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Temporal and Spatial Dynamics of Soil Carbon Cycling and Its Response to Environmental Change in a Northern Hardwood Forest

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ABSTRACT

The timescales over which soil carbon responds to global change are a major uncertainty in the terrestrial carbon cycle. Radiocarbon measurements on archived soil samples are an important tool for addressing this uncertainty. We present time series (1969–2023) of radiocarbon measurements for litter (Oi/Oe and Oa/A) and mineral (0–10 cm) soils from the Hubbard Brook Experimental Forest, a predominantly hardwood forest in the northeastern USA. To estimate soil carbon cycling rates, we built different autonomous linear compartmental models. We found that soil litter carbon cycles on decadal timescales (Oi/Oe: ~7 years), whereas carbon at the organic-mineral interface (Oa/A), and mineral soil (0–10 cm) carbon cycles on centennial timescales (~104 and 302 years, respectively). At the watershed-level, the soil system appears to be at steady-state, with no observed changes in carbon stocks or cycling rates over the study period, despite increases in precipitation, temperature, and soil pH. However, at the site-level, the Oi/Oe is losing carbon (−15 g C m^{-2} $year^{-1}$ since 1998). The observed decline in carbon stocks can be detected when the Oi and Oe layers are modeled separately. This pattern suggests that the rapidly cycling litter layer at the smaller scale is responding to recent environmental changes. Our results highlight the importance of litter carbon as an "early-warning system" for soil responses to environmental change, as well as the challenges of detecting gradual environmental change across spatial scales in natural forest ecosystems.

1 | Introduction

A key uncertainty in the terrestrial carbon cycle is how and at what timescales soil organic matter will respond to environmental changes (Todd-Brown et al. 2013). This challenge is particularly pronounced in natural ecosystems, where gradual environmental changes—as opposed to abrupt shifts in carbon inputs or land management as in agricultural systems—complicate the detection of changes to the soil carbon cycle. Understanding these temporal responses is essential for

improving model predictions and guiding policy makers on the future role of soils in either mitigating or accelerating climate change (Le Noë et al. 2023).

In addition to temporal uncertainties, detecting changes in soil carbon cycling at different spatial scales is a challenge to our understanding of the terrestrial carbon cycle (Bormann and Likens 1994; Jungkunst et al. 2022; Shi et al. 2024). On one hand, spatial variability is caused by local and regional differences such as topography, soil texture, vegetation type, and (micro)climate, which influence soil carbon accumulation and loss (Nave et al. 2021). On the other hand, ecosystems, including soils, are constantly exposed to disturbances, ranging from minor events that leave the structure and function of the ecosystem largely intact, to catastrophic events that drastically alter conditions, or to gradual changes that may induce delayed ecosystem response. These disturbances occur at different spatial scales—from local events, such as a single tree collapse, to large-scale disturbances, such as a drought or fire that affect entire watersheds or regions. This complex pattern means that parts of an ecosystem may be responding to a small disturbance while the entire ecosystem or watershed may still be at steady state at the time of measurement (Sousa 1984).

Long-term ecological research sites, such as the Hubbard Brook Experimental Forest (HBEF) in the northeastern USA (Likens 2013), are critical for tracking changes in soil carbon cycling over time and across spatial scales. Previous research from the HBEF found that the largest carbon pools were in mineral soil organic matter (43%) and living biomass (41%), with the remainder in litter (15%). Based on the ratio of pool size to input (or output) fluxes, the mineral soil organic matter pool had the slowest carbon turnover rate (82 years), while litter carbon turnover was faster (10 years). Repeated sampling of soil carbon stocks showed no significant changes in the late 1990s, although high spatial variability limited detection of small changes in soil organic matter pools (Fahey et al. 2005). Since the late 1990s, the HBEF has experienced significant environmental changes, including an increase in total precipitation (~100 mm; USDA Forest Service, Northern Research Station 2024b), an increase in temperature (~1.4°C; USDA Forest Service, Northern Research Station 2024a) and an increase in soil pH of 0.6, due to the recovery of the ecosystem from acid deposition (Fuss et al. 2015; Groffman and Martel 2024; Ontman et al. 2023; Figure 1). These observations raise the question: Are these environmental changes sufficient to induce measurable changes in soil carbon cycling in different soil layers and across spatial scales? For example, increases in precipitation and temperature may lead to increased above- and belowground biomass accumulation, resulting in increased organic matter input from litter and roots. However, the same factors could also stimulate microbial activity and decomposition, potentially leading to faster turnover of organic matter (San Román et al. 2024; Shi et al. 2020; Xu et al. 2024). In acidic soils, such as those found at the HBEF, low pH can inhibit microbial activity and decomposition, leading to the accumulation of organic matter. As soil pH increases, microbial activity may increase, leading to faster decomposition of organic matter (Malik et al. 2018).

Radiocarbon time series provide a powerful method to assess changes in soil carbon dynamics. The sharp increase in atmospheric radiocarbon from nuclear weapons testing in the 1950s and 1960s serves as an isotopic marker for tracking carbon turnover in soils, making time series that include most of the so-called "bomb" period particularly valuable (Trumbore 2009). By using ^{14}C measurements made on soils sampled in different years at the same site, it is possible to estimate the rate of new carbon incorporation and its persistence in the soil (Baisden et al. 2013; González-Sosa et al. 2024;

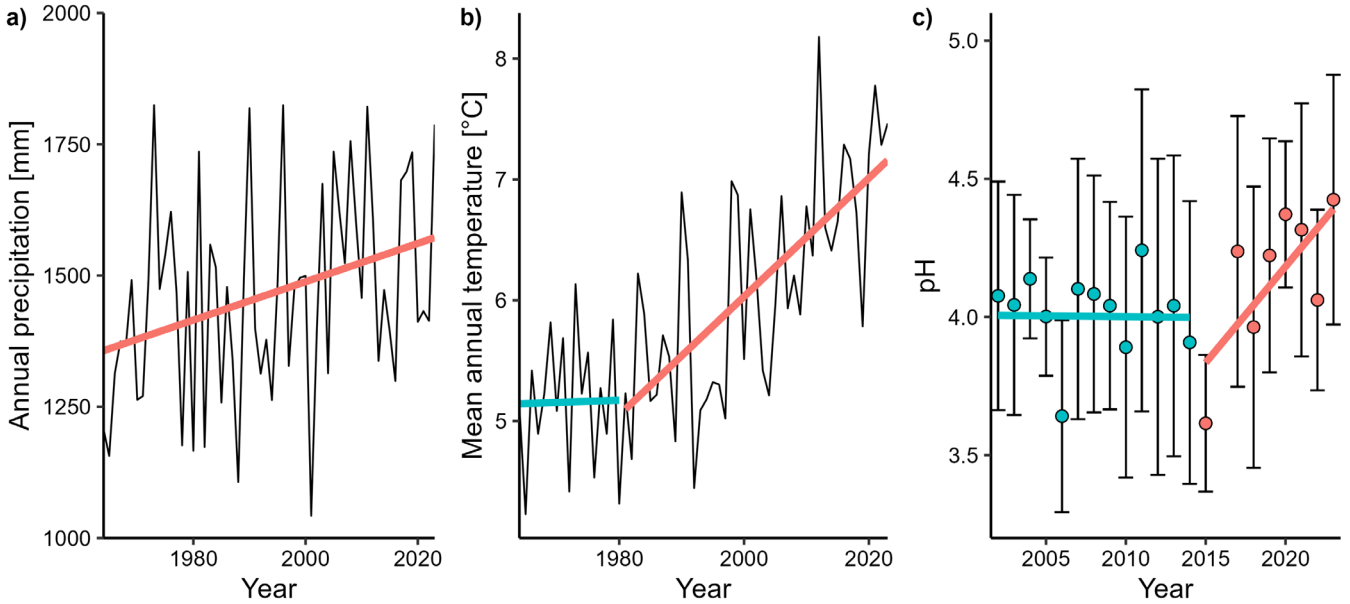

FIGURE 1 | Observed environmental changes at the Hubbard Brook Experimental Forest, including (a) annual precipitation, (b) mean annual temperature, and (c) soil pH (averaged across Oi/Oe, Oa/A, and mineral horizon). Red regression lines indicate significant linear changes, whereas blue regression lines indicate nonsignificant changes. Climate data are from USDA Forest Service, Northern Research Station (2024a, 2024b), and soil pH data are from Groffman and Martel (2024).

Sierra et al. 2012; Spohn et al. 2023; Stoner et al. 2021). However, most of these studies have been conducted on managed soils (agricultural or pasture) or cover relatively short periods, highlighting the need to improve our understanding of soil carbon dynamics in natural forest ecosystems over longer periods.

Previous radiocarbon time series studies have predominantly focused on mineral soils, neglecting the litter layer, which stores approximately 43 Gigatons of carbon in forests worldwide (5% of total C stored in forests; Pan et al. 2011). The few studies that have examined soil carbon cycling rates in the litter layer using radiocarbon have shown that the litter layer usually cycles on decadal timescales, whereas carbon in the upper mineral soil (i.e., A horizon) cycles on centennial timescales (e.g., Gaudinski et al. 2000; Koarashi et al. 2009). Thus, litter carbon is more representative of current atmospheric and biological processes than mineral soil and therefore may be more responsive to changes in atmospheric carbon and environmental conditions. Accounting for the relatively rapid turnover of litter carbon helps to clarify the timescales over which climate change mitigation strategies may affect forest carbon stocks and highlights the need to consider both litter and soil layers when designing and evaluating climate change interventions.

Here, we conducted an analysis of soil carbon dynamics (excluding root dynamics) across spatial scales and for different litter and mineral soil layers. Using two long-term datasets from the HBEF and applying compartmental models to radiocarbon measurements, we aimed to quantify soil carbon ages and turnover rates in a natural forest system. Specifically, our work explored whether there have been changes to carbon cycle dynamics over the past five decades in light of observed environmental changes.

2 | Methods

In this study, we measured carbon content, radiocarbon, and selective dissolution metals (as proxies for organo–mineral interactions) in 164 individual soil samples from the Hubbard Brook Experimental Forest (HBEF). The samples were collected from the litter layer (Oi/Oe), organic-mineral interface (Oa/A), and surface mineral layer (0–10 cm) between 1969 and 2023. We used different compartmental models to best describe the data and to capture differences in soil carbon cycling at different spatial scales over time. We linked our model results to other long-term measurements from the HBEF, including precipitation, temperature, soil pH, and soil respiration.

2.1 | Study Site

The HBEF is located in the White Mountains of New Hampshire, USA (43°56′ N, 71°45′ W) and was established in 1955. It encompasses ~3160 ha of predominantly hardwood forest (Figure S1). The region experiences a humid continental climate with cool summers and cold winters. Annual precipitation between 1964 and 2023 averaged about 1460 mm, with mean air temperatures reaching 18°C in July and decreasing to −8°C in January (USDA Forest Service, Northern Research Station 2024a, 2024b; Figure 1).

Overstory vegetation at the HBEF is dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), with red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) at higher elevation (Schwarz et al. 2003). Much of the region was heavily logged during the late 19th century and the first two decades of the 20th century; most of the modern forest stands date from this period. An exceptional hurricane disturbance in 1938 blew down large forest areas; salvage logging in the aftermath of this event further opened up the remaining forest (Bormann et al. 1970; Holmes and Likens 2016).

Soils are primarily Spodosols (Haplorthods) formed from glacial till, with pH values ranging from 3.4 to 3.8 in the litter layers and from 4.1 to 4.7 in the mineral layers (Johnson et al. 2000). The litter layers, typically 5–9 cm thick, include the organic layers (Oi), a partially decomposed fibrous layer (Oe), and the highly decomposed humic layer at the organic-mineral interface (Oa/A). The mineral soils are shallow, coarse-grained, and predominantly loamy-sand to sandy loam (Johnson et al. 2000).

2.2 | Soil Sampling and Analysis

Soil samples from two different sampling efforts were analyzed, both representing Watershed 6, the biogeochemical reference watershed at the HBEF (Figure S1). Dataset 1 spans from 1969 to 2018 and includes two distinct litter layers (Oi/Oe and Oa) sampled in six different years across Watershed 6. These data comprise litter layer thickness, soil mass, and organic matter content (*measured as part of another project*). In the field, 15 × 15 cm soil blocks of the litter layer were excavated. All samples were oven-dried at 80°C to constant weight. Large solid plant detritus and roots larger than 5 mm, and obviously alive or fresh material were removed from the Oa layer samples. For this study, three archived field replicates were randomly selected for each year sampled ($n = 6$ sampling years × 2 layers × 3 replicates = 36). For the 1969 and 1978 samples, the Oi and Oe layers were sampled and analyzed separately; for subsequent years, the Oi/Oe layers were sampled and analyzed together. Here, the results from the two early sampling years have been C-weighted and combined into a single Oi/Oe value. Organic matter content was converted to soil carbon content using a conversion factor of 0.58 (assuming that roughly 58% of organic matter is composed of carbon; Soil Survey Staff 2022). For more information on the sampling and laboratory analysis of dataset 1, see Johnson (2024).

Dataset 2 ranges from 1998 to 2023 and includes two distinct litter layers (Oi/Oe and Oa/A) and a mineral layer (0–10 cm). The data set is composed of data from nine sampling years, collected from a lower elevation site west of Watershed 6 (*Bear Brook*; Figure S1). In the field, five field replicates were collected each year ($n = 9$ sampling years × 3 layers × 5 replicates = 135). For each replicate, 3–4 soil cores were collected, separated by genetic horizons, merged, and bagged in the field (Groffman and Martel 2024). For this study, all samples

were oven-dried at 60°C to constant weight. Dry samples were passed through a 2 mm sieve; all roots and fresh material were removed. All samples were then finely ground and analyzed for carbon and nitrogen using an elemental analyzer (Carlo Erba NA-1500 analyzer). Based on analytical replicates ($n = 16$), the coefficient of variation was on average 0.51% for carbon (range: 0.04%–2.48%) and 1.34% for nitrogen (range: 0.20%–3.41%). Bulk density for each sample was calculated based on the ovendry weight of total layer mass ($g\,cm^{-2}$) and layer thickness (cm) from Johnson (2024). Since no trend in bulk density was observed over time (*data not shown*), all carbon stocks for each layer were calculated using the mean bulk density value: Oi/Oe = 0.10, Oa/A = 0.25, and mineral = 0.64 $g\,cm^{-3}$, respectively.

Although dataset 1 and dataset 2 both represent Watershed 6, there are notable differences. As described, the samples that were used to create dataset 1 were collected across the entire watershed, which means that the samples cover an area of about 13.2 ha, including gradients in elevation from 549 to 792 m and in slope from 1% to 55%. Northern hardwood forest dominates at lower elevations, with more spruce fir at higher elevations—all of which result in high variability of soil properties within the watershed (Bourgault et al. 2015; Hong et al. 2006; Nezat et al. 2004). In contrast, the samples represented in dataset 2 cover an area of about 30 m^2 at a lower elevation site (~525 m) that is dominated by northern hardwood forest on a gentle slope, resulting in less heterogeneity in soil properties.

To quantify Al and Fe phases of varying crystallinity and their associated organic matter, we performed three common selective dissolution methods: (i) ammonium-oxalate extraction (Al_{ox} and Fe_{ox}), (ii) citrate-dithionite extraction (Al_{dith} and Fe_{dith}), and (iii) sodium-pyrophosphate extraction (Al_{pyr} and Fe_{pyr}). The ammonium-oxalate extraction was adapted from Sparks et al. (1996) and Wagai et al. (2013). In brief, samples were shaken for 4 h and extracted in the dark. This extraction targets amorphous Al and Fe and other noncrystalline phases. The citrate-dithionite and sodium-pyrophosphate extractions were both adapted from Carter and Gregorich (2007); samples were shaken for 16 h for each extraction. Sodium-pyrophosphate is assumed to target organo-metal complexes, whereas citrate-dithionite dissolves crystalline Fe and Al phases. Due to sample availability, selective metal extraction was only performed on samples from dataset 2 (1998–2023) from the Oa/A and mineral (0–10 cm) layers.

Radiocarbon measurements were performed at the Yale Analytical and Stable Isotope Center at Yale University, New Haven, CT, USA, in 2023 (dataset 1) and 2024 (dataset 2) using an IonPlus MIni CArbon DAting System (MICADAS) Accelerator Mass Spectrometer (AMS). Samples were combusted to carbon dioxide (CO_2) in an elemental analyzer (EA). The combusted sample was introduced into the MICADAS via a gas ion source (GIS) system. The gaseous sample was concentrated on a small external trap containing X13 zeolite adsorber material before being transferred to a gastight syringe and subsequently loaded into MICADAS-specific targets (Ruff et al. 2010). Radiocarbon measurements are reported as $\Delta^{14}C$ values, the deviation of the $^{14}C/^{12}C$ ratio in the sample corrected to a common $\delta^{13}C$ of −25‰ from the $^{14}C/^{12}C$ value of oxalic acid decay-corrected to 1950 (Stuiver and Polach 1977). The analytical error for all radiocarbon samples was 6.99‰ ± 1.12‰ (mean ± standard deviation).

2.3 | Mathematical Modeling

To interpret the radiocarbon values and soil carbon stock estimates over time, we built three different autonomous linear compartmental models. The first model included the full dataset (1969–2023) and three pools in series, one for each layer (Oi/Oe, Oa/A, and mineral), with different decomposition rates and transfer rates between the pools (Figure S2). The other two models included only dataset 2 (1998–2023); one had the same pool structure as the first model (three pools in series) and the other had two pools for the Oi/Oe layer instead of one, totaling four pools in series. This model setup was conducted to test if the soil carbon dynamics vary across spatial scales and to separate the litter layer (Oi) from the partially decomposed fibrous layer (Oe), which likely have different carbon cycling rates.

The first model is mathematically defined by three differential equations, each of which describes the temporal changes in C stocks in each pool:

$$\begin{aligned}\frac{dC_{Oi/Oe}}{dt} &= I - k_1 C_{Oi/Oe}\\ \frac{dC_{Oa/A}}{dt} &= \alpha_{21} k_1 C_{Oi/Oe} - k_2 C_{Oa/A}\\ \frac{dC_{min}}{dt} &= \alpha_{32} k_2 C_{Oa/A} - k_3 C_{min},\end{aligned} \tag{1}$$

where I represents carbon inputs from litterfall; $C_{Oi/Oe}$, $C_{Oa/A}$, and C_{min} are the soil carbon stocks in each pool, based on measurements in the same layer; k_1 *to* k_3 are the decomposition rates for each pool, respectively; and α_{21} and α_{32} are the transfer rates from pool 1 (Oi/Oe) to pool 2 (Oa/A) and from pool 2 (Oa/A) to pool 3 (mineral), respectively. The transfer rates correspond to the fluxes between layers. These fluxes include the migration of dissolved organic carbon and the incorporation of highly decomposed organic matter into lower soil layers. Root carbon pools were excluded, as roots were removed prior to sample archiving. For the model constrained with dataset 2 (1998–2023), a fourth pool was added for the Oi/Oe layer while maintaining the same model structure, with all pools connected in series by transfer rates (Figure S2).

We implemented radiocarbon models using the R package *SoilR* (Sierra et al. 2014) and estimated parameters by inverse data assimilation using the R package *FME* (Soetaert and Petzoldt 2010). For all models, we added a lag time of 3 years, which reflects the average time a carbon atom spends in the vegetation before entering the Oi layer at the HBEF (Landis et al. 2024). Parameter optimization involved a two-step process: (i) Levenberg–Marquardt optimization to define priors for parameter values, followed by (ii) Markov Chain Monte Carlo (MCMC) optimization to obtain posterior probability density distribution parameter values.

The cost function incorporated carbon stock and radiocarbon data from all three layers, estimating the best possible values for all k and α values with their respective uncertainties. The models were driven by the atmospheric bomb curve (Hua et al. 2022), which was extended to 2023 using the R package *forecast* (Hyndman and Khandakar 2008). Constant carbon inputs were based on long-term litterfall estimates at the HBEF, which showed no temporal trend (Fahey et al. 2005; Fahey and Cleavitt 2023). Initial parameter values were modified from Fahey et al. (2005) by excluding root carbon inputs for which we do not have data. The optimization procedure minimized errors between model predictions and observed carbon stocks and radiocarbon values, as demonstrated in previous studies (e.g., González-Sosa et al. 2024; Spohn et al. 2023; Stoner et al. 2021).

System age and transit time distributions were calculated using the median values of each parameter from the MCMC procedure and using the method and equations described in Metzler and Sierra (2018). The system age represents the time that carbon atoms have remained in the soil since entering at the time of observation, indicating carbon persistence. Transit time reflects the time between a carbon atom entering and leaving the system, i.e., the age of the particles in the output flux. The definition of transit time in the case for linear autonomous models at steady-state is the same as the turnover time, which conceptually refers to the total carbon stock divided by the total input or output flux in a system (Sierra et al. 2018). Uncertainty in the fitted models was propagated by iteratively drawing parameter sets from the MCMC-derived distributions. These sets were used to run the models, calculating system ages and transit times at each iteration. By recording the values of these variables at each iteration, their distributions were constructed to capture the variability carried over from the parameter populations. System ages and transit times were calculated only for the steady-state model, where carbon inputs equaled carbon outputs.

All analyses were performed in the R computing environment (version 4.4.1; R Core Team 2024). In addition to the R packages mentioned above, we used the R packages "tidyverse" (Wickham et al. 2019), "ggpubr" (Kassambara 2023), and "bayestestR" (Makowski et al. 2019). For full documentation of the data preparation, analyses, including the three different models, we refer to the R code published with this paper (von Fromm, Groffman et al. 2025; von Fromm and Monroe 2025).

3 | Results

The steady-state three-pool model using the full dataset (1969–2023) accurately captures the soil carbon stocks and radiocarbon data at the Hubbard Brook Experimental Forest (HBEF; Figure 2). The modeled median soil carbon stocks without root carbon contributions are 1549 g C m^{-2} for the Oi/Oe, 1860 g C m^{-2} for the Oa/A, and 2282 g C m^{-2} for the mineral layer. Root Mean Squared Errors (RMSE) for radiocarbon are 45‰ (Oi/Oe), 40‰ (Oa/A), and 7‰ (mineral), while RMSE for soil carbon stocks are 415 g C m^{-2} (Oi/Oe), 425 g C m^{-2} (Oa/A), and 168 g C m^{-2} (mineral; Figures S3 and S4 and Table S1). The results suggest that soils at the watershed level have remained at steady-state over the past ~50 years, with no evidence of net carbon sequestration or loss.

Modeled carbon ages range from less than a decade (7.4 ± 0.5 years; mean ± standard deviation) in the Oi/Oe pool

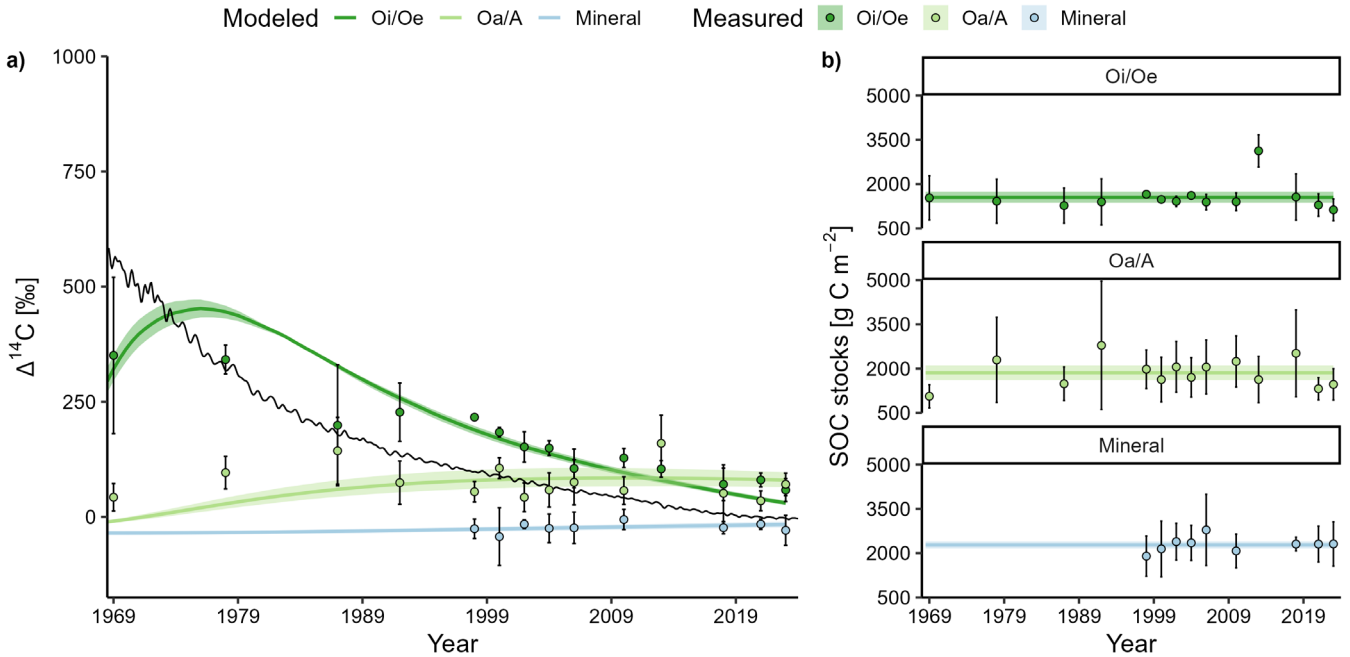

FIGURE 2 | (a) Modeled and measured radiocarbon values ($\Delta^{14}C$ in ‰) and (b) soil organic carbon (SOC) stocks (g C m^{-2}) based on the three-pool model at steady-state using the full dataset (1969–2023) for all three soil layers/pools (Oi/Oe: Dark green, Oa/A: Light green, Mineral: Blue). Circles and error bars for measured values refer to mean plus standard deviation based on field replicates ($n = 3$ for dataset 1 and $n = 5$ for dataset 2). Thick lines refer to the modeled medians and shaded areas to the 95% credible intervals based on the Bayesian Markov Chain Monte Carlo procedure (see 2. Methods).

to centuries in the Oa/A (104 ± 13 years) and mineral pools (302 ± 28 years; Figure 3 and Figure S5). In the Oi/Oe pool, about a quarter of the carbon cycles in less than a year; only 1% of the carbon has an age greater than 33 years. In the Oa/A pool, about 60% of the carbon cycles on decadal timescales, while about 5% of the carbon has an age older than 300 years. In the mineral pool, only 15% of the carbon cycles on decadal timescales, about 84% of the carbon cycles on centennial timescales, and only 1% of the carbon has an age of more than 1000 years.

About 91% (~191 g C m^{-2} $year^{-1}$) of the total carbon litter input is directly respired from the Oi/Oe pool, whereas only 9% (~19 g C m^{-2} $year^{-1}$) is transferred to the Oa/A pool (Figure 4). About 37% (~7 g C m^{-2} $year^{-1}$) of this carbon is respired from the Oa/A pool, while 63% (~12 g C m^{-2} $year^{-1}$) of the carbon is transferred to the mineral pool, from where it eventually leaves the system via respiration or translocation to deeper soil layers that are not part of the model. Since most of the respired carbon comes from the rapidly cycling Oi/Oe pool, the average transit time of the system is about 27 years. The calculated transfer and respiration rates, as well as the decadal transit time, indicate that the carbon stored in the Oi/Oe layer may be most sensitive to changes in environmental conditions and carbon litter inputs.

Soil carbon stocks in the Oi/Oe layer from dataset 2 (1998–2023) show a significant decline of −15 g C m^{-2} $year^{-1}$ since 1998 (Figure 5), but not in the Oa/A and mineral layers. This decline in soil carbon stocks in the Oi/Oe layer coincides with an observed increase in soil CO_2 respiration of +25 g C m^{-2} $year^{-1}$ since 2015 at the same sites based on a different dataset (Figure S6; Groffman and Martel 2023). The quantified Al and Fe phases (Al_{ox}, Fe_{ox}, Al_{dith}, Fe_{dith}, Al_{pyr}, and Fe_{pyr}) show no significant trend over time for the last 25 years in the Oa/A and mineral layers (Figure S7). The extracted amount is always higher in the mineral samples compared to the Oa/A sample, with the difference being greater for Fe than for Al (Figure S8). These findings suggest that only the Oi/Oe layer has experienced changes in soil carbon dynamics over the past 25 years at this site.

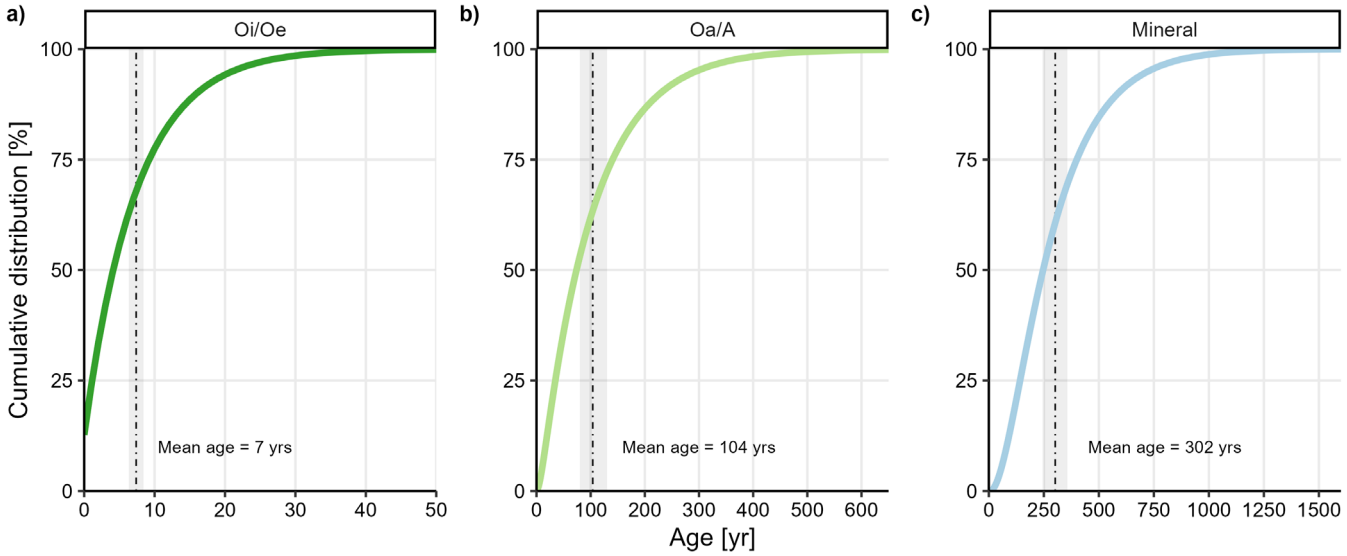

FIGURE 3 | Cumulative soil organic carbon (SOC) pool ages for all three layers/pools: (a) Oi/Oe, (b) Oa/A, and (c) mineral (0–10 cm) based on the three-pool model using the full dataset (1969–2023). Mean SOC ages (black dashed lines) and 95% credible intervals (shaded grey areas) are derived from a subset of accepted model parameters from the Bayesian Markov chain Monte Carlo procedure to calculate the probability distribution of SOC ages for each pool (see 2. Methods).

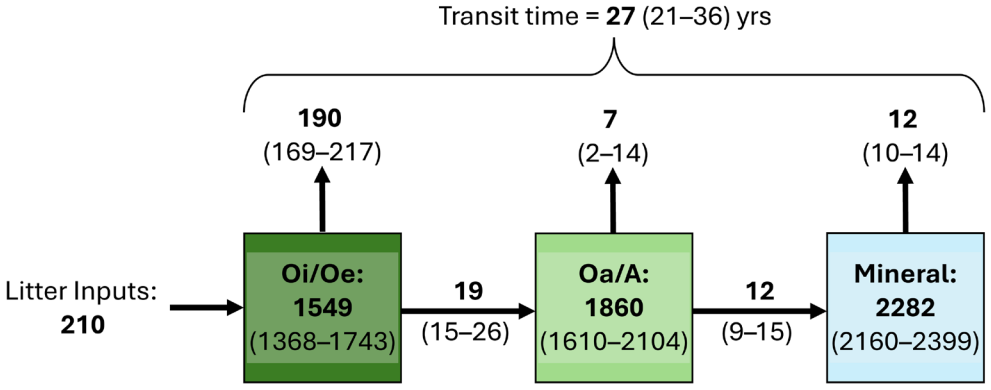

FIGURE 4 | Graphical representation of the steady-state three-pool model using the full dataset (1969–2023; Equation 1). Pool sizes (values inside the boxes) are in g C m^{-2} and fluxes (values next to the arrows) are in g C m^{-2} $year.^{-1}$. Bold values are median values and values in brackets are 95% credible intervals based on the Bayesian Markov Chain Monte Carlo procedure (see 2. Methods).

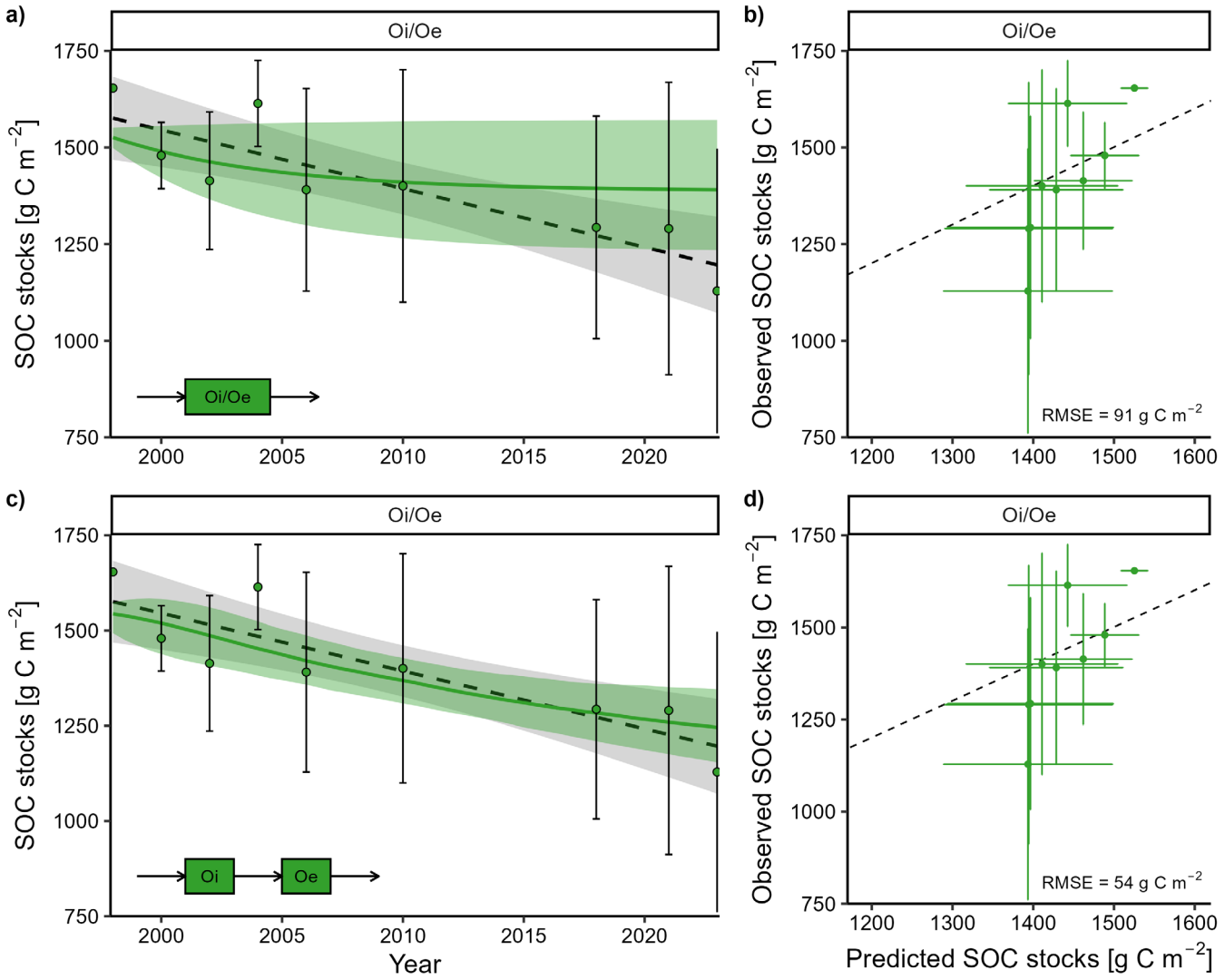

FIGURE 5 | Model results for the Oi/Oe layer using dataset 2 (1998–2023). Panels (a) and (c) show measured mean SOC stocks (green circles) with standard deviation (black error bars) over time and modeled mean values (green line) with 95% credible intervals (green shaded area) for the models with one- and two-pool for the Oi/Oe layer, respectively. The dashed black line and gray shaded area represent the fitted linear regression and standard error for the observed SOC stocks. Panels (b) and (d) show observed versus predicted soil organic carbon (SOC) stocks (g C m^{-2}) for the one- and two-pool models of the Oi/Oe layer, respectively.

The three-pool model, constrained only with dataset 2 (1998–2023), fails to capture the observed decline in soil carbon stocks in the Oi/Oe layer over the past 25 years (Figure 5a,b). This model performs similarly in predicting $\Delta^{14}C$ and soil carbon data compared to the three-pool model using the full dataset (Figures S9–S11 and Table S1). The model also yields similar decomposition rates (k) and transfer rates (α) between the pools, even though it is not at steady state (Table S2). These results suggest that perhaps only a part of the Oi/Oe layer is responding to the environmental changes that have occurred in the forest over the past 25 years.

Interestingly, the model captures the decline in soil carbon stocks in the Oi/Oe layer very well after introducing separate Oi and Oe pools (four pools in total for the entire model; Figure 5c,d). This improved model fit is reflected in a smaller RMSE of 54 g C m^{-2} for the predicted soil carbon stocks in the Oi/Oe pool, while still capturing the radiocarbon data as well as the other two models (Figures S12–S14 and Table S1). The four-pool model shows that most of the carbon in the Oi/Oe layer is stored in the Oe pool (about two-thirds). This observation is in good agreement with the two early sampling years (1969 and 1978), in which the Oi and Oe layers were sampled and analyzed separately for organic matter (see 2. Methods; *data not shown*). Most of the observed carbon loss occurs in the Oe pool (Figure S12). About 21% of the carbon in the Oi pool is transferred to the Oe pool, and 14% of this carbon is transferred to the Oa/A pool (Table S3). The Oa/A pool also shows a trend of decreasing soil carbon stocks over time, which is reflected in the data. However, for both the modeled and observed values, the decline in soil carbon stocks in the Oa/A layer are not significant (Figure S12). About 62% of the carbon in the Oa/A pool is transferred to the mineral layer (Table S3). Overall, the findings from the four-pool model highlight that although the Oi/Oe pool cycles on decadal timescales, subdividing this pool into two provides further information to better understand the observed soil carbon dynamics and their potential response to environmental changes across spatial and temporal scales.

4 | Discussion

At the watershed-level and over the longer period (1969–2023), our model results show that the soil system is at steady-state, neither losing nor gaining carbon (Figure 2). This steady-state finding is consistent with results from Fahey et al. (2005), who reported stable litter and mineral carbon pools at the Hubbard Brook Experimental Forest (HBEF), based on soil carbon stock and flux measurements from about two decades ago. Despite the lack of root carbon inputs in our model, the modeled soil carbon stocks agree well with the measured soil carbon stocks that included root carbon contributions (Fahey et al. 2005). The stability of the soil carbon pools suggests that environmental change at the HBEF, such as increases in temperature, precipitation, and soil pH, may not yet be pronounced enough to disrupt the soil carbon balance at the watershed-level.

The concurrent increases in precipitation, temperature, and soil pH at the HBEF suggest a nuanced and multifaceted set of drivers that have both positive and negative influences on soil carbon dynamics. For example, Rocci et al. (2023) showed that three decades of increased precipitation did not significantly alter surface bulk soil carbon and nitrogen in a grassland ecosystem. Their results corroborated findings from a global meta-analysis that reported no consistent effect of precipitation change on forest SOC content (Xu et al. 2024). In contrast, a 26-year soil warming experiment in a forest approximately 250 km south of the HBEF lost 17% of soil carbon in the top 60 cm (Melillo et al. 2017). Such differences in soil carbon response likely reflect the greater magnitude and abruptness of the experimental warming (+5°C above ambient) compared to the more moderate, gradual temperature increases observed at the HBEF (1.4°C over 35 years). In addition, Melillo et al. (2017) found that soil carbon loss occurred nonlinearly, alternating between periods of rapid carbon loss due to increased microbial activity and intervals of slowed carbon loss, likely due to substrate depletion and microbial community adaptation. The interactions among soil pH, plants, microbial activity, and soil carbon dynamics are even more complex, and the mechanisms by which ecosystems and soils recover from decreases in acid deposition remain unclear (Ontman et al. 2023). Ultimately, our finding of steady-state conditions in soils at the HBEF is consistent with the idea that ecosystems, including soils, are more likely to be in steady-state at larger spatial and temporal scales (Bormann and Likens 1994; Meng et al. 2023; Sundstrom and Allen 2019; Wu and Loucks 1995). This pattern may partly also be due to the high variability of soil carbon across the watershed, which makes it difficult to detect subtle changes (Johnson et al. 1990), as steady-state conditions at the watershed level do not necessarily reflect site-scale dynamics.

In contrast to the stable C pools at the HBEF, soils at Harvard Forest, a comparable long-term study site to the south, have acted as a small carbon sink in recent years, with accumulation rates of 10–30 g C m^{-2} $year^{-1}$ (Finzi et al. 2020). This difference likely reflects the history of Harvard Forest as agricultural land until the late 1800s, with soils still recovering from past disturbances (Finzi et al. 2020)—in contrast to the HBEF, which has never been used for agriculture. In this context, a recent global study found that changes in soil carbon due to land-use change are greater than those due to climate change (Beillouin et al. 2023). However, note that the soil data at Harvard Forest are not conclusive. A radiocarbon study using time series data showed that the soil carbon dynamics at Harvard Forest can also be adequately modeled with a steady-state compartmental model similar to the one used here (Sierra et al. 2012). In summary, these studies and our work highlight the challenges of linking gradual environmental change in natural ecosystems across spatial scales to soil carbon dynamics.

The modeled mean carbon age of 7 years in the Oi/Oe pool agrees well with other estimates that typically show decadal timescales for litter carbon in temperate forests (Gaudinski et al. 2000; Koarashi et al. 2009; Perruchoud et al. 1999). Similarly, the modeled mean carbon ages of about 104 years in the Oa/A pool and of 302 years in the mineral pool are within the range of regional and global estimates for temperate forests (Gaudinski et al. 2000; Shi et al. 2020). The increase in soil carbon ages from the Oa/A to the mineral layer may be attributed to the increase in Al- and Fe-bearing minerals, which are important in forming organo-mineral interactions that protect carbon from decomposition (Hall and Thompson 2022; Masiello et al. 2004; Rasmussen et al. 2018; Torn et al. 1997; von Fromm, Jungkunst et al. 2025; Figures S7 and S8). However, our modeled values may be somewhat biased toward older carbon estimates overall due to the wide distribution of carbon ages in each pool (Figure 3), having only one pool per layer, and the lack of younger root carbon (Sierra et al. 2018).

The young carbon ages for the Oi/Oe layer suggest that litter layers may serve as an "early-warning system" for carbon responses to environmental changes. This conclusion is based on the fact that younger carbon cycles faster on average than older carbon, meaning it is more actively exchanged with the atmosphere and biosphere. As a result, litter carbon is likely to respond more rapidly to changes in environmental conditions (Chen et al. 2024; Gregorich et al. 2017) compared to mineral soil carbon. This conclusion does not necessarily mean that mineral soil carbon will respond in the same way as litter carbon. However, given the larger carbon stocks and slower carbon cycling rates in the mineral soil layer, it is much more difficult to detect subtle short-term changes in this layer. This idea is further supported by the lack of change in the concentration of Al- and Fe-bearing minerals in Oa/A and mineral soil layers over time (Figure S7). Future soil time series studies should emphasize litter carbon dynamics, and not just mineral soil carbon dynamics.

Approximately 90% of the litter carbon input in the model is respired directly from the Oi/Oe pool (Figure 4). This value indicates that despite the large carbon stock of 1549 g C m^{-2}, most of the carbon inputs do not contribute to long-term carbon storage in mineral soils (Kramer et al. 2010). The modeled amount of carbon respired from the litter layer is of the same order of magnitude as heterotrophic respiration estimates for the HBEF and Harvard Forest, although about 30% higher (Fahey et al. 2005; Finzi et al. 2020; Gaudinski et al. 2000). However, other estimates for temperate forests suggest that 50%–94% of foliar litter carbon is respired as CO_2 (Perruchoud et al. 1999). In addition, 25% of the carbon in our modeled Oi/Oe pool cycles in less than 1 year and therefore may not be detected by soil sampling conducted during the growing season (Gaudinski et al. 2000). Furthermore, separating heterotrophic and autotrophic

respiration from different soil layers in field or incubation experiments remains challenging and introduces uncertainties in direct comparisons with modeling results.

The high proportion of respired carbon from the Oi/Oe pool results in a modeled transit time of about 27 years for the entire soil system. This estimate is consistent with previous HBEF estimates of about 37 years (based on carbon stock/flux ratios), with 63% of the respired carbon coming from the litter layer (~10-year turnover time) and the remainder from the mineral layer (~82-year turnover; Fahey et al. 2005). Our modeled organic-to-mineral transfer rates of 12–19 g C m^{-2} $year^{-1}$ agree reasonably well with observed dissolved organic carbon fluxes at the HBEF of about 35 g C m^{-2} $year^{-1}$ (Fahey et al. 2005; Landis et al. 2024). The slight underestimation of this flux may be due to missing contributions from roots in our model (Hagedorn et al. 2004; Uselman et al. 2007). Nevertheless, these results underscore the robustness of our model and the role of northern hardwood forest soils as substantial carbon reservoirs that appear to be able to buffer environmental change to some extent.

The omission of root carbon in our models likely leads to an underestimation of total soil carbon inputs, particularly to the mineral soil layers, where roots are a major carbon source (Fahey et al. 2005). Excluding roots may thus overestimate modeled carbon turnover times and underestimate the responsiveness of soil carbon to environmental changes, such as changes in climate, soil pH, disturbance, or tree physiology (Gaudinski et al. 2000; Hicks Pries et al. 2018). Future studies that include estimates of root carbon inputs and turnover rates will be important for accurately representing the full soil carbon cycle in northern hardwood forests.

Interestingly, at the site scale, and over a shorter period (1998–2023), the Oi/Oe layer showed a decline in carbon stocks of about −15 g C m^{-2} $year^{-1}$ and an increase in soil CO_2 respiration of about +25 g C m^{-2} $year^{-1}$. The four-pool model with two pools for the Oi/Oe layer captured this decline in soil carbon stocks in the Oi/Oe layer well (Figure 5). It appears likely that the observed increases in precipitation, temperature, and soil pH have accelerated litter decomposition rates at the low-elevation site we studied. This is consistent with global estimates of litter carbon response to climate change (Carvalhais et al. 2014; Chen et al. 2024). In contrast to the HBEF, observations at Harvard Forest indicate that the litter layer is a small carbon sink, perhaps due in part to somewhat warmer conditions in central Massachusetts compared to the White Mountains (Finzi et al. 2020). The differences between HBEF and Harvard Forest also point to the importance of legacy effects of land-use history and other local factors in determining modern soil carbon dynamics (Felzer 2023; Vilà-Cabrera et al. 2023). It is therefore critically important to continue to study entire ecosystems over long periods, archive samples, and conduct experiments to better understand the role of multiple global change factors in driving soil response (Rillig et al. 2019).

In summary, our results show a mismatch between soil carbon dynamics at the watershed-level, which appear to be at steady-state, and at an intensively sampled, low-elevation site, where the litter layer is losing carbon. This discrepancy is likely due to variation in spatial and temporal scales between the two datasets and demonstrates the benefit of examining both the long-term persistence of carbon and recent changes in the carbon cycle. The large variability in carbon stocks across the watershed may explain why the data covering the longer period and larger spatial area do not show any significant changes in soil carbon dynamics (Johnson et al. 2000). In contrast, the increase in soil CO_2 respiration is consistent across the elevation gradient within the watershed and is not just seen in the lower elevation site (Groffman and Martel 2023). The scale-dependent nature of ecological processes has long been recognized (e.g., Bormann and Likens 1994; Fan et al. 2023; Sousa 1984) and extends to soils, where the heterogeneity of organic matter combined with a wide distribution of turnover rates complicates the understanding and prediction of soil carbon dynamics (Doetterl et al. 2025; Jungkunst et al. 2022). This complexity again highlights the potential role of litter carbon as an "early-warning system" for soil responses to global change. It also emphasizes the importance of studying the same processes at different scales, and of being cautious when upscaling from the site to the ecosystem level and beyond.

5 | Conclusion

Future research should prioritize integrating root contributions and higher-resolution modeling approaches to refine our understanding of soil carbon responses to environmental change. The exclusion of roots and the use of single pools for the Oa/A and mineral layers in our models are notable limitations, as they may underestimate the presence of younger, more responsive carbon fractions within these layers. Including additional environmental factors, such as changes in temperature seasonality, forest age, and tree physiology may further improve our understanding of short- and long-term soil carbon dynamics in northern hardwood forests.

In summary, our study highlights the temporal and spatial complexity of soil carbon dynamics in a northern hardwood forest at the Hubbard Brook Experimental Forest (HBEF). Using radiocarbon measurements and compartmental models, we demonstrated that carbon in the Oi/Oe layer cycles on decadal timescales, while carbon in the Oa/A and mineral layers cycles on centennial timescales. Despite significant increases in precipitation, temperature, and soil pH over the past five decades, we observed no changes in carbon cycling at the watershed scale, suggesting that these gradual environmental changes have not yet perturbed the overall steady-state of the soil system. The inherent heterogeneity of soil carbon across the watershed complicates the detection of subtle changes and highlights the importance of studying carbon dynamics at multiple scales. In fact, at the site level, we detected a significant decline in carbon stocks within the Oi/Oe layer, coinciding with increased soil respiration rates. The observed scale-dependent responses emphasize the need for caution when extrapolating site-level observations to larger ecosystems or global scales.

Author Contributions

Sophie F. von Fromm: conceptualization, data curation, formal analysis, funding acquisition, methodology, software, visualization, writing – original draft. **Connor I. Olson:** methodology, resources, writing

– review and editing. **Matthew D. Monroe:** data curation, visualization, writing – review and editing. **Carlos A. Sierra:** methodology, software, writing – review and editing. **Charles T. Driscoll:** data curation, resources, writing – review and editing. **Peter M. Groffman:** data curation, funding acquisition, resources, writing – review and editing. **Chris E. Johnson:** data curation, resources, writing – review and editing. **Peter A. Raymond:** data curation, resources, writing – review and editing. **Caitlin Hicks Pries:** conceptualization, funding acquisition, resources, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.15270746 and Github at https://github.com/SophievF/HubbardBrook_Soil (Dataset 1) and the Environmental Data Initiative at https://doi.org/10.6073/pasta/2455ef85807d390f2b95ec277c6a4af7 (Dataset 2).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.