







Evidence for large microbial-mediated losses of soil carbon under anthropogenic warming

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Abstract | Anthropogenic warming is expected to accelerate global soil organic carbon (SOC) losses via microbial decomposition, yet, there is still no consensus on the loss magnitude. In this Perspective, we argue that, despite the mechanistic uncertainty underlying these losses, there is confidence that a strong, positive land carbon–climate feedback can be expected. Two major lines of evidence support net global SOC losses with warming via increases in soil microbial metabolic activity: the increase in soil respiration with temperature and the accumulation of SOC in low mean annual temperature regions. Warming-induced SOC losses are likely to be of a magnitude relevant for emission negotiations and necessitate more aggressive emission reduction targets to limit climate change to 1.5 °C by 2100. We suggest that microbial community–temperature interactions, and how they are influenced by substrate availability, are promising research areas to improve the accuracy and precision of the magnitude estimates of projected SOC losses.

The top two metres of soils store more than 2,200–2,500 Pg of organic carbon (C)^{1,2}, representing the largest biologically active C pool in terrestrial ecosystems³. The size of this C reservoir is annually balanced because large C losses to the atmosphere through soil respiration (defined as the combined flux of autotrophic and heterotrophic respiratory CO₂ from the soil to the atmosphere) are offset by C gains to the soil from plant photosynthesis⁴ (FIG. 1). Ongoing climate change, however, is perturbing this balance and, given the size of the soil organic carbon (SOC) pool, even relatively small SOC losses could represent a substantial contribution to the build-up of atmospheric CO₂ (REF.⁵).

Anthropogenic climate change is expected to accelerate SOC losses via the microbial decomposition of soil organic matter, representing a positive land C–climate feedback⁶. This feedback has received considerable research attention in the past decades, and is represented in the coupled climate–C cycle models of the Intergovernmental Panel on Climate Change (IPCC)⁷. Yet, given considerable

uncertainties about the dynamics of organic matter processing in a warming climate, there appears to be no consensus on the magnitude of this feedback over the rest of this century (whether it will equate to small or large net soil C losses to the atmosphere)^{8,9}. The lack of agreement about the magnitude of net SOC losses represents a major source of uncertainty in projecting climate warming⁵. Further, it means that the potential for SOC losses under warming are not factored into climate policy negotiations, which raises questions about whether agreed emission reductions are likely to translate to climate targets.

This scientific uncertainty is deeply influenced by two fundamental discussions about the temperature sensitivity of soil C fluxes into (plant C inputs) and from (soil respiration) the soil¹⁰. The first discussion about C inputs is based on a large body of literature that suggests that the land C sink is increasing because of greater plant productivity in response to human-induced warming^{11,12}. This effect is thought to be particularly strong in cold regions, where

warmer temperatures increase nitrogen (N) availability via enhanced soil organic matter decomposition, alleviating N limitation for plant growth^{12,13}. However, soil respiration is more affected by elevated temperatures than photosynthetic rates^{4,14}, and new evidence suggests that the land C sink via enhanced plant growth might be slowing down¹⁵. In fact, a global time series analysis of soil heterotrophic respiration and net primary production indicates that Earth greening cannot compensate for warming-induced increases in soil respiration¹⁶. Furthermore, most of the uncertainty around the magnitude of SOC losses with warming is rooted in uncertainty about microbial decomposition mechanisms, as opposed to debates about soil N availability and associated plant growth, particularly when considering SOC losses from cold regions^{8,17}.

In the second discussion, results from long-term warming experiments have shown diverse, sometimes contradictory, responses of soil respiration to rising temperatures. Some experiments indicate overall SOC losses with warming^{18–21}, whereas others have found that soil respiration returns to pre-warming levels after a few years of elevated temperatures^{22,23}. The latter dynamic has been taken to suggest a potential attenuation of the land C–climate feedback, which could be driven by the depletion of labile C sources and/or changes in the temperature dependence for microbial process rates (through physiological adjustments, evolutionary adaptation and/or species turnover; see BOX 1 for an explanation of the concepts used here to describe the microbial–temperature relationship)^{9,24–28}. Debate about the relative role of N availability, plant growth, substrate depletion and changes in microbial temperature dependence in shaping warming effects on SOC stocks generates mechanistic uncertainty about the projected magnitude of SOC losses with warming. This mechanistic uncertainty can also undermine the perceived scientific basis and resulting confidence in the positive direction (SOC loss) and substantive magnitude of the land C–climate feedback.

In this Perspective, we evaluate how changes in microbial communities, their physiology and their substrate use will affect land C cycle feedbacks to climate change (FIG. 1). We highlight that there is

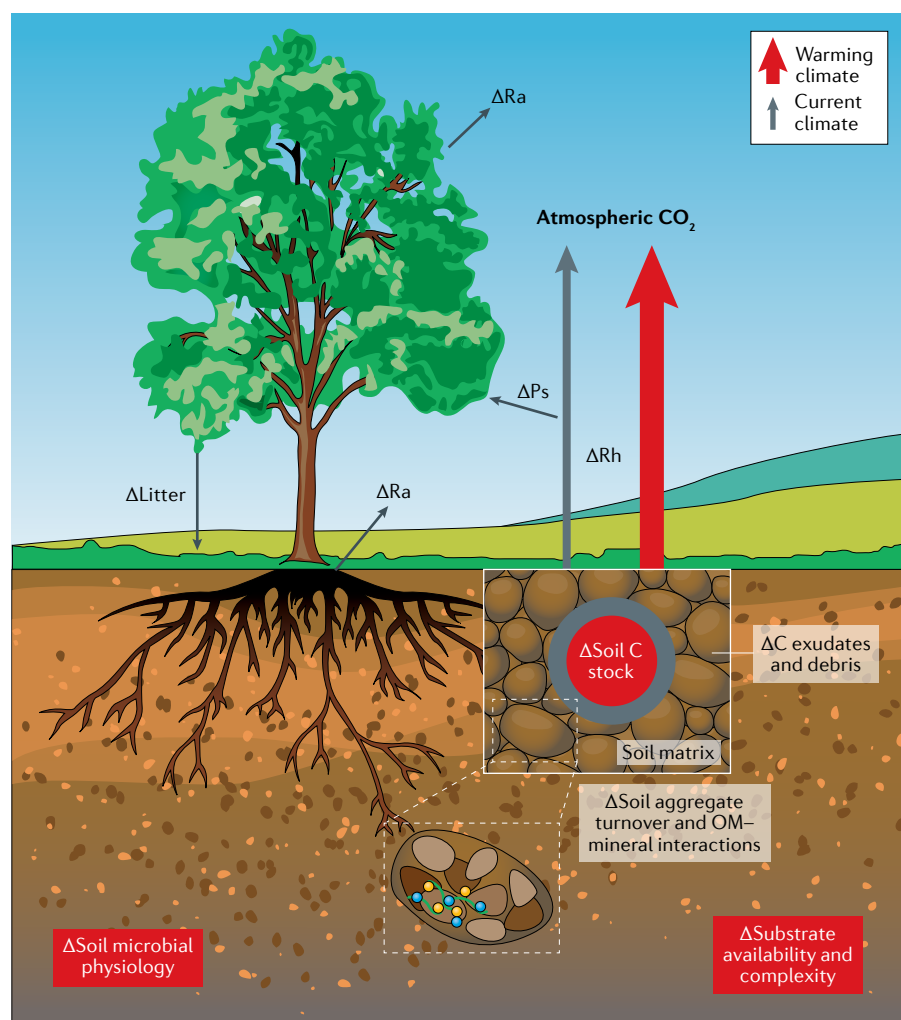


Fig. 1 | Microbial control of soil organic carbon losses to the atmosphere with anthropogenic warming. Soil heterotrophic respiration (Rh) increases with warming, which accelerates the loss of carbon from the soil organic carbon (SOC) stock to the atmosphere (depicted by the thick red arrow under a warming climate versus a thinner grey arrow representing the current climate). The diagram focuses on Rh because the evidence points to it being a major loss pathway of SOC under warming (the smaller red circle within the grey circle) from soils in cold regions. Research in microbial physiology and substrate use can improve the accuracy and precision of the magnitude estimates of SOC losses with warming via Rh (red boxes). Other factors also vary with temperature and can shape the responses of soil microbial communities and SOC to warming, such as plant C inputs to the soil (photosynthesis (Ps), leaf litter, root exudates and root debris), autotrophic respiration (Ra) and associations of the soil organic matter (OM) with soil minerals.

credible scientific confidence supporting the likelihood of a strong, positive land C–climate feedback through microbially mediated decomposition of the particulate SOC that has accumulated in colder regions^{29,30}. Based on evidence from global-scale observational and empirical studies on soil respiration, and a global analysis of SOC density as a function of mean annual temperature (MAT), we assert that there should be high confidence in the expectation that there will be large net losses of SOC to the atmosphere. The necessary research and discussion about the magnitude of SOC losses under

warming should not distract us from the strong consensus that overall soil respiratory losses will increase markedly in a warming world. Finally, we emphasize microbial–temperature relationships and microbial–substrate availability interactions as two research areas that must be addressed to improve the accuracy and precision of the magnitude estimates of SOC losses with warming (FIG. 1).

Positive land C–climate feedback

Two lines of evidence support a self-reinforcing soil C feedback to the climate system. First, soil respiration increases

with temperature across global gradients. Furthermore, field experiments show that warming can modify microbial physiology and resource availability, but these effects do not alter the temperature sensitivity of soil respiration across systems^{31,32}. Instead, the temperature sensitivity remains at least equivalent to that observed in control plots even after a few years of simulated warming^{5,31,32}. Second, SOC accumulates at high latitudes and is inversely correlated with MAT at a global scale³³.

Soil respiration increases with temperature.

Since the seminal review by Raich and Schlesinger in 1992 (REF.³⁴), which suggested that soil respiration will increase with rising temperatures in a positive feedback loop, the number of field studies measuring soil respiration rates has increased dramatically. Currently, at least 10,366 global observations from studies published between 1961 and 2017 have been gathered in the [largest soil respiration database \(SRDB\)](#) available to date³⁵. MAT consistently emerges as the dominant control over soil respiration in this database⁵. Most importantly, when looking at the temperature sensitivity of soil respiration, the Q_{10} remained high (between 2.6 and 3.3) across the temperature range considered³⁶. These findings meant that a simulated global temperature increase of 2°C translated to a 10-Pg C increase in SOC loss to the atmosphere^{5,36}, representing a 17% increase in global annual soil respiration based on estimations from the IPCC⁷. Together with many studies published since^{37,38}, the patterns from the SRDB suggest that there is strong empirical evidence that higher temperatures generally increase SOC losses via microbial respiration.

The patterns from the SRDB are, however, spatial and there are limitations to using spatial observations to make temporal inferences^{5,36}. Yet, two quantitative literature reviews that compared field warming scenarios (imposed by open-top chambers, infrared heaters and soil cables) with control plots at ambient temperature also support the idea that warmer temperatures will not significantly dampen the temperature sensitivity of soil respiration. In the first review³¹, 2°C warming increased soil respiration by 12% across 50 globally distributed experiments within a MAT range of –18.1 to 19.6°C.

In the second review³², the effects of warming on the temperature sensitivity of soil respiration were evaluated across nine global biomes and whether warming-induced increases in soil respiration are dampened by microbial

temperature dependence was assessed. There were no significant differences in the temperature sensitivity of soil respiration for eight of the nine biomes, with all biomes except deserts showing consistent increases in respiratory losses under warmer conditions relative to the controls³². Importantly, in the eight biomes, the shape of the relationship between temperature sensitivity of soil respiration and soil temperature changed across the temperature range evaluated (0–40 °C), following a unimodal response. Specifically, the temperature sensitivity increased with temperature up to ~25 °C, and then started to decrease. This pattern suggests that, in regions where soil temperature is usually below 25 °C (such as in colder regions at higher latitudes), the sensitivity of soil respiration to warming will be higher than in warmer regions at lower latitudes, where soil temperature is more frequently above 25 °C. By contrast, the temperature sensitivity of soil respiration in deserts was significantly lower in warmed than in control plots after the 25-°C threshold was surpassed. Overall, observational studies across global MAT gradients and meta-analyses of field warming experiments consistently support the expectation that warming increases soil respiration, with the strongest and most consistent effects in colder climates.

The major limitation of these data for understanding the magnitude of the land C–climate feedback is that soil respiration might be a poor surrogate for resolving how soil C stocks are responding to warming⁵. Instead, warming-induced changes in soil respiration could simply be a product of altered C input rates to the soil and/or labile C pool sizes⁵, thereby only reflecting altered turnover of very recent soil C¹⁴ without any changes in total SOC stocks. Yet, even in experiments where soil respiration attenuates in response to longer-term warming, microbial activity remains strongly temperature-sensitive^{19,21,32,39}. As such, under experimental warming, soil biota have a continued capacity to mineralize SOC at greater rates under higher temperatures and, hence, release CO₂ from the soil C pool. Determining how temperature affects the balance between C inputs and outputs to and from SOC stocks is key to dramatically increasing the accuracy and precision of future projections of the land C–climate feedback. To do that, data on the response of soil C stocks to warming are necessary.

Soil C accumulates in regions with low mean annual temperature. Given the challenges of using soil respiration data to infer how

SOC stocks respond to warming, confidence in a positive land C–climate feedback relies on a second line of evidence. In the absence of extensive temporal data for soil C change, spatial patterns of SOC storage across the globe provide this additional (albeit correlative) evidence. Specifically, the balance of C between respiratory losses and photosynthetic gains to an ecosystem largely determines the total SOC storage over the

long term in any given region. By regulating the physiology of organisms, temperature consistently emerges as one of the strongest predictors of this balance⁴. As such, SOC accumulates in cold regions such as the Arctic and the sub-Arctic^{33,40}, where C inputs exceed outputs because soil respiration is more temperature-sensitive and, hence, more constrained, than photosynthesis^{4,14,41}. This mechanism suggests a clear latitudinal

Box 1 | Terms and concepts used to describe the microbial–temperature relationship

Carbon use efficiency

The microbial carbon use efficiency is an emergent physiological variable describing the fraction of C that is retained by microbes relative to the total C assimilated^{66–68,97}. It is a critical variable to constrain in order to understand the microbial feedback to climate warming, as it defines the first bifurcation of the flow of C consumed by decomposer microorganisms, leading either to immediate C loss back to the atmosphere as CO₂ or to C storage as soil organic matter via microbial biomass formation^{64,65,70}.

Temperature sensitivity (Q₁₀)

The Q₁₀ is defined as the factor by which the rate increases with a 10-°C rise in temperature, that is, it describes changes in relative reaction rates^{14,48}. Arrhenius first proposed how biochemical reaction rates depend on temperature following Eq. 1, where *k* is a biological rate, *A* is a constant, *E_a* is the activation energy for the studied reaction, *R* is the universal gas constant and *T* is temperature⁴. Most soil C models follow the Arrhenius model and assume a constant Q₁₀ of soil respiration (Q₁₀ = 2–3)^{4,14}. However, it is now widely recognized that the Q₁₀ is not constant with temperature, and that it increases towards lower temperatures and grows complex when temperatures approach the optimum for growth⁴⁹.

$$\ln(k) = \ln A - E_a/RT \quad (1)$$

The macromolecular rate theory

Biological reactions are typically mediated by macromolecules such as enzymes, which have large heat capacities (*C_p*). Changes in the heat capacity leads to a marked temperature dependence of the activation energy. Hence, the Arrhenius model established for biochemical reactions might not match expectations from biological reactions. The macromolecular rate theory develops the Arrhenius model in Eq. 2, where *T₀* is the reference temperature, *k_B* is Boltzmann's constant, *h* is Planck's constant, *H* is enthalpy and *S* is entropy. This representation includes the temperature dependence of Q₁₀ (REF.⁷¹).

$$\ln(k) = \ln(k_B T/h) - [\Delta H_{T_0} + \Delta C_p(T - T_0)]/RT + [\Delta S_{T_0} + \Delta C_p(\ln T - \ln T_0)]/R \quad (2)$$

The square root model

This model effectively captures the increasing Q₁₀ towards lower temperatures, and the derived parameters can yield easily interpretable information characterizing microbial trait distributions with temperature. This model follows Eq. 3, where *a* is the activity rate at temperature *T*, *T_{min}* is the lower temperature limit, *b* is a constant describing the rate of decline when temperatures exceed *T_{opt}* and *T_{max}* is the higher temperature limit. The square root model was originally developed in food microbiology⁷³ and has been applied in different ecosystems^{72,74–76}.

$$\sqrt{k} = a(T - T_{min})(1 - e^{b(T - T_{max})}) \quad (3)$$

Changes in the temperature dependence: enhancing and compensatory thermal responses

The changes in the microbial temperature dependence through physiological adjustments, evolutionary adaptation and/or species turnover can be defined as the subsequent adjustment in the rate of respiration to compensate for an initial change in temperature. Both enhancing and compensatory thermal responses of soil microbial communities to warming have been found^{24,62,66}. In enhancing responses, the Q₁₀ of soil heterotrophic respiration will increase, whereas compensatory responses will dampen the Q₁₀ and/or absolute rates.

Substrate depletion

Labile soil C compounds can be disproportionately used by microbes under elevated temperatures, decreasing their relative abundance. The depletion of these substrates with warming can result in subsequent declines in microbial biomass and activity, reducing C losses via lower soil heterotrophic respiration over time, as found in long-term field studies^{19,22,23}.

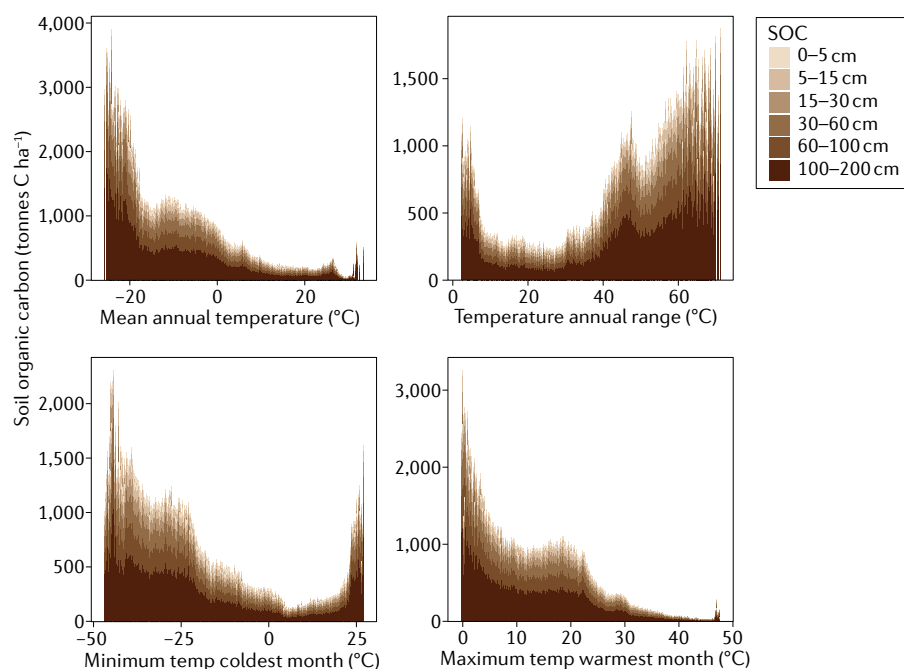


Fig. 2 | SOC stocks are negatively correlated with temperature at the global scale. Soil organic carbon (SOC) stocks (tonnes C ha⁻¹) generally show a negative trend with mean annual temperature (MAT). MAT is a general parameter reflecting broad patterns of climate differences, but it is not likely to be the variable that directly relates to organismal physiology, as it will be differences in temperature ranges, the minimum or the maximum temperatures that ultimately limit activity levels. Using MAT in the representation accounts for regional differences in the SOC stocks pattern that are driven by colder conditions at higher altitudes. Indeed, several mountain ranges located at mid-latitudes, such as the Rocky Mountains, Andes, Pyrenees, Caucasus or Himalayas, have high SOC stocks³³. Soil data from *SoilGrids* v2 (REF.⁴⁰) and climate data from *CHELSA*⁹⁵. The use of C stock per unit area (density) in this figure allows a more comparable assessment of soil C storage in relation to thermal climate, because the amount of land area differs by latitude⁹⁶. Depth bars are stacked along the 0–200 cm soil profile, and represent mean values of tonnes C ha⁻¹ per 0.1°C bins across 100,000 random mapped points. Although the same data were used to develop each figure panel, the binning groups different sets of observations together, which results, for example, in lower maximal SOC density values when the minimum temperature of the coldest month is compared with MAT. Cumulative values to 2-m depth of >2000 tonnes C ha⁻¹ are likely an artefact of poor data on soil bulk density in organic-rich, high-latitude soils in global soil mapping products.

pattern of SOC storage across the globe, as represented in Crowther et al. (2019)³³.

SOC stock spatial patterns suggest a strong temperature signal (visualized here with SOC density as a function of MAT; FIG. 2). Importantly, the latitudinal pattern of SOC storage matches MAT, with lower storage in warmer regions. Although cold regions have relatively slow C input rates to the soil, the rate of respiratory C release through soil respiration is even lower³³. Therefore, the long residence time of C in low MAT soils at high latitudes led to the accumulation of huge soil C stocks over thousands of years^{42,43} (an estimated 1,113 tonnes SOC ha⁻¹ in boreal forests and tundra; FIG. 2). By contrast, both photosynthetic activity of plants and respiratory activity of soil organisms are high in warm and moist regions⁴⁴, which has led to relatively small SOC stocks in the tropics (281 tonnes SOC ha⁻¹ in tropical

forests; FIG. 2). These patterns emerge despite the fact that SOC also accumulates in anaerobic waterlogged ecosystems such as tropical peatlands and wetlands, and in pools of mineral-associated SOC in better drained soils³³.

The difference in C inputs versus outputs, therefore, drives a clear MAT trend in soil C, with massive SOC stocks in high latitude and altitude cold regions^{33,40} (FIG. 2). Of course, MAT does not directly determine organismal physiology, but it is indicative of the extremes in temperature and variation between those extremes that drive microbial activity. It could, ultimately, be the duration of the thawed period that is the most meaningful climate variable in governing the specific activity levels of decomposer organisms in higher latitude regions. Yet, the strong correlation between MAT and other climate variables (minimum temperature, maximum temperature and temperature

seasonality) at a global scale means that the associations between temperature and SOC stocks are apparent across a range of climate variables (FIG. 2).

These patterns (FIG. 2) are supportive but not conclusive evidence of the sensitivity of SOC stock responses to warming because spatial patterns are not necessarily predictive of temporal responses. We also acknowledge that the evidence is observational and, hence, it is possible that other mechanisms might be driving the pattern. Further, recent ¹⁴C-dating evidence suggests that global soil C stocks are, on average, $4,830 \pm 1,730$ years old (with permafrost SOC ranging from 2,800 years mean age at 0–30 cm to 15,000 years mean age at 30–100 cm)⁴³, which is much older than the decadal to centennial age typically assumed through the turnover rates used in soil biogeochemical models⁴⁵. If SOC turnover rates are slower than estimated from soil models, the magnitude of a positive land C–climate feedback might be lower than anticipated from spatial patterns. Yet, that temperature consistently emerges as the strongest predictor of SOC stocks fits with the mechanistic understanding of the physiological responses of organisms to warming. Overall, it seems probable that colder temperatures are likely to be a primary driver of the large SOC stocks found in high latitude and altitude regions, although other abiotic factors such as soil drainage⁴² or lateral C export during thawing⁴⁶ could also play an important role. Nevertheless, if colder conditions drive the accumulation of C in soil, it seems highly plausible that warming those regions is likely to reverse this effect.

Indeed, there is evidence that the rate of SOC release might be high when cold-region soils warm. First, extensive research highlights that the temperature sensitivity of SOC stocks is three times higher in cold than in warm regions^{32,47–49}. Annual cycles of freeze and thaw, and the vertical development of active layer soils could explain some of this high-temperature sensitivity, and sub-annually frozen soils could represent an extreme example in terms of the effects of temperature on C storage⁴⁷. However, reductions in soil C storage with warming are observed both above and below 0°C, including in regions in which soils rarely freeze (FIG. 2). Second, a global network of field warming experiments — with direct measures of SOC — suggested that about 30 Pg of topsoil C could be released to the atmosphere for 1°C of warming by 2050, based on 2016 estimates⁶. Such warming-induced SOC losses represent 12–17% of the amount

of CO₂ emitted from human-related activities over this time, highlighting the importance of cold conditions for trapping C in the soil when addressing biosphere–atmosphere feedbacks. Third, a recent model comparison suggests that, regardless of how SOC responses to warming are represented mechanistically, the response of cold regions predominantly determines the magnitude of net, global C change under various warming scenarios⁸.

Spatial observations, experimental field warming studies and many modelling studies converge to suggest that regions with the largest SOC stocks, for instance, those with low MAT (FIG. 2), are likely to drive large net global losses of soil C under warming. These findings are primarily based on the hypothesis that temperature limitations on SOC decomposition are being alleviated with climate warming. This alleviation will result in larger soil respiratory losses that cannot be compensated by warming-induced increases in net primary production¹⁶ and, hence, will translate to net losses of SOC stocks^{14,47}. Such outcomes could be especially dramatic in the Arctic and the sub-Arctic, because these regions are warming at about two times the global rate⁵⁰.

A growing body of evidence suggests that the huge SOC stocks in cold regions support a larger abundance of soil organisms. Specifically, the size of the SOC stock is a prominent predictor of soil microbial^{51,52} and animal⁵³ abundances. The highest abundances of these soil biota are, therefore, found in high-latitude, organic-rich soils. Yet, the metabolic activity of soil biota (including fungi, bacteria, archaea and invertebrate animals) is low under cold conditions⁵⁴, which explains why C accumulation in cold (high-latitude) areas is likely to have occurred in the first place. However, as these regions warm with ongoing climate change, the metabolic activity of these organisms should increase²⁴, enhancing their potential to mineralize soil C. Given the immense abundances of these organisms in cold regions relative to warmer regions^{51,53}, even slight increases in their metabolic activity could markedly accelerate C losses, highlighting the need to consider decomposer abundance as a factor influencing future SOC stocks^{52,55}.

Magnitude of the feedback

Previous work has discussed the empirical (longer-term field studies, measurements of soil C stocks at deeper soil layers, more studies in tropical and dryland ecosystems, incorporating emerging views on mineral-associated SOC) and modelling

(representing structural uncertainties and microbial-explicit processes) efforts required to robustly assess the effects of warming on SOC stocks^{6,9,56}. Further, given the centrality of soil microbes and their collective metabolic activities to soil respiration and, hence, decomposition rates of soil C compounds, a number of previous studies have recently reviewed the consequences of microbial responses to warming for SOC turnover and storage^{57–59}. In this section, we focus on the need for an improved understanding of microbial–temperature relationships and microbial–substrate availability–temperature interactions. The nature of these relationships has high potential to dictate the magnitude of net SOC losses under warming and, hence, are important to constrain in order to make accurate and precise estimates of the magnitude of estimated SOC losses.

Alternative metrics for microbial–temperature relationships. There is compelling evidence suggesting that there will be marked changes in microbial activity–temperature relationships in response to warmer temperatures.

For instance, warming-induced changes in microbial metabolism can decrease, not affect or increase temperature sensitivities of soil heterotrophic respiration^{24,26,60–62}; these are phenomena that cannot be represented with the Arrhenius response depicted in the Q₁₀ coefficient (BOX 1). However, the coupled climate–C models of the IPCC represent a monotonic increase in soil microbial respiration with warmer temperatures based on Q₁₀ coefficients^{56,63}. To improve the representation of microbial processes in soil biogeochemical models, the complex interaction between climate and the structure, function and physiology of soil microbial communities must be captured^{9,28}.

Microbial physiology–temperature relationships reveal potentially contrasting responses to warming for different microbial parameters such as respiration versus growth^{28,64}. These contrasting responses mean that net SOC losses might occur under warming because of respiration, even if microbial biomass production increases and provides a source of microbial necromass and secondary compounds for greater formation of persistent soil C pools⁶⁵. Such possibilities depend on the response of the carbon use efficiency (CUE, BOX 1) of soil microbial communities to warming.

CUE is an emergent physiological variable of multiple anabolic and catabolic processes⁶⁶, making its interpretation complicated. The influence of these

contrasting properties could explain why soil incubations in the laboratory suggest that microbial CUE is unresponsive⁶⁷, reduced⁶⁸ or increased⁶⁹ by greater temperatures. Further, given the methodological challenges in measuring CUE in situ, field assessments of how microbial CUE responds to experimental warming are rare. The single study to date has investigated how field experimental warming changes microbial CUE, based on estimates of substrate use efficiency. It was found that, although CUE declined with increased temperatures in the laboratory, long-term field warming had a minor, if any, impact on the temperature response of CUE⁷⁰. These results were consistent with CUE responses to natural geothermal warming of soil⁶⁷. More field warming experiments measuring microbial CUE across a wide range of environmental conditions are required to improve our understanding of the CUE–temperature relationship and its consequences for the magnitude of projected SOC losses as the direct effect of warming.

Given the shortcomings of the Q₁₀ coefficient for understanding microbial metabolic responses to sustained warming, and the paucity of field data for CUE responses, there is a need to explore additional metrics. For instance, the macromolecular rate theory (BOX 1) allows the calculation of temperature response traits such as the maximum activity or the maximum temperature sensitivity of soil heterotrophic respiration⁷¹. In particular, the minimum temperature index (T_{\min} ; FIG. 3a) of the square root model⁷² appears to be ecologically meaningful for understanding soil C responses to warming (BOX 1). T_{\min} is the theoretical minimal temperature for growth or activity, but is also one of the key variables that define microbial–temperature relationships⁷³, along with the optimal temperature and maximal temperature. The T_{\min} index is estimated to be 0.3 °C higher per 1 °C increase in soil temperature^{72,74}, as soil microbial growth and CUE are expected to adapt to the selection pressure under climate warming⁷⁵, resulting in a more warm-adapted microbial community.

Empirical support for warm-adapted communities comes from studies of bacterial growth, which has been shown to adapt to field experimental warming⁷⁶ and across gradients of MAT⁷⁴. A shift in T_{\min} of soil bacterial growth across a wide gradient of increasing temperatures (FIG. 3a) also results in higher Q₁₀ (FIG. 3b), indicating higher temperature sensitivity of soil heterotrophic respiration in warm-adapted than in cold-adapted microbial communities

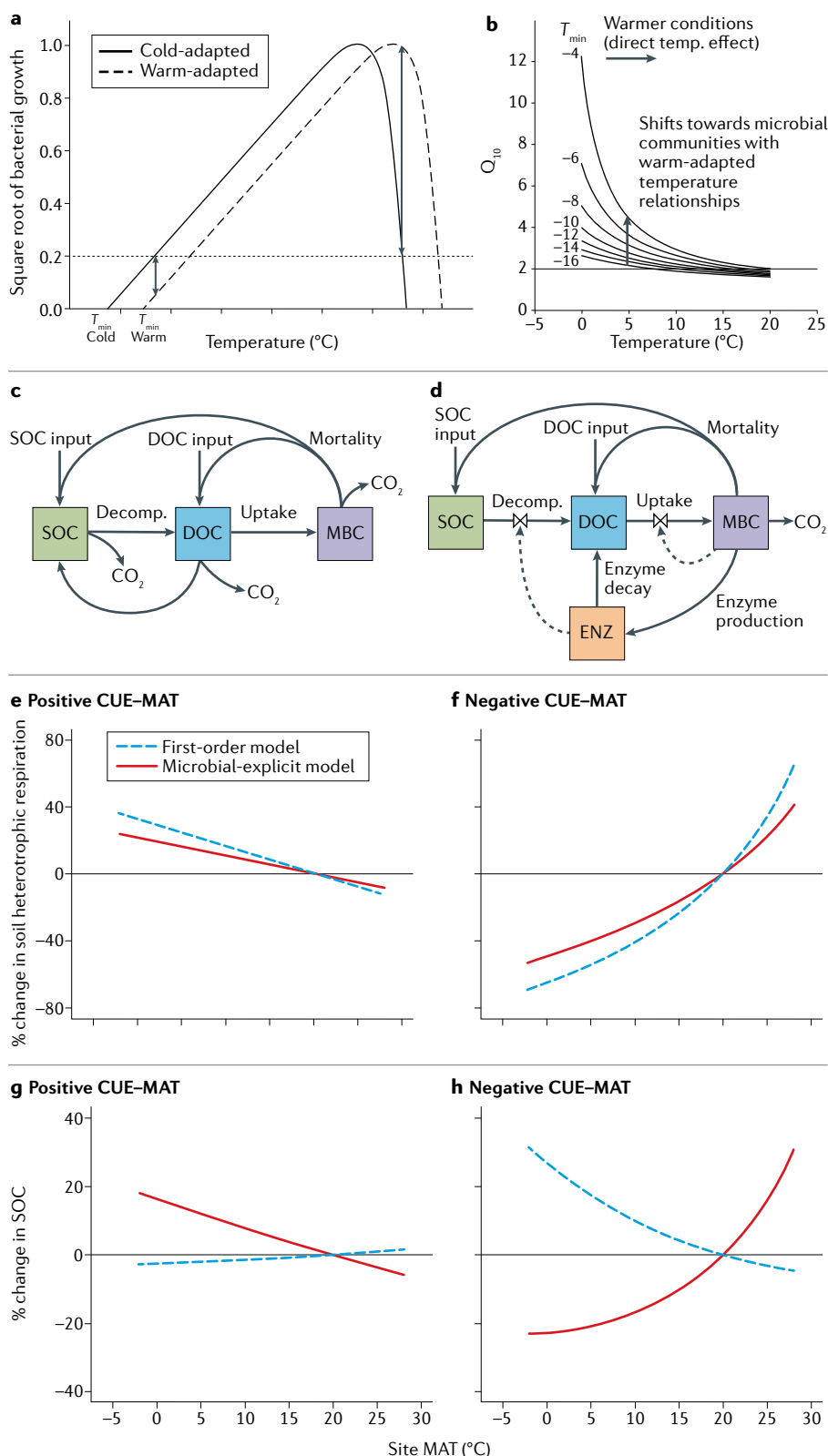


Fig. 3 | Exploring the microbial-temperature relationship to improve estimates of SOC losses. These relationships need to be explored in empirical studies and soil organic carbon (SOC) models to improve the accuracy and precision of the magnitude of losses with warming. **a** | Temperature relationship of square-root-transformed bacterial growth derived from a minimum temperature (T_{min}) in a cold and a warm climate. Arrows indicate the competitive advantage of thermal adaptation at low versus high temperatures. **b** | Warm-adapted temperature relationships (high T_{min} curves) have higher sensitivity of soil respiration (Q_{10}) than cold-adapted temperature relationships (low T_{min} curves). **c** | First-order linear model with SOC, dissolved organic carbon (DOC) and microbial biomass carbon (MBC) pools. **d** | Four-pool microbial-explicit model with enzymatic (ENZ) decomposition of SOC and subsequent assimilation (uptake) of DOC by microbes. Solid and dashed arrows represent C fluxes and controls, respectively. **e** | Long-term (30 years) simulated effects of mean annual temperature (MAT) on soil microbial respiration rates with first-order versus microbial-explicit models assuming positive microbial carbon use efficiency (CUE)-MAT relationship (modelling details in Supplementary Information). **f** | MAT effects on respiration assuming negative CUE-MAT. **g** | MAT effects on SOC stocks assuming positive CUE-MAT. **h** | MAT effects on SOC stocks assuming negative CUE-MAT. Soil respiration was measured as mass-specific rates, to account for changes in microbial biomass. The relative changes (%) of both variables as compared with equilibrium values at 20°C (the black line) are provided to facilitate comparisons between models. The scenario in panels **e** and **g** with the microbial-explicit model is consistent with the global SOC-MAT relationship shown in FIG. 2 and with large-scale field experiments evaluating microbial physiological responses to spatial variation in MAT³². This scenario suggests that prolonged warming is likely to lead to net losses of the global SOC stock.

sensitivity of a suite of microbial traits, which is fundamental for determining the absolute magnitude of net SOC losses under warming.

Addressing microbial-temperature relationships in soil C models. The soil sub-models typically used in the projections of Earth system models include several assumptions about how microbes influence SOC dynamics. For instance, conventional SOC models such as Century⁴⁵ (Daycent) and RothC⁷⁷ assume that SOC losses to the atmosphere through microbial respiration are a product of microbial activity, but that microbial communities do not regulate soil C dynamics independently of other factors, such as temperature. Specifically, soil microbial responses to temperature are represented in these models

(low T_{min} curves). The macromolecular rate theory and the square root model have yet to be extended to global scales. To do so, field and laboratory studies performed across different biomes and ecosystems that measure microbial physiology at multiple temperatures within a range

that is biologically relevant are needed. Regardless, both are promising frameworks to move beyond the use of a constant Q_{10} coefficient across the entire temperature range (BOX 1). Indeed, these new models allow the calculation of alternative metrics that better represent the temperature

as a first-order process (FIG. 3c), whereby the respired CO₂ is proportional to the SOC stock. The implicit representation of microbial processes in SOC models can lead to marked differences between field observations and model predictions of respiration rates^{9,78}, generating low confidence in model abilities to project the magnitude of the land C–climate feedback⁵⁶.

Emerging empirical evidence suggests that a suite of microbial responses to thermal regimes occur that deviate from the first-order representation in models^{9,21,24,70}. Notably, the compensatory thermal response of soil heterotrophic respiration (BOX 1) emerges across major biomes when other driving factors, such as substrate depletion and changes in microbial biomass, are controlled for^{61,62}. Physiological traits such as CUE and enzyme kinetics likely underlie these compensatory thermal patterns (BOX 1). To explicitly represent these traits in SOC models, innovative modelling efforts assume particular microbial physiology–temperature relationships^{25,28,79}. For instance, CUE is typically represented as decreasing as climate becomes warmer in microbial-explicit models^{25,80}. However, recent large-scale field observations across contrasting temperature regimes suggest that the opposite relationship could occur^{69,81} (although it is worth noting that CUE was inferred and not directly measured in these studies). The lack of consensus about how microbial processes will respond to warming highlights the need to represent multiple competing assumptions of microbial metabolic response in models. These representations then need to be tested against field observations gathered over a wide range of environmental conditions in order to refine the representation of microbial processes.

This approach has been attempted in two studies exploring how effectively different microbial–temperature representations recreate large-spatial-scale empirical observations, using model–data integration and database cross-validation. In the first study⁸², positive and negative relationships between CUE and MAT were simulated in both first-order (FIG. 3c) and microbial-explicit (FIG. 3d) SOC models. The model predictions were then compared with the microbial respiration rates (per unit microbial biomass) observed in independent, controlled laboratory incubations of 110 soils from global drylands⁶² and 22 soils from boreal to tropical biomes⁶¹. The microbial-explicit models assuming a positive CUE–MAT relationship best predicted the observations,

suggesting that the compensatory thermal response of soil microbial respiration^{61,62} was associated with higher CUE under warmer climates.

In the second study⁸³, observations from two independent field datasets from global croplands^{52,81} were most consistent with positive, empirical relationships between CUE and MAT. When represented in a microbial-explicit SOC model, this positive relationship best predicted the compensatory response of soil metabolic quotient (decreased respiration rate per unit of biomass with MAT) that was empirically observed. However, the SOC models^{82,83} were run at a very fine temporal resolution (10h), matching the short-term laboratory incubations conducted to measure soil microbial respiration at different temperatures in the two empirical studies^{61,62}. Only respiration outcomes were queried because SOC stock changes are not detectable at such short timescales. It, therefore, remains unclear how the observed respiratory responses to warmer temperatures translate to changes in SOC stocks.

Here, we incorporated positive and negative relationships between physiological attributes of soil microbial communities, such as CUE, and MAT into these SOC models to demonstrate the potential for such microbial information to make testable predictions about SOC stock responses to warming (FIG. 3c–h). The implications of these assumptions in both first-order and microbial-explicit SOC models were then tested on long-term (30 years) soil microbial respiration and SOC stocks (FIG. 3e,f; more details on the SOC modelling in the Supplementary Information). The sign of the hypothesized CUE–MAT relationship generated opposite responses of mass-specific soil respiration and SOC stocks to variation in MAT (FIG. 3e,f). Unfortunately, such simulated results cannot be validated with 30-year soil incubations, as these studies have not been conducted. However, it has been demonstrated⁸² that a positive CUE–MAT relationship is more likely to represent the microbial temperature-sensitivity patterns observed across space for soils from different biomes^{61,62}.

Invoking this positive relationship, both the first-order and microbial-explicit model representations reproduced the expected decrease in respiration rates per unit microbial biomass expected under compensatory thermal responses (FIG. 3e). By contrast, the negative CUE–MAT relationship led to model predictions of increased respiration rates per unit

biomass, a pattern inconsistent with empirical observations (FIG. 3f). Notably, the implications for SOC stocks were markedly different even when the first-order and microbial-explicit models predicted qualitatively similar respiration patterns. Specifically, in the first-order model with a positive CUE–MAT relationship, SOC stocks slightly increased with MAT, whereas they decreased with increasing MAT in the microbial-explicit model (FIG. 3g). As such, only the latitudinal pattern in SOC stocks (increasing stocks with decreasing MAT) was generated by the microbial-explicit model when a positive temperature–CUE relationship was assumed (FIG. 3g). Presumably, the mechanism explaining this pattern was because the microbial-explicit model permitted the microbial pool to feed back to SOC decomposition²⁵, as in FIG. 3d. Therefore, higher CUE led to higher microbial biomass and SOC consumption, and, thereby, lower SOC stocks with elevated MAT. The advantage, then, of microbial-explicit model structures is that they provide an effective way to test how microbial metabolic shifts under warming might influence soil C dynamics.

A negative CUE–MAT relationship (for which there is limited field support^{52,81–83}) fails to recreate the observed MAT by soil C pattern generated by large SOC stocks in cold regions (FIG. 2). Indeed, the microbial-explicit model indicated SOC gains with increasing temperature (FIG. 3h). Notably, the first-order model did create the pattern of lower SOC stocks with elevated MAT (FIGS 2,3h), but it failed to capture the expected respiration pattern (FIG. 3g).

Given the lack of empirical data or consensus on decadal responses of SOC stocks to warming, the evaluation of competing microbial–temperature relationships against spatial field data appears to be an effective tool for building near-term confidence in model projections of SOC stocks under a warmer climate. A positive CUE–MAT relationship recreates both expected respiratory responses and the global SOC–MAT patterning when represented in models that explicitly consider microbes as controls (FIGS 2,3e,g). In short, the model–data integration most consistent with large-spatial-scale field observations suggests a positive land C–climate feedback.

Microbial–substrate availability–temperature interactions. When addressing the relationship between soil microbial metabolism and temperature, it is important to consider the interplay with other

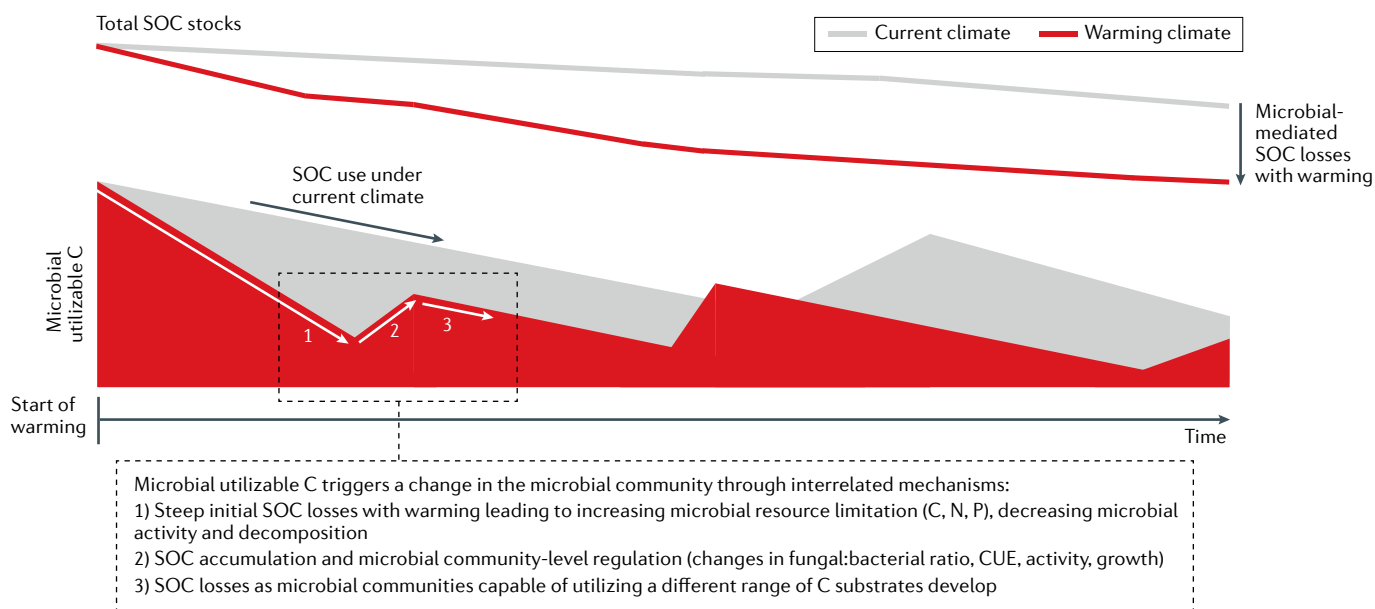


Fig. 4 | Changes in the interactions between microbes and substrate availability under warming. Changes in these interactions can determine the magnitude of net soil organic carbon (SOC) losses. A steep decline in SOC response to initial warming is commonly found via the reduction in the availability of readily decomposable SOC for microbial growth and activity. However, instead of translating to stabilization of the SOC pool, C losses can continue under long-term warming as a consequence of multiple mechanisms that alter the capacity of microbial communities to decompose complex and persistent SOC components. CUE, carbon use efficiency.

environmental factors. Long-term storage of C in mineral soils is strongly controlled by physicochemical mechanisms that control the accessibility of SOC to decomposers⁸⁴. For example, occlusion in aggregates and the formation of organo-mineral interactions are critical in preventing microbial degradation of SOC. The resulting low accessibility to microbes of a substantial proportion of the SOC pool could help explain why rates of decomposition decline with warming, even when only a small proportion of SOC has been released^{19,23}. The depletion of small pools of readily decomposable and unprotected SOC can result in subsequent declines in microbial biomass and activity^{67,74,85}, reducing SOC losses with warming over time⁶⁷.

Incubated samples from a grassland warming experiment at common temperatures provided evidence for the role of substrate depletion in reducing fluxes⁸⁵. Lower respiration rates were observed in samples from warmed plots, and differences between control and warmed cores increased over time. These observations suggest that substrate loss, rather than changes in microbial thermal dependence, was the dominant mechanism explaining the lower fluxes from warmed soils. Furthermore, when physicochemical persistence mechanisms were disrupted by homogenizing the soil with sieving, differences between warmed and control samples were largely eliminated — the

warming-induced reduction in unprotected SOC was swamped by the release of aggregate-associated C following the disturbance of the soil structure.

Although the depletion of available soil organic matter should translate into reduced SOC losses under prolonged warming, losses are often still observed after several years of elevated temperatures^{19,67,86,87}. Recent evidence suggests that this discrepancy could be the result of shifts in the soil microbial community (FIG. 4), which are associated with accelerated decomposition of SOC components that were less biochemically available at lower temperatures. For example, the response of the enzyme lignase — which is involved in the degradation of biochemically recalcitrant SOC — to warming was positively correlated with changes in soil respiration⁸⁸. In long-term warming experiments, there was a higher stimulation of microbial genes related to the degradation of labile SOC compounds in warmed plots²¹. However, an increase in microbial genes related to the decomposition of recalcitrant SOC was found after 4 years of warming in the same grassland experiment⁸⁷.

Warming studies that evaluate microbial functional information provide strong evidence that, as the relative availabilities of different SOC pools change under warming, there is selection for microbes that specialize on more biochemically recalcitrant C. This selection drives shifts

in microbial community composition and function (FIG. 4). As such, interactions between substrate supply, complexity and warming appear to result in the development of microbial communities capable of utilizing a broader range of substrates^{21,70,87}. Whether these shifts are related to microbial communities responding to the loss of readily decomposable SOC or to a relaxation of the thermal constraints for the decomposition of complex C compounds, is unknown.

The magnitude of SOC losses resulting from these microbial community shifts will likely depend on additional mechanisms. For example, substrate complexity affects microbial growth rates and physiological variables such as CUE⁸⁹, so the magnitude of losses will likely depend on whether these responses enhance or mitigate increases in microbial activity under warming. One field warming study suggests that these responses might enhance activity⁸⁵. Specifically, when warming was periodically switched off, carbon fluxes remained elevated in previously warmed plots for extended time periods (days to weeks) during the cold season. These observations indicate that the changes in microbial community function with warming had long-term impacts on activity that could not be explained by the direct effects of temperature alone.

Shifts in soil microbial communities that expedite C mineralization rates might

be restricted to unprotected SOC pools, given mounting evidence that biochemical recalcitrance is unlikely to explain the long-term persistence of mineral-associated SOC⁹⁰. However, SOC persistence might be influenced by interactions between biochemical recalcitrance and mineral association. Thus, warming effects are likely also to extend to the large global pools of mineral-associated SOC⁶⁵. Nevertheless, the extent to which physicochemical persistence mechanisms are temperature-sensitive and the amounts of SOC that could be released on timescales relevant to twenty-first century climate change remain controversial. Indeed, these mechanisms and values could vary between soil types, depending on the affinity of the mineral surfaces for the organic matter¹⁴.

For example, in many cold regions, much of the SOC seems to be in particulate forms^{29,30}, which are not associated with mineral surfaces and might remain accessible to microbes. Unlike mineral-associated SOC, increases in particulate forms of SOC do not appear to asymptote as total SOC increases⁹¹, presumably because they are not dependent on a finite availability of mineral surfaces to associate with. Therefore, it seems likely that large SOC losses under warming in cold regions will likely result from how shifts in microbial communities under warming affect their functional effects on the decomposition rate of particulate SOC pools. At the same time, the extent to which mineral protection is found across soils in colder regions is little understood. Overall, microbial–substrate availability–temperature interactions demand immediate research to better constrain how microbial community responses to temperature-induced changes in SOC influence C loss from warmed soils (BOX 2).

Broader implications

The sensitivity of SOC decomposition rates to warming remains a strong point of academic disagreement^{6,92}. New evidence is constantly emerging that supports expectations ranging from minimal to large losses of SOC to the atmospheric CO₂ pool⁴³. Yet, scientists are typically trained to present more conservative estimates of change, even when higher estimates are equally, if not more, plausible. The academic uncertainty around the sensitivity of SOC decomposition rates to warming generates low confidence in the magnitude of the land C–climate feedback, meaning it is omitted from consideration during negotiations on emissions. However, there is an academic

responsibility to weigh the evidence and not tend towards overly conservative projections as the default, because the reality is that academic debates around the magnitude of change — including for SOC — can have substantive societal consequences. Inclusion of the land C–climate feedback in climate negotiations would, if it is substantive, require aggressive emission reductions to meet climate change targets.

We believe that there is reasonable scientific confidence that SOC losses caused by microbial-mediated decomposition under warming are likely to be of a magnitude relevant for emission negotiations. Although long-term warming might partially dampen microbial activity via changes in substrate availability or physiology, there is no evidence as yet to suggest that these mechanisms would override or preclude net losses of SOC under warming. Instead, evidence that microbial communities might shift their substrate-use patterns to more

rapidly decompose more biochemically recalcitrant particulate forms of SOC suggests that long-term warming could actually amplify microbial activity (FIG. 4). Overall, the pattern of increasing soil C stocks in regions with lower MAT and the positive response of soil respiration to temperature both plausibly support the notion that warming is likely to substantially reduce the global soil C stock. That lower MAT regions are warming most rapidly raises the possibility that the most vulnerable, large SOC stocks will respond most in the near term to ongoing climate warming.

We acknowledge that the role of variables such as soil moisture and plant production, which can regulate the responses of the soil microbial community and, thus, alter warming-induced changes in soil respiration and SOC^{9,20,93,94}, are not considered here. The assessment of these and other factors will help to strengthen confidence in

Box 2 | Road map to build confidence in the magnitude of the land C–climate feedback

Research needs (in *italics*) and suggested approaches are listed.

Soil organic carbon in cold regions

Quantify how much of the large soil organic carbon (SOC) stock in cold regions is in particulate versus mineral-associated forms. Develop a comprehensive field database for high latitude and altitude sites using standardized protocols and consistent separation schemes of soil organic matter fractions.

Determine how the high abundance of soil decomposers influences SOC mineralization rates with warming in cold regions. Explore soil decomposer abundance in estimates of warming effects on SOC stocks using microbial-explicit biogeochemical models and observations across gradients in soil microbial biomass.

Soil organic carbon modelling

Integrate complex microbial–temperature relationships into SOC models that go beyond the use of a constant Q_{10} coefficient. Test the macromolecular rate theory and the square root model across wide environmental conditions, with a particular focus in cold regions.

Explore through SOC modelling the sensitivity of model projections to the opposite findings in the literature regarding microbial–temperature relationships. Represent multiple competing assumptions of microbial metabolic response to temperature in first-order and microbial-explicit SOC models, and refine the largest structural and parameter sensitivities among models.

Soil organic carbon stocks and warming

Determine the extent to which soil microbial communities respond to changes in SOC complexity with warming, and what the outcomes are for SOC stocks. Develop microbial functional information using omics and other advanced technologies in concert with SOC physicochemical characterizations, to develop robust structure–function relationships between microbial communities and SOC turnover.

Quantify how factors such as moisture and plant inputs shape the responses of soil microbial communities and SOC to warming. Monitor these factors in observational studies capturing wide environmental variation, and include them in multi-factor global change experiments, to develop microbial functional and SOC fraction data for modelling.

Communication

Ascertain what information on SOC responses under warming is most useful to and needed by climate policy audiences. Use co-production approaches to engage soil scientists and ecologists with climate policymakers in a manner that efficiently and productively discerns the information the policymakers need.

Resolve how soil scientists and ecologists should present information on SOC responses under warming to climate policy audiences, especially in terms of uncertainty and variance. Collaborate with social scientists working in areas such as communication, political philosophy, epistemology and ethics to evaluate the most effective ways that soil scientists and ecologists can present uncertainty to climate policymakers.

the magnitude of the land C–climate feedback, and we suggest a road map for future research and synthesis (BOX 2). Still, latitudinal patterns in SOC stocks are simulated through model–data integration and cross-validation of broad-scale, field observational and experimental patterns in microbial physiological processes such as CUE under different thermal regimes. Thus, it is both academically and societally important to examine shifts in microbial activities under warming, to help rapidly build a robust, inferential basis on which to estimate the magnitude of C cycle–climate feedbacks with reasonable confidence.

Even if the exact magnitude is unknown, the positive relationship between soil respiration and temperature, and SOC accumulation in low MAT regions, together build compelling evidence for an expectation of substantive net losses of SOC under warming. Therefore, we suggest that there is enough confidence in a positive land C–climate feedback to warrant its inclusion in the setting of greenhouse gas emission allowances to meet stated climate targets.

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Author contributions

P.G.-P. and M.A.B. conceived the idea for the paper. T.W.C., J.R., J.v.d.H. and J.-S.Y. conducted the analyses. The paper was drafted by P.G.-P., T.W.C., M.D., I.P.H., S.R., R.R., J.R. and M.A.B., and all authors contributed to the final version.

Competing interests

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