effect of Ca, because they usually co-vary. Earthworms can utilize Ca in respiration, forming biogenic CaCO₃ (Lambkin et al., 2011) and thus may have a preference for high-Ca soils. This calciferous respiration requires a calciferous gland which is present in lumbricid earthworms (Pierce, 1972) of mostly of European origins, but not in some species in the Megascolecidae family of Asian origins (James and Davidson, 2012; Plisko and Nxele, 2015). A common garden experiment of 14 conifer and hardwood species showed that Ca-rich litter increased earthworm abundance (Reich et al., 2005). Similar results were found in a six-species common garden experiment in Denmark, which also found a negative effect of soil exchangeable Al³⁺

(Schelfhout et al., 2017). In reestablished forests, earthworm presence can prevent the creation of a new forest floor (Ma et al., 2013). The presence or absence of earthworms clearly can have a strong effect on soil profile development.

In 2008–2009, we established 18 study sites in managed forests distributed around the state of Vermont with the purpose of monitoring long-term changes in SOC stocks and soil nutrients before and after harvesting. Earthworms were noticed in about half the sites during the initial soil sampling but not identified or enumerated. In 2012–2013, we returned to the sites with the explicit aim of quantifying earthworm numbers and identifying adults to the species level. In addition, a detailed land-use history was developed for each specific site location. Along with tree species, basal area measurements and a broad range of environmental factors, these data help explain the distribution of SOC throughout the profile of the soils. We hypothesized that earthworms would be more prevalent at sites with a more intensive agricultural land-use history and that the forest floor at these impacted sites would be thinner, with more of the profile carbon pool within the mineral soil.

2. Methods

2.1. Site selection and plot layout

Sites were selected based on the following criteria: i) having soils mapped as one of the major soil series (in terms of area) in Vermont, ii) having a forest management plan that included possible harvest within the next 5–10 years and iii) having one of the major forest types found in Vermont. The soil series extents were taken from the SSURGO database that included 13 of Vermont’s 14 counties (Soil Survey Staff, 2007). The major soil series included five Spodosols (Tunbridge, Berkshire, Lyman, Peru and Marlow) and three Inceptisols (Cabot, Buckland and Vershire) that covered 40.2% of the state’s land area. After locating potential cooperators, site selection was GIS-based, using available layers for forest management, soils and forest type. The forest type (Table 1) classification defined by the land manager sometimes represented the natural community type, as defined in Thompson and Sorensen (2005), and not the current species composition. The resulting 18 sites (Table 1) represented most of the biophysical regions of Vermont (Fig. 1).

Each site had a plot laid out in a design adapted from the US Department of Agriculture Forest Service (USDA-FS) Forest Inventory and Analysis (FIA) (USDA FS, 2005), with three additional soil sampling locations added (Supplemental Fig. S1). Plots were chosen to be relatively uniform in slope and forest composition, to limit variability within plots. The six soil sampling locations were located every 60 degrees, 27.4 m from the center of the plot. Three soil pits were excavated and described at every other soil sampling location (at an azimuth of 0, 120 and 240 degrees from the center). Vegetation subplots were 7.32 m in diameter; one was located at the center of the plot and three were located 36.6 m from the center of the plot, every 120 degrees (at an azimuth of 0, 120 and 240 degrees from the center).

2.2. Vegetation measurements

In order to calculate carbon stored aboveground in tree biomass, we measured diameter at breast height (137 cm) and tree height for trees ≥ 5 cm DBH, by species, in each of the four vegetation subplots. Biomass was calculated using the allometric equations of Jenkins et al. (2003) and C was assumed to be 50% of this biomass.

2.3. Soil sampling and analysis

The three soil pits were excavated to a mineral soil depth of 100 cm when possible, otherwise ~20 cm into the C horizon (usually a dense Cd horizon inherited from glacial till) or an impenetrable rock layer—whichever was encountered first (see Fig. 2 for average depth). Standard soil descriptions were made and used to determine the soil series and

Table 1
Site characteristics.

Site abbr.	Site	Forest Community	Elevation Center (m)	Average Aspect (°)	Average Slope
EML	Emerald Lake State Park	Enriched Northern Hardwood	299	142	21
GAR	Atlas Partnership 'Garfield'	Northern Hardwood	488	97	16
GRO	Groton State Forest	Spruce-Fir	425	245	3
HIN	Hinesburg Town Forest 'Poor'	Northern Hardwood	403	326	5
HIR	Hinesburg Town Forest 'Rich'	Enriched Northern Hardwood	370	349	21
JER	Jericho Research Forest (UVM)	Northern Hardwood	154	269	18
MBR	Marsh-Billings-Rockefeller National Park	Northern Hardwood	397	90	24
NFS	Green Mountain National Forest	Northern Hardwood	493	50	14
NIN	Coolidge State Forest 'Ninevah'	Spruce-Fir	552	182	7
PCB	Coolidge State Forest 'PCB'	Enriched Northern Hardwood	651	193	10
SKR	Starksboro Town Forest 'Rich'	Enriched Northern Hardwood	349	278	24
SMB	Steam Mill Brook Wildlife Management Area	Spruce-Fir	649	254	5
SQU	Atlas Partnership 'Square'	Enriched Northern Hardwood	589	100	15
STE	Sterling Town Forest (Stowe) 'Hardwoods'	Northern Hardwood	528	250	6
STK	Starksboro Town Forest	Northern Hardwood	333	215	13
STS	Sterling Town Forest (Stowe) 'Spruce-Fir'	Spruce-Fir	524	94	6
WAT	Waterworks Property (VT Family Forests)	Northern Hardwood	237	279	18
WIL	Willoughby State Forest	Northern Hardwood	465	79	7

drainage class of each soil, using USDA National Resources Conservation Service (NRCS) criteria (Soil Survey Staff, 2006). Samples were taken from the side of the pit from each mineral horizon. As detailed below, these three pit samples were used to measure exchangeable cations and pH whereas carbon was measured in the mineral soil in samples from six corings performed at each site. Forest floor samples were taken separately, using a 15 by 15 cm frame to obtain a quantitative sample. Separate Oi, Oe and Oa horizon samples were taken unless a horizon was too thin to be collected separately (<1 cm), in which case it was combined with the overlying horizon. Twigs present on top of the Oi horizon were discarded but roots and twigs within a horizon were collected with each soil sample and included in the carbon analysis. Three replicates were collected at each of the six soil sampling locations, resulting in 18 samples per horizon per plot. Organic soil horizons were air-dried within 24 h of collection, then oven-dried to a constant weight at 60 °C. The Oi and Oe samples were ground using an Udy cyclone mill (Udy Corp., Fort Collins, Colorado) and Oa samples were ground to pass a 0.425 mm sieve.

Mineral soil samples were air-dried within 48 h of collection. Samples were oven-dried to constant weight at 105 °C, sieved through 2-mm mesh and a subsample for C analysis ground to pass a 0.425 mm sieve to ensure sample homogeneity. Rocks, twigs and large roots were removed from all samples by sieving and when grinding.

Samples of mineral soils were also collected for carbon analysis at each of the six locations using a diamond-tipped core (inner diameter of 6.9 cm) mounted on a power auger. The exact depth of each core increment (usually about 10 cm) was measured in the coring hole progressively after each sampling. The forest floor was removed and coring proceeded to about the same depth as the soil pits with each increment saved quantitatively in a polyethylene bag. The corer could drill slowly through rock but if a large rock was encountered at a depth shallower than the closest soil pit, a new coring hole was started. These cores were also used to measure coarse fragments content and bulk density. Core samples were oven dried to constant weight at 105 °C, and sieved to pass a 2 mm sieve; the weight of rocks and roots was recorded. Soil bulk density for mineral soil was calculated on oven-dry soils, accounting for the volume and weight of coarse material (coarse roots and rocks). The separated weight of the >2 mm rocks was used to calculate the fraction of coarse fragments. A subsample of each soil (<2 mm) was ground to pass a 0.425 mm sieve to facilitate accurate C analysis.

For carbon analysis, 25–80 mg of ground soil was weighed into tin capsules and analyzed on a Thermo Scientific Flash EA 1112 NC Analyzer (CE Elantech Inc., Lakewood, New Jersey). Mineral soil samples and Oa samples were run in triplicate; Oi and Oe horizons were run

in duplicate. Soils obtained from the North American Proficiency Testing program were used both to calibrate the instrument and as quality controls. One site, EML, was shallow to limestone bedrock and had CaCO₃ in the lower horizons. Organic C was determined in soils from this site by weighing subsamples into silver capsules and incubating with sufficient HCl to remove the carbonate. Samples were also run without pretreatment to provide total soil C.

The total profile mineral soil organic carbon was determined by summing the C in the core depth increments for each of the six cores. The weight of each increment (median thickness of 440 core samples was 10.4 cm), minus coarse fragments >2 mm, was used to convert the C result (mg/Kg) to a mass of carbon that was then expressed as Mg/ha after summation. At seven of the sites (in 1–5 of the six soil sampling locations), the C analysis revealed that the presumed Oa horizon sampled in the 15 × 15 cm square was <200 g/kg C and, by definition, an A horizon. In these cases the mass of C in this horizon in the three squares taken at the site of each core sample were averaged, converted to Mg/ha and added to the mineral soil summation instead of the forest floor, because the coring started below what was thought to be an Oa (forest floor) horizon. At three sites, a core as deep as an adjacent pit was not successfully obtained and the profile C for these was calculated from samples taken from the pits adjusted by using the average coarse fragment content and bulk densities for the depth increments from the other five corings at that site. This provided an *n* of six for the C results for all eighteen sites.

Exchangeable cations in the pit samples (not the core samples because of possible contamination with freshly ground rock) were determined by extraction with 1 M NH₄Cl (Ross et al., 2015). Solution: soil ratios of 10:1 or 12.5:1 were used for mineral horizons while 40:1 was used for Oa horizons to ensure complete exchange. Samples were shaken for 2 hr, centrifuged at ~1500g and run on an ICP-OES (Optima 3000 DV, Perkin-Elmer Corp., Norwalk, CT) for Al, Ca, Mg, K and Na using standard techniques. To calculate profile pools of these cations, the horizon depths from the pits were used along with bulk density measurements from the corresponding depth in the nearby coring. For pools in the uppermost humified horizon, the Oa and A were combined into an Oa/A because two sites had no A horizon, nine sites had no Oa horizon and seven sites had both (Fig. 2). Another rationale for combining the Oa and A was that, at some sites, there were horizons both closely above and below the US Taxonomy threshold of 20% carbon for differentiating an A from an Oa horizon. The Oa/A designation avoids the problem of this perhaps arbitrary threshold and we use that term throughout this paper.

The pH was measured in water (2:1 V:V) on samples from one

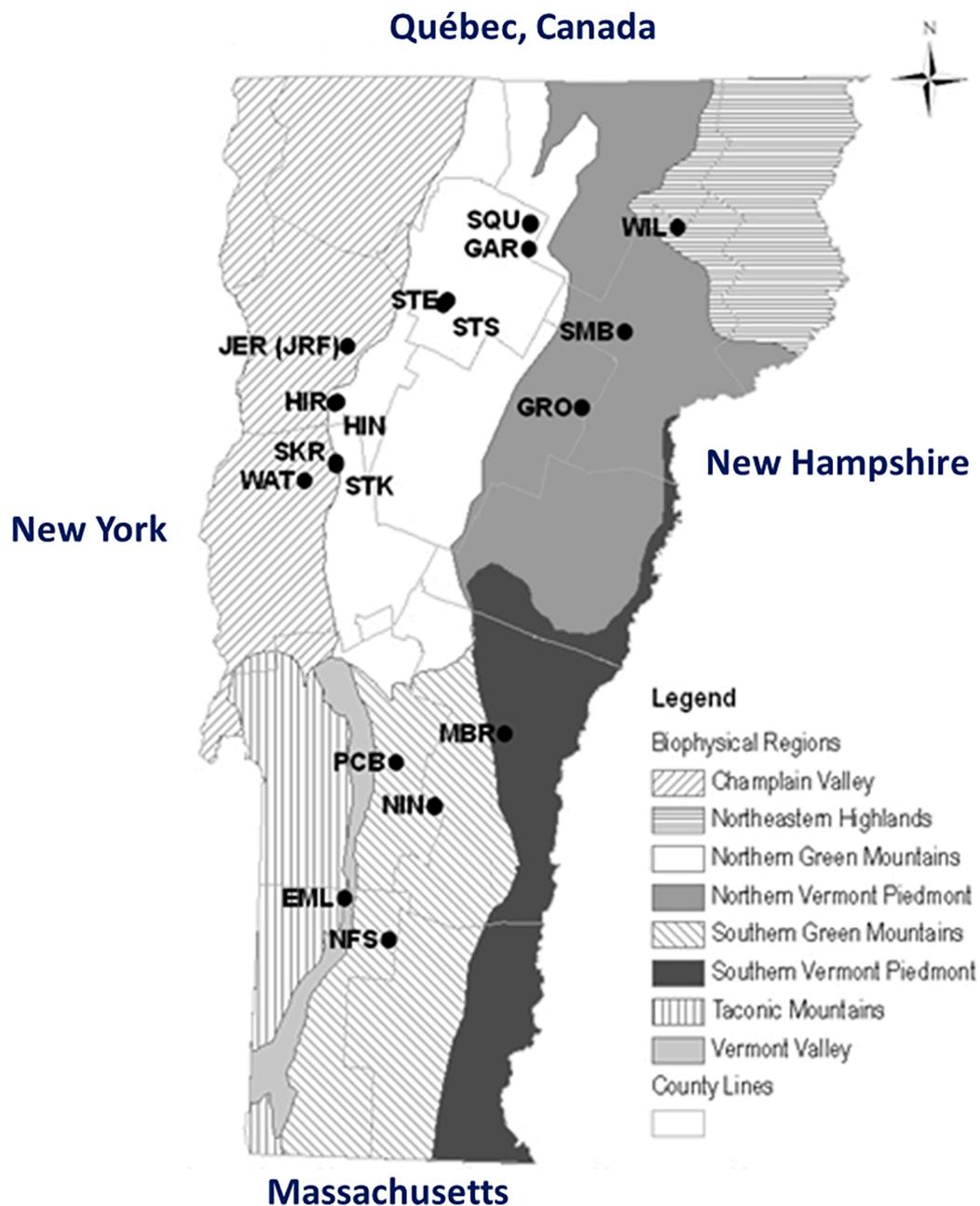


Fig. 1. Location of study sites in Vermont. The biophysical regions are from the [VT Biodiversity Project \(1998\)](#). See [Table 1](#) for complete site names.

mineral soil sample nearest to the surface (A or upper B, not E) for each pit. Particle size was determined on each of the six plots sampled for earthworms at nine sites in 2012. The hydrometer method was used after overnight dispersion with 1% sodium hexametaphosphate ([Gee and Or, 2002](#)).

2.4. Earthworms

To determine earthworm species and numbers, six 50 × 50 cm survey pits were added to the existing plots. Pits were placed 32 m from plot center at 30, 90, 150, 210, 270 and 330° magnetic north. Depths of litter (Oi, Oe, Oa) were measured, and the complete Oi and Oe horizons collected separately, sorted for earthworm counts and subsequently dried and weighed in the lab. Soil from 0 to 10 cm (including the Oa horizon), followed by 10–20 cm, was removed and hand sorted for earthworms. Earthworms were enumerated and identified on site based on external characteristics using the keys in [Hale \(2013\)](#) and

[WormWatch \(NatureWatch, 2014\)](#). Anecic worms were enumerated by their midden mounds, with a 1:1 correspondence to individual earthworms assumed. The earthworm survey was conducted in May through October of 2012 and 2013.

2.5. Land-use history

The site-specific history of each site was documented with a combination of historical analyses and on-site field survey. The history of agricultural and forest management land use was determined by deriving the town's original forest composition (from the Cogbill witness tree database); the ownership history (from 19th century cadastral maps); 19th century agricultural use (from U.S. agricultural censuses, gazetteers, town histories), and 20th century land use (from topographic maps, aerial photographs, and field landscape investigations, including forest structure, stone wall analysis, and soil descriptions). Each location was effectively limited to one known property/field/woodlot with a

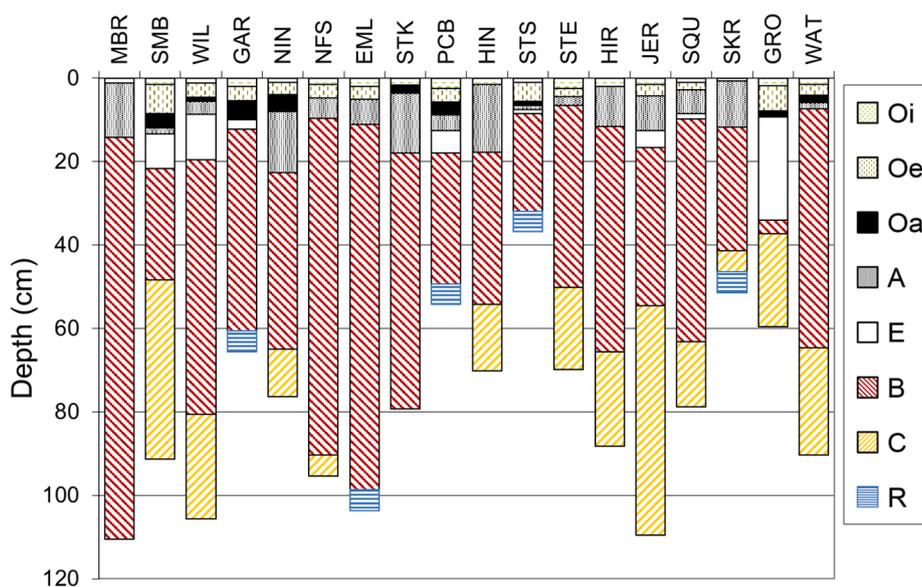


Fig. 2. Soil depth and horizon sequence from the average of the three pits. If bedrock (R) was not encountered, sampling depth was either ~20 cm into the C horizon or to ~100 cm below the forest floor. Sites are sorted left-to-right from highest to lowest total profile organic carbon.

single decipherable history. The timing and intensity of specific changes at the site over the past 200 years was categorized. We produced a time line of major historical events at each site and the proximity of the soil sampling pits to those historical factors. The specific land use history of each site was classified into one of five categories (i.e. cultivation, improved pasture, back pasture, woodlot, woodland) directly reflecting the definition (i.e. tilled, improved pasture, unimproved pasture, woodlot, remainder of land, respectively) and site specific location from the 1880 U.S. Agricultural Census. The pastures were untilled and separated by the intensity of use for production or grazing.

2.6. Statistical analyses

Because of the relatively few sites (n = 18), standard regression with more than one independent variable was not considered. Correlation matrices of all data were used to explore for the best single predictors of soil carbon and earthworm metrics, followed by simple linear regression. Spearman’s rank correlation was used because many of the

Table 2
Organic carbon in the soil and aboveground live trees. Values in parentheses are the standard error of the means.

	Aboveground C in live trees (Mg/ha)	Mineral Soil C (Mg/ha)	Forest Floor C (Mg/ha)	Belowground mineral + forest floor C (Mg/ha)
EML	118.4	171.0 (19.7)	8.3 (1.3)	179.3 (27.0)
GAR	79.6	153.4 (28.4)	20.1 (3.0)	173.5 (30.0)
GRO	62.4	82.1 (23.1)	20.2 (2.6)	102.3 (21.5)
HIN	101.4	149.2 (10.9)	1.6 (0.1)	150.9 (11.8)
HIR	101.7	126.6 (11.7)	3.2 (0.5)	129.8 (9.6)
JER	125.0	128.6 (11.3)	6.7 (1.2)	135.3 (12.6)
MBR	179.7	210.8 (17.2)	3.2 (0.4)	214.0 (16.9)
NFS	117.6	172.5 (27.4)	10.5 (0.6)	183.0 (19.0)
NIN	76.0	167.5 (17.3)	23.3 (2.7)	190.7 (20.5)
PCB	113.7	96.5 (7.9)	22.7 (5.0)	119.2 (11.3)
SKR	106.7	86.2 (7.4)	1.5 (0.2)	87.8 (7.4)
SMB	128.4	167.9 (21.2)	31.0 (2.4)	198.9 (19.7)
SQU	115.9	109.7 (8.5)	7.3 (0.5)	117.0 (8.5)
STE	132.3	115.6 (9.4)	6.5 (0.7)	122.0 (11.9)
STK	131.2	151.4 (24.4)	1.7 (0.2)	153.1 (24.4)
STS	85.3	119.9 (10.1)	14.0 (1.3)	133.9 (10.8)
WAT	129.1	48.2 (3.1)	9.6 (1.2)	57.9 (3.1)
WIL	77.2	181.2 (10.5)	16.5 (2.1)	197.7 (9.8)

variables were not normally distributed. We also used regression tree analysis to demonstrate partitioning of SOC by one or two independent variables. A multivariate modeling approach, partial least squares (PLS), was investigated because it is suited for data like ours in which the number of independent variables far exceeds the number of observations and where there is high multicollinearity among the predictors. PLS creates explanatory factors from the independent variables while maximizing the variability explained within both the predictors and the response. Use of this approach has increased over recent decades in areas such as genomics (Boulesteix and Strimmer, 2007) and chemometrics, e.g. predicting soil carbon from spectroscopy (Winowiecki et al., 2017). Fifty continuous variables were employed including: elevation, aspect (converted to an index of southness: cosine of 180+ degrees), and slope from Table 1; exchangeable cation pools in the Oa/A horizon and pH from Table 3; distance to 1880 farmhouse from Table 4; earthworm metrics from Table 5; tree species basal area from Table S1 (13 species that were present at four or more sites); and exchangeable cation total pools and concentrations in the Oa/A and upper B horizon (Tables S4, S5 and S6, respectively). Soil horizon depths were not included because of the a priori correspondence between forest floor depth and carbon content. For modeling the forest floor carbon, these variables were initially screened with individual simple linear regressions and the 22 with p values <0.10 were used (presented in Table S7). PLS was run using the standard NIPALS method with K-fold cross validation (K = 7). For modeling the mineral soil carbon, initial screening found an insufficient number of variables for PLS, i.e. only three with a p < 0.10. Modeling earthworm metrics, e.g. total individuals/m², with PLS was not possible with the large proportion of observations with zero values. Although PLS was not appropriate, logistic regression with data converted to dichotomous outcome was investigated, but a multivariate model with all significant predictors could not be found. One site, WAT, was at or near the Bristol Ore Bed, which was mined for iron from 1791 to 1832 (Rolando, 1992). A century later in 1935, a municipal reservoir was created downslope from our plot location. Because of the unusually low profile SOC at WAT and the unusual history of disturbance, this site was omitted from statistical analysis of SOC with other variables. All statistics were run with JMP (SAS Institute, 2018).

Table 3
Exchangeable cation pools in the Oa/A horizons, and pH in the upper mineral horizon (A or B).

	Ca (cmol _c /m ²)	Al (cmol _c /m ²)	Mg (cmol _c /m ²)	K (cmol _c /m ²)	Na (cmol _c /m ²)	Mn (cmol _c /m ²)	pH in upper mineral horizon
EML	852	133	311	11.7	0.89	0.65	6.3
GAR	9.4	10.8	1.3	0.7	0.09	0.34	4.0
GRO	13	9.8	3.1	1.9	0.47	0.04	4.6
HIN	281	235	39.7	20.3	4.23	9.22	4.5
HIR	398	120	78.8	23.4	1.22	17.2	4.4
JER	153	189	37.3	9.9	1.04	2.44	3.9
MBR	794	8.0	75.9	31.3	1.04	7.69	5.7
NFS	39	144	22.7	10.5	0.84	1.10	3.9
NIN	20	565	16.6	10	2.49	1.16	3.9
PCB	65	3.0	7.8	1.8	0.21	0.55	4.6
SKR	513	147	51.1	14	2.16	24.0	4.4
SMB	107	57.5	29.2	8.2	1.08	0.40	3.3
SQU	147	2.5	25.1	2.5	0.74	2.40	4.8
STE	85	40.1	14.4	4.3	0.70	25.0	4.9
STK	1288	59.1	101	38.8	3.59	32.8	5.2
STS	12	50.5	5.2	4.5	0.82	3.18	4.3
WAT	34	37.1	6.8	3.4	0.27	4.66	4.1
WIL	76	35.8	12.8	4.9	0.86	0.82	3.7

Table 4
Land use history, including distance from closest dwelling. Land use history scalar: 1 = cultivation, 2 = improved pasture, 3 = back pasture, 4 = farm woodlot, 5 = woodland.

Site	Land use history scalar	Distance to 1880 farm house (km)	Farm dates	Summary of use
EML	2	0.50	1769–1957	cow pasture, heavy use 1850–1957
GAR	4	1.77	1802–1955	heavy use included sugaring, heavily cut since 1950
GRO	5	1.14	1873–1933	industrial woodland lots, heavily cut 1873–1933, state forest 1933 to present
HIN	2	0.43	1875–1950	dairy farm fields, with sheep
HIR	2	0.39	1875–1950	dairy farm fields
JER	2	0.31	1790–1910	dairy farm fields, perhaps woods pasture to 1941, selective cutting since
MBR	2	0.63	1790–1930	improved pasture with perhaps some woods pasture on gentleman farm
NFS	2	0.48	1790–1950	intensive dairy farm, with sheep, remnant stone walls
NIN	1	0.39	1837–1950	1759 Crown Point road; 1837–1872 Tyson Furnace land cleared for charcoal; after 1870 s medium scale dairy & sheep farm; stone walls and plow layer
PCB	2	0.31	1838–1940	dairy farm, remnant stone walls
SKR	2	0.31	1810–1940	dairy farm, perhaps some sugarbush, remnant stone walls
SMB	3	0.42	1810–1960	dairy farm; back pasture & possibly some woodland; to state WMA 1971, selective cutting since
SQU	4	1.14	1830–1960	cow, sheep farm; selectively cut since 1960
STE	2	0.61	1799–1950	diversified farm, formerly Sterling Hollow
STK	1	0.19	1810–1940	dairy farm, plow layer, stone wall
STS	2	0.64	1799–1950	diversified farm, formerly Sterling Hollow, cleared stone piles
WAT	2	1.24	1840–1930	Bristol Ore Bed 1791–1832; pasture 1840–1930, stone walls and barb wire; Municipal Forest with reservoir 1935–1997
WIL	4	1.03	1850–1940	sawmill at summit in 1800; 1939 CCC camp; 1960 State forest, heavily cut since

3. Results

3.1. Tree species

Sugar maple (*Acer saccharum*) was the dominant species at most of the hardwood sites, comprising 19–97% of the basal area (Fig. 3, Supplemental Table S1). The two other key northern hardwood species, American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*), were much less common, with maximum basal area contributions of 20% and 11% respectively. White ash (*Fraxinus americana*) comprised over 20% of the basal area at five of the sites while paper birch (*Betula papyrifera*) and red oak (*Quercus rubra*) each contributed 20% or greater at two sites. Basal areas in the lowland spruce-fir sites were 1–44% red spruce (*Picea rubens*) and 15–53% balsam fir (*Abies balsamea*). Red maple (*Acer rubrum*) comprised 28–44% of the basal area at the spruce-fir sites and was actually the dominant species at STS. Eastern hemlock (*Tsuga canadensis*) was only present at two sites but made up 58% of the basal area at EML. The aboveground carbon in 2008/2009 in live trees (Table 2) ranged from 62.4 Mg/ha at GRO

(lowland spruce-fir) to 179.7 at MBR (91% sugar maple).

3.2. Soil characteristics

Fifteen different soil series were found in the 18 sites (Supplemental Table S2), all Spodosols or Inceptisols. The most common were Typic Haplorthods followed by Oxyaquic Dystrudepts. Both are naturally base-poor and undergoing podsolization but the poorer drainage of the Oxyaquic Dystrudepts has limited leaching and profile development. A few sites had three different series, varying either by depth to bedrock or drainage. Soils at one site, EML, were developed on limestone bedrock and were base-rich Eutrudepts, with CaCO₃ found in some of the lower horizons. Particle size analysis on the earthworm plots sampled in 2012 (nine sites, data not shown), found a range in texture from sandy loam to loam, consistent with the soil series descriptions. The remaining nine sites had similar soils and, based on field examination, would also be loams and sandy loams. Coarse fragment content ranged from 3.0% at JER to 25.1% at EML, with a median of 15.8% (Supplemental Table S3). Soil depth averaged 79 cm and ranged from 33 cm at STS to greater than

Table 5
Numbers of earthworm species and individuals, also broken down by habitat type (ecotype).

Site	Number of earthworm species	Epigeic earthworms (individuals/m ²)	Endogeic earthworms (individuals/m ²)	Epi-endogeic earthworms (individuals/m ²)	Anecic earthworms (individuals/m ²)	Total earthworms (individuals/m ²)	Fraction of plots with earthworms
EML	3	2	15	1	0	17	0.67
GAR	0	0	0	0	0	0	0.00
GRO	0	0	0	0	0	0	0.00
HIN	6	10	130	5	13	153	1.00
HIR	4	4	4	7	1	16	0.83
JER	5	2	31	4	0	37	0.50
MBR	3	118	1.3	2	4	121	1.00
NFS	0	0	0	0	0	0	0.00
NIN	0	0	0	0	0	0	0.00
PCB	1	0	0.7	0	0	0.7	0.17
SKR	6	29	49	23	4	103	1.00
SMB	0	0	0	0	0	0	0.00
SQU	1	0	12	0	0	12	0.33
STE	1	2	0	0	0	2	0.17
STK	4	23	226	66	3	319	1.00
STS	0	0	0	0	0	0	0.00
WAT	0	0	0	0	0	0	0.00
WIL	0	0	0	0	0	0	0.00

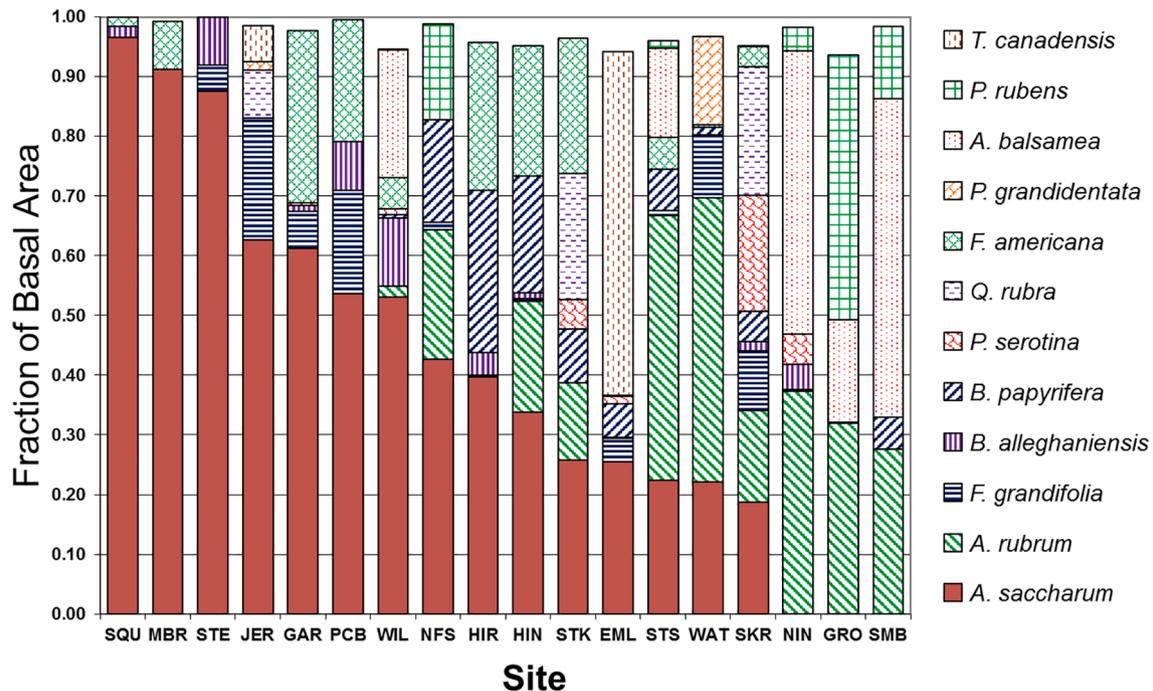


Fig. 3. Major tree species basal area. Sites are sorted left-to-right by *Acer saccharum* (sugar maple).

100 cm at MBR, WIL and JER (Fig. 2). All sites had B horizons (Bs and Bhs in the Spodosols or Bw in the Inceptisols) ranging in thickness from 3.3 cm at GRO (shallow, wet soil) to 96.3 cm at MBR (unusually deep Dystrudept). C horizons were found in two thirds of the profiles, with four sites having a B horizon over bedrock and two sites having a B horizon extending beyond the sampling depth. Nine of the sites had Oa horizons (C > 200 g/kg) and two of these nine had no A horizons (C < 200 g/kg), with the Oa immediately over an E horizon.

Full profile (forest floor and mineral soil) SOC varied between 57.9 Mg/ha at WAT to 214 Mg/ha at MBR (Table 2, Fig. 4). When inorganic C was included in the totals, EML contained 441 Mg/ha C. Forest floor SOC ranged from 1.5 to 31.0 Mg/ha (Table 2), and varied from 1.1 to 19.7% of the total profile SOC, with a median of 6.0% (Table S3). In the 16 sites where present, the A horizons had a broad range (<1% to ~46%) in

percentage of the total mineral SOC, with a median of 14% (Table S3).

A wide range in exchangeable Ca pools was found in the combined Oa/A horizons (9.4–1288 cmol_c/m², Table 3) and in the full profile (58–11122 cmol_c/m², Supplemental Table S4).

Exchangeable Al also had a broad range in both the Oa/A horizons (2.5–565 cmol_c/m², Table 3) and the full profile (159–2138 cmol_c/m², Table S4). As would be expected, the highest profile exchangeable Ca was found in the calcareous soil at EML, which also had the highest pH in the upper mineral soil (Table 3). Soil pH ranged from this high of 6.3 in the A horizon at EML to a low of 3.3 at SMB, one of the spruce-fir sites. Thirteen of the 18 sites had a pH in a relatively narrow range between 3.9 and 4.6.

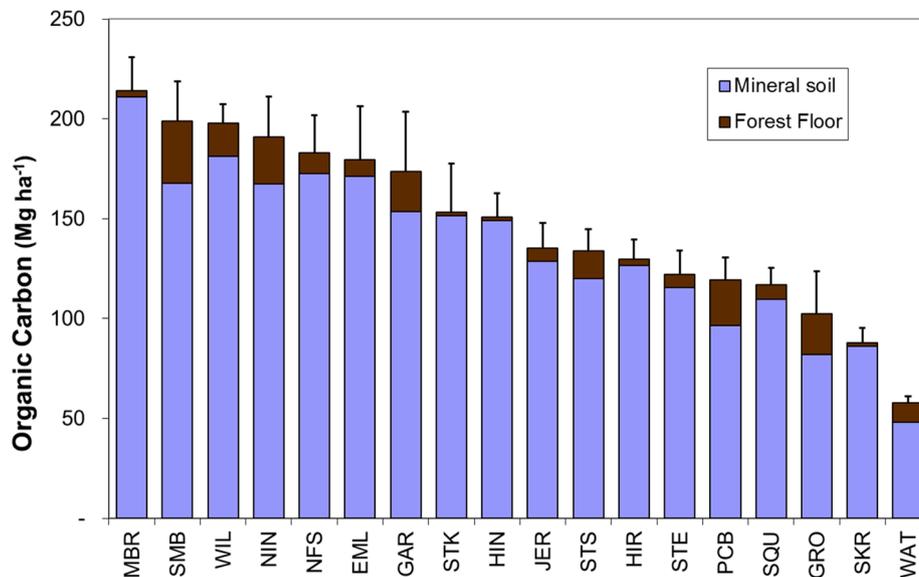


Fig. 4. Soil profile organic carbon at each site. Sites are sorted left-to-right by the total amount of organic carbon to the depth sampled. Error bars represent the standard error of the mean for the combined mineral and forest floor data ($n = 6$).

Table 6

Species of earthworms found and their distribution. See Table 1 for explanation of site abbreviations.

Type	Species	Sites found
Epigeic	<i>Dendrobaena octaedra</i>	EML, JER, MBR
	<i>Dendrobaena rubida</i>	HIN, HIR, SKR
Endogeic	<i>Aporrectodea turgida</i>	HIN, HIR, SKR
	<i>Aporrectodea rosea</i>	EML, HIN, STK
	<i>Aporrectodea tuberculata</i>	HIN, HIR, JER, MBR, SKR, SQU, STK
	<i>Aporrectodea trapazoides</i>	JER, SKR, STK
	<i>Octolasion cyaneum</i>	HIN
	<i>Octolasion tyrtaeum</i>	EML, HIN, SKR
Epi-Endogeic	<i>Lumbricus rubellus</i>	JER, SKR, STK
	<i>Amyntas agrestis</i>	JER
Anecic	<i>Lumbricus terrestris</i>	SKR
Juvenile	Pigmented	EML, HIN, HIR, MBR, SKR, STK
	Unpigmented	EML, HIN, HIR, JER, MBR, PCB, SKR, STK, SQU

3.3. Land-use history

All but one site (GRO) were part of farms that were in operation beginning as early as 1769 (EML in southeastern Vermont) and ending as late as 1960 (SMB and SQU in northern Vermont). The dominant land use (11 sites) was improved pasture (Table 4), with one site as 'back' pasture, two cultivated and three as farm woodlots. The distance from the plot center to the farm house that existed in 1880 varied between 0.2 and 1.8 km. Of historical interest, one cultivated site (NIN) was on the 1759 road from Crown Point, NY to Boston, MA that played a role in the Revolutionary War. NIN also was cleared for charcoal in the 19th century to supply a nearby iron forge (Rolando, 1992).

3.4. Earthworms

Eight of the 18 sites were completely earthworm free (Table 5) with two other sites (PCB and STE) only having worms in one of the six sampling plots. Overall, earthworm presence was patchy with only four sites having earthworms in all six plots. These four sites (HIN, MBR, SKR and STK) also had much higher numbers than the other sites, ranging from 103 to 319 individuals/m². Genera found included *Dendrobaena*, *Aporrectodea*, *Octolasion* and *Lumbricus*; all of European origin (Table 6). The Asian species, *Amyntas agrestis*, was found only at JER, the site with the lowest elevation and the closest in proximity to Vermont's major urban/suburban area. The number of species found at each site varied between 0 and 6. The four sites with the highest earthworm numbers, mentioned above, also had earthworms in all four ecotypes: epigeic, endogeic, epi-endogeic and anecic (Table 5). Overall, there were more endogeic species found than any other earthworm type (Table 6). Differences in earthworm abundance and their patchy distribution may have been partially due to the extended period over which sampling was spread. Some European earthworms go into aestivation when soils become dry and temperature get higher.

3.5. Interactions explaining forest floor carbon

The best single predictor of forest floor SOC was elevation ($R^2 = 0.42$, $P = 0.005$, Fig. 5). Our sites spanned about 500 m in elevation (154–651 m) and the higher elevation sites usually had thicker Oa and Oe horizons and thinner A horizons than the lower sites (with the exception of NIN, discussed below). Total earthworm numbers and earthworm species richness were negatively correlated with elevation (Spearman's $r = -0.64$ and -0.65 respectively, $P = 0.005$), as were the number of epi-endogeic earthworms (Spearman's $r = -0.81$, $P < 0.001$) and the number of epigeic earthworms (Spearman's $r = -0.71$, $P = 0.001$). Total earthworm numbers decreased from a range of 16–319 individuals/m² below about 400 m in elevation to a range of 0–12 individuals/m² at higher elevation, with 7 out of the 10 higher elevation

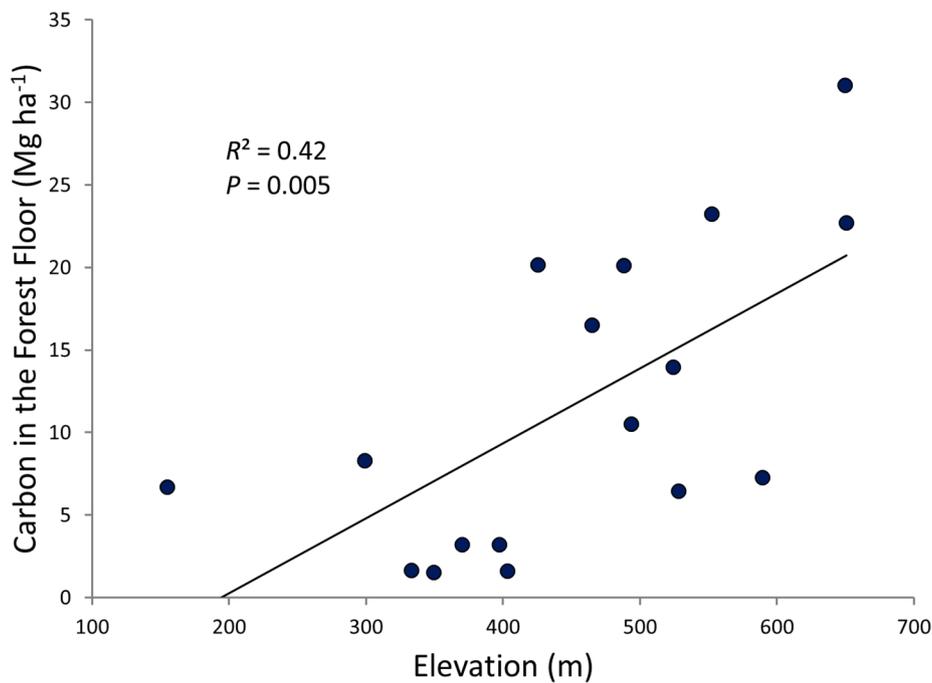


Fig. 5. Carbon in the forest floor as a function of site elevation.

sites having no earthworms (Fig. 6a). Regression tree analysis partitioned the forest floor SOC mass by the number of earthworms found: 9 sites with >1 individuals/m² had a mean SOC of 4.45 Mg/ha and the 8 sites with ≤ 1 individuals/m² had a mean SOC of 19.8 Mg/ha, ($R^2 = 0.75$, Fig. 6b).

Further evidence for the controlling effect of earthworms on the forest floor can be seen when examining both the prior land use and the current earthworm density (Fig. 7). Prior cultivation and pasturing should have largely eliminated the forest floor yet 60–70 years after reforestation on the two cultivated soils, NIN (0 earthworms) developed an 8-cm thick forest floor with 23.3 Mg/ha SOC over an Ap horizon but STK (319 earthworms/m², highest in any site) only accumulated 1.7 Mg/ha. The former pasture sites that had no earthworms (or 0.7 individuals/m² at PCB) were all higher in forest floor SOC than sites with greater earthworm densities (Fig. 7). One former woodlot, SQU, had a relatively thick average forest floor (10 cm) but with only moderate SOC (7.29 Mg/ha) because of relatively low-carbon Oa horizons. SQU had one endogeic species of earthworms found in two of the six plots (overall mean of 12 individuals/m²).

Partial least squares regression confirmed the negative influence of earthworms on forest floor carbon pools and showed the positive influence of some variables that may relate to inhibition of earthworms (Fig. 8). The PLS analysis created three factors (minimal root mean predictive error sum of squares of 0.429) that explained 65.0% of the variability in the explanatory variables and 94.8% of the variability in the forest floor carbon. Seventeen predictors were above the 0.80 threshold for Wold's variable importance (Fig. 8), a metric of influence on the overall model. The variables of highest importance with negative coefficients (i.e. predicting lower forest floor carbon) were the fraction of plots at each site that had earthworms and the number of earthworm species at each site. Two soil chemistry variables, Mn pools in the Oa/A horizons and in the full profile, had the highest negative normalized coefficients. Variables of high importance with positive coefficients included one tree species basal area (*Abies balsamea*), a site physical metric (aspect expressed as index of southern exposure (southness) in

which -1 is the most south and $+1$ the most north) and a soil chemistry metric (Al concentration in the uppermost B horizon). Interestingly, elevation and the Oa/A horizon Ca pool, both discussed above individually, had somewhat lower importance and less positive coefficients (Fig. 8). Implications of the PLS model are discussed further in Section 4.2.

3.6. Interactions explaining earthworm density

A number of factors beyond elevation help explain the differences in earthworm densities. All six sites with a spruce-fir component (Fig. 2, Table S1) were earthworm free, but earthworms were also quite low or absent (≤ 2 individuals/m²) from three other sites with no conifers. The single best predictor was the Ca pool in the Oa/A horizon (combined because some sites only had one of these two horizons, $R^2 = 0.62$, $P < 0.001$). We binned the Ca data into three ranges to better show the relationship with earthworm numbers (Fig. 9). Calcium concentrations and pools were positively correlated with soil pH (e.g. upper B horizon Ca concentration vs. pH, Spearman's $r = 0.75$, $P = 0.001$) and negatively correlated with Al concentrations and pools (e.g. the total profile pools of Ca and Al showed a linear negative ln/ln relationship, $R^2 = 0.72$, $P < 0.001$, Supplemental Fig. S2). Soil pH (Table 3) was not as clear an indicator of earthworm density as was Ca and the pH ranges for sites with <1 earthworm individual/m² (3.3–4.6) and those with >1 /m² (3.9–6.3) overlapped. Overall, the pH did not vary numerically as much as Ca, with 12 of the 17 sites within one pH unit (3.9–4.9).

3.7. Interactions explaining mineral soil carbon

Land-use history explained the depth of the mineral A horizon, with only the two cultivated sites showing clear Ap horizons or plow layers (Fig. 10). There was, however, no apparent effect of prior land use on total profile SOC. The best single overall predictor of mineral SOC was the thickness of the B horizon ($R^2 = 0.53$, $P = 0.001$, Fig. 11) but the total mineral soil depth was nearly as good ($R^2 = 0.52$, $P = 0.001$).

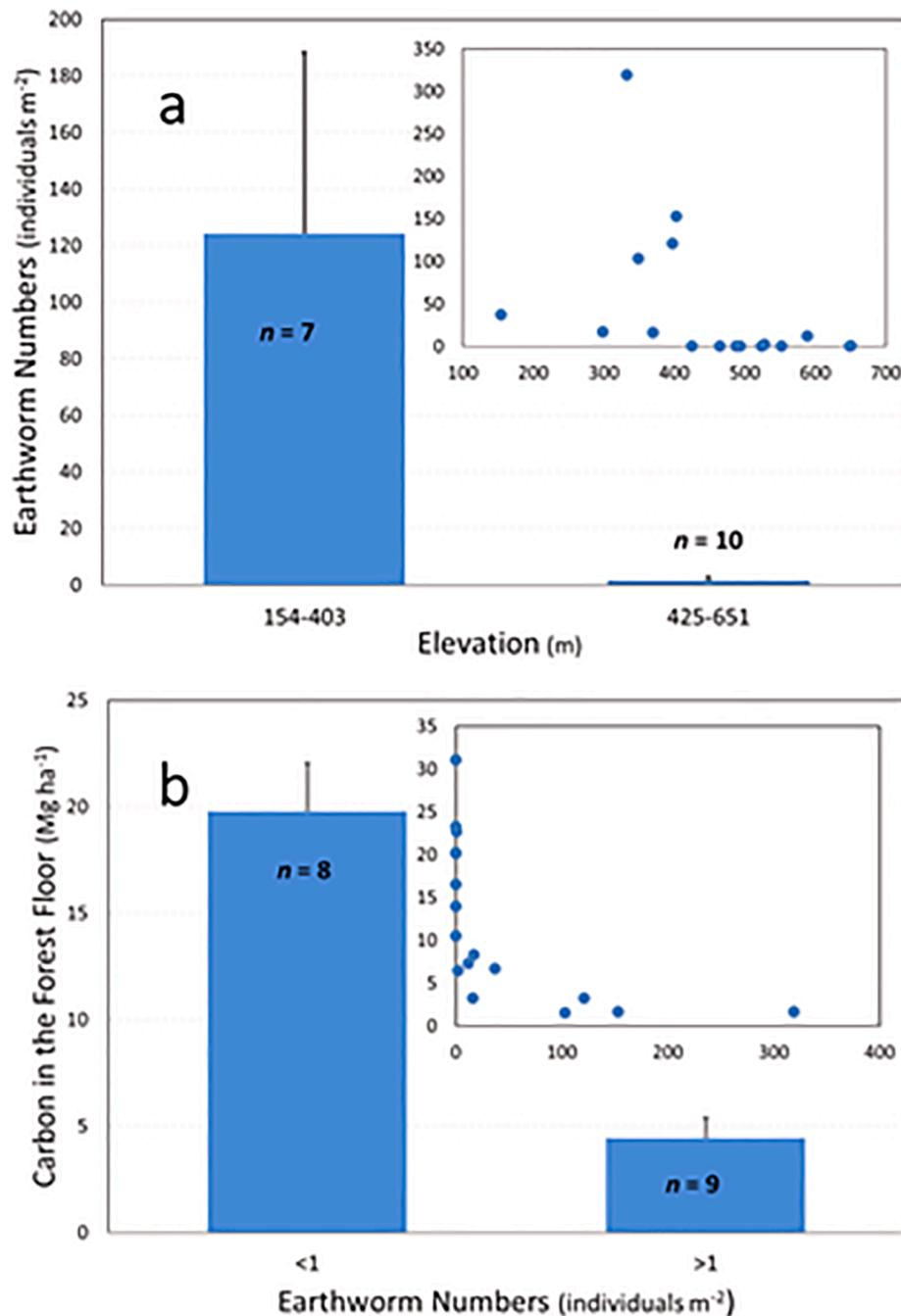


Fig. 6. (a) Earthworm numbers binned by elevation above and below ~400 m. (b) Carbon in the forest floor separated by regression tree analysis into sites with <1 or >1 individual/m². Error bars in both panels represent the standard error of the mean. Inset graphs show the individual points.

Regression tree analysis partitioned the sites to 12 with a total profile exchangeable Al pool being < or ≥ 1310 cmol_c/m² with mean SOC of 103.1 and 147.4 Mg/ha respectively. Earthworm density did not explain differences in mineral or total profile SOC; sites with earthworm densities <1 individual/m² had a mean mineral SOC of 143 Mg/ha while sites with higher earthworm densities had a mean of 139 Mg/ha. The site with the highest profile SOC (and highest live-tree carbon), MBR, had an earthworm density of 121 individuals/m², which was the third highest in our study. As mentioned in the methods section 2.6, there were insufficient candidate variables to model the mineral soil carbon using the multivariate approach, PLS, employed for the forest floor.

4. Discussion

The current forest in Vermont is predominately northern hardwood and this was reflected in the species composition of most of our plots. However, the pre-colonial forest had a much higher proportion of American beech and lower proportion of maple species (Cogbill et al., 2002). The strong present-day sugar maple component (>40% of the basal area at half our sites) is a likely result of both better regeneration and selection of this valued species. The stock of C in standing live trees varies both because of harvest history and site quality. The lowest live tree C was at GRO, the one site under continuous woodland management and, probably not coincidentally, the site with the overall wettest soils (Humaquepts along with Haplorthods, Table S2) and low total SOC from shallowness. Because of the shallow, wet and bouldery soils, this area

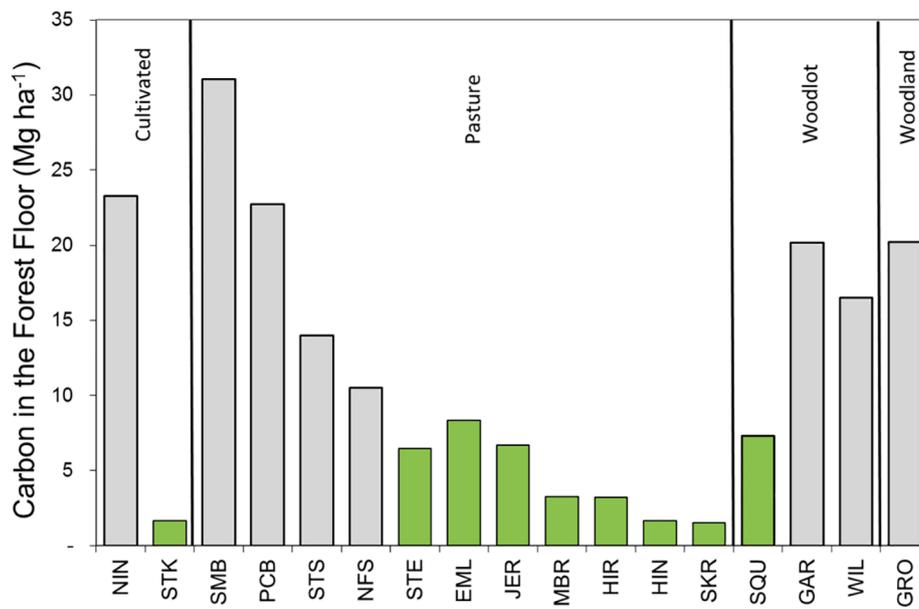


Fig. 7. Organic carbon pools in the forest floor sorted by land use history (see Table 4). Sites with light bars had low earthworm densities (<1 individual/m²).

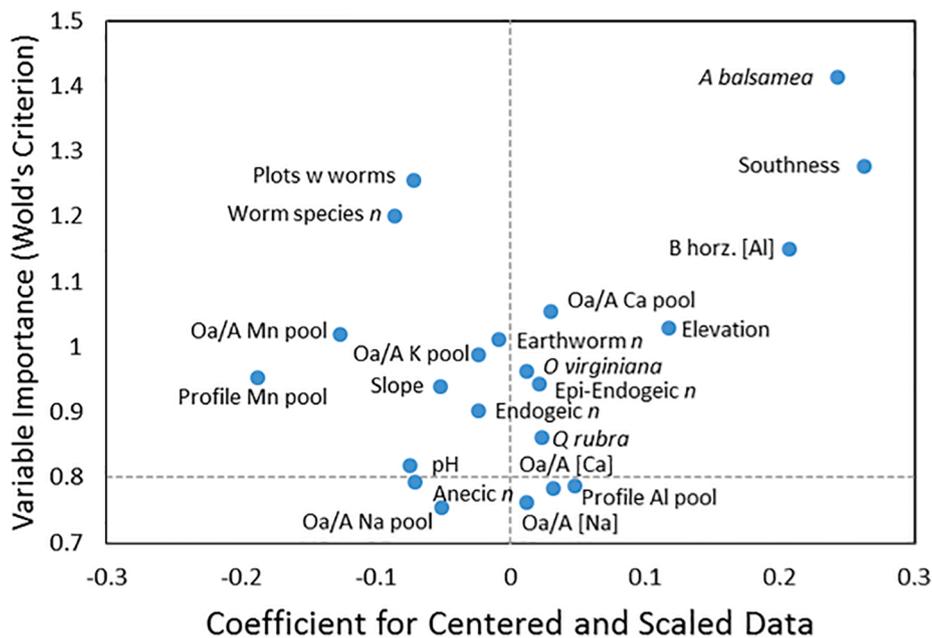


Fig. 8. Partial least squares analysis of carbon in the forest floor showing the relative variable importance (y axis, >0.8 is considered important) and the normalized coefficient for each variable's contribution to the prediction of forest floor carbon (x axis).

would not have easily been converted to agriculture. The site with the highest live tree C, MBR, had an exceptionally thick B horizon and the highest total SOC of all of our sites. Our plot was just south of MBR's reference stand 30, which was established in 1900 through natural regeneration (Urbano and Keeton, 2017) and was likely the site with the oldest trees in our study. Even with these two sites 'book-ending' the high and low live-tree C and SOC, there was not a significant correlation between these two C pools. Jevon et al. (2019) found aboveground C to be the best predictor of SOC in two actively managed forest areas of nearby New Hampshire but the variability in our site histories may have masked the potential relationship in our study. The average total profile SOC at our sites was 147.0 Mg/ha with a wide range (Table 2), which compares well to the 156.1 Mg/ha average for Vermont soils derived from FIA data (Domke et al., 2017). Clark and Johnson (2011) found a

mean of ~110 Mg/ha SOC, normalized to a depth of 55 cm, for soils in western New England (including southwestern Vermont) that had been reforested for >90 yrs. Hooker and Compton (2003) measured ~130 Mg/ha in 115-yr reforested soils in southern New England under *Pinus strobus* (to a depth of 70 cm). Sampling to a depth of 1 m, Richardson and Stolt (2013), also in southern New England, found a mean SOC of 152 Mg/ha in reforested soils under a variety of tree species. The latter study was more comparable to ours in sampling depth and tree species, and the SOC means are close.

Our hypothesis that greater earthworm abundance would be associated with less carbon in the forest floor appears, not surprisingly, to be valid. The supposition that earthworm numbers would be higher at sites with more intensive agricultural land-use history, e.g. tillage, was not clearly supported by our results. Most of our sites, and most of

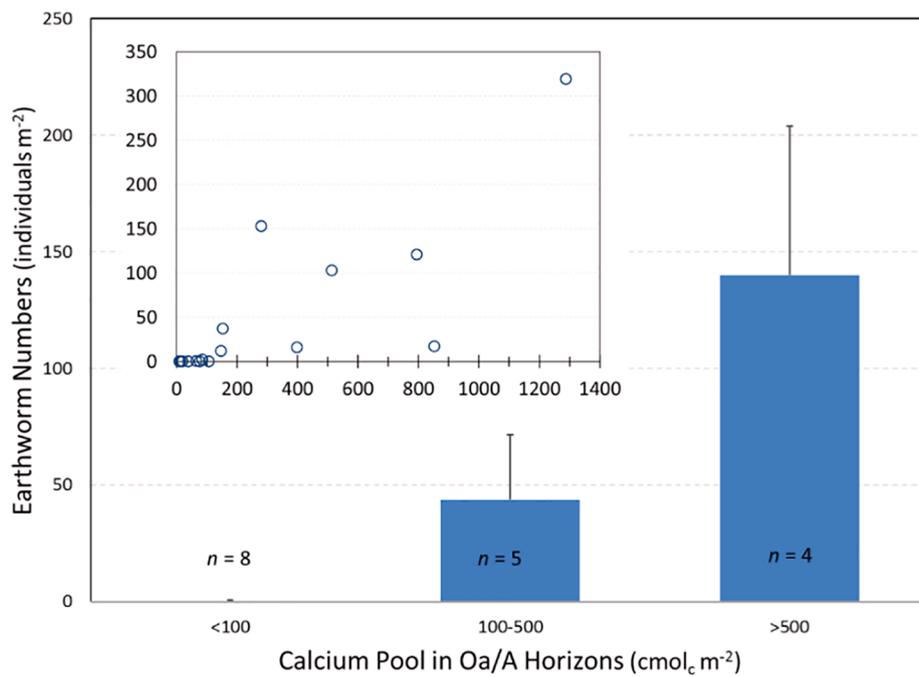


Fig. 9. Earthworm numbers in three different ranges of exchangeable Ca pools in the Oa/A horizon. Error bars represent the standard error of the mean. Inset graph provides the individual points.

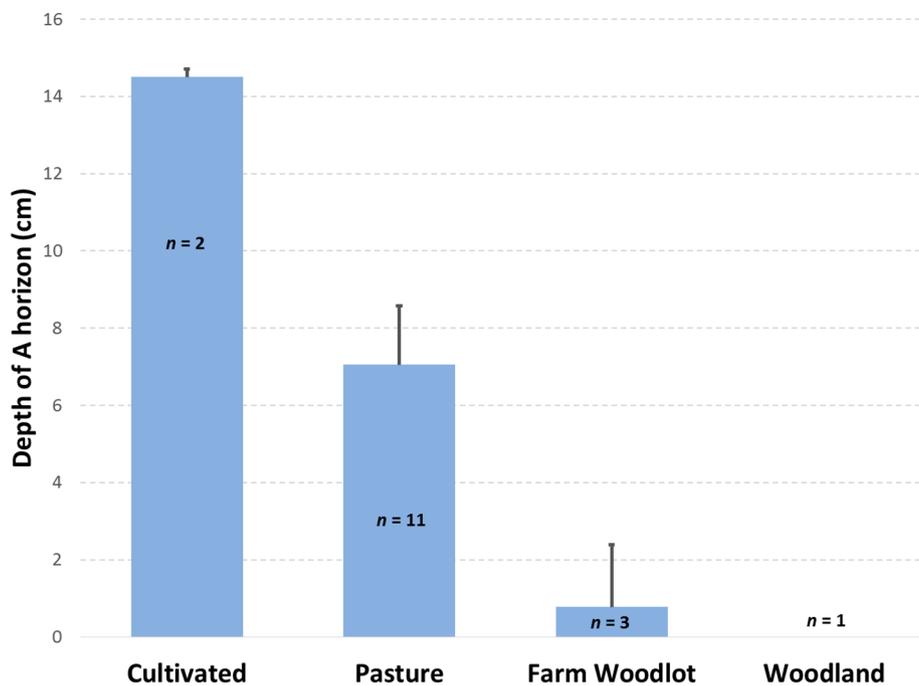


Fig. 10. The average depth of the A horizon in four different past land uses (see Table 4). The pasture bar combines the one back pasture with improved pasture. Error bars represent the standard error of the mean.

Vermont’s formerly cleared land, were in pasture, with only two having a history of tillage as evidenced by the presence of an Ap horizon. As discussed further below, these two sites, NIN and STK, had clear differences in earthworm numbers and forest floor depth that appear to be related to differences in soil chemistry and tree species.

4.1. Tree species, earthworm, site and soil chemistry interactions

A number of studies have shown tree species effects on SOC accumulation patterns. Conifers are generally assumed to promote faster and greater forest floor accumulation than broadleaf deciduous trees and recent work has confirmed this after land-use change (afforestation) in Europe (Poeplau and Don, 2013; Barcena et al., 2014) and also in New

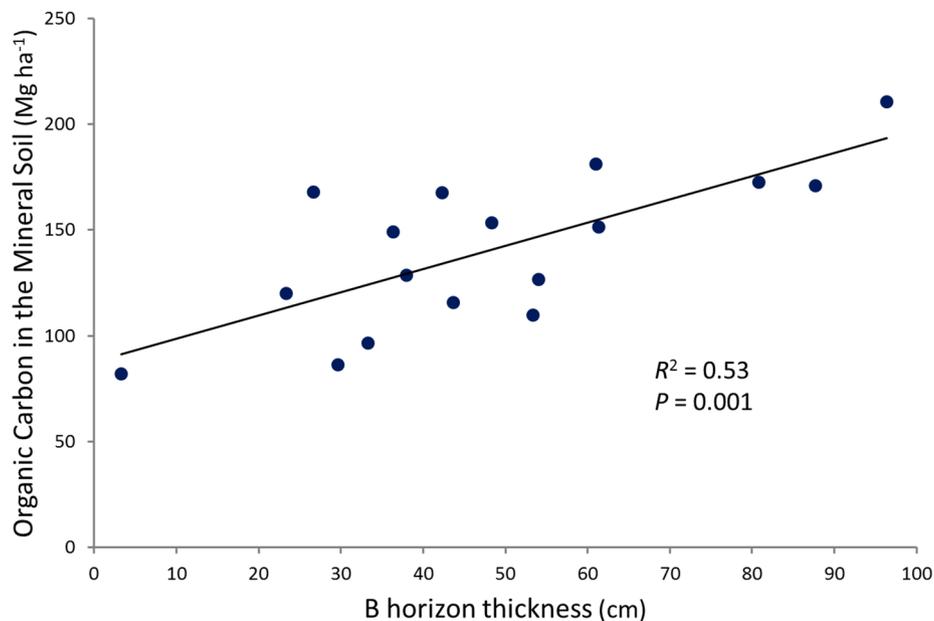


Fig. 11. Organic carbon in the mineral soil as a function of B horizon thickness.

England (Compton and Boone, 2000). In our study, the highest forest floor SOC was found in a spruce-fir site but two of the five highest-SOC forest floors were sites with >50% basal area from sugar maple, no conifers and <1 earthworm/m² (PCB and GAR). One of these sites (GAR) was a farm woodlot and may not have lost the forest floor during that period of land use. The litter from sugar maple is generally assumed to be rapidly decomposed and not conducive to SOC accumulation (Lovett et al., 2004). However, common garden experiments have shown an interaction among earthworms, tree species, pH and Ca (Reich et al., 2005; Mueller et al., 2015) and the effect of tree species on SOC may be strongly influenced by earthworm numbers (Vesterdal et al., 2013). The eight sites with the highest forest floor SOC, regardless of current dominant tree species (spruce-fir vs. sugar maple) or prior land-use (cultivated, pasture or woodlot), all had low earthworm presence (Fig. 6b), with seven of the eight having none. In a common garden experiment of 14 different species, Reich et al. (2005) showed that different species' litter varied in Ca concentration and created large differences in pH and fertility in the surface soil. This Ca-rich litter increased native earthworm abundance and diversity. At the same common garden, Mueller et al. (2015) found that earthworm abundance was strongly negatively correlated with SOC in the forest floor and upper 20 cm of the mineral soil (the SOC was positively correlated with Al, Fe and proton concentration). The effect on the total profile SOC pool was minimal but there was a strong effect on the vertical distribution. Sugar maple can have an effect on soil pH and Ca status (Finzi et al., 1998) but our two sites with both high sugar maple basal area and high forest floor SOC (GAR and PCB) both had relatively low Ca pools in the Oa/A horizons (65 and 9.4 cmol_c/m² respectively, Table 3). The relatively low soil pH (4.0 and 4.6 in the top mineral soil layer in GAR and PCB respectively, Table 3) could have contributed to the low earthworm numbers at these two sites, which in turn resulted in forest floor SOC accumulation. Drouin et al. (2016) found a weak but significant relationship between pH (range from 4.1 to 6.4) and earthworm presence in 40 sugar maple stands in southern Québec. In acid forest soils, especially Oa horizons, the pH is not necessarily well correlated with the 'base' cation content, which is dominated by Ca (Ross et al., 2008). Thus Ca, which many species of earthworms utilize in the secretion of CaCO₃ (Lambkin et al., 2011), may be a better predictor of earthworm numbers than pH. This suggests that soil chemistry could have a stronger influence on earthworm numbers than tree species, although other evidence

discussed below may not support this.

4.2. Interactions in the forest floor

The interaction of SOC distribution with tree species and soil chemistry, through effects on earthworms, may be evident in the two formerly cultivated sites, NIN and STK. With a relatively thick forest floor, NIN was dominated by balsam fir and red maple, had a low Ca pool (20 cmol_c/m² in the Oa/A horizons), low pH (3.9) and no earthworms. The site with the highest earthworm density (319/m²), STK, had a mix of hardwoods, a thin forest floor, the highest exchangeable Ca pool in the Oa/A (1288 cmol_c/m²) and a pH of 5.2. The high Ca and pH may reflect added fertility amendments while this site was cultivated. The conifer site, NIN, had the lowest full profile exchangeable Ca pool (58 cmol_c/m²) and the combination of base-poor soils and conifers likely created an unsuitable earthworm habitat. Further evidence for the importance of conifer species was shown in the PLS analysis of forest floor carbon. *Abies balsamea* had highest 'importance' value for the model and the second highest positive normalized coefficient, i.e. a higher basal area predicts greater forest floor carbon (Fig. 8). The five sites with *A. balsamea*, ranging from 16 to 54% of live tree basal area, had zero earthworms. If *P. rubens* is added (but not the other conifer *T. canadensis*), six sites with spruce/fir basal areas of 16–66% had zero earthworms. A recent continental-scale study in Europe found that the proportion of evergreen leaf litter was negatively related to both earthworm biomass and species richness (De Wandeler et al., 2018). Our results, although with a limited number of sites, also support a negative effect of two evergreen species on earthworm abundance, and a positive effect on forest floor carbon.

The multivariate analysis (Fig. 8) also found two site factors with an influence on forest floor carbon—southern exposure (southness) and elevation. Sites with more southern exposure had lower carbon in the forest floor and the most likely explanation would be higher temperatures promoting faster decomposition. The effect of elevation on greater forest floor carbon was also clear in simple linear regression (Fig. 5) and an elevation effect on fewer earthworms was clear in Fig. 6a. Other factors associated with higher elevation, such as fewer roads and less human access (Cameron and Bayne, 2009), may have limited earthworm introductions and activity or perhaps earthworms were only recent invaders at these sites. There was also an interaction of tree species with

elevation because the seven lowest-elevation sites had no spruce/fir component, although many of the higher elevation sites also were all broadleaf.

Two soil chemistry factors, exchangeable Al^{3+} and Mn^{2+} , had relatively strong influence in the PLS model. The concentration of exchangeable Al^{3+} in the uppermost B horizon was the third strongest positive factor on forest floor carbon (Fig. 8). This could relate to an inhibition of earthworm activity due to either Al toxicity, low pH or low Ca (see the inverse relationship between exchangeable Al^{3+} and Ca^{2+} in Fig. S2). It could also suggest a greater availability of Al for complexing and stabilizing SOC. In a common garden experiment in Denmark, Schelfhout et al. (2017) found that six tree species induced differences in exchangeable Al^{3+} that helped explain differences in earthworm abundance. While Al^{3+} had a negative effect that varied in strength among the different earthworm ecotypes, the Ca-richness of the litter layer had an interacting positive effect. In our study, the exchangeable Mn^{2+} pool in both the Oa/A horizon and the full profile had the highest negative coefficients and relatively high importance values (Fig. 8). This could be related to a little-known (and perhaps not well tested) hypothesis that the presence of Mn can stimulate SOC decomposition, resulting in A horizon formation instead of an Oa (Bartlett, 1990). Manganese oxides have long been known to promote oxidation of organic compounds (e.g. McBride, 1987) and higher exchangeable Mn^{2+} would suggest higher Mn oxide activity. This is clearly speculative but worthy of further investigation. The most important PLS model variables with a negative effect on forest floor carbon were, as expected, earthworm metrics—the fraction of plots at each sites that had earthworms and the total number of species at each site (Fig. 8).

4.3. Interactions in the mineral soil and full soil profile

While it is not surprising that there was greater soil profile C with greater soil depth, the positive relationship (Fig. 10) between the thickness of the B horizons and the C pool in the mineral soil (including the A horizon) might not be expected. Many of the sites in this study had unusually thick spodic (Bs or Bhs) or weakly spodic Bw horizons that had accumulated C through pedogenesis. The contribution of these thick B horizons (Fig. 2) to profile C was much greater than the thinner higher-C A horizons and the variable low-carbon C horizons. The potential influence of exchangeable Al in retaining greater C, shown by the regression tree analysis, is consistent with podzolization processes (accumulation of amorphous organometallic complexes in the B horizon) and with other studies on factors controlling C stabilization (Mueller et al., 2015).

There was no apparent relationship between any earthworm metric and the C pool in the mineral soil or full profile. This may simply be due to a lack of a sufficient number of sites to show statistical differences but it does contrast with the clear effect of earthworms on the forest floor. The forest floor made up a relatively small portion of the full profile C (median of 6.0%) and low C in the forest floor did not necessarily correspond with high C in the mineral soil. While earthworms certainly can alter the depth of the forest floor (Bohlen et al., 2004; Hale et al., 2005), it is not known whether they might have an effect on the depth of the B horizons—the best predictor of mineral soil C stocks in our study. Zhang et al. (2013) proposed an earthworm-mediated ‘carbon trap’ in which their effect on stabilization outweighed their effect on mineralization of soil C. The meta-analysis of Ferlian et al. (2020) found that earthworms had a strong significant negative effect on C stocks in the organic soil layer and a small significant positive effect in the mineral soil. Carbon translocated downward through earthworm activity may comprise a more stable C pool and offset the negative effect on shallow C.

4.4. Implications for management

Forest regrowth has the potential to offset an appreciable amount of anthropogenic CO_2 emissions, especially in mid- to high-latitudes where forest ages are relatively young (Pugh et al., 2019). In reforestation after clear cutting, aboveground C gains may be partially offset by belowground losses (Diochon et al., 2009; Petrenko and Friedland, 2015; Hamburg et al., 2019). The effect of less intensive forest harvesting practices commonly used in Vermont, e.g. shelterwood and single tree selection cuts, on belowground C stores has not been thoroughly studied but appears to be less dramatic (e.g. Jevon et al., 2019). Where forest carbon management is a priority, harvesting techniques that reduce forest floor disturbance and avoid mineral soil scarification would minimize SOC loss and/or improve recovery time. Our sites are all in managed forests and at least four have undergone harvesting activity since we sampled. Resampling of the forest floor at these sites (data not shown) has found decreased forest floor depths but no decreases in carbon pools. Future resampling should help elucidate the effects of forest management on SOC changes over time.

Two other factors, possibly related, will affect forest SOC accumulation over time—continued climate change and possible invasion by new exotic earthworm species (or increases in populations already present). Predicting the effect of warmer temperatures on SOC is confounded by likely changes in seasonality, snow cover, aboveground/belowground allocation of fixed C, etc. (Rustad et al., 2012). Warmer winters can initially lead to colder soils from loss of snowpack (Groffman et al., 2001; Brown and DeGaetano, 2011), which will affect carbon cycling in the absence of earthworms and also have an effect on invasive earthworm distribution activity. Also largely unknown is the invasion potential of *Amyntas* earthworm species originating from Asia (Chang et al., 2016). The European species have likely been present in Vermont since colonial settlement in the 1700s and may have spread to their most suitable habitat, i.e. soils relatively high in Ca. The habitat limitations of the *Amyntas* species are not well known and they appear to be more aggressive invaders than the other species. Further dramatic changes to forest soil SOC distribution may be occurring in the future, although the long-term effect may still be greater SOC stabilization in the mineral soil.

Our study supports the findings of others that coniferous species, specifically *A. balsamea* and *P. rubens* foster greater carbon pools in the forest floor and inhibit earthworms. Where current forest types are maintained as hardwood sites through selective harvesting, but are more conducive to spruce/fir natural communities, shifting species composition to a more coniferous forest type during management may lead to fairly rapid increases in near-surface carbon storage. Recent downward elevational shifts in the spruce/fir ecotone in the northeast USA (Foster and D’Amato, 2015), along with increased growth rate of *P. rubens* (Kosiba et al., 2018) suggests that this is a potential strategy for at least this region. Low impact forest harvesting techniques will clearly be needed to preserve any increases in carbon pools.

Further research is clearly needed on the long-term effect of earthworm species on carbon accumulation and persistence in the mineral soil. Our research did not show any negative effects of earthworm on full-profile carbon storage and it is possible, as suggested by Zhang et al. (2013), that earthworm activity can have an overall long-term positive effect on soil carbon stabilization.

5. Conclusions

The major drivers of SOC were past land use, earthworms, and correlated higher elevation/coniferous environment. Past land use has created diversity in above and below ground forest characteristics across our New England landscape. Understanding interactions between soil nutrients, SOC, and earthworm activity can be crucial in predicting

future forest dynamics, especially where management strategies focus on carbon sequestration and storage. Our eighteen study sites showed that the amount of SOC on the forest floor was lower on lower elevation plots and where earthworms were present. There was also a positive correlation between earthworm abundance and Ca levels in the Oa/A horizons. The presence of coniferous species, specifically *A. balsamea*, was associated with a lack of earthworms. Earthworm distribution can be spotty but predictable by the factors discussed above. Past land use influenced the thickness of the A horizon, and its contribution to the entire profile C pool. Future sampling at these sites following forest management will provide more chronological information on relationships between land use, soil carbon, and earthworms.

CRedit authorship contribution statement

Donald S. Ross: Conceptualization, Methodology, Validation, Investigation, Writing - original draft, Visualization, Supervision, Project administration, Funding acquisition. **Meghan E. Knowles:** Conceptualization, Methodology, Validation, Investigation. **Juliette I. Juillerat:** Conceptualization, Methodology, Validation, Investigation. **Josef H. Görres:** Conceptualization, Methodology, Validation, Investigation, Writing - review & editing, Supervision, Funding acquisition. **Charles V. Cogbill:** Conceptualization, Methodology, Validation, Investigation, Writing - review & editing, Funding acquisition. **Sandy Wilmot:** Conceptualization, Methodology, Validation, Investigation, Writing - review & editing, Supervision, Funding acquisition. **Kristen D'Agati:** Investigation.

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 data

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References

Bárcena, T.G., Kiær, L.P., Vesterdal, L., Stefánsdóttir, H.M., Gundersen, P., Sigurdsson, B. D., 2014. Soil carbon stock change following afforestation in Northern Europe: a meta-analysis. *Glob Chang. Biol.* 20 (8), 2393–2405. <https://doi.org/10.1111/gcb.2014.20.issue-810.1111/gcb.12576>.

Bartlett, R.J., 1990. An A or an E: Which will it be? p. 7–18. In: Kimble, J.M., Yeck, R.D. (Eds.), *Proc. 5th Int. Soil Correlation Meeting (VISCCOM). Characterization, Classification, and Utilization of Spodosols*, Oct. 1–14, 1987. USDA Soil Conserv. Serv., Lincoln, NE.

Bernard, M.J., Neatrou, M.A., McCay, T.S., 2009. Influence of soil buffering capacity on earthworm growth, survival, and community composition in the western Adirondacks and central New York. *Northeastern Naturalist* 16 (2), 269–284.

Bohlen, P.J., Pelletier, D.M., Groffman, P.M., Fahey, T.J., Fisk, M.C., 2004. Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests. *Ecosystems* 7 (1), 13–27.

Boulesteix, A.L., Strimmer, K., 2007. Partial least squares: a versatile tool for the analysis of high-dimensional genomic data. *Briefings Bioinf.* 8, 32–44. <https://doi.org/10.1093/bib/bbl016>.

Bossio, D.A., Cook-Patton, S.C., Ellis, P.W., Fargione, J., Sanderman, J., Smith, P., Wood, S., Zomer, R.J., von Unger, M., Emmer, I.M., Griscom, B.W., 2020. The role of soil carbon in natural climate solutions. *Nat. Sustainability* 3 (5), 391–398. <https://doi.org/10.1038/s41893-020-0491-z>.

Brown, P.J., DeGaetano, A.T., 2011. A paradox of cooling winter soil surface temperatures in a warming northeastern United States. *Agric. For. Meteorol.* 151 (7), 947–956.

Cameron, E.K., Bayne, E.M., 2009. Road age and its importance in earthworm invasion of northern boreal forests. *J. Appl. Ecol.* 46 (1), 28–36.

Chang, C.H., Snyder, B.A., Szlavecz, K., 2016. Asian pheretimid earthworms in North America north of Mexico: an illustrated key to the genera *Amyntas*. *Zootaxa* 4179, 495–529.

Clark, J.D., Johnson, A.H., 2011. Carbon nitrogen accumulation in post-agricultural forest soils of Western New England. *Soil Sci. Soc. Am. J.* 75 (4), 1530–1542. <https://doi.org/10.2136/sssaj2010.0180>.

Cogbill, C.V., Burk, J., Motzkin, G., 2002. The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys. *J. Biogeogr.* 29 (10–11), 1279–1304. <https://doi.org/10.1046/j.1365-2699.2002.00757.x>.

Compton, J.E., Boone, R.D., 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecol.* 81, 2314–2330. [https://doi.org/10.1890/0012-9658\(2000\)081\[2314:ltioao\]2.0.co;2](https://doi.org/10.1890/0012-9658(2000)081[2314:ltioao]2.0.co;2).

De Wandeler, H., Bruelheide, H., Dawud, S.M., Dănilă, G., Domisch, T., Finér, L., Hermy, M., Jaroszewicz, B., Joly, F.-X., Müller, S., Ratcliffe, S., Raulund-Rasmussen, K., Rota, E., Van Meerbeek, K., Vesterdal, L., Muys, B., 2018. Tree identity rather than tree diversity drives earthworm communities in European forests. *Pedobiologia* 67, 16–25. <https://doi.org/10.1016/j.pedobi.2018.01.003>.

De Wandeler, H., Sousa-Silva, R., Ampoorter, E., Bruelheide, H., Carnol, M., Dawud, S. M., Dănilă, G., Finér, L., Hättenschwiler, S., Hermy, M., Jaroszewicz, B., Joly, F.-X., Müller, S., Pollastrini, M., Ratcliffe, S., Raulund-Rasmussen, K., Selvi, F., Valladares, F., Van Meerbeek, K., Verheyen, K., Vesterdal, L., Muys, B., 2016. Drivers of earthworm incidence and abundance across European forests. *Soil Biol. Biochem.* 99, 167–178. <https://doi.org/10.1016/j.soilbio.2016.05.003>.

Diochon, A., Kellman, L., Beltrami, H., 2009. Looking deeper: An investigation of soil carbon losses following harvesting from a managed northeastern red spruce (*Picea rubens* Sarg.) forest chronosequence. *For. Ecol. Manage.* 257 (2), 413–420.

Domke, G.M., Perry, C.H., Walters, B.F., Nave, L.E., Woodall, C.W., Swanson, C.W., 2017. Toward inventory-based estimates of soil organic carbon in forests of the United States. *Ecol. Appl.* 27 (4), 1223–1235. <https://doi.org/10.1002/eap.1516>.

Drouin, M., Bradley, R., Lapointe, L., 2016. Linkage between exotic earthworms, understory vegetation and soil properties in sugar maple forests. *For. Ecol. Manage.* 364, 113–121. <https://doi.org/10.1016/j.foreco.2016.01.010>.

Fahey, T.J., Yavitt, J.B., Sherman, R.E., Maerz, J.C., Groffman, P.M., Fisk, M.C., Bohlen, P.J., 2013. Earthworms, litter and soil carbon in a northern hardwood forest. *Biogeochemistry* 114 (1–3), 269–280. <https://doi.org/10.1007/s10533-012-9808-y>.

Ferlian, O., Thakur, M.P., Castañeda González, A., San Emeterio, L.M., Marr, S., Silva Rocha, B., Eisenhauer, N., 2020. Soil chemistry turned upside down: a meta-analysis of invasive earthworm effects on soil chemical properties. *Ecology* 101 (3). <https://doi.org/10.1002/ecy.v101.310.1002/ecy.2936>.

Finzi, A.C., Van Breemen, N., Canham, C.D., 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecol. Appl.* 8 (2), 440–446.

Foster, J.R., D'Amato, A.W., 2015. Montane forest ecotones moved downslope in northeastern USA in spite of warming between 1984 and 2011. *Glob Change Biology* 21 (12), 4497–4507. <https://doi.org/10.1111/gcb.13046>.

Frellich, L.E., Hale, C.M., Scheu, S., Holdsworth, A.R., Heneghan, L., Bohlen, P.J., Reich, P.B., 2006. Earthworm invasion into previously earthworm-free temperate and boreal forests. *Biol. Invasions* 8 (6), 1235–1245. <https://doi.org/10.1007/s10530-006-9019-3>.

Groffman, P.M., Driscoll, C.T., Fahey, T.J., Hardy, J.P., Fitzhugh, R.D., Tierney, G.L., 2001. Colder soils in a warmer world: A snow manipulation study in a northern hardwood forest ecosystem. *Biogeochemistry* 56 (2), 135–150. <https://doi.org/10.1023/A:1013039830323>.

Gee, G.W., Or, D., 2002. Particle size analysis. In: Dane, J.H., Topp, G.C. (Eds.), *Methods of Soil Analysis, Part 4, Physical Methods*. Soil Science Society of America, Madison, WI, pp. 255–293.

Hale, C.M., 2013. Earthworms of the Great Lakes. Kollath+Stensaas, Duluth, MN.

Hale, C.M., Frellich, L.E., Reich, P.B., 2005. Exotic European earthworm invasion dynamics in northern hardwood forests of Minnesota, USA. *Ecol. Appl.* 15 (3), 848–860. <https://doi.org/10.1890/03-5345>.

Hamburg, S.P., 1984. Effects of forest growth on soil nitrogen and organic matter pools following release from subsistence agriculture. In: Stone, E.L. (Ed.), *North American Forest Soils Conference*. University of Tennessee, Knoxville, TN, pp. 145–158.

Hamburg, S.P., Vadeboncoeur, M.A., Johnson, C.E., Sanderman, J., 2019. Losses of mineral soil carbon largely offset biomass accumulation 15 years after whole-tree harvest in a northern hardwood forest. *Biogeochemistry* 144 (1), 1–14. <https://doi.org/10.1007/s10533-019-00568-3>.

- Homan, C., Beier, C., McCay, T., Lawrence, G., 2016. Application of lime (CaCO₃) to promote forest recovery from severe acidification increases potential for earthworm invasion. *For. Ecol. Manage.* 368, 39–44. <https://doi.org/10.1016/j.foreco.2016.03.002>.
- Hooker, T.D., Compton, J.E., 2003. Forest ecosystem carbon and nitrogen accumulation during the first century after agricultural abandonment. *Ecol. Appl.* 13 (2), 299–313.
- Houghton, R.A., Hackler, J.L., 2000. Changes in terrestrial carbon storage in the United States. 1: The roles of agriculture and forestry. *Glob. Ecol. Biogeogr.* 9, 125–144. <https://doi.org/10.1046/j.1365-2699.2000.00166.x>.
- James, S.W., Davidson, S.K., 2012. Molecular phylogeny of earthworms (Annelida: Crassidellata) based on 28S, 18S and 16S gene sequences. *Invertebrate Systematics* 26 (2), 213. <https://doi.org/10.1071/IS11012>.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D. W., Minkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? *Geoderma* 137 (3–4), 253–268.
- Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49, 12–35.
- Jevon, F.V., D'Amato, A.W., Woodall, C.W., Evans, K., Ayres, M.P., Matthes, J.H., 2019. Tree basal area and conifer abundance predict soil carbon stocks and concentrations in an actively managed forest of northern New Hampshire, USA. *For. Ecol. Manage.* 451, 117534. <https://doi.org/10.1016/j.foreco.2019.117534>.
- Knowles, M.E., Ross, D.S., Görres, J.H., 2016. Effect of the endogeic earthworm *Aporrectodea tuberculata* on aggregation and carbon redistribution in uninvaded forest soil columns. *Soil Biol. Biochem.* 100, 192–200. <https://doi.org/10.1016/j.soilbio.2016.06.016>.
- Kosiba, A.M., Schaberg, P.G., Rayback, S.A., Hawley, G.J., 2018. The surprising recovery of red spruce growth shows links to decreased acid deposition and elevated temperature. *Sci. Total Environ.* 637–638, 1480–1491. <https://doi.org/10.1016/j.scitotenv.2018.05.010>.
- Laganière, J., Angers, D.A., Paré, D., 2010. Carbon accumulation in agricultural soils after afforestation: a meta-analysis. *Global Change Biology* 16, 439–453. <http://doi.org/10.1111/j.1365-2486.2009.01930.x>.
- Lambkin, D.C., Gwilliam, K.H., Layton, C., Canti, M.G., Pearce, T.G., Hodson, M.E., 2011. Production and dissolution rates of earthworm-secreted calcium carbonate. *Pedobiologia* 54, S119–S129. <https://doi.org/10.1016/j.pedobi.2011.09.003>.
- Li, D., Niu, S., Luo, Y., 2012. Global patterns of the dynamics of soil carbon and nitrogen stocks following afforestation: a meta-analysis. *New Phytol.* 195, 172–181. <https://doi.org/10.1111/j.1469-8137.2012.04150.x>.
- Lovett, G.M., Weathers, K.C., Arthur, M.A., Schultz, J.C., 2004. Nitrogen cycling in a northern hardwood forest: Do species matter? *Biogeochemistry* 67 (3), 289–308.
- Lyu, M., Noormets, A., Ukonmaanaho, L., Li, Y., Yang, Y., Xie, J., 2021. Stability of soil organic carbon during forest conversion is more sensitive in deep soil than in topsoil in subtropical forests. *Pedobiologia* 84, 150706. <https://doi.org/10.1016/j.pedobi.2020.150706>.
- Ma, Y., Filley, T.R., Johnston, C.T., Crow, S.E., Szlavec, K., McCormick, M.K., 2013. The combined controls of land use legacy and earthworm activity on soil organic matter chemistry and particle association during afforestation. *Org. Geochem.* 58, 56–68. <https://doi.org/10.1016/j.orggeochem.2013.02.010>.
- Mayer, M., Prescott, C.E., Abaker, W.E.A., Augusto, L., Cécillon, L., Ferreira, G.W.D., James, J., Jandl, R., Katzensteiner, K., Laclau, J.-P., Laganière, J., Nouvellon, Y., Paré, D., Stanturf, J.A., Vanguelova, E.I., Vesterdal, L., 2020. Tamm Review: Influence of forest management activities on soil organic carbon stocks: a knowledge synthesis. *For. Ecol. Manage.* 466, 118127. <https://doi.org/10.1016/j.foreco.2020.118127>.
- McBride, M.B., 1987. Adsorption and oxidation of phenolic compounds by iron and manganese oxides. *Soil Sci. Soc. Am. J.* 51, 1466–1472. <http://doi:10.2136/sssaj1987.03615995005100060012x>.
- Moore, J.-D., Ouimet, R., Bohlen, P.J., 2013. Effects of liming on survival and reproduction of two potentially invasive earthworm species in a northern forest. *Soil Biol. Biochem.* 64, 174–180. <https://doi.org/10.1016/j.soilbio.2013.04.013>.
- Mueller, K.E., Hobbie, S.E., Chorover, J., Reich, P.B., Eisenhauer, N., Castellano, M.J., Chadwick, O.A., Dobies, T., Hale, C.M., Jagodzinski, A.M., Kałucka, I., Kieliszewska-Rokicka, B., Modrzyński, J., Rozen, A., Skorupski, M., Sobczyk, Ł., Stasińska, M., Trocha, L.K., Weiner, J., Wierzbicka, A., Oleksyn, J., 2015. Effects of litter traits, soil biota, and soil chemistry on soil carbon stocks at a common garden with 14 tree species. *Biogeochemistry* 123 (3), 313–327. <https://doi.org/10.1007/s10533-015-0083-6>.
- NatureWatch, 2014. WormWatch. Field guide to worms. <http://www.naturewatch.ca/wormwatch/how-to-guide/field-guide-to-earthworms/>.
- Nave, L.E., Domke, G.M., Hofmeister, K.L., Mishra, U., Perry, C.H., Walters, B.F., Swanston, C.W., 2018. Reforestation can sequester two petagrams of carbon in US topsoils in a century. *Proc. Natl. Acad. Sci.* 115 (11), 2776–2781. <https://doi.org/10.1073/pnas.1719685115>.
- Nave, L.E., Swanston, C.W., Mishra, U., Nadelhoffer, K.J., 2013. Afforestation effects on soil carbon storage in the United States: a synthesis. *Soil Sci. Soc. Am. J.* 77 (3), 1035–1047. <https://doi.org/10.2136/sssaj2012.0236>.
- Petrenko, C.L., Friedland, A.J., 2015. Mineral soil carbon pool responses to forest clearing in Northeastern hardwood forests. *GCB Bioenergy* 7 (6), 1283–1293. <https://doi.org/10.1111/gcbb.12221>.
- Pearce, T., 1972. The calcium relations of selected Lumbricidae. *J. Animal Ecol.* 41, 167–188. <https://doi.org/10.2307/3511>.
- Plisko, J.D., Nxele, T.C., 2015. An annotated key separating foreign earthworm species from the indigenous South African taxa (Oligochaeta: Acanthodrilidae, Eudrilidae, Glossoscolecidae, Lumbricidae, Megascolecidae, Microchaetidae, Ocnerodrilidae and Tritogeniidae). *African Invertebrates* 56 (3), 663–708.
- Poeplert, C., Don, A., 2013. Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. *Geoderma* 192, 189–201. <https://doi.org/10.1016/j.geoderma.2012.08.003>.
- Pugh, T.A.M., Lindeskog, M., Smith, B., Poulter, B., Arneeth, A., Haverd, V., Calle, L., 2019. Role of forest regrowth in global carbon sink dynamics. *Proc. Natl. Acad. Sci.* 116 (10), 4382–4387. <https://doi.org/10.1073/pnas.1810512116>.
- Reich, P.B., Oleksyn, J., Modrzyński, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J., Chadwick, O.A., Hale, C.M., Tjoelker, M.G., 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. *Ecol. Lett.* 8, 811–818. <https://doi.org/10.1111/j.1461-0248.2005.00779.x>.
- Richardson, M., Stolt, M., 2013. Measuring soil organic carbon sequestration in aggrading temperate forests. *Soil Sci. Soc. Am. J.* 77 (6), 2164–2172. <https://doi.org/10.2136/sssaj2012.0411>.
- Rolando, V.R., 1992. 200 years of soot and sweat: The history and archeology of Vermont's iron, charcoal, and lime industries. Vermont Archaeological Society, Montpelier, VT.
- Ross, D.S., Bailey, S.W., Briggs, R.D., Curry, J., Fernandez, I.J., Fredriksen, G., Goodale, C.L., Hazlett, P.W., Heine, P.R., Johnson, C.E., Larson, J.T., Lawrence, G.B., Kolka, R.K., Ouimet, R., Paré, D., Richter, D. deB., Schirmer, C.D., Warby, R.A., 2015. Inter-laboratory variation in the chemical analysis of acidic forest soil reference samples from eastern North America. *Ecosphere* 6 (5), art73. <https://doi.org/10.1890/ES14-00209.1>.
- Ross, D.S., Matschonat, G., Skjellberg, U., 2008. Cation exchange in forest soils: the need for a new perspective. *Eur. J. Soil Sci.* 59, 1141–1159. <https://doi.org/10.1111/j.1365-2389.2008.01069.x>.
- Rustad, L., Campbell, J., Dukes, J.S., Huntington, T., Lambert, K.F., Mohan, J., Rodenhouse, N., 2012. Changing climate, changing forests: the impacts of climate change on forests of the northeastern United States and eastern Canada. USDA-Forest Service. General Technical Report NRS-99.
- SAS Institute, 2018. JMP Statistical Discovery Software, version 14. SAS Institute Inc., Cary, North Carolina, USA.
- Schellhout, S., Mertens, J., Verheyen, K., Vesterdal, L., Baeten, L., Muys, B., De Schrijver, A., 2017. Tree species identity shapes earthworm communities. *Forests* 8 (3), 85. <https://doi.org/10.3390/f8030085>.
- Shartell, L.M., Lilleskov, E.A., Storer, A.J., 2013. Predicting exotic earthworm distribution in the northern Great Lakes region. *Biol. Invasions* 15 (8), 1665–1675. <https://doi.org/10.1007/s10530-012-0399-2>.
- Shi, S., Zhang, W., Zhang, P., Yu, Y., Ding, F., 2013. A synthesis of change in deep soil organic carbon stores with afforestation of agricultural soils. *For. Ecol. Manage.* 296, 53–63. <https://doi.org/10.1016/j.foreco.2013.01.026>.
- Soil Survey Staff, 2006. Keys to Soil Taxonomy. USDA-Natural Resources Conservation Service, Washington, DC.
- Soil Survey Staff, 2007. Natural Resources Conservation Service, United States Department of Agriculture, Web Soil Survey. <http://websoilsurvey.nrcs.usda.gov/>.
- Stoscheck, L.M., Sherman, R.E., Suarez, E.R., Fahey, T.J., 2012. Exotic earthworm distributions did not expand over a decade in a hardwood forest in New York State. *Appl. Soil Ecol.* 62, 124–130. <https://doi.org/10.1016/j.apsoil.2012.07.002>.
- Templer, P., Findlay, S., Lovett, G., 2003. Soil microbial biomass and nitrogen transformations among five tree species of the Catskill Mountains, New York, USA. *Soil Biol. Biochem.* 35, 607–613.
- Thompson, E.H., Sorensen, E.R., 2005. Wetland, woodland, wildland. A guide to the natural communities of Vermont. University Press of New England, Hanover, NH.
- Urbano, A.R., Keeton, W.S., 2017. Carbon dynamics and structural development in recovering secondary forests of the northeastern U.S. *For. Ecol. Manage.* 392, 21–35. <https://doi.org/10.1016/j.foreco.2017.02.037>.
- USDA FS, 2005. Forest inventory and analysis national core field guide, Version 3.0. In: United States Department of Agriculture Forest Service (Ed.). Forest Inventory and Analysis Program.
- Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? *For. Ecol. Manage.* 309, 4–18. <https://doi.org/10.1016/j.foreco.2013.01.017>.
- VT Biodiversity Project, 1998. <https://geodata.vermont.gov/datasets/vt-biodiversity-project-representative-landscapes-boundary-lines>.
- Winowiecki, L.A., Vågen, T.-G., Boeckx, P., Dungait, J.A.J., 2017. Landscape-scale assessments of stable carbon isotopes in soil under diverse vegetation classes in East Africa: application of near-infrared spectroscopy. *Plant Soil* 421 (1–2), 259–272. <https://doi.org/10.1007/s11104-017-3418-3>.
- Zhang, W., Hendrix, P.F., Dame, L.E., Burke, R.A., Wu, J., Neher, D.A., Li, J., Shao, Y., Fu, S., 2013. Earthworms facilitate carbon sequestration through unequal amplification of carbon stabilization compared with mineralization. *Nat. Commun.* 4, 2576. <https://doi.org/10.1038/ncomms3576>.