Global Change Biology

WILEY

Global Change Biology

RESEARCH ARTICLE OPEN ACCESS

Shifts in Microbial Thermal Traits Mitigate Heat-Induced Carbon Losses in Soils

Albert C. Brangarí[1,2,3] | Melissa A. Knorr[4] | Serita D. Frey[4] | Johannes Rousk[3,5]

[1]Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity & Ecosystem Dynamics, University of Amsterdam, Amsterdam, the Netherlands | [2]Institute for Physical Geography and Ecosystem Science, Lund University, Lund, Sweden | [3]Microbial Biogeochemistry in Lund (MBLU), Department of Biology, Lund University, Lund, Sweden | [4]Center for Soil Biogeochemistry and Microbial Ecology, Department of Natural Resources and the Environment, University of New Hampshire, Durham, New Hampshire, USA | [5]Microbial Ecology, Department of Biology, Lund University, Lund, Sweden

Correspondence: Albert C. Brangarí (a.carlesbrangari@uva.nl)

Received: 3 July 2025 | **Revised:** 8 September 2025 | **Accepted:** 7 October 2025

Funding: This work was supported by grants from the Swedish Research Council Formas (grant no. 2022-01478), the Carl Tryggers Stiftelse för vetenskaplig forskning (grant no. CTS 22: 2131) and the Knut and Alice Wallenberg Foundation (grant no. KAW 2022.0175; KAW 2023.0384). The Soil Warming × Nitrogen Addition Study at Harvard Forest is maintained with support from the National Science Foundation (NSF) Long-Term Ecological Research Program (DEB-1832110) and a Long-Term Research in Environmental Biology grant (DEB-1456610).

Keywords: carbon cycling | carbon use efficiency (CUE) | climate change mitigation | global warming | microbial ecology | Soil Warming × Nitrogen Addition (SWaN) Study at the Harvard Forest Long-Term Ecological Research (LTER) site | temperature sensitivity

ABSTRACT

Global warming is expected to transfer carbon from soil organic matter to atmospheric CO_2, with microbial communities playing a crucial role in regulating this exchange. While the immediate impact of temperature on microbial functions is well understood and causes soil carbon losses, the long-term response remains unclear, with losses stabilising over time, reducing the overall effect of chronic warming on soil organic carbon (SOC) stocks. Here, we examined the temperature dependence of microbial respiration and growth after 9 years of +5°C warming in a temperate forest. Using these temperature dependences and field temperature data, we modelled in situ carbon fluxes and changes in SOC stocks. Results showed that the direct effect of temperature initially increased respiration and growth, projecting a potential 31% SOC stock loss if the trend had persisted. However, the gradual optimisation of microbial traits to warming balanced the direct temperature effects, enhanced carbon use efficiency and offset CO_2 emissions. Together, these microbial trait shifts limited the heat-induced SOC loss to 15%, closely aligning with empirical observations. These findings suggest that microbial trait optimisation can moderate carbon emissions, providing a parsimonious mechanistic explanation for observations worldwide and underscoring the need to integrate microbial dynamics into models.

1 | Introduction

Soils store over 2000 Pg of carbon globally, amounting to a several times larger pool than that currently held in the atmosphere (Le Quéré et al. 2018). This reservoir results from the long-term balance between primary production carbon input from plants and loss via microbial decomposition of soil organic matter (Davidson and Janssens 2006). Climate warming disrupts this balance, as microbial decomposition rates respond more strongly to temperature than primary production (Smith and Dukes 2013). As a result, higher temperatures are expected to lead to a net transfer of carbon from soils to the atmosphere (Melillo et al. 2017; Soong et al. 2021), potentially reducing soil organic carbon (SOC) stocks and accelerating climate change (Heimann and Reichstein 2008). However, the situation is more complex than initially anticipated: warming-induced carbon losses tend to decline over time (Melillo et al. 2002; Verbrigghe et al. 2022), diminishing the long-term impact of warming on

SOC stocks. Soil microbial decomposers are thought to play a key role in this attenuation, but their contribution remains uncertain (Bradford 2013; Wieder et al. 2018), leaving the biological feedback that governs land-atmosphere carbon exchange yet to be explained.

To understand the impact of chronic warming on SOC stocks, a mechanistic understanding of both the direct and indirect effects of temperature on microbial decomposition is essential, along with their integration into models. Short-term experiments have consistently shown microbial respiration increases with temperature (Cruz-Paredes et al. 2021; Schindlbacher et al. 2015), reflecting the direct effect of temperature on decomposition rates. This knowledge has been incorporated into biogeochemical and Earth system models through temperature reduction functions (Bauer et al. 2008; Brangarí and Rousk 2025; Sierra et al. 2015). However, despite recent advances in representing complex interactions between abiotic and biotic factors in models (Abramoff et al. 2018; Ahrens et al. 2015), their treatment of temperature effects remains simplistic. The widespread use of universal and unresponsive reduction functions fails to capture the recently uncovered biological variance across climates and responses to climate change. For example, soil respiration and microbial growth depend differently on temperature (Birgander et al. 2013; Brangarí and Rousk 2025; Tian et al. 2023), leading to variations in microbial carbon use efficiency (CUE) across temperatures. This affects the fraction of carbon respired back into the atmosphere versus that incorporated into microbial biomass, with the potential to be stored as SOC. Studies have reported reduced (Li et al. 2019; Tian et al. 2023), increased (Frey et al. 2013; Zheng et al. 2019) or unchanged (Hagerty et al. 2014; Simon et al. 2020; Walker et al. 2018) CUEs in response to chronic warming. These differences may arise from the alignment between microbial thermal traits and environmental temperatures (Donhauser et al. 2020; Nottingham et al. 2022), with mismatches reducing microbial performance and CUE, and indirect effects of temperature on microbial composition and resource availability (Frey et al. 2013; García et al. 2023; Propster et al. 2023). The uncertain impact of direct and indirect effects of temperature on SOC stocks, coupled with the lack of a clear conceptual framework linking physiological, ecological and functional principles (Bradford 2013; Lennon et al. 2024; Trivedi et al. 2013), hinders our ability to integrate trait adaptation into models and predict how climate change is, and will continue, modulating soil-atmosphere carbon exchange.

Here, we investigated microbial thermal traits in a global change field experiment, where the soil of a temperate mixed deciduous forest had been continuously warmed 5°C above ambient for 9 years. Our main objective was to determine whether changes in thermal traits caused by chronic warming could help explain the initially large warming-induced SOC losses that diminished over time, thereby providing a mechanistic explanation for an important biological feedback modulating the land-atmosphere carbon exchange. We experimentally determined the temperature relationships of respiration and growth for the dominant decomposer organisms in soils (i.e., bacteria and fungi) from the ambient and warming treatments. These relationships served as proxies for microbial thermal traits specific to the soil and treatment, as they described microbial utilisation of carbon at different temperatures—whether respired or incorporated into microbial biomass—making them crucial for understanding how SOC cycling responds to temperature changes. From these relationships, we derived CUE and trait indices of minimum temperature ($T_{\min}$) and temperature sensitivity (Q_{10}). Integrating these thermal relationships with high-resolution soil temperature and moisture data collected in the field, we estimated in situ soil heterotrophic respiration and microbial growth throughout a natural year, being able to assess annual carbon budgets. By comparing these to estimates without thermal optimisation, we could differentiate direct and indirect effects of temperature on carbon fluxes. Finally, we used a basic input–output SOC conceptual model to quantify the implications of shifts in microbial thermal traits for carbon cycling under warming. We expected that such shifts would explain the initially large losses that diminished over time, providing a microbial-based mechanistic explanation for this attenuation and for the observed 15% reduction in SOC stocks after 9 years of warming (Table 1).

2 | Materials and Methods

2.1 | Field Experiment and Sample Collection

Soil samples were collected from the Soil Warming × Nitrogen Addition (SWaN) Study located at the Harvard Forest Long-Term Ecological Research (LTER) site in Petersham,

TABLE 1 | Main soil characteristics and their statistics.

	Total C [mg C/g]	Total N [mg N/g]	C:N	pH	WC [g/g]	ρ [g/cm^3]	SOC [g C/m^2]
Ambient ORG	319 ± 26	13.7 ± 1.3	22.5 ± 0.3	4.05 ± 0.06	1.02 ± 0.09	0.22 ± 0.02	5879 ± 346
Ambient MIN	63 ± 5	3.1 ± 0.2	20.5 ± 0.7	4.86 ± 0.06	0.37 ± 0.02	0.54 ± 0.04	
Warming ORG	264 ± 42	10.9 ± 1.8	22.1 ± 1.1	4.05 ± 0.11	0.60 ± 0.09	0.27 ± 0.03	5010 ± 602
Warming MIN	55 ± 4	3.0 ± 0.3	18.8 ± 0.8	5.02 ± 0.03	0.31 ± 0.02	0.54 ± 0.04	
p-T	*	ns	ns	ns	***	ns	ns
p-D	***	***	***	***	***	***	—
p-N	ns	ns	ns	ns	ns	ns	ns

Note: The table presents mean values ± standard error. It includes total carbon, total nitrogen, carbon to nitrogen ratio, pH, water content, bulk density and soil organic carbon stocks in the organic (ORG) and mineral (MIN) soil horizons. The *p*-values are the values of significance for differences between temperature treatments (T), soil depths (D) and nitrogen treatments (N). Significance levels: ***$p < 0.001$; *$p < 0.05$; ns, not significant. Refer to Table S1 for detailed statistics.

Massachusetts, USA. Initiated in 2006, the fully factorial experiment includes twenty-four 3 × 3 m plots randomly assigned to one of four treatments with six replicates each: 'control', 'heated', 'N-addition' or 'heated × *N*-addition' (see Supporting Information S1; Contosta et al. 2011). Soils in all heated plots had been continuously warmed to ca. 5°C above ambient (Figure S1) using buried electrical cables, representing a plausible warming scenario projected for the end of the century under climate change (IPCC 2021). In ambient plots, the temperature range recorded spanned from −1.0°C to 23.2°C, while in warmed plots, the range extended from 3.7°C to 27.1°C. For the purpose of this study, we specifically focused on the differences generated by temperature differences. To assess the warming effect, we grouped the 'heated' and 'heated × *N*-addition' treatments and hereafter are referred to as 'warming'. The 'control' and 'N-addition' treatments were also pooled and are referred to as 'ambient'. Soil cores were collected in October 2015 from each one of the experimental plots, with one core per plot, except for one heated replicate plot, where cable damage in 2009 had resulted in it no longer being heated. Cores were extracted using a 5.7 cm diameter stainless steel corer to a depth of 10 cm, encompassing both an organic layer (upper 3–5 cm) and the mineral horizon underneath (10 cm), which were separated immediately upon collection. The soil samples were gently homogenised, sieved (2 mm) and stored in gas-permeable plastic bags at ~5°C during shipping and until analyses were initiated within 10 days after sampling.

2.2 | Microbial Analyses

We measured the temperature relationships for respiration rates and for growth rates of the bacteria and fungi as previously described (Cruz-Paredes et al. 2021), incubating the samples at the screening temperatures of 4°C, 16°C, 25°C and 35°C. Incubation times were kept short (0.75–7 h at 35°C, depending on the method used; see Supporting Information S1 for details) to ensure comparable levels of carbon and nutrient use. Times were adjusted for temperature using a Q_{10} of 2, meaning that the duration was doubled for every 10°C decrease in incubation temperature. This approach was selected to isolate the direct effect of temperature on microbial rates and minimise the influence of altered conditions (Cruz-Paredes et al. 2021; Hartley et al. 2008; Kirschbaum 2006; Rousk and Bååth 2011). This maximised the preservation of field characteristics of soils and microbial communities, along with the respective effects of treatments on microbial traits, carbon and nutrient resources.

Soil respiration rates were assessed through gas chromatography, quantifying the accumulation of headspace CO_2 in the incubation vials (as in Rousk and Frey 2015). Bacterial growth was estimated by the leucine incorporation method (Rousk and Bååth 2011), using the tracking of trace concentrations of added radiolabels into bacterial proteins. Fungal growth was assessed using the acetate-in-ergosterol method (Rousk and Bååth 2011), in which actively growing fungi incorporate radiolabelled acetate into the fungal-specific lipid ergosterol. The incorporation of these radiolabelled tracers was then quantified and converted to fungal and bacterial carbon production per unit time (Soares and Rousk 2019), which was summed to total microbial growth. See Supporting Information S1 for additional details on laboratory techniques.

2.3 | Microbial Temperature Relationships

The rates of respiration, bacterial growth and fungal growth performed at the different screening temperatures were subjected to fitting using the Lloyd and Taylor model (Lloyd and Taylor 1994) for respiration and the Ratkowsky model (Ratkowsky et al. 1983) for growth. For consistency, the Ratkowsky model was additionally used to estimate the thermal trait indices T_{min} and Q_{10} for both respiration and growth. This combined approach allowed for optimal fitting of data across the entire temperature range under study and facilitated comparison among treatments (see Supporting Information S1 for details).

Microbial CUE was then determined by dividing the temperature relationships of the total microbial production (i.e., bacterial and fungal growth combined) by the total amount of carbon used (i.e., the sum of total microbial growth and respiration). To establish the temperature relationship of in situ CUE, we standardised the temperature relationships per unit of surface area and depth, calculated their CUEs across temperatures and then averaged them for each temperature treatment. Subsequently, we estimated the 'optimal' temperature (tipping point) of CUE, marking the temperature at which microbial functioning becomes compromised as temperature nears the limits of microbial physiology of the community.

2.4 | Modelling In Situ Microbial Biomass Production and Microbial CO_2 Emissions

To model in situ microbial process rates, we combined high-resolution soil temperature data (measured hourly throughout a full annual cycle in both ambient and warmed plots at the field site; Figure S1) with the intrinsic temperature relationships derived from the Ratkowsky and the Lloyd and Taylor models. To incorporate the effects of water limitation on carbon fluxes, we utilised soil moisture data continuously recorded in the field and applied the moisture reduction function implemented in the CENTURY model (see Supporting Information S1 for details).

For each treatment, microbial process rates were estimated by coupling the temperature response functions with the corresponding in situ soil temperature records: ambient temperature relationships with ambient temperature data and warming temperature relationships from all heated plots with the warmed temperature data. Bacterial and fungal growth were combined to obtain total microbial production. Fluxes were scaled to the field level by normalising per unit of soil surface area and accounting for soil bulk density and SOC concentration.

We then assessed the direct effect of warming by comparing the flux estimates using the temperature relationships derived from the ambient temperature treatments at ambient temperature (scenario in all unheated plots) to those using ambient temperature traits but simulated as exposed to the temperature recorded in the warmed plots at +5°C (crossed scenario). To distinguish the indirect effect of temperature (i.e., due to the changes in microbial temperature sensitivities and resource availability) from the direct, we compared the rate estimates simulated by using the temperature relationships derived from the ambient temperature treatments at +5°C (crossed scenario) to those using the warm-tolerant temperature relationships parameterised with the same warmed temperature data (scenario in warmed plots).

The total annual production of microbial carbon and respired carbon was estimated by summing up each hourly rate, determined with a 1-h time step, over the entire year.

2.5 | Modelling SOC Stocks

The impact of temperature treatments on SOC stocks was assessed through a fundamental conceptual model that delineates the mass balance of carbon between input and output fluxes within the soil system. Soil heterotrophic respiration served as the exclusive output flux from soils, with litter and root exudates acting as the input. Autotrophic respiration was not considered due to its negligible impact on SOC stocks at the plot scale. Microbial growth was conceptualised as a loop flux in the soil system, involving the utilisation of SOC to generate new microbial biomass, considered a form of SOC, without altering the pool's size.

Following the establishment of the model structure, we quantified changes in SOC stocks over time for each treatment. For this, we used the modelled in situ annual rates for microbial respiration (output) and microbial growth (loop). Annual inputs were estimated to sustain equilibrium in the ambient treatment, ensuring no change in SOC stocks and considered uniform across treatments (i.e., the 9-year warming had no significant impact on plant inputs at the time of sampling; unpublished results in SWaN).

We first estimated SOC changes in the ambient and warmed treatments by modelling their cumulative effects on SOC stocks over 9 years. In addition to these, we examined two crossed scenarios. The first scenario isolated the direct effect of temperature by applying microbial traits derived from ambient plots to the warmed temperature regime (‘ambient +5°C’). The second scenario investigated the effects of a realistic microbial trait adaptation to the warmed temperature regime by simulating a gradual transition (linear) in traits from the ambient to the warm-adapted state (‘ambient +5°C to warming’), which is considered to represent the actual and most mechanistic representation of the microbially induced carbon transformation over time.

2.6 | Model Considerations

The estimation of carbon fluxes and SOC stocks in natural environments using temperature relationships established in the laboratory is a simplification with associated caveats. Even though the model incorporates the role of soil moisture as a key control on microbial growth and respiration (Brangarí et al. 2020; Sierra et al. 2015), this study did not explicitly account for treatment-specific differences in water limitation or the potential optimisation of microbial responses to moisture. However, point measurements from the SWaN study site indicate negligible reductions in soil moisture in warmed plots for most of the year (Knorr et al. 2024), supporting the assumption of similar moisture conditions across treatments. Moreover, the temperature-driven variation in our estimates remains robust, as temperature and moisture act as independent rate modifiers (Cruz-Paredes et al. 2021) and treatment effects are persistent across seasons and soil depths (Tian et al. 2023). In addition to temperature and moisture, microbial rates are influenced by resource availability. Our model implicitly captures these effects, as the short-term incubations used to derive temperature relationships aim to preserve field conditions, including treatment-specific differences in nutrient and carbon availability. Oxygen was not explicitly considered, given that it is unlikely to be limiting in the well-drained silty loam soils of the Harvard Forest. Despite its simplicity, the use of Lloyd and Taylor and Ratkowsky formulations has consistently proven effective in capturing immediate temperature effects on carbon fluxes across a wide range of settings, from controlled experiments to complex field conditions (Bååth 2018; Del Grosso et al. 2005; Li et al. 2021; Lloyd and Taylor 1994; Portner et al. 2010; Ratkowsky et al. 1983; Rijkers et al. 2022).

The input–output model also simplifies the representation of organic matter in soils, considering a single, homogeneous SOC pool in the top 10 cm of the soil profile and focusing on fluxes derived from measured relationships for heterotrophic respiration and microbial growth. As a result, direct comparisons with field chamber measurements, which include autotrophic respiration from plants and potential contributions from deeper layers, are not straightforward. Nevertheless, by focusing on the core microbial processes that govern SOC dynamics, the model provides valuable insights into complex soil-ecosystem responses to warming.

2.7 | Statistics

Treatment effects in temperature relationships were assessed using three-way analyses of variance (ANOVA), considering temperature, depth and N-addition as fixed factors. For analyses of production per unit soil surface area and the temperature sensitivity of CUE, we used two-way ANOVA with temperature and N-addition as factors. Similarly, to evaluate the direct and indirect effects of temperature, we applied two-way ANOVA with warming treatment and model assumptions (e.g., simulations combining temperatures and trait relationships) as fixed factors. Statistical significance was reported using p-values and F-values, with subscripts indicating the degrees of freedom for the effect and error terms, respectively. Although the figures display only the ambient and warming treatments, and nitrogen-fertilisation treatments are not plotted separately, all four treatment combinations were included in the statistical analyses. To meet assumptions of normality and homogeneity of variance, data were log-transformed prior to analysis. All statistical tests were conducted using JMP 17.0.0 for Mac (SAS Institute, Cary, NC, 1989-2023).

3 | Results

3.1 | Shifts in Microbial Traits Under Chronic Soil Warming

Rates of heterotrophic soil respiration and microbial growth, as measured in lab incubations across a temperature gradient, exhibited consistent patterns across soil depths and warming treatments (Figure 1). Respiration rates increased monotonically throughout the measured temperature range (Figure 1a), and were well matched by the Lloyd and Taylor model (Lloyd and Taylor 1994) (all $R^2 \geq 0.99$). The indices for thermal traits $T_{\min}$ and Q_{10} for respiration were unaffected by warming (all $p > 0.1$) (Table S2). Bacterial and fungal growth rates increased with temperature until an optimum value—around 30°C for bacteria and 35°C–40°C for fungi—beyond which rates dropped (Figure 1b,c). These patterns were well described by the Ratkowsky model (Ratkowsky et al. 1983) (all $R^2 \geq 0.93$). Warming caused significant shifts in growth-temperature relationships, indexed as higher $T_{\min}$ values for bacteria ($p < 0.05$) and fungi ($p < 0.001$) (Figure 1, Table S2), along with increased Q_{10} values for both groups ($p < 0.01$). These temperature-dependent respiration and growth relationships were consistent across soil horizons (all $p > 0.1$) and nitrogen addition treatments (all $p > 0.1$). Additionally, exposure to chronic warming generally altered the absolute rates of respiration and growth at all temperatures during incubations, quantified here as rates per gram of SOC at 25°C (bottom panels in Figure 1). Respiration rates consistently decreased by 23% in all warmed soils ($p = 0.01$, Table S3) (Figure 1d). In contrast, fungal growth rates increased by about 20% ($p = 0.03$) (Figure 1e,f) and bacterial growth rates did not detectably respond ($p = 0.85$).

On average, CUE increased with temperature (Figure S2), reaching a maximum of 17% at 14°C in warmed plots and 14% at 12°C in the ambient treatment ($p = 0.02$; Table S4), followed by a slow decrease with further temperature rise. CUE in warmed plots exhibited an increase of approximately +2.1% CUE units across the studied temperature range.

3.2 | Implications of Microbial Traits for Field Carbon Fluxes

Modelled in situ microbial respiration rates per unit SOC were ~13% higher throughout the year in warmed compared to ambient plots (Figure 2a), whereas microbial growth rates were consistently ~39% higher (Figure 2b).

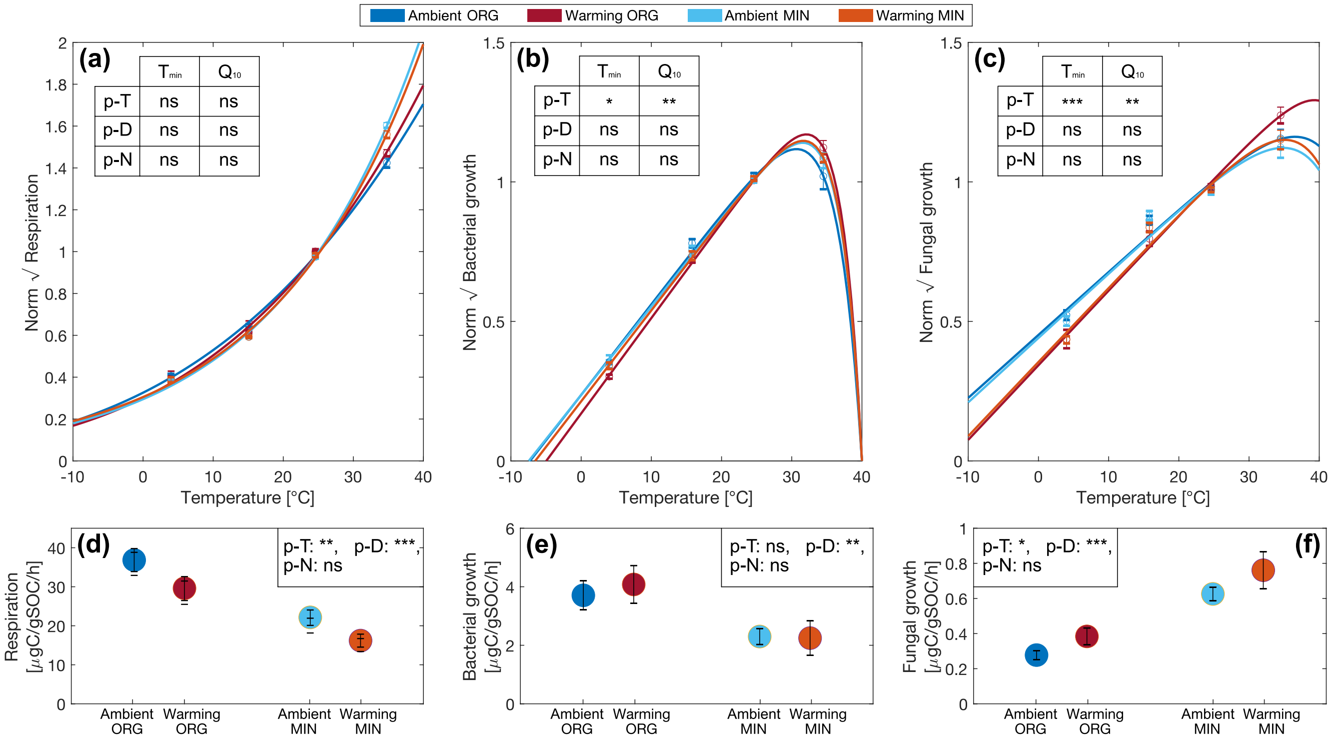

FIGURE 1 | Temperature dependences of microbial respiration and growth. The figure shows the temperature relationships associated with the organic (ORG) versus mineral (MIN) soil horizons under the field temperature treatments 'Ambient' versus 'Warming' as measured in short-term lab incubations across a temperature gradient. Panels (a), (b) and (c) display the normalised rates of soil respiration, bacterial growth and fungal growth, respectively, along with the best-fit curves obtained from the Lloyd and Taylor model (for respiration) and the Ratkowsky model (for growth). Panels (d), (e) and (f) show the non-normalised rates at 25°C for respiration, bacterial growth and fungal growth, respectively. Error bars represent standard errors. The *p*-values indicate the significance of the differences between temperature treatments (p-T), soil depths (p-D) and nitrogen addition treatments (p-N). Significance levels: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; ns, not significant. Refer to Tables S2 and S3 for sensitivity indexes and detailed statistics.

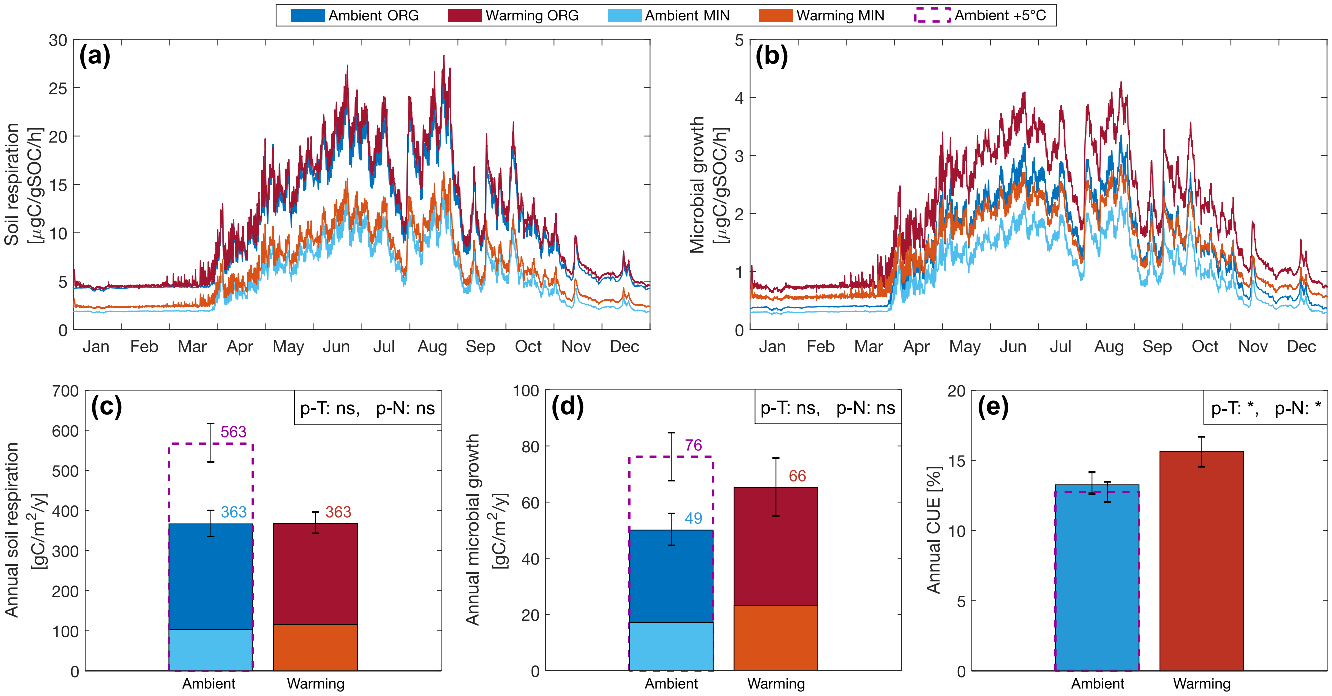

FIGURE 2 | Modelled annual dynamics of soil respiration and microbial growth. Panels show soil heterotrophic respiration (panel a) and microbial growth (panel b) throughout a natural year in the organic (ORG) and mineral (MIN) soil horizons under 'Ambient' and 'Warming' treatments and total annual rates for respiration (panel c), growth (panel d) and carbon use efficiency (panel e). Rates obtained by combining empirical thermal relationships with high-resolution field-collected soil temperature data and incorporating the effect of moisture limitation. Stacked bars show the implications of the temperature treatments across both soil horizons. Bars with dashed patterns show the direct effect of temperature on rates, obtained by combining the ambient temperature relationships (unheated) with field temperatures of the warmed plots (+5°C). Error bars represent standard errors. The p-values indicate the significance of the differences between temperature treatments (p-T) and nitrogen addition treatments (p-N). Significance levels: $^*0.01 < p < 0.05$; ns, not significant. Refer to Table S5 for detailed statistics and to Table S6 for detailed statistics on differences between direct and indirect effects.

Assessing the modelled annual gross fluxes at the field scale, we estimated the influence of field temperature treatments on the in situ annual cumulative rates per land area (solid bars in Figure 2). Modelled annual soil emissions (Figure 2c) were unaffected by warming ($p > 0.1$, Table S5); however, annual microbial growth, considering bacteria and fungi together, exhibited a 33% increasing trend in warmed soils (Figure 2d), although this effect was not statistically significant ($p = 0.14$). These distinct patterns yielded an 18% increase in the annual plot-level CUE in warmed plots, from 13.3% to 15.7% ($p = 0.03$) (Figure 2e).

The simulated effects of soil moisture limitation on in situ microbial activity were primarily evident during the peak of the dry season (Figure 2), from late June to mid-September (Figure S3a). During this period, microbial rates showed a slight but non-significant decrease compared to the scenario that considered only temperature effects (Figure S4a,b) ($p > 0.1$, Table S7). This resulted in a minor reduction (~7%) in the cumulative carbon fluxes by the end of the year (Figure S4c,d) and minimal differences in CUE (<1%) (Figure S4e).

3.3 | Direct and Indirect Effects of Temperature on Carbon Cycling and SOC Stocks

Modelling in situ heterotrophic respiration using the temperature relationships obtained from the lab incubations indicated that the direct effect of warming (i.e., considering only the temperature increase, without shifts in thermal traits) would increase annual heterotrophic CO_2 emissions by 55% ($p = 0.049$, Table S6) (Figure 2c) and annual microbial growth by 53% ($p = 0.048$) (compare the empty bars with dashed lines to blue bars in Figure 2d). These fluxes counteracted each other, resulting in unchanged CUE ($p = 0.78$) (Figure 2e). The cumulative impact of these microbial warming responses over 9 years, however, would lead to a substantial 31% reduction in modelled stocks of SOC by direct warming effects (Figure 3b,e).

When examining the indirect effect of temperature (i.e., considering both the temperature increase and the shift in thermal traits; compare the empty bars with dashed lines to red bars in Figure 2), the model revealed a moderate 36% decrease in total respiration ($p = 0.07$) and a slight 13% decrease in total microbial growth ($p = 0.81$), together resulting in a complete neutralisation of the direct effects of temperature (all $p > 0.05$). These responses combined to produce an 18% increase in CUE in the warmed soils (Figure 2c), resulting in a new equilibrium between carbon inputs and outputs, and consequently, no further changes to SOC stocks (Figure 3c,e).

The scenario where microbial thermal traits would undergo a linear shift over 9 years of warming, transitioning from ambient to warming-optimised traits while exposed to a +5°C throughout, projected a progressive reduction of heat-induced CO_2

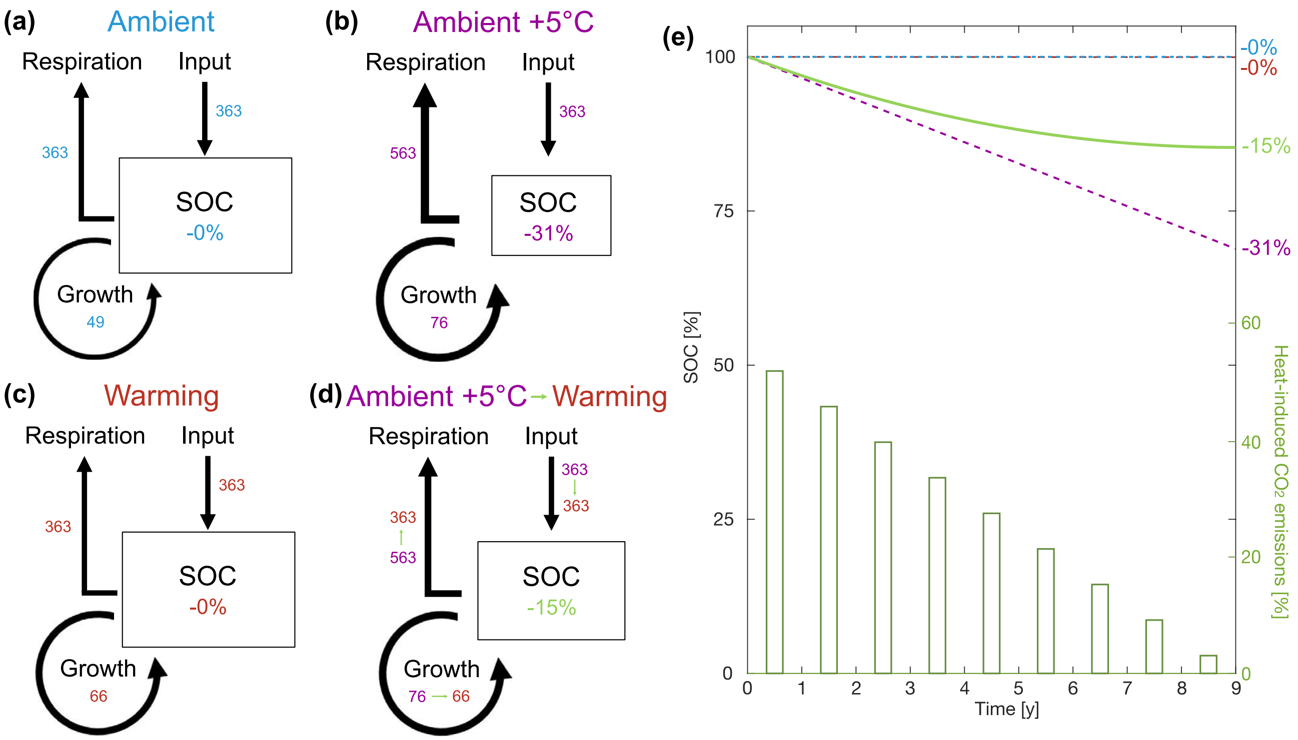

FIGURE 3 | Predicted carbon cycling and changes in SOC stocks using the input–output model. Panels (a), (b) and (c) present a conceptual sketch with the annual fluxes for the 'Ambient', 'Ambient +5°C' and 'Warming' scenarios based on the annual microbial respiration, annual growth and plant input estimates. Panel (d) depicts the sketch of the scenario where 'Ambient +5°C' gradually transforms into 'Warming', indicating the shift in microbial traits over time. Panel (e) illustrates the changes in SOC over 9 years for all scenarios (left *y*-axis) and the modulation of heat-induced CO_2 emissions assuming gradual optimisation of traits (right *y*-axis). The thickness of arrows in the figure indicates the size of fluxes, while the size of boxes represents the changes in SOC stocks.

emissions, ultimately resulting in a 15% reduction of SOC stocks (Figure 3d,e).

4 | Discussion

The consequences of climate warming for SOC storage are yet to be fully understood. Although warming initially accelerates microbial decomposition and CO_2 release to the atmosphere, long-term field studies consistently report a dampening of this response within the first decade after warming (Melillo et al. 2017, 2002; Verbrigghe et al. 2022). Microbial temperature relationships established in the laboratory cannot readily explain these dynamics. However, our simple modelling approach permitted upscaling laboratory data to the soil-ecosystem level, enabling an assessment of the in situ microbially induced carbon cycling dynamics affecting land-atmosphere exchange and matching the SOC reductions observed at the Harvard Forest. While the framework was not designed to identify specific drivers of changes in microbial thermal traits, it provides a basis for interpreting their implications for carbon cycling over time and their consequent effects on soil carbon stocks.

Warming treatments induced shifts in the thermal traits that defined the temperature relationships of both bacterial and fungal growth, as evidenced by significant differences in T_{min} and Q_{10} indices, while the temperature relationship for respiration was unaffected (Figure 1). Similarly, when assessing the annual rates in plots subjected to 9 years of +5°C warming, microbial growth was stimulated compared to the ambient plots, leading to higher cumulative microbial biomass production, yet with a residual impact on soil respiration, resulting in equivalent levels of modelled microbial CO_2 emissions by the end of the year for both treatments (Figure 2). As a direct outcome of these two opposing responses—moderately increased microbial growth and maintained respiration—the CUE of soil microorganisms subjected to chronic warming increased by 18%. Simulations also revealed that the direct effect of temperature would have led to a cumulative increase of over 50% in both microbial growth and microbial CO_2 emissions in warmed plots. These increases align with the principles of basic thermodynamics and reports of immediate responses to rising temperatures (Birgander et al. 2013; Kirschbaum 2006; Nottingham et al. 2022; Schindlbacher et al. 2015). However, when also accounting for indirect effects of warming (i.e., including changes in microbial thermal traits), the actual impact on microbial growth was reduced by nearly half and eliminated for microbial respiration.

Explaining the causes of these patterns poses a challenge. Reductions in microbial growth rates in long-term warmed plots have previously been associated with decreased resource availability (Domeignoz-Horta et al. 2022; Melillo et al. 2017, 2002; Walker et al. 2018) and increased nitrogen availability in warmed plots (Frey et al. 2013; Tian et al. 2023) has been reported to increase total soil respiration (Knorr et al. 2024). However, the asymmetric impact on microbial rates, where respiration is more strongly downregulated than growth, suggests that resource availability alone does not explain the observed trait shifts. Instead, 9 years of warming likely induced a combination of physiological, evolutionary and community-level changes accumulated over time (Bradford 2013; Martiny et al. 2023; Pold et al. 2020), resulting in microbial communities with traits optimised for efficient growth (Roller and Schmidt 2015) under warmed conditions, thereby minimising carbon losses. The observed changes in microbial community structure under chronic warming (Figure S5) are consistent with a causal relationship where compositional changes led to a shift in functional traits. This finding is consistent with studies at the Harvard Forest that reported shifts in microbial community composition and diversity in heated plots (Anthony et al. 2021; Frey et al. 2008; Pec et al. 2021).

These observed shifts in thermal traits have profound and persistent implications for SOC stocks. The fact that warm-adjusted microbial traits do not lead to increased microbial emissions compared to the ambient, yet still result in SOC losses, is not immediately intuitive. However, a gradual optimisation of thermal traits does provide a simple explanation for the mitigation of CO_2 emissions over time and the reduction in SOC stocks observed (Figure 4), underscoring the importance of temporal dynamics in ecosystems. Following the application of warming treatments, microbial traits initially remained aligned with ambient conditions (no trait adaptation). As a consequence, the direct effect of temperature led to accelerated microbial metabolism and enhanced CO_2 emissions, driven by the direct effect of temperature, causing an estimated ~4.5% loss in SOC during the first year, which, if sustained, would have resulted in a 31% loss over 9 years (Figures 3 and 4). However, the gradual optimisation of microbial traits progressively reduced CO_2 emissions, resulting in a stabilisation of SOC stocks around the observed 15% reduction. This phenomenon is consistent with earlier observations of enhanced soil emissions occurring only in the initial years after warming treatment application (Melillo et al. 2002), followed by a gradual cessation of this effect (Melillo et al. 2017; Verbrigghe et al. 2022). It would be valuable to explore whether these patterns emerge as properties of trait optimisation in microbially explicit models that incorporate complex biotic and abiotic interactions. It also remains unassessed if the reported state of stability with microbial traits aligning with field temperatures will persist, a question that should guide future investigations.

Longer-term observations suggest that such stability may not be maintained, as other processes, mechanisms and their dynamics come into influencing soil carbon cycling. A 26-year soil warming experiment at the Harvard Forest reported alternating phases with and without carbon loss over time (Melillo et al. 2017). Following the stabilisation of soil respiration in the warmed plots during the first decade, a reversal of the trend

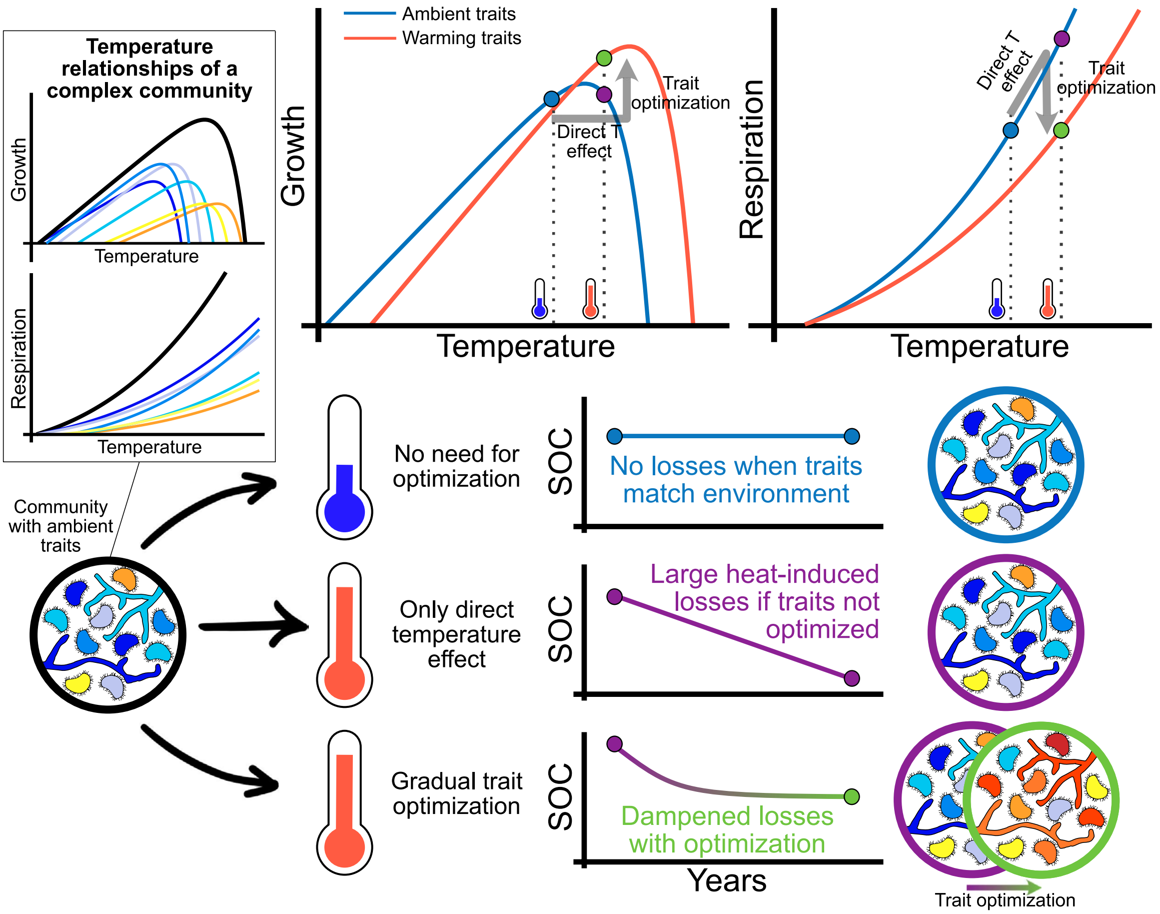

FIGURE 4 | Conceptual model of microbial and carbon responses to chronic warming. The schematic illustrates how long-term warming alters the temperature relationships of microbial growth and respiration (shown as absolute rates) within composite microbial communities and the resulting consequences for soil organic carbon stocks over time. Distinguishing between direct and indirect effects of temperature (T) provides a comprehensive explanation for the initially accelerated carbon losses, which were gradually mitigated over time by trait optimisation.

was observed, with emissions once again exceeding those of the unheated plots. This oscillatory behaviour may be explained by differences in the timing of temperature-trait adaptation to warming, driven mainly by soil microorganisms during the first decade and subsequently by vegetation, which caused a renewed disequilibrium in the plant–soil-microbe system and an associated increase in respiration. Such dynamics could potentially be captured by the model if supplemented with microbial trait estimates and plant-level responses, leading to further SOC reductions at the site (as in Knorr et al. 2024; Muratore et al. 2025), although this was not tested. Several non-microbial factors can also interact to influence the timing and magnitude of soil carbon loss (Melillo et al. 2017), including changes in the amount and quality of soil carbon pools (Davidson and Janssens 2006; Frey et al. 2013) and in root-derived carbon inputs to the soil (Muratore et al. 2025).

In conclusion, our study shows that shifts in microbial temperature relationships have the potential to mitigate warming-induced carbon emissions in soils, where a combination of direct and indirect effects of temperature on microbial traits can explain the observed patterns. Our analysis suggests that the gradual optimisation of microbial thermal traits over time alone could reduce soil CO_2 emissions, dampening SOC losses from 31% (as predicted under constant traits) to just a 15% reduction after 9 years of warming, closely matching SOC stock estimates at the time of sampling. Our findings can thus offer a parsimonious explanation for the biological feedback driving warming effects on soil carbon globally, calling for validation in independent ecosystems to enable a broader generalisation. Our study also accentuates the significance of accounting for the dynamic alignment of microbial traits to environmental change, highlighting the limitations of biogeochemical and Earth system models that assume static and universal microbial traits when projecting SOC responses to global warming.

Acknowledgements

This work was supported by grants from the Swedish Research Council Formas (grant no. 2022-01478), the Carl Tryggers Stiftelse för vetenskaplig forskning (grant no. CTS 22: 2131) and the Knut and Alice Wallenberg Foundation (grant no. KAW 2022.0175; KAW 2023.0384). The Soil Warming × Nitrogen Addition Study at Harvard Forest is maintained with support from the National Science Foundation (NSF) Long-Term Ecological Research Program (DEB-1832110) and a Long-Term Research in Environmental Biology grant (DEB-1456610).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and MATLAB scripts used to generate model results and figures are publicly available via GitHub at https://github.com/Brangari/HarvardForest.git and Zenodo at https://doi.org/10.5281/zenodo.17293274.

References

Abramoff, R., X. Xu, M. Hartman, et al. 2018. "The Millennial Model: In Search of Measurable Pools and Transformations for Modeling Soil Carbon in the New Century." *Biogeochemistry* 137, no. 1–2: 51–71. https://doi.org/10.1007/s10533-017-0409-7.

Ahrens, B., M. C. Braakhekke, G. Guggenberger, M. Schrumpf, and M. Reichstein. 2015. "Contribution of Sorption, DOC Transport and Microbial Interactions to the ^{14}C Age of a Soil Organic Carbon Profile: Insights From a Calibrated Process Model." *Soil Biology and Biochemistry* 88: 390–402. https://doi.org/10.1016/j.soilbio.2015.06.008.

Anthony, M. A., M. Knorr, J. A. M. Moore, M. Simpson, and S. D. Frey. 2021. "Fungal Community and Functional Responses to Soil Warming Are Greater Than for Soil Nitrogen Enrichment." *Elementa* 9, no. 1: 1–15. https://doi.org/10.1525/elementa.2021.000059.

Bååth, E. 2018. "Temperature Sensitivity of Soil Microbial Activity Modeled by the Square Root Equation as a Unifying Model to Differentiate Between Direct Temperature Effects and Microbial Community Adaptation." *Global Change Biology* 24, no. 7: 2850–2861. https://doi.org/10.1111/gcb.14285.

Bauer, J., M. Herbst, J. A. Huisman, L. Weihermüller, and H. Vereecken. 2008. "Sensitivity of Simulated Soil Heterotrophic Respiration to Temperature and Moisture Reduction Functions." *Geoderma* 145, no. 1–2: 17–27. https://doi.org/10.3987/REV-08-634.

Birgander, J., S. Reischke, D. L. Jones, and J. Rousk. 2013. "Temperature Adaptation of Bacterial Growth and ^{14}C-Glucose Mineralisation in a Laboratory Study." *Soil Biology and Biochemistry* 65: 294–303. https://doi.org/10.1016/j.soilbio.2013.06.006.

Bradford, M. A. 2013. "Thermal Adaptation of Decomposer Communities in Warming Soils." *Frontiers in Microbiology* 4: 1–16. https://doi.org/10.3389/fmicb.2013.00333.

Brangarí, A. C., S. Manzoni, and J. Rousk. 2020. "A Soil Microbial Model to Analyze Decoupled Microbial Growth and Respiration During Soil Drying and Rewetting." *Soil Biology and Biochemistry* 148: 107871. https://doi.org/10.1016/j.soilbio.2020.107871.

Brangarí, A. C., and J. Rousk. 2025. "A Unified Representation of the Temperature Dependences of Soil Microbial Growth and Respiration." *Communications Earth & Environment* 6, no. 1: 724. https://doi.org/10.1038/s43247-025-02707-1.

Contosta, A. R., S. D. Frey, and A. B. Cooper. 2011. "Seasonal Dynamics of Soil Respiration and N Mineralization in Chronically Warmed and Fertilized Soils." *Ecosphere* 2, no. 3: art36. https://doi.org/10.1890/ES10-00133.1.

Cruz-Paredes, C., D. Tájmel, and J. Rousk. 2021. "Can Moisture Affect Temperature Dependences of Microbial Growth and Respiration?" *Soil Biology and Biochemistry* 156: 108223. https://doi.org/10.1016/j.soilbio.2021.108223.

Davidson, E. A., and I. A. Janssens. 2006. "Temperature Sensitivity of Soil Carbon Decomposition and Feedbacks to Climate Change." *Nature* 440: 165–173.

Del Grosso, S. J., W. J. Parton, A. R. Mosier, et al. 2005. "Modeling Soil CO_2 Emissions From Ecosystems." *Biogeochemistry* 73, no. 1: 71–91. https://doi.org/10.1007/s10533-004-0898-z.

Domeignoz-Horta, L. A., G. Pold, H. Erb, et al. 2022. "Substrate Availability and Not Thermal Acclimateion Controls Microbial Temperature Sensitivity Response to Long-Term Warming." *Global Change Biology* 29: 1–17. https://doi.org/10.1111/gcb.16544.

Donhauser, J., P. A. Niklaus, J. Rousk, C. Larose, and B. Frey. 2020. "Temperatures Beyond the Community Optimum Promote the Dominance of Heat-Adapted, Fast Growing and Stress Resistant Bacteria in Alpine Soils." *Soil Biology and Biochemistry* 148: 107873. https://doi.org/10.1016/j.soilbio.2020.107873.

Frey, S. D., R. Drijber, H. Smith, and J. Melillo. 2008. "Microbial Biomass, Functional Capacity, and Community Structure After 12 Years of Soil Warming." *Soil Biology and Biochemistry* 40, no. 11: 2904–2907. https://doi.org/10.1016/j.soilbio.2008.07.020.

Frey, S. D., J. Lee, J. M. Melillo, and J. Six. 2013. “The Temperature Response of Soil Microbial Efficiency and Its Feedback to Climate.” *Nature Climate Change* 3, no. 4: 395–398. https://doi.org/10.1038/nclimate1796.

García, F. C., T. Clegg, D. B. O'Neill, R. Warfield, S. Pawar, and G. Yvon-Durocher. 2023. “The Temperature Dependence of Microbial Community Respiration Is Amplified by Changes in Species Interactions.” *Nature Microbiology* 8, no. 2: 272–283. https://doi.org/10.1038/s41564-022-01283-w.

Hagerty, S. B., K. J. van Groenigen, S. D. Allison, et al. 2014. “Accelerated Microbial Turnover but Constant Growth Efficiency With Warming in Soil.” *Nature Climate Change* 4, no. 10: 903–906. https://doi.org/10.1038/nclimate2361.

Hartley, I. P., D. W. Hopkins, M. H. Garnett, M. Sommerkorn, and P. A. Wookey. 2008. “Soil Microbial Respiration in Arctic Soil Does Not Acclimate to Temperature.” *Ecology Letters* 11, no. 10: 1092–1100. https://doi.org/10.1111/j.1461-0248.2008.01223.x.

Heimann, M., and M. Reichstein. 2008. “Terrestrial Ecosystem Carbon Dynamics and Climate Feedbacks.” *Nature* 451, no. 7176: 289–292. https://doi.org/10.1038/nature06591.

IPCC. 2021. “IPCC, 2021: Climate Change 2021: The Physical Science Basis.” In *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press. https://doi.org/10.1017/cbo9781316146705.014.

Kirschbaum, M. U. F. 2006. “The Temperature Dependence of Organic-Matter Decomposition - Still a Topic of Debate.” *Soil Biology and Biochemistry* 38, no. 9: 2510–2518. https://doi.org/10.1016/j.soilbio.2006.01.030.

Knorr, M. A., A. R. Contosta, E. W. Morrison, et al. 2024. “Unexpected Sustained Soil Carbon Flux in Response to Simultaneous Warming and Nitrogen Enrichment Compared With Single Factors Alone.” *Nature Ecology & Evolution* 8, no. 12: 2277–2285. https://doi.org/10.1038/s41559-024-02546-x.

Le Quéré, C., R. M. Andrew, P. Friedlingstein, et al. 2018. “Global Carbon Budget 2018.” *Earth System Science Data* 10, no. 4: 1–28.

Lennon, J. T., R. Z. Abramoff, S. D. Allison, et al. 2024. “Priorities, Opportunities, and Challenges for Integrating Microorganisms Into Earth System Models for Climate Change Prediction.” *MBio* 15, no. 5: 1–9. https://doi.org/10.1128/mbio.00455-24.

Li, J., E. Bååth, J. Pei, C. Fang, and M. Nie. 2021. “Temperature Adaptation of Soil Microbial Respiration in Alpine, Boreal and Tropical Soils: An Application of the Square Root (Ratkowsky) Model.” *Global Change Biology* 27, no. 6: 1281–1292. https://doi.org/10.1111/gcb.15476.

Li, J., G. Wang, M. A. Mayes, et al. 2019. “Reduced Carbon Use Efficiency and Increased Microbial Turnover With Soil Warming.” *Global Change Biology* 25, no. 3: 900–910. https://doi.org/10.1111/gcb.14517.

Lloyd, J., and J. A. Taylor. 1994. “On the Temperature Dependence of Soil Respiration.” *Functional Ecology* 8, no. 3: 315–323.

Martiny, J. B. H., A. C. Martiny, E. Brodie, et al. 2023. “Investigating the Eco-Evolutionary Response of Microbiomes to Environmental Change.” *Ecology Letters* 26, no. S1: S81–S90. https://doi.org/10.1111/ele.14209.

Melillo, J. M., S. D. Frey, K. M. DeAngelis, et al. 2017. “Long-Term Pattern and Magnitude of Soil Carbon Feedback to the Climate System in a Warming World.” *Science* 358, no. 6359: 101–105. https://doi.org/10.1126/science.aan2874.

Melillo, J. M., P. A. Steudler, J. D. Aber, et al. 2002. “Soil Warming and Carbon-Cycle Feedbacks to the Climate System.” *Science* 298, no. 5601: 2173–2176.

Muratore, T., N. R. Chari, R. P. Phillips, B. N. Taylor, M. A. Knorr, and S. D. Frey. 2025. “Increased Root-Derived Carbon Offsets Soil Carbon Loss Under Simultaneous Warming and Nitrogen Addition.” *Authorea*. https://doi.org/10.22541/au.175165200.06761123/v1.

Nottingham, A. T., J. J. Scott, K. Saltonstall, et al. 2022. “Microbial Diversity Declines in Warmed Tropical Soil and Respiration Rise Exceed Predictions as Communities Adapt.” *Nature Microbiology* 7, no. 10: 1650–1660. https://doi.org/10.1038/s41564-022-01200-1.

Pec, G. J., L. T. A. van Diepen, M. Knorr, et al. 2021. “Fungal Community Response to Long-Term Soil Warming With Potential Implications for Soil Carbon Dynamics.” *Ecosphere* 12, no. 5: e03460. https://doi.org/10.1002/ecs2.3460.

Pold, G., L. A. Domeignoz-Horta, E. W. Morrison, S. D. Frey, S. A. Sistla, and K. M. Deangelis. 2020. “Carbon Use Efficiency and Its Temperature Sensitivity Covary in Soil Bacteria.” *MBio* 11, no. 1: e02293-19. https://doi.org/10.1128/mBio.02293-19.

Portner, H., H. Bugmann, and A. Wolf. 2010. “Temperature Response Functions Introduce High Uncertainty in Modelled Carbon Stocks in Cold Temperature Regimes.” *Biogeosciences* 7, no. 11: 3669–3684. https://doi.org/10.5194/bg-7-3669-2010.

Propster, J. R., E. Schwartz, M. Hayer, et al. 2023. “Distinct Growth Responses of Tundra Soil Bacteria to Short-Term and Long-Term Warming.” *Applied and Environmental Microbiology* 89, no. 3: e0154322. https://doi.org/10.1128/aem.01543-22.

Ratkowsky, D. A., R. K. Lowry, T. A. McMeekin, A. N. Stokes, and R. E. Chandler. 1983. “Model for Bacterial Culture Growth Rate Throughout the Entire Biokinetic Temperature Range.” *Journal of Bacteriology* 154, no. 3: 1222–1226. https://doi.org/10.1128/jb.154.3.1222-1226.1983.

Rijkers, R., J. Rousk, R. Aerts, B. D. Sigurdsson, and J. T. Weedon. 2022. “Optimal Growth Temperature of Arctic Soil Bacterial Communities Increases Under Experimental Warming.” *Global Change Biology* 28, no. 20: 6050–6064. https://doi.org/10.1111/gcb.16342.

Roller, B. R. K., and T. M. Schmidt. 2015. “The Physiology and Ecological Implications of Efficient Growth.” *ISME Journal* 9, no. 7: 1481–1487. https://doi.org/10.1038/ismej.2014.235.

Rousk, J., and E. Bååth. 2011. “Growth of Saprotrophic Fungi and Bacteria in Soil.” *FEMS Microbiology Ecology* 78: 17–30. https://doi.org/10.1111/j.1574-6941.2011.01106.x.

Rousk, J., and S. D. Frey. 2015. “Revisiting the Hypothesis That Fungal-to-Bacterial Dominance Characterizes Turnover of Soil Organic Matter and Nutrients.” *Ecological Monographs* 85, no. 3: 457–472. https://doi.org/10.1890/14-1796.1.

Schindlbacher, A., J. Schnecker, M. Takriti, W. Borken, and W. Wanek. 2015. “Microbial Physiology and Soil CO_2 Efflux After 9 Years of Soil Warming in a Temperate Forest - No Indications for Thermal Adaptations.” *Global Change Biology* 21, no. 11: 4265–4277. https://doi.org/10.1111/gcb.12996.

Sierra, C. A., S. E. Trumbore, E. A. Davidson, S. Vicca, and I. Janssens. 2015. “Sensitivity of Decomposition Rates of Soil Organic Matter With Respect to Simultaneous Changes in Temperature and Moisture.” *Journal of Advances in Modeling Earth Systems* 7, no. 1: 335–356. https://doi.org/10.1002/2014MS000358.

Simon, E., A. Canarini, V. Martin, et al. 2020. “Microbial Growth and Carbon Use Efficiency Show Seasonal Responses in a Multifactorial Climate Change Experiment.” *Communications Biology* 3, no. 1: 584. https://doi.org/10.1038/s42003-020-01317-1.

Smith, N. G., and J. S. Dukes. 2013. “Plant Respiration and Photosynthesis in Global-Scale Models: Incorporating Acclimation to Temperature and CO_2.” *Global Change Biology* 19, no. 1: 45–63. https://doi.org/10.1111/j.1365-2486.2012.02797.x.

Soares, M., and J. Rousk. 2019. “Microbial Growth and Carbon Use Efficiency in Soil: Links to Fungal-Bacterial Dominance, SOC-Quality and Stoichiometry.” *Soil Biology and Biochemistry* 131: 195–205. https://doi.org/10.1016/j.soilbio.2019.01.010.

Soong, J. L., C. Castanha, C. E. Hicks Pries, et al. 2021. “Five Years of Whole-Soil Warming Led to Loss of Subsoil Carbon Stocks and

Increased CO_2 Efflux." *Science Advances* 7, no. 21: eabd1343. https://doi.org/10.1126/sciadv.abd1343.

Tian, Y., A. Schindlbacher, C. U. Malo, et al. 2023. "Long-Term Warming of a Forest Soil Reduces Microbial Biomass and Its Carbon and Nitrogen Use Efficiencies." *Soil Biology and Biochemistry* 184: 109109. https://doi.org/10.1016/j.soilbio.2023.109109.

Trivedi, P., I. C. Anderson, and B. K. Singh. 2013. "Microbial Modulators of Soil Carbon Storage: Integrating Genomic and Metabolic Knowledge for Global Prediction." *Trends in Microbiology* 21, no. 12: 641–651. https://doi.org/10.1016/j.tim.2013.09.005.

Verbrigghe, N., N. I. W. Leblans, B. D. Sigurdsson, et al. 2022. "Soil Carbon Loss in Warmed Subarctic Grasslands Is Rapid and Restricted to Topsoil." *Biogeosciences* 19, no. 14: 3381–3393. https://doi.org/10.5194/bg-19-3381-2022.

Walker, T. W. N., C. Kaiser, F. Strasser, et al. 2018. "Microbial Temperature Sensitivity and Biomass Change Explain Soil Carbon Loss With Warming." *Nature Climate Change* 8, no. 10: 885–889. https://doi.org/10.1038/s41558-018-0259-x.

Wieder, W. R., M. D. Hartman, B. N. Sulman, Y. P. Wang, C. D. Koven, and G. B. Bonan. 2018. "Carbon Cycle Confidence and Uncertainty: Exploring Variation Among Soil Biogeochemical Models." *Global Change Biology* 24, no. 4: 1563–1579. https://doi.org/10.1111/gcb.13979.

Zheng, Q., Y. Hu, S. Zhang, et al. 2019. "Growth Explains Microbial Carbon Use Efficiency Across Soils Differing in Land Use and Geology." *Soil Biology and Biochemistry* 128: 45–55. https://doi.org/10.1016/j.soilbio.2018.10.006.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcb70579-sup-0001-Supinfo.pdf.