LETTER

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Quantifying global soil carbon losses in response to warming

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The majority of the Earth's terrestrial carbon is stored in the soil. If anthropogenic warming stimulates the loss of this carbon to the atmosphere, it could drive further planetary warming[1–4]. Despite evidence that warming enhances carbon fluxes to and from the soil[5,6], the net global balance between these responses remains uncertain. Here we present a comprehensive analysis of warming-induced changes in soil carbon stocks by assembling data from 49 field experiments located across North America, Europe and Asia. We find that the effects of warming are contingent on the size of the initial soil carbon stock, with considerable losses occurring in high-latitude areas. By extrapolating this empirical relationship to the global scale, we provide estimates of soil carbon sensitivity to warming that may help to constrain Earth system model projections. Our empirical relationship suggests that global soil carbon stocks in the upper soil horizons will fall by 30 ± 30 petagrams of carbon to 203 ± 161 petagrams of carbon under one degree of warming, depending on the rate at which the effects of warming are realized. Under the conservative assumption that the response of soil carbon to warming occurs within a year, a business-as-usual climate scenario would drive the loss of 55 ± 50 petagrams of carbon from the upper soil horizons by 2050. This value is around 12–17 per cent of the expected anthropogenic emissions over this period[7,8]. Despite the considerable uncertainty in our estimates, the direction of the global soil carbon response is consistent across all scenarios. This provides strong empirical support for the idea that rising temperatures will stimulate the net loss of soil carbon to the atmosphere, driving a positive land carbon–climate feedback that could accelerate climate change.

The exchange of carbon (C) between the soil and atmosphere represent a prominent control on atmospheric C concentrations and the climate[1,6,9]. These processes are driven by the organisms (plants, microbes and animals) that live in the soil, the activity of which could be accelerated by anthropogenic warming[10]. If warming stimulates the loss of C into the atmosphere, it could drive a land C–climate feedback that could accelerate climate change. Yet despite considerable scientific attention in recent decades, there remains no consensus on the direction or magnitude of warming-induced changes in soil C[11,12]. There is growing confidence that warming generally enhances fluxes to and from the soil[8,12], but the net global balance between these responses remains uncertain and direct estimates of soil C stocks are limited to single-site experiments that generally reveal no detectable effects[5,13–15].

Given the paucity of direct measurements of the responses of soil C stocks to warming, Earth system models (ESMs) must rely heavily on the short-term temperature responses of soil respiration (Q_{10}) to infer long-term changes in global C stocks. Without empirical observations that capture longer-term C dynamics, we are limited in our ability to evaluate model performance or to constrain the uncertainty in model projections[16]. As such, the land C–climate feedback remains one of the largest sources of uncertainty in current ESMs[12,14,17], restricting our capacity to develop C emissions targets that are compatible with specific climate change scenarios. Direct field measurements

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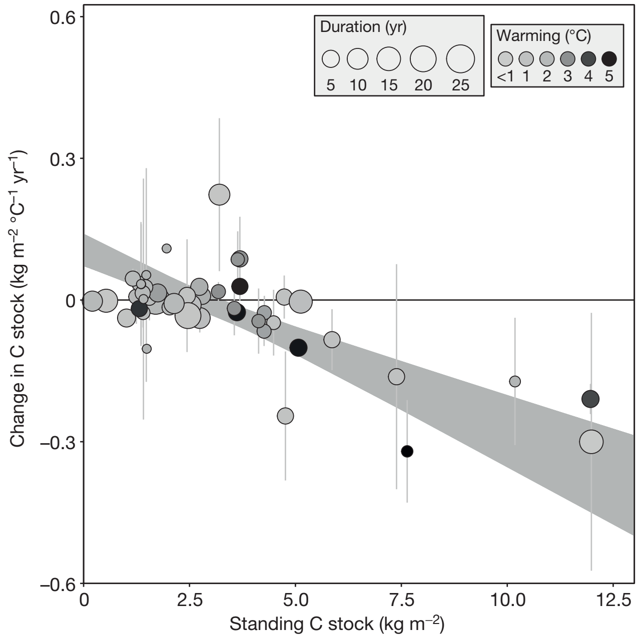

Figure 1 | The effect of warming on soil C losses depends on the initial standing soil C stock. The interaction between warming (degree-years) and standing C stocks is a primary determinant of the final warmed soil C stocks in the top 10 cm of soil (estimated using a mixed effects model; $n = 229$; see Supplementary Information). Each point represents the difference (mean ± standard error) between soil C stocks in warmed and ambient plots within an individual experiment. The size of each point represents the length of the individual study and the colour indicates the amount of warming. The shaded area represents the bootstrapped 95% confidence interval ($R^2 = 0.49$: see Supplementary Information for details).

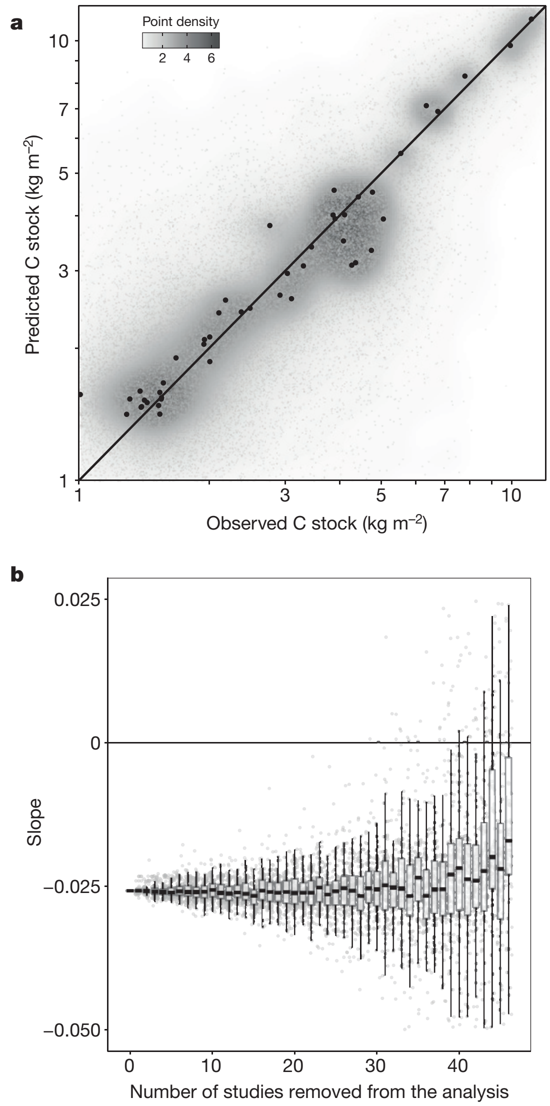

Figure 2 | Validation plots highlighting the predictive strength of the statistical model. a, Predicted versus observed soil C stock values in warmed treatment plots (estimated using statistical Equation (1), $R^2 = 0.95$; this high value is driven by the correlation between C values in the control and warmed plots). The black points represent the mean values for each study, and the shaded area represents the density of 1,000 simulated points randomly selected from within the normal distribution for each study. The 1:1 line is included to highlight perfect correspondence between the predicted and observed points and distributions. **b**, Bootstrapped estimates of the model (Equation (2)) slope values for different sample sizes. Studies were removed at random, the slope coefficient was calculated and this was repeated 1,000 times. Each point represents a bootstrapped estimate of slope for the model that included any given number of studies, and we include the interquartile range and median slope estimates for each number. The average slope value remains unchanged until >38 studies have been removed from the initial analysis (with 49 studies), highlighting that the relationship we present is not disproportionately influenced by the effects of warming in any specific study or site.

of warming-induced changes in soil C stocks are urgently needed to increase confidence in future climate projections[16].

We took advantage of the growing number of climate change experiments around the world to compile a global database of soil C stock responses to warming. Soil samples were collected from replicate plots in 49 climate change experiments conducted across six biomes, ranging from arctic permafrost to dry Mediterranean forests (Extended Data Fig. 1). We compared soil C stocks across warmed (treatment) and ambient (control) plots to explore the effects of temperature across sites. The measured differences in the soil C stocks represent the net result of long-term changes in soil C inputs (plant production) and outputs (respiration) in response to warming. By linking these soil C responses to climatic and soil characteristics, we are able to generate a spatial understanding of the temperature sensitivity of soil C stocks at a global scale. To standardize collection protocols and account for the considerable variability in soil horizon depths, we focus on C stocks in the top 10 cm of soil. At a global scale, this upper soil horizon contains the greatest proportion of biologically active soil C[9].

The effects of warming on soil C stocks were variable, with positive, negative and neutral impacts observed across sites (Fig. 1). However, the direction and magnitude of these warming-induced changes were predictable (Fig. 2) as they are contingent on the size of the standing soil C stocks and the extent and duration of warming. The interaction between control C stocks and degree-years (the standardized metric used to represent the multiplicative product of the extent (in °C) and duration (in years) of warming) was a strong explanatory variable when predicting warmed C stocks (additive model Akaike information criterion (AIC) = 383 versus multiplicative model AIC = 381; see Supplementary Information and Equation (1)). Specifically, the effects of warming were negligible in areas with small initial C stocks, but losses occurred beyond a threshold of 2–5 kgC m^{-2} and were considerable in soils with ≥7 kgC m^{-2} (Fig. 1). No other environmental characteristics (mean annual temperature, precipitation, soil texture or pH) significantly ($P > 0.1$) influenced the responses of soil C stocks to warming in our statistical models (additive environmental with degree-year model AIC = 388; see Supplementary Information).

The dominant role of standing C stocks in governing the magnitude of warming-induced soil C losses is in line with both empirical and theoretical expectations[17–19]. The thawing of permafrost soils, where

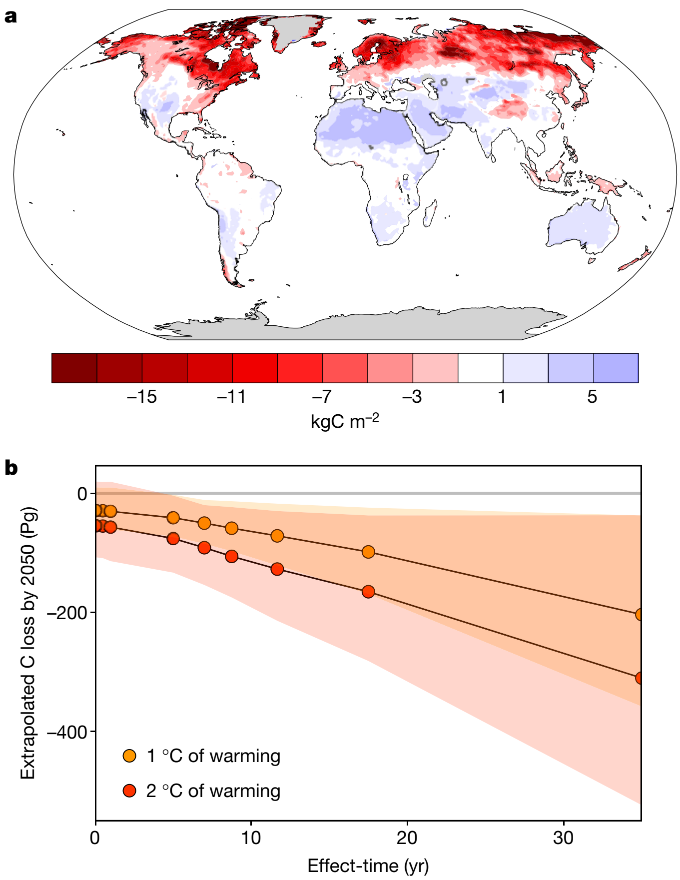

Figure 3 | Spatial extrapolation of the temperature vulnerability of soil C stocks. a, Map of predicted changes in soil C stocks per pixel by 2050 under the 'no acclimatization' scenario. This map was generated by extrapolating Equation (2) using spatially explicit estimates of soil C stocks[19] and soil surface temperature change[22] to reveal the spatial variation in projected changes in surface soil C stocks (0–15 cm depth) expected under a 1 °C rise in global average soil surface temperature. Note that Equation (2) reflects the maximum effect-time scenario, which generates the largest possible estimates of soil C change. This map also predicts C gains in tropical/desert regions that contain almost no soil C at present, but our lack of data in these mid-latitude regions means that we have low confidence in these effects. **b**, Total reductions in the global C pool under 1 °C and 2 °C global average soil surface warming by 2050, as expected under a full range of different soil C effect-time scenarios (*x* axis). Note that effect-time refers to the rate at which the full soil C response to warming is realized. Shaded areas indicate the 95% confidence intervals around the average C losses (dots) for each scenario. The rapid effect-time scenarios (for example, one week to one year) result in lower total soil C losses than the maximum effect-time scenario, but all simulations reveal considerable global losses of soil C under warming over the next 35 years.

limited C decomposition has led to the accumulation of large C stocks, will undoubtedly contribute to this phenomenon[20,21]. However, our analysis also revealed considerable soil C losses in several non-permafrost regions, suggesting that additional mechanisms may contribute to the vulnerability of large soil C stocks. Presumably, the vulnerability of soils that contain large C stocks stems from the high temperature sensitivity of C decomposition and biogeochemical restrictions on the processes driving soil C inputs. In ecosystems with low initial soil C stocks, minor losses that result from accelerated decomposition under warming may be offset by concurrent increases in plant growth and soil C stabilization[13,22]. In contrast, in areas with larger standing soil C stocks, accelerated decomposition outpaces potential C accumulation from enhanced plant growth, driving considerable C losses to the atmosphere.

By combining our measured soil C responses with spatially explicit estimates of standing C stocks[20] and soil surface temperature change[23], we reveal the global patterns in the vulnerability of soil C stocks (Fig. 3). Given that high-latitude regions have the largest standing soil C stocks[20] and the fastest expected rates of warming[18,23], our results suggest that the overwhelming majority of warming-induced soil C losses are likely to occur in Arctic and subarctic regions (Fig. 3). These high-latitude C losses considerably outweigh any minor changes expected in mid- and lower-latitude regions, providing further support for the idea of Arctic amplification of climate change feedbacks[18] (Fig. 3). These warming-induced soil C losses need to be considered in light of future changes in moisture stress and vegetation growth, which are also likely to increase disproportionately in high-latitude areas[18]. Notably, the spatial distribution of soil C changes from our extrapolation contradicts projections from the CMIP5 archive of ESMs[24], which show increases in soil C at high latitudes—presumably due to the increases in plant productivity[25]. The warming-induced losses of soil C that we observe have the potential to offset these vegetation responses, emphasizing the importance of representing soil C vulnerability in the process-based models that are used in climate change projections.

We extrapolated this relationship over the next 35 years to indicate how global soil C stocks might respond by 2050. The simple extrapolation of our empirical relationship suggests that 1 °C of warming over 35 years would drive the loss of 203 ± 161 PgC from the upper soil horizon (Fig. 3). However, this approach implicitly assumes that the effects of a given amount of warming are never fully realized (that is, C stocks fall continuously even under a small amount of warming), so are likely to markedly overestimate total soil C losses (see Methods for details). As with mechanistic models[26], our assumptions about the rate at which soil C responds to warming will strongly influence the magnitude of our predicted C losses (see Fig. 3b). If we make the conservative assumption that the full effects of warming are fully realized within a year, then approximately 30 ± 30 PgC would be lost from the surface soil for 1 °C of warming. Given that global average soil surface temperatures are projected to increase by around 2 °C over the next 35 years under a business-as-usual emissions scenario[16], this extrapolation would suggest that warming could drive the net loss of approximately 55 ± 50 PgC from the upper soil horizon. If, as expected, this C entered the atmospheric pool, the atmospheric burden of CO_2 would increase by approximately 25 parts per million over this period.

The global extrapolation of our empirical data is broadly intended to contextualize our measured changes in soil C stocks. We stress that such statistical approaches cannot be used to project soil C losses far into the future because, unlike process-based models, they cannot capture the complex processes that govern long-term C dynamics. For example, extending the observed relationship over several centuries would lead to a global convergence of soil C stocks. Conversely, soil C stocks would increase exponentially in response to environmental cooling. Our linear extrapolation inherits weaknesses from simple single-pool models[17,27]. However, the value of such linear approximations lies in their descriptive strengths rather than their predictive capabilities: instead of using short-term flux estimates to project long-term changes in C stocks, our approach allows the scaling of measured C differences over time frames (that is, decades) represented by the experimental studies. Our results capture the realized temperature sensitivity of current soil C stocks and can serve as a guideline (or target) for multi-pool process-based models. Specifically, these models can run forward simulations that attempt to reflect the outcomes of the warming experiments that we present. Those models that accurately capture the observed relationships between standing soil C stocks and losses under gradual step increases in global temperature are likely to be the most successful at projecting the land C–climate feedback into the future.

Our analysis reveals a number of outstanding challenges facing empiricists and modellers that limit the certainty of current land C–climate

Table 1 | List of the major remaining gaps in our understanding of the land C–climate feedback

Limitation	Consequence
Limited data on the sensitivity of C socks in deeper soil horizons	Our global estimates of warming-induced C losses cannot represent the C losses from lower soil horizons, which are likely to enhance the magnitude of our reported effects
Uncertainty regarding current estimates of global soil C stocks	Our analysis highlights that soil C losses are highly dependent on the size of standing C stocks. Constraining our estimates of global soil C stocks should therefore be a research priority.
Limited spatial scale of field warming experiments. None of our data were collected from tropical ecosystems.	This leads to considerable uncertainty regarding the sensitivity of C stocks in many parts of the world—the tropics in particular
Practical difference between soil warming experiments and ecosystem warming experiments	Although most studies experimentally warm both the soil and plants within an ecosystem (that is, the whole ecosystem), many studies in forests are unable to capture the temperature responses of trees, which can limit comparison across ecosystem types. Depending on how trees respond to warming, soil C stock data from these sites might over-, or under-represent C losses.
Limited global data on warming-induced changes in primary productivity	Projecting these changes in soil C stocks into the future requires a mechanistic understanding of how warming affects each of the separate components of the ecosystem C cycle. The outstanding limitation, and major source of uncertainty, is the lack of data on warming-induced changes in soil C inputs at a global scale.
Our analysis does not incorporate the interactive effects of other global change drivers	Although temperature is a dominant factor driving changes in Earth system dynamics, the responses of other abiotic factors (including CO_2 concentration, N enrichment and moisture availability) have potential to influence the strength of the relationships presented here.
Limited global data on the effects of biotic responses to warming at a global scale.	Our current understanding of global feedbacks is dominated by the physical sciences, but changes in the physiology and community compositions of organisms have been shown to have strong effects on the strength of this feedback. It is critical that we understand the importance of these effects at a global scale.
We do not know how long it takes for the effects of warming to be realized. That is, we do not know how long soil communities take to acclimatize to warming.	Extrapolating these over time necessitates that we understand the rate at which the effects of warming occur (that is, how fast soils acclimatize to warming). If the effects or warming are realized slowly, then the estimated warming-induced losses of soil C by 2050 will be towards the upper end of the uncertainty bounds that we present (approximately 200 PgC), but if soils acclimatize rapidly, then they will be towards the lower end (around 50 PgC).

Each of these limitations represents a practical challenge that can be addressed by empiricists to improve the accuracy of benchmarking estimates or to parameterize process-based models that project soil C dynamics into the future.

feedback predictions (see the list of critical research gaps in Table 1). These limitations fall into two distinct categories: more data are necessary to improve both our current global estimates of the temperature sensitivity of soil C and modelling efforts to project these soil C responses into the future. First, along with the limited spatial and temporal scale of current warming experiments, perhaps the most critical limitation to our present analysis is the paucity of information about the responses of soil C stocks at depth (below 10 cm). Although the sizes of C stocks decrease down the soil profile[28], any extra C losses from these deeper soil horizons will undoubtedly enhance the effects we present. Second, incorporating global soil C information into modelling frameworks requires a mechanistic understanding of how warming affects each of the individual components of the ecosystem C cycle. Now that we are beginning to generate a global picture of the temperature sensitivity of soil C losses (respiration)[6] and total C stocks, our limited understanding of how warming influences global soil C inputs remains a major source of uncertainty for modelling efforts[14,25]. These efforts also require more information about the interacting effects of other global change factors that may simultaneously influence soil C dynamics. This non-exclusive set of practical challenges calls for concerted, coordinated investment in multi-factor climate change experiments for an extended period of time to generate the data necessary to improve confidence in future climate projections.

In conclusion, our global compilation of experimental data allows us to see past the conflicting results from single-site studies and capture larger patterns in the sensitivity of soil C to warming. The warming-induced changes in soil C stocks reflect the net result of changes in C fluxes into and from the soil, which can augment modelling efforts to project Earth system dynamics into the future. Ultimately, our analysis provides empirical support for the long-held concern that rising temperatures stimulate the loss of soil C to the atmosphere, driving a positive land C–climate feedback that could accelerate planetary warming over the twenty-first century[3,4]. Reductions in greenhouse gas emissions are essential if we are to avoid the most damaging effects of this feedback over the rest of the century.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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METHODS

Data collection and standardization. Total percentage C and bulk density (BD) data ($n = 456$) were collected from each of the replicated warmed and ambient plots within 49 experimental warming studies located across North America, Europe and Asia. In several of these sites, it was not possible to access these data for deeper soil horizons. We therefore standardized collection protocols and account for the considerable variability in soil horizon depths by focusing on the top 10 cm of soil, which contains the majority of the biologically active C. Soil C stocks were then calculated for each plot (percentage C × BD/100), and expressed as the total mass of C (kg m^{-3} soil) in the top 10 cm of each plot. Metadata for each study included the mean annual difference in soil surface temperature between warmed and ambient plots and the duration of experimental warming. These were multiplied together to generate the standardized degree-years metric (which reflects the extent and duration of warming) to permit the comparison of warming effects across sites. Other collected data included a site-specific geospatial reference (latitude and longitude), which was linked to spatially explicit estimates of soil characteristics (pH and texture using the SoilGrids database[19]) and climate (using the Bioclim database) following the procedure used in ref. 29. These climate and soil characteristics were then used to explore the dominant controls on the sensitivity of soil C stocks to warming across our global compilation of experimental studies.

Some of the climate change studies in this analysis contained multiple separate warming experiments. Degree-years and soil C were calculated independently for each study within a site, but all other environmental data were shared. In addition, some sites included multifactor climate change studies. For these studies, ambient and warmed plots were only compared under equivalent experimental conditions so that all other conditions remained consistent between treatments.

Statistical analysis. We fitted linear mixed models (LMMs) to evaluate the factors that correlate with the measured soil C stocks following warming. Study site was included as a random factor because clustering replicates by location could introduce spatial autocorrelation[30]. The LMMs were fitted assuming a Gaussian error distribution in the lme4 package for the R statistical program. We constructed LMMs that included all of the putative explanatory variables to explain warmed soil C stocks including treatment variables (degrees warmed and degree-years) and environmental characteristics (standing soil C stocks (control C stocks), mean annual temperature, mean annual precipitation, pH (as H^+ ion concentration) and soil texture (with percentage clay as the representative variable)). Given the markedly different ranges in magnitudes of the explanatory variables at a global scale, variables were standardized using a z transformation before use in final models[30] although the response variable (soil C stock) was not standardized. Further, given a positive skew in the distributions of degrees, degree-year and control soil C, these variables were also natural-log transformed. Neither of these data transformations significantly altered the statistical outputs, so both were retained in final models. The only independent variables that were strongly correlated (pairwise coefficients >0.4) were mean annual temperature and mean annual precipitation, and mean annual temperature and percentage clay.

Model selection was performed using maximum likelihood comparison of competing models (see Supplementary Information), using AIC and Bayesian information criterion (BIC) approaches that provided identical results. Only warming (degrees and degree-years) and standing C stock (control soil C) were retained in the most parsimonious models, (full model AIC = 381 versus final model AIC = 372; Supplementary Tables 6 and 7) and the best-fit model included an interaction between these two variables (additive model AIC = 375 versus multiplicative model AIC = 372; Supplementary Table 7). All reported P values are quasi-Bayesian, rather than the classical frequentist P values, but retain the same interpretation. We considered coefficients with $P < 0.05$ significant and coefficients with $P < 0.10$ marginally significant. Variance explained by the model was also estimated by calculating R^2 values for the minimally adequate LMM to retain the random effects structure.

The final statistical model was:

$$C_w = aC_c(\Delta T \Delta t) + bC_c + d(\Delta T \Delta t) + \varepsilon \qquad (1)$$

where C_w is the C stock in the warmed treatment, C_c is the C stock in the control plots, $\Delta T \Delta t$ is the degree-years calculated by multiplying the degrees warmed by the length of the treatment, ε is the random effects term that controls for study site (see Supplementary Information) and a,b,d represent fitted coefficients for the statistical model.

Statistical model development. To scale the changes in soil C stocks, we rearranged our statistical equation to describe the relationship between standing soil C stocks (control C stocks) and warming (degree-years) over time:

$$\frac{C_w - C_c}{\Delta T \Delta t} = fC_c + g \qquad (2)$$

This new model explained a considerable proportion ($R^2 = 0.606$; Supplementary Table 7) of the difference in soil C stocks between studies over treatment. This is further highlighted in Fig. 2.

We used sample-based bootstrapping (as opposed to the study-based bootstrapping in Fig. 2b) to evaluate the strength of this simple statistical relationship and to generate a margin of error for global soil C stock projections. Equation (1) was extrapolated with 95% confidence interval bounds by randomly selecting 200 samples from all studies, randomizing the control–warmed pairings and repeating the regression 1,000 times. This resulted in normally distributed parameters (see Supplementary Table 4) with the following 95% confidence interval. The intercept–slope pairs were then sampled to create the grey margin of error seen in Fig. 1.

The inclusion of a linear effect of time in our analysis implicitly assumes that the effects of warming on soil C stocks are never fully realized. That is, it assumes that even a small amount of warming would continue to drive C losses indefinitely, even if the temperature were held constant. However, it is likely that C stocks would ultimately plateau (that is, acclimatize), as the full effects of warming are realized after a given period of time. As such, the assumption that the warming effects are never fully realized is likely to overestimate total soil C losses (see Fig. 3). But we do not know how long it takes for the full effects of warming to be realized (that is, how long it takes the soil to plateau/acclimatize after warming). To explore the importance of this effect-time in determining the magnitude of soil C losses in our extrapolation, we repeated the analysis across a full range of scenarios, where the effect-time of warming varied continuously. To simulate different effect-times, we successively capped the study years (or experiment duration) at 1 week, 1 month, 6 months and 1, 5, 7, 8.75, 11.6 and 17.5 years, then re-ran the linear regression described above (Equation (2) with the sample-based bootstrapping). The resulting coefficients are in Supplementary Table 4.

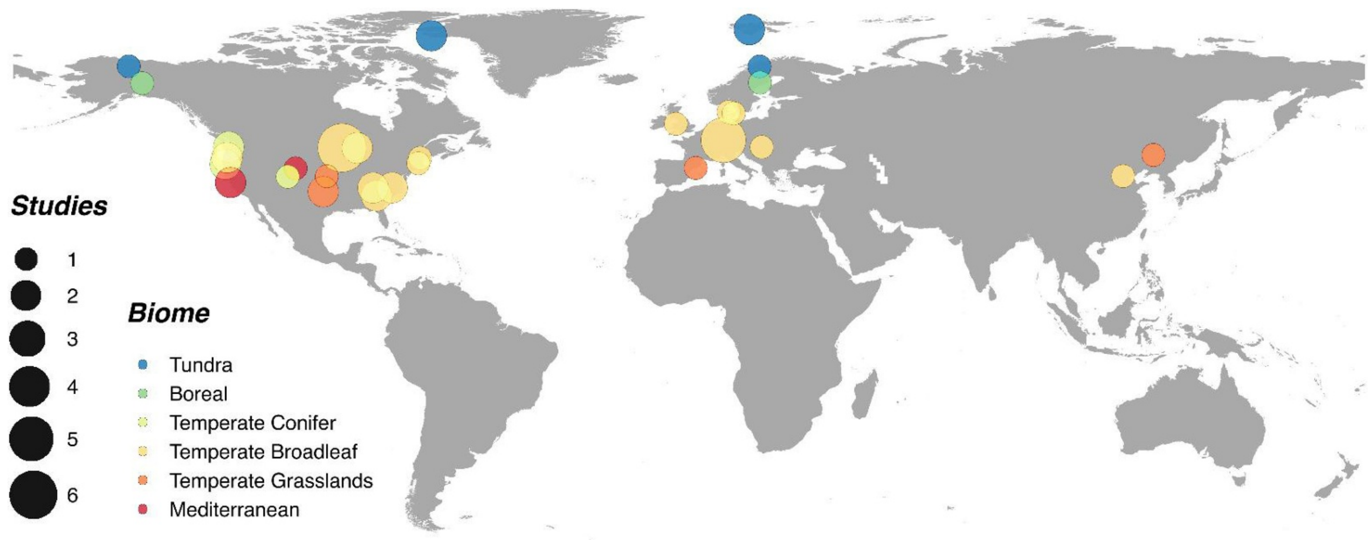
Extrapolation. To estimate the changes in global soil C stocks under projected warming scenarios we applied linear changes in soil temperature that result in a mean warming of 1 °C or 2 °C by 2050 (over 35 years); this warming is spatially distributed in a manner consistent with surface soil temperature projections from a single ensemble of the Community Earth System Model (CESM) that was submitted to the CMIP5 archive under RCP8.5 run from 2005 to 2050. We estimated initial soil C stocks in the upper soil horizon (0–15 cm) from the SoilGrids 50 km^2 product[20], which was regridded using bilinear interpolation to the same spatial scale of soil surface temperature projections (roughly 1°).

The temporal extrapolations across the 35 years (until 2050) were applied separately for each of the possible effect-time scenarios described above. First, the single-time-step approach used the coefficients listed above and illustrated in Fig. 1 to generate a 95% confidence interval for projected C losses. On average, roughly 17.5 degree-years and 35 degree-years were seen cumulatively across the globe for the 1 °C and 2 °C warming scenarios, respectively. The exact warming seen by any individual grid cell was determined by the relative temperature shifts predicted by the CESM run described above. Each subsequent effect-time scenario was then extrapolated using a given time step for a forward integration where the change in soil C over that time was based on the soil C stock at the beginning and the degree-year change experienced by that site over the duration of at respective time step. For example, the 1 yr effect-time scenario used the coefficients from the analysis where experimental duration was capped at 1 yr (see Supplementary Table 4), and was extrapolated to 2050 using the sum of 35 annual time steps. The predicted soil C losses for a global average warming of 1 °C and 2 °C over 35 years, based on each of the full range of effect-time scenarios, is presented in Fig. 3b. This reveals how our assumption about effect-time influences the magnitude of our final expected C losses. Given that the effects of warming are likely to be realized within a year, we have expanded on the annual time-step option.

Code availability. The R code for the full analysis can be found in Supplementary Information.

Data availability. The data that support the findings of this study are available from the corresponding author upon reasonable request.

29. Crowther, T. W. *et al.* Mapping tree density at a global scale. *Nature* **525,** 201–205 (2015).
30. Gelman, A. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27,** 2865–2873 (2008).



Extended Data Figure 1 | Map of the study locations. The sizes of the points represent the number of separate warming experiments at that location and the colours indicate the biomes (as delineated by The Nature Conservancy; http://www.nature.org).