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Key Points:
- Soil warming decreased soil organic matter and water holding capacity in a temperate deciduous forest in the northeastern United States
- Decreased soil organic matter content accounted for part but not all of the decrease in water holding capacity
- Lower water holding capacity decreased thermal and hydrological buffering, leading to warmer and drier soil conditions

Supporting Information:
- Supporting Information S1

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Decreased Soil Organic Matter in a Long-Term Soil Warming Experiment Lowers Soil Water Holding Capacity and Affects Soil Thermal and Hydrological Buffering

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Abstract Long-term soil warming can decrease soil organic matter (SOM), resulting in self-reinforcing feedback to the global climate system. We investigated additional consequences of SOM reduction for soil water holding capacity (WHC) and soil thermal and hydrological buffering. At a long-term soil warming experiment in a temperate forest in the northeastern United States, we suspended the warming treatment for 104 days during the summer of 2017. The formerly heated plot remained warmer (+0.39 °C) and drier (-0.024 cm^3 H_2O cm^{-3} soil) than the control plot throughout the suspension. We measured decreased SOM content (-0.184 g SOM g^{-1} for O horizon soil, -0.010 g SOM g^{-1} for A horizon soil) and WHC (-0.82 g H_2O g^{-1} for O horizon soil, -0.18 g H_2O g^{-1} for A horizon soil) in the formerly heated plot relative to the control plot. Reduced SOM content accounted for 62% of the WHC reduction in the O horizon and 22% in the A horizon. We investigated differences in SOM composition as a possible explanation for the remaining reductions with Fourier transform infrared (FTIR) spectra. We found FTIR spectra that correlated more strongly with WHC than SOM, but those particular spectra did not differ between the heated and control plots, suggesting that SOM composition affects WHC but does not explain treatment differences in this study. We conclude that SOM reductions due to soil warming can reduce WHC and hydrological and thermal buffering, further warming soil and decreasing SOM. This feedback may operate in parallel, and perhaps synergistically, with carbon cycle feedbacks to climate change.

Plain Language Summary Soil warming in temperate deciduous forests of the northeastern United States may result in a series of consequences that ultimately reinforce climate change. Reduced soil carbon storage is one well-studied consequence; changes in soil water holding capacity are less well studied. At a long-term soil warming experiment in Harvard Forest, we suspended the warming treatment for 104 days to investigate how long-term warming might have altered water holding capacity. We measured both reduced soil organic matter and reduced water holding capacity, as well as a statistically significant link between the two. We also observed the formerly heated plot remaining warmer and drier than the control plot throughout the suspension, despite having received no artificial warming for several months. This could have important implications for a warming world. Soil water storage plays a crucial role in holding water in an ecosystem between rain events, making water continuously available for both the ecological and for human use. Reduced soil water storage capacity could make both ecosystems and human infrastructure more sensitive to the weather variability, which is expected to increase with climate change. This could result in reduced forest growth and carbon storage, further reinforcing climate change.

1. Introduction

Soil water holding capacity (WHC) can be an important constraint on the water balance (e.g., the partitioning of precipitation between runoff and evapotranspiration) of terrestrial ecosystems. Soil water storage provides a hydrological buffering function, matching episodic water supply (precipitation) to continuous water demand (evapotranspiration). Insufficient buffering capacity can alter water balance if the seasonality of precipitation is not synchronized with the seasonality of potential evapotranspiration (Milly, 1994; Wolock & McCabe, 1999). When WHC constrains water balance, it also constrains soil moisture by imposing a maximum post-drainage moisture level following a soil-saturating precipitation event. In such a scenario,

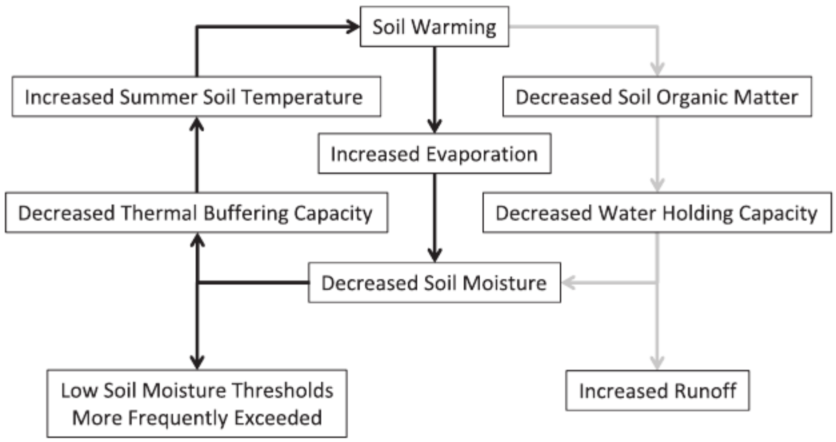

Figure 1. Conceptual diagram of hypothesized feedbacks between soil warming, water holding capacity, and soil thermal buffering capacity. The black arrows indicate feedback via the direct effect of warmer soil temperatures on soil moisture, which we refer to as the "evaporative feedback." the gray arrows indicate feedback via long-term reduction of soil organic matte content and water holding capacity, which we refer to as the "WHC feedback."

any reduction in WHC would result in a generally drier soil moisture regime, as evapotranspiration would begin drawing down soil moisture from a lower starting point. Since water has a much higher specific heat than dry soil (Bowers & Hanks, 1962), reducing soil moisture also reduces the soil's thermal buffering capacity, causing soil temperature to be more strongly influenced by air temperature. Therefore, if reductions in WHC increase the runoff fraction of water balance and lower soil moisture, it should also lead to increased summer soil temperature, since summer air temperatures are generally warmer than concurrent soil temperatures. Soil moisture and soil temperature are two central controls on biologically mediated soil processes, so reduced WHC could have far-reaching ripple effects if water balance is affected.

While much attention has been devoted to the relationship between soil organic matter (SOM) content and WHC, most of it has been in the context of soils with low to moderate SOM content (typically <10% *w*/w). In such soils, WHC is primarily a function of soil texture and depth (Kern, 1992), and the effects of SOM on WHC tend to be minor (Minasny & McBratney, 2017). In SOM-rich soils, especially those with prominent organic horizons, SOM content can play a much larger role in determining WHC (Ankenbauer & Loheide, 2017; Jordan et al., 2010; Ramirez et al., 2017; Yang et al., 2014), especially if combined with coarse soil texture (Dunne & Willmott, 1996; Rawls et al., 2003). SOM may also play an elevated role in determining WHC for more mesic ecosystems, as soil water retention becomes more strongly determined by soil physical structure (relative to adsorption/desorption dynamics) as soil water content increases (Yang et al., 2014), and increasing soil porosity is a major mechanism by which SOM content is thought to enhance WHC (Pollacco, 2008).

A central finding of several long-term soil warming experiments in temperate and boreal forests with SOM-rich soils has been large initial increases in soil respiration (Bronson et al., 2008; Contosta et al., 2011; Eliasson et al., 2005; Hicks Pries et al., 2017; McHale et al., 1998; Melillo et al., 2002, 2011; Noh et al., 2017; Rustad & Fernandez, 1998; Schindlebacher et al., 2009; Teramoto et al., 2016, 2018). This is typically assumed to imply an eventual drawing down of SOM stocks, which has been directly confirmed in at least one of the longer-running experiments (Melillo et al., 2017). If this response to warming occurs in contexts where SOM content is relevant to WHC and WHC is relevant to water balance, or if warming-induced SOM losses diminish hydrological buffering capacity to a point where WHC becomes relevant to water balance, then soil warming could have several additional implications for ecosystem processes beyond its well-appreciated carbon cycle feedback to the climate system (Figure 1).

Lower soil moisture in heated plots is a common observation at soil warming experiments (Bronson et al., 2008; Eliasson et al., 2005; Peterjohn et al., 1994; Rustad & Fernandez, 1998) and is typically assumed to be a direct consequence of increased physical evaporation; we will refer to this as the "evaporative feedback." Here, we propose a second indirect feedback, which we will refer to as the "WHC feedback," where soil moisture is further reduced due to reductions in WHC caused by SOM loss. We hypothesize that the evaporative feedback reduces soil moisture, increases summer soil temperature by reducing soil thermal buffering (an effect not ordinarily observable in soil warming experiments that actively regulate temperature in their heated plots), and elevates the role of soil moisture in constraining ecosystem processes. We hypothesize that the WHC feedback compounds these effects by further reducing soil moisture, while additionally altering water balance by diverting water into runoff that otherwise would have been partitioned into evapotranspiration. Any water diverted from evapotranspiration into runoff would no longer be readily accessible to terrestrial ecosystems.

The WHC feedback loop depicted in Figure 1 has three prerequisites: SOM levels must be sensitive to soil warming, WHC must be sensitive to SOM levels, and water balance must be sensitive to WHC. We would expect most sites at the Harvard Forest Long-Term Ecological Research Station to meet all three of these criteria. Three on-site soil warming experiments have either measured reduced SOM levels as a consequence of long-term warming (Melillo et al., 2017) or persistently increased soil respiration (Contosta et al., 2011; Melillo et al., 2011). Soils at Harvard Forest are generally coarse textured with high SOM content. The United States Geological Survey hydrological region in which the Harvard Forest is located has high runoff efficiency (>20% of total precipitation becomes runoff; McCabe & Wolock, 2016). Although productivity at this site is not ordinarily water limited, while analyzing 13 years of eddy covariance data, Urbanski et al. (2007) found evidence for water limitation of productivity during midsummer (the 206th–250th days of the year). High runoff efficiency and seasonal soil moisture limitation of productivity suggest that in a typical year, some water is partitioned into runoff that otherwise could have been utilized by vegetation for transpiration; in other words, annual evapotranspiration was constrained by hydrological buffering capacity. This is consistent with Harvard Forest's climatic context: its very even seasonal distribution of precipitation (Finkelstein & Truppi, 1991) contrasts with the highly uneven seasonal distribution of potential evapotranspiration expected of midlatitude forests. The relevance of hydrological buffering capacity to ecosystem processes at Harvard Forest is further suggested by Savage and Davidson (2001), who analyzed 6 years of soil respiration data and concluded that the seasonal timing of precipitation events was at least as important as total annual precipitation for determining if soil moisture limited annual soil respiration during a given year.

In addition to reducing SOM content, soil warming can also affect SOM composition by the preferential loss of particular classes of organic compounds (Feng et al., 2008; Pold et al., 2017), potentially shifting SOM composition toward a more hydrophobic profile. While most historical work on soil water repellency (SWR) has focused on highly water repellent soils, more recent studies have found low levels SWR to be the rule rather than the exception (de Jonge et al., 2009). While positive correlations between SWR and SOM content have historically been observed, recent work has revealed a more complex relationship between the two factors (Goebel et al., 2011; Yang et al., 2014), leading to the conclusion that SOM per se does not induce SWR; particular classes of SOM compounds or functional groups do (Doerr et al., 2000; Ellerbrock et al., 2005). Therefore, alterations to SOM composition could affect WHC independently of changes in SOM content.

At the Barre Woods soil warming experiment at Harvard Forest, where soils have been continuously warmed to +5 °C above control temperatures since 2003, we investigated the indirect effects of long-term soil warming on soil moisture and thermal buffering by suspending the warming treatment for 104 days during the growing season of 2017. During this period, we recorded hourly soil temperature and soil moisture measurements in the previously heated plot and the adjacent control plot. We also measured WHC and SOM content of soils taken from the two plots and used Fourier transform infrared (FTIR) spectroscopy to assess SOM composition. We then investigated if treatment differences in WHC could be explained by differences in either SOM content or composition.

2. Materials and Methods

2.1. Study Site

The Barre Woods soil warming experiment is located in an even-aged, mixed deciduous forest in central Massachusetts, USA (42°28′N, 72°10′W). Mean weekly air temperature varies from a high of 20 °C in July to a low of −6 °C in January. Mean total annual precipitation is 108 cm, evenly distributed throughout the year. Soils are of the Canton series (coarse-loamy over sandy or sandy-skeletal, mixed, semiactive, mesic Typic Dystrudepts), and include a distinct organic horizon about 5.5 cm thick. Surface (O horizon) pH is about 5.2, and a subsurface (A horizon) pH is about 5.5. Dominant tree species at the study site are *Quercus rubra*, *Quercus velutina*, and *Acer rubrum*. Historical records, stone walls, and the presence of a plow layer suggest that the site was used for either pasture or low-intensity agriculture prior to 1908. A hurricane in 1938 knocked down most trees on the site; blowdowns were salvaged, and the site was allowed to naturally regenerate to its current state. See Melillo et al. (2011) for more details.

2.2. Soil Warming Experiment Design

The warming experiment consists of one 30 × 30-m heated plot and an adjacent 30 × 30-m control plot separated by a 5-m buffer strip. Soil in the heated plot has been continually warmed to +5 °C above control plot temperatures since May of 2003 by electrical resistance cables buried 10 cm deep and spaced 20 cm apart. Soil temperature and moisture are recorded hourly by a Campbell Scientific CR1000 datalogger, with Campbell Scientific Type 107 thermistors and Campbell Scientific CR-616 soil moisture probes. The heated plot contains 80 thermistors and 12 soil moisture probes; the control plot contains 12 thermistors and 12 soil moisture probes. Thermistors were installed at a depth of 5 cm; soil moisture probes have 30-cm tines and were installed vertically from the soil surface. See Melillo et al. (2011) for more details. During the summer of 2017, the warming treatment was suspended on 30 May and resumed on 11 September.

2.3. Soil Sampling

Soil samples were collected on multiple dates, 13, 27, 71, 104, and 106 days after the suspension of warming, from eight randomly selected 1 × 1-m sampling plots within each treatment. Sampling plots under the crowns of Eastern Hemlocks (*Tsuga canadensis*) were avoided, as they are a minor presence at this site but have strong localized effects on soil properties. Cores were collected with a 5.5-cm diameter by 10-cm deep tulip bulb corer. The cores were separated into organic and mineral (A) horizons, sieved at 2 mm, and subsamples from each horizon of each core were taken for SOM, WHC, and FTIR assays.

2.4. SOM and WHC Measurements

SOM content was measured by mass loss on ignition. Five to ten grams of field-moist soil were weighed into drying tins, dried at 105 °C for 48 hr and reweighed to get dry weight. The dried soil was then placed in a furnace set at 550 °C for 4 hr and reweighed to get the ash weight. Organic matter content was calculated as the mass ratio of organic matter to mineral material ([dry wt. − ash wt.]/ash wt.).

We measured SOM content by loss on ignition instead of by %C because we believe it to be a more appropriate measurement for the purpose of accounting for variation in WHC. We expect WHC to be a function of soil pore structure and the way pore surfaces interact with water. Entire organic molecules should be relevant to these properties, not just their carbon atoms. But it should be noted that loss on ignition is not an exact measurement of soil carbon, since the carbon content of SOM can vary.

WHC was measured as field capacity (water retained by the soil after gravity drainage). Five to ten grams of field-moist soil was transferred into modified 50-ml centrifuge tubes with the conical bottom section cut off and replaced with a fine mesh. Tubes were loosely capped during the assay to limit evaporation. Tubes containing the soil samples were placed upright in water and soaked for 24 hr. Additional water was applied to the top of the tubes as necessary to prevent organic horizon soil from floating on the surface and remaining dry. After 24 hr, the tubes were removed from the water, placed on a metal grate, and allowed to drain for another 24 hr. After draining, the soil was removed from the tubes, placed in a drying tin and weighed to get the wet weight, then dried at 105 °C for 48 hr and reweighed to get dry weight. WHC was calculated as the mass ratio of the water to soil dry weight following saturation and 24 hr of draining ([wet wt. − dry wt.]/dry wt.).

2.5. FTIR Assays

Diffuse reflectance FTIR spectroscopy was used to evaluate differences in organic matter chemistry between control and heated plots. Dried and finely ground samples were diluted 20-fold in spectroscopy grade potassium bromide (KBr) and then analyzed on a Bruker Vertex 70 FTIR equipped with a wide-range Si beam splitter and detector and a Pike AutoDiff diffuse reflectance accessory. Ultradry CO_2-free air was provided via a Parker-Hannifin FTIR purge gas generator. For each sample, 60 coadded spectra were acquired from

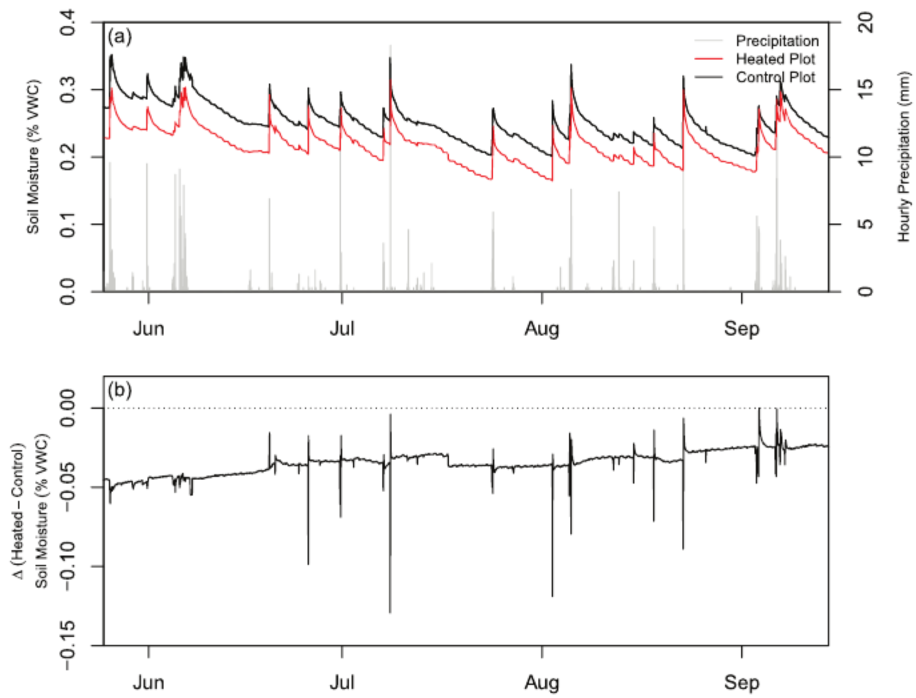

Figure 2. (a) Hourly soil moisture and precipitation from immediately prior to the shutoff (30 May) to immediate after the shutoff (11 September). Hourly precipitation was measured at a nearby (~5 km) meteorological station (Boose, 2018). (b) Δ(heated − control) soil moisture during the same time period.

6,000 to 400 cm^{-1} with a resolution of 4 cm^{-1}. With each set of 20 samples, a new background spectrum was obtained on a clean mirror.

2.6. Statistical Analysis

Since there was minimal overlap in either SOM or WHC between organic and mineral horizon samples, separate statistical tests were run for organic and mineral horizons. Samples from different sampling dates were pooled, as we do not expect SOM or WHC to change on the time scales separating the different samplings.

The effect of treatment (heated vs. control) on WHC and SOM content was evaluated using two-sample t tests. The effect of SOM content and treatment (heated vs. control) on WHC was analyzed using type II analysis of covariance (ANCOVA), with SOM content as a covariate and treatment as a fixed factor. Nonsignificant interaction terms were dropped, reducing the ANCOVA models to multiple linear regression models with common slopes but treatment-specific intercepts. We interpreted the difference between the heated and control plot intercepts as the effect of treatment on WHC independent of differences in SOM content; we refer to this as the "warming effect." We calculated the effect of SOM differences between the heated and control plots on WHC (the "SOM effect") as the mean difference in WHC between the heated and control plots minus the warming effect. t tests, ANCOVAs, and linear regressions were performed in R 3.5.0.

Prior to analysis of the FTIR data, all spectra were baseline corrected at 6,000 cm^{-1}, and the region between 627 and 587 cm^{-1} was removed due to low throughput. After computing a dissimilarity matrix on the FTIR spectra (1,440 data points) using Euclidean distance, a one-way permutational analysis of variance (PERMANOVA, Anderson, 2001) was used to assess overall differences in FTIR-observed chemistry between heated and control plots for the organic and mineral horizons using the Primer 6 software package. For organic horizon soil, we constructed and compared partial least squares regression (PLSR) models to predict SOM and WHC data using FTIR data as independent variables to further explore which FTIR-observed features most strongly correlate with differences in these two soil properties. All were pooled ($n = 50$), and models were validated using a full leave-one-out cross validation procedure in the Unscrambler

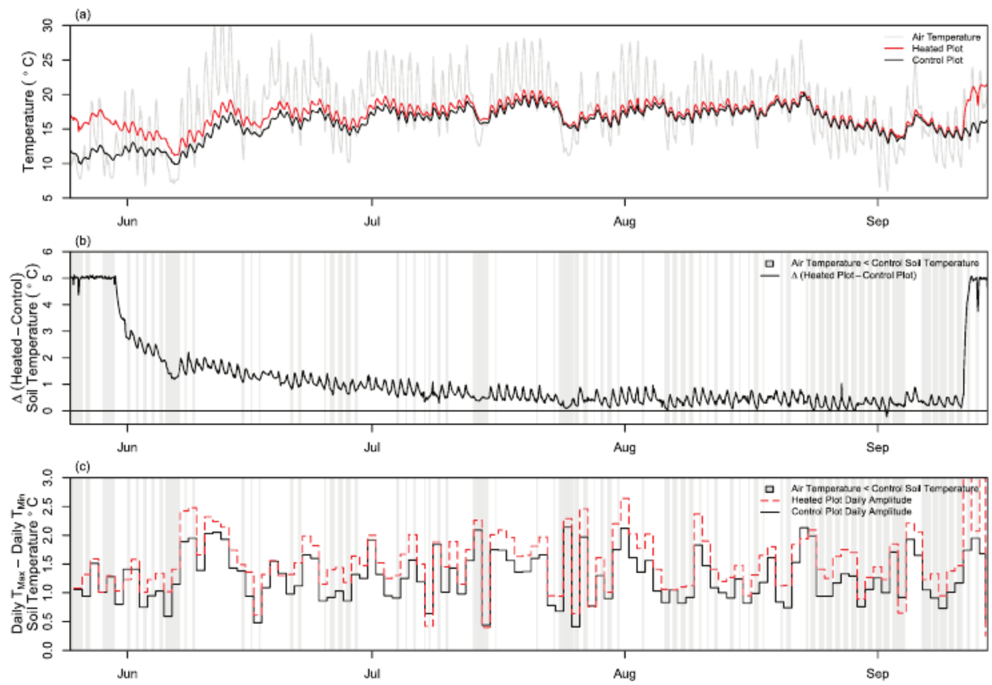

Figure 3. Hourly soil temperature in the control and heated plots. Panel (a) depicts soil temperature from immediately prior to shutting down the warming system (30 May) to immediately after the shutoff (11 September) in the formerly heated and control plots, as well as air temperature. Panel (b) depicts the difference between the formerly heated and control plot soil temperature (solid line), with gray shading indicating time periods where the air temperature was cooler than the control plot soil temperature. Panel (c) depicts the difference between the maximum and minimum temperatures within each day for the heated and control plots, illustrating the magnitude of the diurnal soil temperature cycle.

X software package. Mineral horizon soil was not analyzed this way due to minimal treatment effects on FTIR spectra.

3. Results and Discussion

3.1. Soil Moisture

Throughout the entire 104-day suspension of the warming treatment, soil moisture remained lower in the formerly heated plot than in the control plot (Figure 2). During the week prior to the suspension, we measured a mean water content of 0.294 cm^3 H_2O cm^{-3} soil in the top 30 cm of soil in the control plot and 0.253 cm^3 H_2O cm^{-3} soil in the heated plot, for a warming effect of −0.041 cm^3 H_2O cm^{-3} soil, which is representative of typical soil moisture deficits observed at this experiment. During the final week of the warming suspension, we measured an average water content of 0.265 cm^3 H_2O cm^{-3} soil in the control plot and 0.241 cm^3 H_2O cm^{-3} soil in the formerly heated plot, for a difference of −0.024 cm^3 H_2O cm^{-3} soil. This difference persisted despite 2017 being a relatively cool and wet summer compared to long-term trends at Harvard Forest (Figure S1 in the supporting information; Boose & Gould, 2004; Boose, 2018), and including multiple rain events that briefly raised formerly heated plot soil moisture above the level which control plot soil moisture would drain to in subsequent days (Figure 2a). Formerly warmed plot soil moisture often had a slightly delayed response to precipitation relative to the control plot, leading to the cardiograph-like pattern in $\Delta(H - C)$ soil moisture (Figure 2b).

3.2. Soil Temperature

The formerly heated plot also remained consistently warmer than the control plot throughout the suspension (Figure 3; see Figure S2 for more a more detailed view of selected periods). After the first few days when the temperature difference between the plots rapidly diminished, we also observed an amplified diurnal soil temperature cycle in the formerly heated plot relative to the control plot (Figure 3c). Air temperatures

Table 1
WHC and SOM Content

	Water holding capacity (g H_2O g^{-1} soil dry weight)		SOM content (g SOM g^{-1} mineral soil)	
	Organic horizon	Mineral horizon	Organic horizon	Mineral horizon
Control plot	2.91 ± 0.15	1.09 ± 0.02	0.569 ± 0.046	0.107 ± 0.004
Heated plot	2.09 ± 0.08	0.91 ± 0.02	0.385 ± 0.025	0.097 ± 0.005
Δ (heated − control)	−0.82 ± 0.17	−0.18 ± 0.03	−0.184 ± 0.052	−0.010 ± 0.006
Statistical significance (P)	1.3×10^{-5}	5.7×10^{-7}	0.001	0.087
N (control, heated)	34, 34	36, 39	34, 34	36, 39
SOM effect on Δ(H − C)	−0.51	−0.04		
Warming Effect on Δ(H − C)	−0.31	−0.14		

Note. Numbers in the first three lines are mean ± standard error. Standard errors for Δ(heated − control) were propagated from the standard error estimates of the component terms. Statistical significance refers to the contrast between heated and control plot samples, determined by Welch's two-sample *t* test. The difference between the intercepts of heated and control regression models (Figure 5 and Table S1) was interpreted as the Treatment Effect on Δ(H − C). The difference between Δ(H − C) and the Treatment Effect on Δ (H-C) was interpreted as the SOM Effect on Δ(H − C). Mineral horizon refers to A horizon soil.

remained generally warmer than soil temperatures until the final few weeks of the warming treatment suspension.

Three unusually cool periods occurred during which air temperatures became cooler than soil temperatures for a few days each (5 June to 6 June; 13 July to 15 July; 24 July to 26 July) (Figure S2). On 24 July, the soil temperatures of the formerly heated and control plots converged within 0.1 °C and subsequently diverged again with the return of warmer air temperatures. For the remainder of the warming treatment suspension (26 July to 11 September), antecedent soil temperature could no longer explain the persistent temperature elevation in the formerly heated plot relative to the control plot. During this time period, the difference between control and formerly heated soil temperature was tightly correlated with the difference between control soil temperature and the air temperature ($r^2 = 0.80$, $P < 2.2 \times 10^{-16}$; Figure S3), suggesting that air temperature was exerting a stronger influence on soil temperature in the formerly warmed plot than in the control plot. The mean temperature difference between the formerly heated and control plots during this period was +0.39 °C, with an increase in the mean amplitude of the diurnal temperature cycle (mean daily $T_{max} - T_{min}$) of +0.28 °C.

3.3. SOM Content and WHC

We measured lower SOM content and lower WHC in the heated plot relative to control plot soil in both organic and mineral (A) horizons (Table 1). All these differences were statistically significant except for SOM content in the mineral soil ($P = 0.087$). We suspect the lack of statistical significance for this comparison is driven by a small effect size relative to the variability. Analysis of a larger SOM dataset from this experiment lacking paired WHC approximately reproduces the means presented in Table 1 and is statistically significant (Table S2).

3.4. FTIR Spectra

For mineral horizon soil, FTIR spectra were not significantly different between the heated and control plots (PERMANOVA pseudo-F = 1.764, P (perm) = 0.137). For organic horizon soil, we observed significant differences (PERMANOVA pseudo-F = 8.341, P (perm) = 0.005) with a general enhancement of mineral features and a general diminishment of most organic features in the heated plot relative to the control plot (Figure 4), consistent with the finding of reduced SOM content in the heated plot.

3.5. Statistical Relationship Between WHC and SOM Content

To determine if measured reductions in WHC could be accounted for by reductions in SOM content, we conducted an analysis of covariance on WHC with SOM as a covariate and treatment (control vs. heated) as a fixed factor. Both factors were strongly significant for both soil horizons ($P < 0.005$; Table S1), suggesting that reduced SOM content can explain some, but not all, of our measured reductions in WHC. Since the interaction term was not significant in either model, we reduced the ANCOVA models to multiple linear regression models with common slopes but different intercepts for the control and heated plots (adj. $r^2 = 0.77$ for organic soil, adj. $r^2 = 0.69$ for mineral soil; Figure 5, Table S1). We interpreted the difference between the

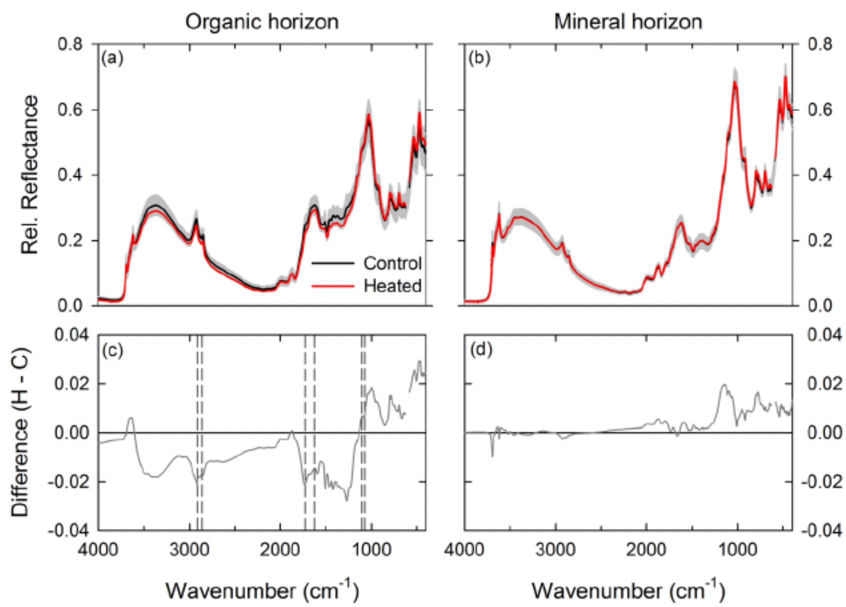

Figure 4. Mean baseline corrected FTIR spectra for control and heated plots in (a) organic and (b) mineral horizons. Gray shaded region represents 1 s.d. about the overall mean spectra for each horizon. The difference spectra between heated and control are given for organic and mineral horizons in (c) and (d). On panel (c), drop lines indicate locations of adsorption features for aliphatic CH– (2,920 and 2,860 cm^{-1}), hydrophilic C=O– (1,725 and 1,630 cm^{-1}) and polysaccharide C–O (1,100 and 1,080 cm^{-1}) functional groups using in calculation of FTIR indices.

intercepts (−0.31 g H_2O g^{-1} dry soil for organic horizon, −0.14 g H_2O g^{-1} dry soil for the mineral horizon) as the difference in mean WHC not attributable to differences in SOM, or the "warming effect." Given this interpretation, we can calculate the difference in mean WHC attributable to differences in SOM content, or the "SOM effect," as the total measured reduction in mean WHC minus the warming effect. By this analysis, reduced SOM content can explain 62% of the WHC reduction measured in the heated plot relative to the control plot for organic horizon soil. In contrast, reduced SOM content can only explain 22% of the mean WHC reduction measured in the mineral horizon soil.

3.6. Statistical Relationship Between WHC and FTIR Spectra

To test if SOM composition was contributing to the measured differences in WHC capacity between heated and control plots, we compared PLSR models predicting SOM and WHC as a function of FTIR spectra (Figure S4). Even with a limited sample size ($n = 50$), the FTIR spectra explained about 70% of the variance in both SOM and WHC for organic horizon soil (Figures S4a & S4b). The loading spectra were very similar for both models (Figures S4c and S4d), suggesting that a similar set of factors could explain differences in both SOM and WHC. However, the best linear combinations of the loading spectra (i.e., the PLSR model beta coefficients) produced quite different final PLSR models for SOM and WHC (Figure S4e), suggesting that some factors are especially or uniquely important to one property over the other. The most prominent differences were that aliphatic functional groups (2,920 and 2,860 cm^{-1}) and a peak at 3,700 cm^{-1} (most likely –OH associated with kaolinite; Madejova et al., 2017) were strong positive predictors of WHC but not SOM. In the mineral horizons, while the PLSR models could not explain as much variance in the data, exploration of the beta coefficients suggested that while some of the same functional groups best explained SOM and WHC, there were also several functional groups unique to explaining differences in WHC (Figure S5). But within both horizons, the FTIR peaks best able to uniquely explain variation in WHC did not differ much between heated and control soil. Therefore, our FTIR results support the hypothesis that SOM composition can affect WHC independently of SOM content, but they cannot explain the warming effect on WHC (i.e., the remaining difference between treatments after the SOM Effect is accounted for) in our data.

3.7. Interpretation of Results From Unreplicated Ecological Manipulations

As noted in the site description, the Barre Woods Soil Warming Experiment lacks plot-scale replication. Autocorrelation of soil and/or ecological conditions within our plots is unlikely as they do not correspond

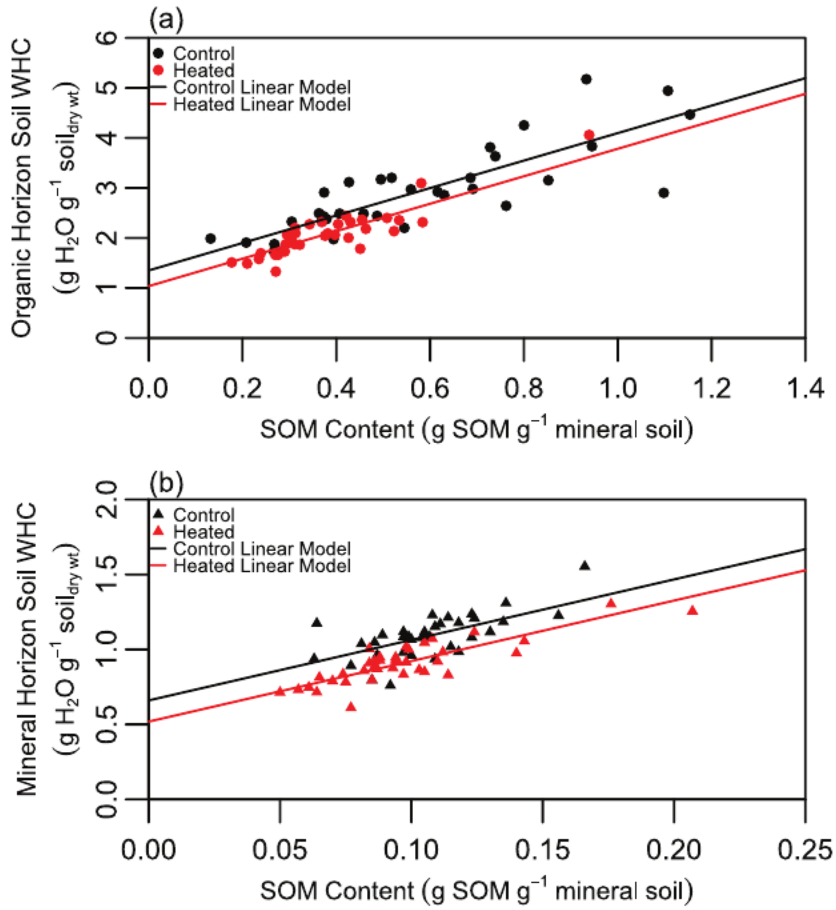

Figure 5. Water holding capacity of organic horizon (a; circles) and mineral horizon (b; triangles) soil from the control plot (black points) and heated plot (red points). Solid lines represent the linear relationship between water holding capacity and soil organic matter content in control plot soil (black lines) and heated plot soil (red lines) for organic soil (a) and mineral soil (b). See Table S1 for model information.

to natural boundaries, but are arbitrary units superimposed over a continuous landscape. However, spatial heterogeneity may still be an issue. Statistical inference in the context of this study can only address spatial heterogeneity on scales much smaller than the plot size, which can be captured by the replication and spatial dispersion of sampling plots within the experimental plots. Heterogeneity on scales much larger than the plot size are unlikely to affect our measurements due to the immediate proximity of the plots. But heterogeneity on scales similar to the plot size cannot be empirically addressed without plot-level replication. The essential implication is that the statistics we present can demonstrate that the differences between the heated and control plot are statistically significant, but they cannot statistically attribute those differences to the experimental manipulation.

Experimental manipulation of whole ecosystems is a very powerful analytical approach, as ecosystem processes are often shaped by nuanced emergent properties that are difficult or impossible to preserve in more controlled settings (Likens, 1985). Classic examples of successful whole-system manipulations include the paired lake studies in northern Michigan by Arthur Hassler and his students beginning in the 1950s (e.g., Johnson & Hasler, 1954) and the paired forested watershed studies at Hubbard Brook in New Hampshire by F. Herbert Bormann and Gene Likens (e.g., Bormann et al., 1968). While these studies were unreplicated due to cost and feasibility constraints, they have produced important ecological information that has shaped ecosystem science over the past half century and lead it down productive paths.

While there is widespread recognition that these studies (alongside others with similar studies unavoidable limitations) have produced valuable information, there has also been extensive and ongoing debate in the

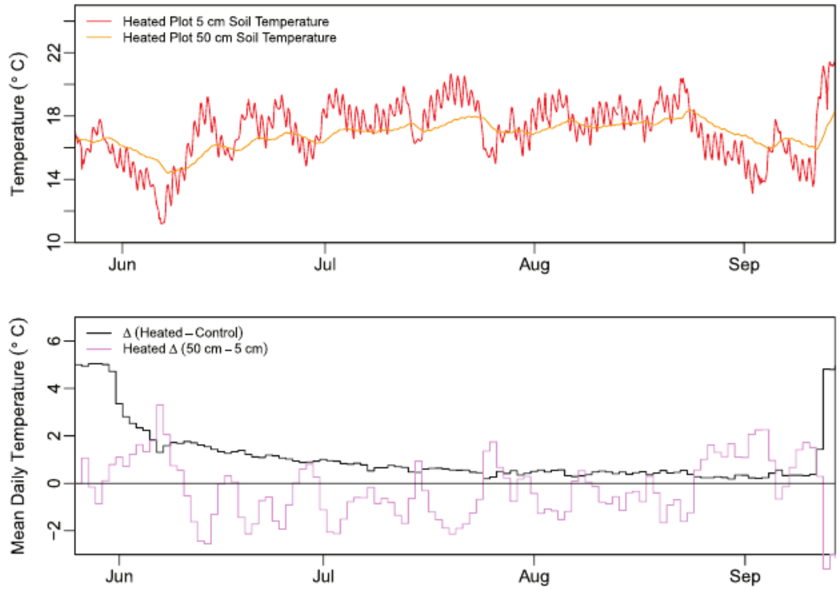

Figure 6. Comparison between the surface (5 cm) and subsurface (50 cm) soil temperatures in the formerly warmed plot throughout the suspension of the warming treatment, and how the thermal gradient between the two relates to the temperature elevation observed in the formerly warmed plot. Panel (a) compares hourly soil temperature at the two depths in the formerly warmed plot. Panel (b) compares the difference between 5- and 50-cm soil temperature within the formerly warmed plot with the difference between surface soil temperature between the formerly warmed plot or the control plot (analogous to the data presented in Figure 3b). For greater clarity of overall trends, the data in (b) is displayed as daily average temperatures instead of hourly temperatures.

ecological literature over their limitations (Carpenter, 1989; Davis & Gray, 2015; Hargrove & Pickering, 1992; Heffner et al., 1996; Hurlbert, 1984; Hurlbert, 2004; Oksansen, 2001). We believe everyone agrees that replication is a foundational component of ecosystem science. We also believe that valuable scientific information can and should be extracted from imperfect experiments when they are what we have, or what can be feasibly achieved. Oksansen (2001) suggested that even when replication of an experimental manipulation is not feasible, the control plots can still be replicated. Although such a design enables narrower statistical inference than a fully replicated design, it at least allows for some evaluation of plot-scale variability that the treatment effects can be tested against. For future ecological manipulation experiments, we recommend that full replication be utilized whenever possible, and replication of control plots be strongly considered for the remainder.

3.8. Extrapolation of WHC Reductions Through the B Horizon

All measurements presented above were from the top 10 cm of soil from the surface of the organic horizon. WHC in the O through B horizons, the most relevant portion of the soil profile for biological processes and carbon cycling, is 147.8 mm (Borken et al., 2006); the majority (78%) of this is in the B horizons. While we were not able to assess the effect of soil warming on WHC for B horizon soil in this study since the warming treatment is applied to the top 10 cm of soil, we can use the data reported here to set logical boundary conditions on its expected response to warming. The lower boundary would be to assume no reduction in WHC with warming in B horizon soil. If WHC loss was confined to the O and A horizons, this would result in an 8% reduction of O through B WHC (Table S3). This calculation accounts for an observed reduction in organic horizon thickness, from 5.4 cm in the control plot to 3.3 cm in the heated plot, measured in 2016 after 14 years of warming. We consider this scenario unlikely, especially in light of a recent deep profile soil warming experiment in California that showed accelerated SOM processing at soil depths down to 100 cm (Hicks Pries et al., 2017). The upper boundary would be to assume that the entire B horizon showed a similar relative reduction in WHC to our mineral (A horizon) soil. We consider this scenario unlikely as well; SOM content typically declines with depth, and as it declines, we would expect its importance to WHC relative to soil texture to decline. Under this assumption, we would estimate a 21% reduction of O through B WHC.

Realistically, we would expect B horizon soils to lose some WHC with warming, but less than what we measured for A horizon soil; so based on these results, we would predict a O through B WHC loss of somewhere between 8% and 21% based on 15 years of +5 °C of soil warming.

3.9. Thermal Storage in Subsurface Soil as an Alternate Explanation to Reduced Thermal Buffering

Heat stored in the thermal mass of the subsurface soil could theoretically continue to warm the surface soil long after the suspension of the warming treatment. If present, lagged warming could be an alternate explanation for the persistent temperature elevation observed in the formerly warmed plot throughout the suspension period. Additional soil temperature data collected at a depth of 50 cm does not support this possibility (Figure 6a). Through most of the time period we report here, the soil at 50 cm in the formerly warmed plot was cooler than the surface soil, reflecting that the magnitude of our warming treatment (5 °C) is substantially smaller than the amplitude of the seasonal soil temperature cycle (approximately 20 °C). This implies that for most of the suspension of the warming treatment, we'd expect the subsurface soil (50 cm) in the formerly warmed plot to exert a cooling effect on the surface soil (5 cm) rather than a warming effect. The most prominent exception to this trend occurs during the final few weeks of the warming suspension, where air temperatures dropped and mostly remained below both surface and subsurface soil temperatures. During this time, surface soil temperatures did drop below subsurface soil temperatures, and therefore the subsurface soil could in principle have exerted a warming effect on the surface soil, perpetuating or increasing the elevation in formerly warmed plot soil temperature relative to the control plot. Instead, the gap between the formerly warmed and control plot temperatures diminished relative to the preceding weeks (Figure 6b). This suggests that air temperature had a stronger influence on surface soil temperature than subsurface soil temperature did, at least in the context of the patterns illustrated in Figure 2 and Figure 6.

3.10. Plot Differences in LAI as an Alternate Explanation to Reduced Thermal Buffering

Another possible alternative explanation to the persistence of elevated soil temperature in the formerly warmed plot would be reduction in leaf area index (LAI), increasing energy imputes into the soil from solar radiation. Although we did not measure LAI, we did measure litterfall quantity in the fall of 2017 and found no significant difference between the heated and control plot (n = c(10,12), $P = 0.46$) (Melillo, unpublished data). While litterfall does not account for the distribution of leaves within the canopy and therefore may not perfectly correspond to LAI, it is unlikely that we would see a large change in LAI alongside no significant change in litterfall. We therefore consider it unlikely that LAI differences were a major confounding factor in our results.

4. Conclusions

4.1. Causes of Reduced WHC

Although differences in SOM content explained much of our measured reductions in WHC, it could not explain the entire reduction, especially for mineral soil. Analysis of the FTIR data do suggest that SOM composition can explain some variability in WHC at our site, as some FTIR spectra associated with specific organic matter classes and functional groups are better predictors of WHC than of SOM (Figure S4 and S5). But the differences in the FTIR spectra between the heated and control plot do not suggest an enhancement or diminishment of these spectra as a consequence of warming and therefore cannot explain WHC differences between our treatments. This is especially notable for the mineral soil, where SOM content differences can only account for a modest percent of our measured WHC differences. We therefore conclude that factors other than SOM quantity and composition have contributed to diminished WHC in the heated plot relative to the control plot and that these factors are especially important in the mineral soil.

Warming-induced changes to soil structure due to changes in soil biological activity are a plausible explanation. Plant roots and mycorrhizae can alter soil structure in a manner resulting in greater WHC (Daynes et al., 2013). We have previously reported reduced fine root biomass in the heated plot relative to the control plot at this experiment (Zhou et al., 2011). We have also observed a functional shift in the mycorrhizal community (as characterized by Agerer, 2001) away from long-distance explorers that build extensive hyphal networks and toward contact-type explorers that only colonize soil in the immediate vicinity of the root tip (Melillo, unpublished data). These reductions in biological activity could result in reduced generation and persistence of WHC-enhancing soil structures.

4.2. Consequences for Water Balance and Hydrological Buffering

The partial, but incomplete, recovery of soil moisture despite ample rainfall during the warming suspension implies that both the evaporative and WHC feedbacks illustrated in Figure 1 contributed to the reduced soil moisture levels previously observed at this experiment, and potentially at other warming experiments as well. This suggests that for sites where WHC feedback operates, future reductions in soil moisture driven by higher soil temperatures are likely to exceed predictions based on first-order principles. Even at Harvard Forest, a generally mesic site with high WHC, carefully designed studies have revealed thresholds below which soil moisture begins to constrain processes such as net ecosystem exchange (Urbanski et al., 2007) and soil respiration (Savage & Davidson, 2001). In contrast, another study in the same tract of Harvard Forest but taking place during different years found no evidence for moisture limitation of soil respiration (Philips et al., 2010). Taken together, these studies suggest that soil moisture does not ordinarily constrain ecosystem processes at Harvard Forest but can episodically become relevant. All else equal, a generally drier soil moisture regime would expand both the frequency and duration of episodes where water availability constrains ecosystem processes.

The evaporative and WHC feedback mechanisms for reducing soil moisture have different implications for the fate of water that is diverted from soil storage. Water diverted via evaporation becomes water vapor. Water diverted via decreased hydrological buffering capacity becomes runoff or percolates to deep water tables. These have different implications for feedbacks to weather systems, the water cycle, water resource management, and potentially even landscape patterns. At Harvard Forest, the landscape is a patchwork of well-drained upland and poorly drained lowland sites, with the latter often becoming wetlands. Since the lowland sites' hydrology is maintained by lack of drainage, additional runoff from upland sites to the lowland sites could offset lowland site water losses due to increased evapotranspiration with climate change. This could have significant implications for the ecosystem processes investigated by Savage and Davidson (2001) and Urbanski et al. (2007). In contrast to the upland sites, at lowland sites belowground processes are often constrained by anoxic soil conditions due to persistent saturation. In other cases, additional runoff diverted to rivers and groundwater could increase water availability for human use; though it could make floods more frequent (Gioia et al., 2012).

We would also expect the evaporative and WHC feedback mechanisms to interact differently with altered precipitation patterns. During the 20th century in the northeastern United States, total annual precipitation increased, as well as the fraction of annual precipitation arriving in large precipitation events (Kunkel et al., 2013). These trends are expected to continue over the 21st century, leading to a wetter and more variable climate for the region with fewer but larger precipitation events, wetter winters, and increased occurrence of summer and fall droughts (Horton et al., 2014). To the extent that the reduced soil moisture we have observed is a consequence of increased evaporation, it could be thought of as a consequence of increased water demand, which could be offset by a concurrent increase in water supply. But to the extent that the decrease in soil moisture was the consequence of reduced hydrological buffering capacity, increases in precipitation would not be able to counteract it, and more precipitation would just result in more runoff. In fact, a future scenario where precipitation comes in fewer but larger events and is more seasonally desynchronized from potential evapotranspiration would make the soil's hydrological buffering capacity more consequential at the same time that reduced WHC could diminish it. In this scenario, the modest present importance of hydrological buffering at Harvard Forest could belie a greater future importance.

4.3. Feedback Between Soil Temperature, Soil Moisture, and SOM Stocks

Our observation of persistently elevated soil temperatures during the warming treatment suspension demonstrate that the feedback loop depicted in Figure 1 extends to soil temperature in a manner that would be undetectable during normal operations of the warming experiment, since heated plot soil temperatures are manipulated to a defined point above concurrent control plot temperatures. The link between the persistent temperature elevation and reduced thermal buffering capacity is suggested by the enhanced diurnal temperature cycle in the heated plot relative to the control plot depicted in Figure 3 and the tight correlation between Δ(air temperature − control plot soil temperature) and Δ(heated plot soil temperature − control plot soil temperature) depicted in Figure S3. The prospect of a self-reinforcing feedback between soil warming and the global climate system driven by the redistribution of soil carbon into atmospheric pools is well appreciated. Our results suggest the possibility of an additional self-reinforcing feedback involving reduced WHC, reduced soil moisture, and reduced thermal buffering which may operate in parallel, and perhaps synergistically, with the carbon cycle feedback between soil warming and global climate. In addition to the prerequisites already discussed (SOM content must be sensitive to soil warming, WHC must be sensitive to SOM content, and water balance must be sensitive to WHC), the final stipulation for completing the SOM-WHC-thermal buffering feedback is that the stimulatory effect of warmer soil temperatures on SOM processing exceeds the dampening effect of drier soil conditions. This appears to generally be the case at Harvard Forest (Philips et al., 2010; Savage & Davidson, 2001), at least regarding upland sites during the recent past. Since the dampening effect of dry conditions on SOM processing should grow stronger as soil becomes drier and the stimulatory effect of warmer soil temperatures on SOM processing should grow weaker as the soil becomes warmer, we hypothesize this to be the most likely backstop to eventually limit this feedback. This would imply a more prominent role for soil moisture in regulating SOM processing in the future than it has played in the past, along with decreases in both the thermal and hydrological buffering capacity of the soil, alterations of water balance in favor of lower evapotranspiration and higher runoff, and further reductions in soil carbon storage enhancing the feedback between soil warming and global climate change.

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References

Agerer, R. (2001). Exploration types of ectomycorrhizae. *Mycorrhiza*, *11*(2), 107–114.
Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46.
Ankenbauer, K., & Loheide, S. P. (2017). The effects of soil organic matter on soil water retention and plant use in a meadow of the Sierra Nevada, CA. *Hydrological Processes*, *31*(4), 891–901.
Boose, E. (2018). Fisher Meteorological Station at Harvard Forest since 2001. Harvard Forest Data Archive, HF001.
Boose, E., & Gould, E. (2004). Shaler Meteorological Station at Harvard Forest 1964-2002. Harvard Forest Data Archive, HF000.
Borken, W., Savage, K., Davidson, E. A., & Trumbore, S. E. (2006). Effects of experimental drought on soil respiration and radiocarbon efflux from a temperature forest soil. *Global Change Biology*, *12*(2), 177–193.
Bormann, F. H., Likens, G. E., Fisher, D. W., & Pierce, R. S. (1968). Nutrient loss accelerated by clear-cutting of a forest ecosystem. *Science*, *159*(3817), 882–884. https://doi.org/10.1126/science.159.3817.882
Bowers, S., & Hanks, R. (1962). Specific heat capacity of soils and minerals as determined with a radiation calorimeter. *Soil Science*, *94*(6), 392–396.
Bronson, D. R., Gower, S. T., Tanner, M., Linder, S., & Van Herk, I. (2008). Response of soil surface CO_2 flux in a boreal forest to ecosystem warming. *Global Change Biology*, *14*(4), 856–867.
Carpenter, S. R. (1989). Replication and treatment strength in whole-lake experiments. *Ecology*, *70*(2), 453–463.
Contosta, A. R., Frey, S. D., & Cooper, A. B. (2011). Seasonal dynamics of soil respiration and N mineralization in chronically warmed and fertilized soils. *Ecosphere*, *2*(3), 36.
Davis, G. M., & Gray, A. (2015). Don't let spurious accusations of psuedoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution*, *5*(22), 5295–5304.
Daynes, C. N., Field, D. J., Saleeba, J. A., Cole, M. A., & McGee, P. A. (2013). Development and stabilization of soil structure via interactions between organic matter, arbuscular mycorrhizal fungi and plant roots. *Soil Biology and Biochemistry*, *57*, 683–694.
de Jonge, L. W., Moldrup, P., & Schjønning, P. (2009). Soil infrastructure, interfaces & translocation processes in inner space ("Soil-it-is"): Towards a road map for the constraints and crossroads of soil architecture and biophysical processes. *Hydrology and Earth System Sciences*, *6*(2), 2633–2678.
Doerr, S. H., Shakesby, R. A., & Walsh, R. P. D. (2000). Soil water repellency: Its causes, characteristics and hydro-geomorphological significance. *Earth-Science Reviews*, *51*(1–4), 33–65.
Dunne, K. A., & Willmott, C. J. (1996). Global distribution of plant-extractable water capacity of soil. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, *16*(8), 841–859.
Eliasson, P. E., McMurtrie, R. E., Pepper, D. A., Stromgren, M., Linder, S., & Argen, G. I. (2005). The response of heterotrophic CO_2 flux to soil warming. *Global Change Biology*, *11*(1), 167–181.
Ellerbrock, R. H., Gerke, H. H., Bachmann, J., & Goebel, M. O. (2005). Composition of organic matter fractions for explaining wettability of three forest soils. *Soil Science Society of America Journal*, *69*(1), 57–66.
Feng, X., Simpson, A. J., Wilson, P. K., Williams, D. D., & Simpson, M. J. (2008). Increased cuticular carbon sequestration and lignin oxidation in response to soil warming. *Nature Geoscience*, *1*(12), 836–839.
Finkelstein, P. L., & Truppi, L. E. (1991). Spatial distribution of precipitation seasonality in the United States. *Journal of Climate*, *4*(4), 373–385.
Gioia, A., Iacobellis, V., Manfreda, S., & Fiorentino, M. (2012). Influence of infiltration and soil storage capacity on the skewness of the annual maximum flood peaks in a theoretically derived distribution. *Hydrology and Earth System Sciences*, *16*(3), 937–951.
Goebel, M. O., Bachmann, J., Reichstein, M., Janssens, I. A., & Guggenberger, G. (2011). Soil water repellency and its implications for organic matter decomposition—Is there a link to extreme climatic events? *Global Change Biology*, *17*(8), 2640–2656.
Hargrove, W. W., & Pickering, J. (1992). Pseudoreplication: A sina qua non for regional ecology. *Landscape Ecology*, *6*(4), 251–258.
Heffner, R. A., Butler, M. J., & Reilly, C. K. (1996). Pseudoreplication revisited. *Ecology*, *77*(8), 2558–2562.
Hicks Pries, C. E., Castanha, C., Porras, R. C., & Torn, M. S. (2017). The whole-soil carbon flux in response to warming. *Science*, *355*(6332), 1420–1423. https://doi.org/10.1126/science.aal1319

Horton, R., Yohe, G., Easterling, W., Kates, R., Ruth, M., Sussman, E, et al. (2014). Ch. 16: Northeast. In J.M. Melillo, T.C. Richmond, G.W. (Eds.), *Climate change impacts in the United States: Third National Climate Assessment.* US Global Change Research Program, 16-1-nn.

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological experiments. *Ecological Monographs*, *54*(2), 187–211.

Hurlbert, S. H. (2004). On misrepresentations of pseudoreplication and related issues: A reply to Oksansen. *Oikos*, *104*(3), 591–597.

Johnson, W. E., & Hasler, A. D. (1954). Rainbow trout population in dystrophic lakes. *Journal of Wildlife Management*, *18*, 113–134.

Jordan, A., Zavala, L. M., & Gil, J. (2010). Effects of mulching on soil physical properties and runoff under semi-arid conditions in southern Spain. *Catena*, *81*(1), 77–85.

Kern, J. S. (1992). Geographic patterns of soil water-holding capacity in the contiguous United States. *Soil Science Society of America Journal*, *59*(4), 1126–1133.

Kunkel, K. E., Karl, T. R., Brooks, H., Kossin, J., Lawrimore, J. H., Arndt, D., et al. (2013). Monitoring and understanding trends in extreme storms. *Bulletin of the American Meteorological Society*, *94*(4), 499–514.

Likens, G. E. (1985). An experimental approach to the study of ecosystems. *Journal of Ecology*, *73*(2), 381–396.

Madejova, J., Gates, W. P., & Petit, S. (2017). IR spectra of clay minerals. In W. P. Gates, J. T. Kloprogge, J. Madejova, & F. Bergaya (Eds.), *Infrared and Raman spectroscopies of clay minerals* (Vol. 8, pp. 107–149). Amsterdam, The Netherlands: Elsevier.

McCabe, G. J., & Wolock, D. M. (2016). Variability and trend sin runoff efficiency in the coterminous United States. *Journal of the American Water Resources Association*, *52*(5), 1046–1055.

McHale, P. J., Mitchell, M. J., & Bowles, F. P. (1998). Soil warming in a northern hardwood forest: Trace gas fluxes and leaf litter decomposition. *Canadian Journal of Forest Research*, *28*, 1365–1372.

Melillo, J. M., Butler, S., Johnson, J., Mohan, J., Steudler, P. A., Lux, H., et al. (2011). Soil warming, carbon-nitrogen interactions, and forest carbon budgets. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(23), 9508–9512. https://doi.org/10.1073/pnas.1018189108

Melillo, J. M., Frey, S. D., Deangelis, K. M., Werner, W. J., Bernard, M. J., Bowles, F. P., et al. (2017). Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science*, *358*(6359), 101–105. https://doi.org/10.1126/science.aan2874

Melillo, J. M., Steudler, P. A., Aber, J. D., Newkirk, K., Lux, H., Bowles, F. P., et al. (2002). Soil warming and carbon-cycle feedbacks to the climate system. *Science*, *298*(5601), 2173–2176. https://doi.org/10.1126/science.1074153

Milly, P. C. D. (1994). Climate, soil water storage, and the average annual water balance. *Water Resources Research*, *30*(7), 2143–2156.

Minasny, B., & McBratney, A. B. (2017). Limited effect of organic matter on soil available water capacity. *European Journal of Soil Science*, *69*(1), 39–47.

Noh, N. J., Kuribayashi, M., Saitoh, T. M., & Muraoka, H. (2017). Different responses of soil, heterotrophic and autotrophic respirations to a 4-year soil warming experiment in a cool-temperate deciduous broadleaved forest in central Japan. *Agricultural and Forest Meteorology*, *247*, 560–570.

Oksansen, L. (2001). Logic of experiments in ecology: Is pseudoreplication a pseudoissue? *Oikos*, *94*, 27–38.

Peterjohn, W. T., Melillo, J. M., Steudler, P. A., Newkirk, K. M., Bowles, F. P., & Aber, J. D. (1994). Response of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecological Applications*, *4*(3), 617–625.

Philips, S. C., Varner, R. K., Frolking, S., Munger, J. W., Bubier, J. L., Wofsy, S. C., & Crill, P. M. (2010). Interannual, seasonal, and diel variation in soil respiration relative to ecosystem respiration at a wetland to upland slope at Harvard Forest. *Journal of Geophysical Research*, *115*, G02019. https://doi.org/10.1029/2008JG000858

Pold, G., Grandy, A. S., Melillo, J. M., & DeAngelis, K. M. (2017). Changes in substrate availability drive carbon cycle response to chronic warming. *Soil Biology and Biochemistry*, *110*, 68–78.

Pollacco, J. A. P. (2008). A generally applicable pedotransfer function that estimates field capacity and permanent wilting point from soil texture and bulk density. *Canadian Journal of Soil Science*, *88*(5), 761–774.

Ramirez, B. H., van der Ploeg, M., Teuling, A. J., Ganzeveld, L., & Keemans, R. (2017). Tropical montane cloud forests in the Orinoco river basin: The role of soil organic layers in water storage and release. *Geoderma*, *298*, 14–26.

Rawls, W. J., Pachepsky, Y. A., Ritchie, J. C., Sobecki, T. M., & Bloodworth, H. (2003). Effect of soil organic carbon on soil water retention. *Geoderma*, *116*(1– 2), 61–76.

Rustad, L. E., & Fernandez, I. J. (1998). Experimental soil warming effects on CO_2 and CH_4 flux from a low elevation spruce-fir forest soil in Maine, USA. *Global Change Biology*, *4*(6), 597–605.

Savage, K. E., & Davidson, E. A. (2001). Interannual variation of soil respiration in two New England forests. *Global Biogeochemical Cycles*, *15*(2), 337–350.

Schindlebacher, A., Zechmeister-Bolternstern, S., & Jandal, R. (2009). Carbon losses due to soil warming: Do autotrophic and heterotrophic soil respiration respond equally? *Global Change Biology*, *15*(4), 901–913.

Teramoto, M., Liang, N., Ishida, S., & Zeng, J. (2018). Long-term stimulatory warming effect on soil heterotrophic respiration in a cool-temperate broadleaved deciduous forest in Northern Japan. *Journal of Geophysical Research: Biogeosciences*, *123*, 1161–1177. https://doi.org/10.1002/2018JG004432

Teramoto, M., Liang, N., Takagi, M., Zeng, J., & Grace, J. (2016). Sustained acceleration of soil carbon decomposition observed in a 6-year warming experiment in a warm-temperate forest in southern Japan. *Scientific Reports*, *6*, 1–14.

Urbanski, S., Barford, C., Wofsy, S., Kucharik, C., Pyle, E., Budney, J., et al. (2007). Factors controlling CO_2 exchange on timescales from hourly to decadal at Harvard Forest. *Journal of Geophysical Research*, *112*, G02020. https://doi.org/10.1029/2006JG000293

Wolock, D. M., & McCabe, G. J. (1999). Explaining spatial variability in mean annual runoff in the coterminous United States. *Climate Research*, *11*(2), 149–159.

Yang, F., Zhang, G., Yang, J., Li, D., Zhao, Y., Liu, F., et al. (2014). Organic matter controls of soil water retention in an alpine grassland and its significance for hydrological processes. *Journal of Hydrology*, *519*, 3086–3093.

Zhou, Y., Melillo, J. M., Butler, S., & Mohan, J. E. (2011). Root standing crop and chemistry after six years of soil warming in a temperate forest. *Tree Physiology*, *31*(7), 707–717. https://doi.org/10.1093/treephys/tpr066