QUANTIFYING GLOBAL SOIL C LOSSES IN RESPONSE TO WARMING

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Generating meaningful greenhouse gas (GHG) emission targets requires an understanding of Earth system dynamics and projections about how they will respond to global change[1–3]. If anthropogenic warming stimulates the loss of carbon from the Earth's surface into the atmosphere, it could drive additional planetary warming. Despite growing evidence that warming enhances soil carbon fluxes to and from the soil[8,12], the net global balance between these responses remains uncertain[1]. 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 upon the size of the initial soil carbon stock, with considerable carbon losses occurring in high-latitude areas. By extrapolating this empirical relationship to the global scale, we provide estimates of global soil carbon sensitivity 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) to 203 (± 161) Pg C for 1 degree of continuous warming, depending upon the potential acclimatization rate of soil organic matter decomposition. An assumption of annual acclimation yields a conservative estimate that soil C stocks will fall by 55 (± 50) Pg C from the upper soil horizons by 2050, a value that is 12-17% of anthropogenic emissions over this period. Despite the uncertainty in these estimates, the direction of the global soil carbon response is consistent across all acclimatization scenarios. Our analysis provides strong empirical support for the assumption that rising temperatures will stimulate the net loss of soil carbon to the atmosphere, driving a positive land carbon-climate feedback that could accelerate climatic change.

The majority of the Earth's terrestrial C is stored in the soil and changes in the size of this C stock represent a prominent control on atmospheric C concentrations[6–8]. If anthropogenic warming stimulates the loss of even a small proportion of soil C, it could drive substantive additional planetary warming[7,9]. Yet, despite considerable scientific attention in recent decades, there remains no consensus on the direction or magnitude of warming-induced changes in soil C[3,10]. Although there is growing confidence that warming generally enhances fluxes to and from the soil[8,12], 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[1,11–13].

Given the paucity of direct measurements of soil C stock responses to warming, Earth System Models (ESMs) must rely heavily on 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 constrain the uncertainty in model projections[14]. As such, the land C-climate feedback remains one of the largest sources of uncertainty in current ESMs[1–3], restricting our capacity to develop C emissions targets that are compatible with specific climate change scenarios. Direct field measurements of warming-induced changes in soil C stocks are urgently needed to increase confidence in future climate projections[14].

We take advantage of the growing number of climate change experiments around the world to compile the first 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 Figure 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 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 standardise 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 by depth[6].

The effects of warming on soil C stocks were variable, with positive, negative and neutral impacts observed across sites (Figure 1). However, the direction and magnitude of these warming-induced changes were predictable (Figure 2), being contingent upon the size of

156 standing soil C stocks and the extent and duration of warming. The interaction between
157 'control C stocks' and 'degree-years' (the standardised metric to represent the
158 multiplicative product of the extent (°C) and duration (years) of warming) was a strong
159 explanatory variable when predicting warmed C stocks (additive model AIC=383 vs.
160 multiplicative model AIC=381; see SI and Equation 1). Specifically, the impacts of
161 warming were negligible in areas with small initial C stocks, but losses occured beyond a
162 threshold of 20 – 40 kg C m^{-3} and were considerable in soils with ≥ 60 kg C m^{-3} (Figure
163 1). No other environmental characteristics (mean annual temperature, precipitation, soil
164 texture or pH) significantly ($P > 0.1$) influenced the responses of soil C stocks to
165 warming in our statistical models (additive enviromental with degree-year model
166 AIC=388; see SI).
167
168 The dominant role of standing C stocks in governing the magnitude of warming-induced
169 soil C losses is in line with both empirical and theoretical expectations[2,15,16]. The thawing
170 of permafrost soils, where limited C decomposition has led to the accumulation of large
171 C stocks, will undoubtedly contribute to this phenomenon[17,18]. However, our analysis also
172 revealed considerable soil C losses in several non-permafrost regions, suggesting that
173 additional mechanisms may contribute to the vulnerability of large soil C stocks.
174 Presumably, the vulnerability of soils containing large C stocks stems from the high
175 temperature-sensitivity of C decomposition and biogeochemical restrictions on the
176 processes driving soil C inputs. In ecosystems with low initial soil C stocks, minor losses
177 that result from accelerated decomposition under warming may be offset by concurrent
178 increases in plant growth and soil C stabilization[12,19]. In contrast, in areas with larger
179 standing soil C stocks, accelerated decomposition outpaces potential C accumulation
180 from enhanced plant growth, driving considerable C losses into the atmosphere.
181
182 By combining our measured soil C responses with spatially-explicit estimates of standing
183 C stocks[17] and soil surface temperature change[20] (using Equation 2), we reveal the global
184 patterns in the vulnerability of soil C stocks (Figure 3). Given that high-latitude regions
185 have the largest standing soil C stocks[17] and the fastest expected rates of warming[15,20],
186 our results suggest that the overwhelming majority of warming-induced soil C losses are

likely to occur in Arctic and sub-Arctic regions (Figure 3). These high-latitude C losses drastically outweigh any minor changes expected in mid- and lower latitude regions, providing additional support for the idea of Arctic amplification of climate change feedbacks[15] (Figure 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 respond disproportionately to climate change in high-latitude areas[15]. Notably, the spatial distribution of soil C changes from our extrapolation contradicts projections from the CMIP5 archive of Earth system models[21], which show increases in soil C at high latitudes, presumably due to the increases in plant producitity[22]. 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 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 degree of warming over 35 years would drive the loss of 203 (±161) Pg C from the upper soil horizon (Figure 3). However, this approach implicitly assumes that soil communities never acclimatize to changes in temperature, so are likely to drastically over-estimate total soil C losses. Indeed, as with mechanistic models[23], our assumptions about the rate of soil C acclimatization will strongly influence the magnitude of our predicted C losses (see Figure 3B). For example, a range of recent analyses suggest that soil communities can acclimatize to warming within a year[24–26]. If we assume annual acclimatization to warming in our extrapolation, then approximately 30 (± 30) Pg C would be lost from the surface soil for 1 degree (ºC) of warming. Given that global average soil surface temperatures are projected to increase by ~2 ºC over the next 35 years under a business-as-usual emissions scenario[16], this annual time step extrapolation would suggest that warming could drive the net loss of ~55 (± 50) Pg C from the upper soil horizon. If, as expected, this C entered the atmospheric pool, it would increase the atmospheric burden of CO_2 by approximately 25 ppm 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, which can over-predict the magnitude of responses in the long term[2,27]. However, the value of such linear approximations lie in their descriptive strength 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 (i.e. decades) represented by the experimental studies. Our results capture the realised 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 which 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 modelers, which currently limit the certainty of current land C-climate feedback predictions (see Supplemenrary Table 1). These limitations fall into two distinct categories, as more data are necessary to improve (i) our current global estimates of soil C temperature sensitivity, and (ii) 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 size of C stocks decrease down the soil profile[28], any additional 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)[8] and total C stocks, our limited understanding of how warming influences global soil C inputs remains a major outstanding source of uncertainty for modelling efforts[1,22]. 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 into the atmosphere, driving a positive land C-climate feedback that could accelerate planetary warming over the 21st century. Reductions in greenhouse gas emissions are essential if we are to avoid the most damaging impacts of the land C-climate feedback over the rest of this century.

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AUTHOR CONTRIBUTIONS

The study was conceived and designed by TWC and NS. Statistical analysis was performed by KEOTB , MAB, and BLS. Spatial scaling and mapping was performed by WRW and CWR. The manuscript was written by TWC with assistance from CWR, MAB, WRW, KEOTB, SDA and PBR. All other authors reviewed and provided input on the manuscript. Measurements of soil carbon, bulk density and geospatial data from climate change experiments around the world were provided by JCC, MBM, SF, GZ, AJB, BE, SR, AJH, HL, YL, AM, JP, ME, SDF, GK, CP, PHT, LLR, EP, SS, JML, SDA, KKT, BE, LNM, IKS, KSL, YC, FAD, SM, SN, ATC, JMB, SB, JSC, FAD, JG, BRJ, JM, LPM and PBR.

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FIGURE LEGENDS

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 final warmed soil C stocks (estimated using a mixed effects model; n = 229; see SI). Here, each point represents the difference (mean±SE) between soil C stocks in warmed and ambient plots within an individual experiment. The size of points represents the length of each individual study, and the colour indicates the amount

of warming. The shaded area represents the bootstraped 95% conficence interval (R^2 = 0.49: see supplemental for details).

Figure 2: Validation plots highlighting the predictive strength of the statistical model. Plate A: predicted vs. observed soil C stock values in warmed treatment plots (estimated using statistical Equation 1: $R^2 = 0.95$ – high value is driven by the correlation between C values in control and warmed plots). Black points represent mean values for each study, and the coloured area represents the density of 1000 simulated points randomly selected from within the normal distribution for each study. The 1:1 line is included to highlight perfect correspondence between predicted and observed points and distributions. Plate B: Bootstrapped estimates of model (Equation 2) slope values for different sample sizes. Studies were removed at random, the slope coefficient was calculated and this was repeated 1000 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 an 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(s) or site(s).

Figure 3: Spatial and temporal extrapolation of the temperature-vulnerability of soil C stocks. Plate A: Map of soil C vulnerability to warming. This map was generated by extrapolating Equation 2 (i.e. the no-acclimation scenario) using spatially explicit estimates of soil C stocks[17], and soil surface temperature change[20], and reveals the spatial variation in projected surface soil C stock changes (0-15 cm) expected under a 1ºC rise in global average soil surface temperature. Panel B: Total reductions in the global C pool under a 1, and 2ºC global average soil surface warming by 2050, as expected under a full range of different soil acclimatization scenarios (x axis). Shaded areas indicate 95% confidence intervals around the average C losses (dots) for each scenario. The rapid acclimatization scenarios (e.g. 1 week – 1 year) result in lower total soil C losses than the no acclimatization scenario, but all simulations reveal considerable global losses of soil C under warming over the next 35 years. Note that our map predicts some C gains in desert

402 regions that currently contain almost no soil C. Removing these biochemically
403 questionable responses would marginally enhance the size of the global C losses reported
404 in Pannel B.
405
406
407 **METHODS**
408
409 **Data collection and standardisation**
410 Total percentage C and bulk density (BD) data (n=456) were collected from each of the
411 replicated warmed and ambient plots within 49 experimental warming studies located
412 across North America, Europe and Asia. In several of these sites, it was not possible to
413 access these data for deeper soil horizons. Therefore, we standardised collection
414 protocols and account for the considerable variability in soil horizon depths by focusing
415 on the top 10 cm of soil, which contains the majority of the biologically active C. Soil C
416 stocks were then calculated for each plot (percentage C * BD / 100), and expressed as the
417 total mass of C (kg m^{-3} soil) in each plot. Metadata for each study included the mean
418 annual difference in soil surface temperature between warmed and ambient plots and the
419 duration of experimental warming. These were multiplied together to generate the
420 standardised metric 'degree-years', (reflecting the extent and duration of warming) to
421 permit the comparison of warming effects across sites. Other collected data included a
422 site-specific geospatial reference (latitude and longitude), which was linked to spatially-
423 explicit estimates of soil characteristics (pH and texture using the SoilGrids database[17])
424 and climate (using the Bioclim database) following Crowther *et al.*[29]. These climate and
425 soil characteristics were then used to explore the dominant controls on soil C stock
426 sensitivity to warming across our global compilation of experimental studies.
427
428 Some of the climate change studies in this analysis containted multiple separate warming
429 experiments. Degree-years and soil C were calculated independently for each study
430 within a site, but all other environmental data were shared. In addition, some sites
431 included multi-factor 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 fit assuming a Gaussian error distribution in the "lme4" package for the R statistical program[31]. We constructed LMMs that included all of the putative explanatory variables to explain warmed soil C stocks including treatment variables (degrees warmed and degrees warmed across years of study (degree-years)), and environmental characteristics (Standing soil C stocks (control C stocks), Mean Annual Temperature (MAT), Mean Annual Precipitation (MAP), 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 standardised using a z-transformation prior to use in final models[32], though the response variable (soil C stock) was not standardised. Further, given 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 were retained in final models. The only independent variables that were strongly correlated (pairwise coefficients >0.4) were MAT and MAP, and MAT and percentage clay.

Model selection was performed using maximum likelihood comparison of competing models (see SI), using Akaike information criterion (AIC) and Bayesian information criterion (BIC) approaches providing identical results. Only warming (degrees and degree-years) and standing C stock (control soil C) were the most parsimonious final models, (full model AIC=381 vs. final model AIC=372; Tables S6, S7) and the best-fit model included an interaction between these two variables (addItive model AIC=375 vs. multiplicative model AIC=372; Table S7). 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 following Nakagawa and Schielzeth to retain the random effects structure.

The final statistical model was:

$$C_w = a \cdot C_c \cdot (\Delta T \Delta t) + b \cdot C_c + d \cdot (\Delta T \Delta t) + e \qquad \text{Eqn 1}$$

where *Cw* is the carbon stock in the warmed treatment, Cc the carbon stock in the control plots, $\Delta T \Delta t$ the degree-years calculated by multiplying the degrees warmed times the length of the treatment, ε the random effects term controlling for study site (see SI), and *(a, b, d*) represent fitted coefficients for the statistical model.

Statistical model development

To scale the changes in soil C stocks, we re-arranged our statistical equation in order to describe the relationship between standing soil C stocks (control C stocks) and warming (degree-years) over time:

$$\frac{C_w - C_c}{\Delta T \cdot \Delta t} = f \cdot C_c + g \qquad \text{Eqn 2}$$

where *Cw* is the carbon stock in the warmed treatment, Cc the carbon stock in the control plots, $\Delta T \Delta t$ the degree-years calculated by multiplying the degrees warmed times the length of the tratement. This new model explained a considerable proportion (R^2=0.606; SI Table 7) of the difference in soil C stocks between studies over treatment. This is futher highlighted in Figure 2.

We used sample-based bootstrapping (as opposed to the study-based bootstrapping in Figure 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%CI bounds by randomly selecting 200 samples from all studies, randomising the

control-warmed pairings, and repeating the regression 1000 times. This resulted in normally distributed parameters (see SI Table 4) with the following 95%CI. The intercept-slope pairs were then sampled to create the grey margin of error seen in Figure 1.

The inclusion of a linear effect of 'time' in our analysis implicitly assumes that soils never acclimatize to warming. However, recent studies suggest that soils can acclimatize to warming within an annual time-frame[24–26], so the assumption of no acclimatization is likely to over-estimate total soil C losses. To explore the importance of this acclimatization assumption in determining the magnitude of soil C losses in our extrapolation, we repeated the analysis across a full range of acclimatization scenarios. To simulate different acclimatization rates, we sucessively capped the study years (or experiment duration) at 1 week, 1 month, 6 months, and 1, 5, 7, 8.75, 11.6, 17.5 years, then re-ran the linear regression described above (Eqn 2) with the sample-based bootstrapping. The resulting coefficients are in SI Table 4.

Extrapolation

To estimate changes in global soil C stocks under projected warming scenarios we applied linear changes in soil temperature that result in 1 or 2^{o}C mean warming by 2050 (35 years) that 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[17], that was regridded using bilinear interpolation to the same spatial scale of soil surface temperature projections (roughly 1 degree).

The temporal extrapolations across the 35 years (until 2050) were applied separately for each of the possible acclimatization scenarios described above. First, the single time step approach used the coefficients listed above and illustrated in Figure 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 and 2^{o}C warming

scenarios, respectively. The exact warming seen by any individual grid was determined by their relative temperature shifts predicted by the CESM run described above. Each subsequent acclimatization 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-year acclimation scenario used the coefficients from the analysis where or experimental duration was capped at 1 year (see SI, 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 and 2 C by 35 years, based on each of the full range of acclimatization scenarios, is presented in Figure 3B. This reveals how our assumption about acclimatization time influences the magnitude of our final expected C losses.

The R code for the full analysis can be found in the Supplementary Material.

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Extended data table 1: List of current limitations in the availability of global data that restrict confidence in our current understanding of the land C-climate feedback. Each of these limitations represents a practical challenge that can be adressed by empiricists to improve the accuracy of benchmarking estimates or to perameterize process-based

models that project Earth system dynamics into the future.

Extended Data Figure 1: Map of study locations. The size of points represents the number of separate warming experiments at that location and colour indicates the biome, as delineated by The Nature Conservancy (http://www.nature.org).

Extended Data Figure 2: Extended extrapolation of our linear model that illustrates some of the limitations of this statistical scaling approach. Figures show soil C projections for initial stocks under (A) 1 degree warming per decade, which converge on the same soil C stocks; or (B) 2 degree cooling per decade, which show exponential increases in soil C stocks. Although both of these responses are unrealistic, we note the time scales (and amount of warming) needed to observe such dynamics are well outside the range of observed manipulations or climate change projections. This highlights that our extrapolation cannot represent a substitute for process-based models, which capture long-term C dynamics. However, under more realistic warming (< 5 degrees C) our extrapolation makes plausible projections over decadal time scale that represent the current temperature sensitivity of soil C stocks.