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The sensitivity of carbon turnover in the Community Land Model to modified assumptions about soil processes

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Abstract. Soil organic matter (SOM) is the largest store of organic carbon (C) in the biosphere, but the turnover of SOM is still incompletely understood and not well described in global C cycle models. Here we use the Community Land Model (CLM) and compare the output for soil organic C stocks (SOC) to estimates from a global data set. We also modify the assumptions about SOC turnover in two ways: (1) we assume distinct temperature sensitivities of SOC pools with different turnover time and (2) we assume a priming effect, such that the decomposition rate of native SOC increases in response to a supply of fresh organic matter. The standard model predicted the global distribution of SOC reasonably well in most areas, but it failed to predict the very high stocks of SOC at high latitudes. It also predicted too much SOC in areas with high plant productivity, such as tropical rainforests and some midlatitude areas. Total SOC at equilibrium was reduced by a small amount ($< 1\%$ globally) when we assume that the temperature sensitivity of SOC decomposition is dependent on the turnover rate of the component pools. Including a priming effect reduced total global SOC more (6.6% globally) and led to decreased SOC in areas with high plant input (tropical and temperate forests), which were also the areas where the unmodified model overpredicted SOC (by about 40%). The model was then run with climate change prediction until 2100 for the standard and modified versions. Future simulations showed that differences between the standard and modified versions were maintained in a future with climate change (4–6 and 23–47 Pg difference in soil carbon between standard simulation and the modified simulation with temperature sensitivity and priming respectively). Although the relative changes are small, they are likely to be larger in a fully coupled simulation, and thus warrant future work.

1 Introduction

Soil organic matter (SOM) is the largest store of organic carbon (C) in the biosphere (Batjes, 1996). Even relatively small percentage changes in this store can lead to large changes in atmospheric CO_2 concentrations. However, there is still large uncertainty associated with the response of SOM dynamics to perturbations such as changes in temperature, moisture and plant-derived inputs to soils that are predicted under environmental change (Heimann and Reichstein, 2008; Ostle et al., 2009; Billings et al., 2010; Conant et al., 2011; Zhu and Cheng, 2011). In large part, this uncertainty is a result of incomplete understanding of the complex chemical, physical and biological processes (and interactions) that govern SOM decomposition, and the influence of environmental factors on these processes (Paterson et al., 2009; Subke and Bahn, 2010; Dungait et al., 2012). This has limited the extent to which the processes mediating SOM decomposition have been represented explicitly in models, potentially limiting their accuracy in predicting impacts of environmental change across ecosystems.

Terrestrial models predict fluxes of C and water and more recently also N and fire in the earth system. Several terrestrial

models exist, such as the Lund–Potsdam–Jena (LPJ), the Joint UK Land Environment Simulator (JULES) and the Community Land Model (CLM) (Sitch et al., 2003; Best, 2005; Oleson et al., 2010). These models can be integrated into earth system models (ESMs) to predict the biotic feedback to climate change. ESM studies have demonstrated that climate–carbon-cycle feedbacks over the next century may have a large impact on future CO_2 levels and climate (Cox et al., 2000; Friedlingstein et al., 2001), although this is not true in all simulations (Thornton et al., 2009). As well as being a tool in climate prediction, ESMs also provide tools for integration of knowledge about the land surface. A comparison of earth system models included in the Intergovernmental Panel on Climate Change (IPCC) showed that one of the largest uncertainties in predicting biotic feedback to climate change is how the soil will respond (Friedlingstein et al., 2006). The soil response to global warming is a critical parameter in determining future CO_2 concentrations and therefore the magnitude of feedbacks to the rate of future climate change (Jones et al., 2003) and represents a large uncertainty in future climate prediction overall, including physical climate effects (Huntingford et al., 2009). Improving the soil part of the model is therefore a priority for earth system modellers.

Soils receive inputs of organic matter from plants via living roots (rhizodeposition) and senescent tissue (litter), whereas the dominant loss is as CO_2 from microbial decomposition of these inputs and of native SOM (Yuste et al., 2007; Paterson et al., 2008, 2009; Metcalfe et al., 2011). A large proportion of plant-derived inputs is rapidly mineralised to CO_2 (supporting the activities of diverse microbial communities) with the remainder contributing to the stock of SOM and, for soils in equilibrium, balancing the decay of SOM pools. In simulation models, SOM is usually represented as 2–6 pools defined by their respective rates of C turnover. In almost all models the temperature sensitivity of soil organic C (SOC) turnover is assumed to be constant for all pools, irrespective of their mineralisation rate, or other factors controlling relative turnover rates (e.g. Jenkinson et al., 1987; Parton et al., 1987, 1988, 1994; Williams, 1990; Li, 2000). In addition, SOC content is modelled to increase as a direct function of increasing rates of plant inputs, which makes the implicit assumption that the decomposition rates of individual pools do not affect each other, i.e. that there is no priming (Kuzyakov, 2010). However, in recent years, evidence derived from mechanistic studies of soil processes has challenged the validity of these assumptions. Firstly, some studies have now reported that SOC pools exhibit distinct temperature sensitivities, although this is still debated (Waldrop and Firestone, 2004; Fang et al., 2005; Knorr et al., 2005; Reichstein et al., 2005; Davidson and Janssens, 2006). Differential temperature sensitivity of SOC pools has been interpreted as being consistent with kinetic theory, where reactions with high activation energy (e.g. decomposition of relatively recalcitrant SOC) have greater temperature

sensitivity (Conant et al., 2011). Therefore, it has been suggested that incorporation of pool-specific temperature sensitivity into models could be approached through inclusion of an Arrhenius-form equation to modify pool turnover rates (Knorr et al., 2005). Secondly, increased decomposition of native SOM pools in response to fresh inputs from plants (priming effects) has now been demonstrated in many laboratory and field-based experiments (e.g. Fontaine et al., 2003, 2007, 2011; Paterson et al., 2008, 2013; Paterson and Sim, 2013; Kuzyakov, 2010; Zhu and Cheng, 2011). It is increasingly recognised that such priming effects are general phenomena intrinsic to plant–soil interactions, but have only recently become reliably quantifiable (Paterson et al., 2009; Kuzyakov, 2010). Plant-mediated decomposition of native SOM is an important means of sustaining plant biomass production, through mobilisation of limiting nutrients from organic forms, and may be a key process mediating the balance of ecosystem C exchange (Paterson, 2003). Therefore, particularly under future environmental conditions where plant growth may be enhanced (e.g. in response to increased atmospheric CO_2 concentration) and result in increased inputs of plant-derived organic matter to soil, consideration of priming effects may be necessary for prediction of soil C dynamics.

Here we carry out a sensitivity study using the CLM with both a carbon and a nitrogen cycle (CN) (Thornton et al., 2007; Oleson et al., 2010) to assess the potential global effects of changing the assumptions about temperature sensitivities of SOM pools and the effect of organic matter input on SOC mineralisation rate. We assess the effects on a global scale and compare model output to available observational data, and conduct simulations using both standard and modified SOM models with predicted climate change.

2 Materials and methods

2.1 Model

All model experiments were conducted with the terrestrial model CLM version 4.0, which simulates photosynthesis, C fluxes and storage, heat and water transfer in soils, and vegetation–radiation interactions (Oleson et al., 2010). The model has been updated to include the N cycle in addition to the C cycle (Thornton et al., 2007, 2009). The model is described in detail in the CLM technical description and appropriate papers (Thornton et al., 2007, 2009; Oleson et al., 2010).

The SOC submodel in CLM is described in detail by Thornton and Rosenbloom (2005). The model has three litter pools and four SOC pools with different turnover time, similar to most SOM models. The fraction of plant litter allocated to each of the three litter pools depends on which plant functional type it is from. In addition, woody material is assumed to fractionate before it enters any litter pool, using a fractionation constant (K_{frag}). As the litter pools decompose, a

fraction of the C is released as CO_2 and a fraction is transformed into the corresponding SOC pool. The SOC pools either mineralise to CO_2 or decompose to enter another pool except the last (and slowest turning over SOC pool) that only mineralises to CO_2. The response of the model to climate change in offline and fully coupled simulations has been explored (Thornton et al., 2007, 2009), and comparisons to detailed observations has been examined (Randerson et al., 2009). A version of this model was included in the Coupled Model Intercomparison Project (CMIP5) analysis prepared in part for the 5th Assessment Report of the IPCC (Lindsay et al., 2013). The model has also been compared to other fully coupled models (e.g. Arora et al., 2013; Jones et al., 2013).

2.2 Modifications

The model was modified in two ways to assess the effect of other plausible assumptions about soil processes than those currently in the model. These modifications are described below.

2.2.1 Temperature sensitivity of pools

In the standard version of the model, decomposition rates of all soil and litter organic C pools are equally sensitive to temperature, using a Q_{10} formulae ($Q_{10} = 1.5$). Knorr et al. (2005) suggested how decomposition rates of pools could be calculated based on Arrhenius kinetics:

$$k(T) = A e^{\frac{-E_a}{RT}} k = A e^{\frac{-E_a}{RT}}, \tag{1}$$

where k is the decomposition rate, E_a is activation energy, R is the universal gas constant, T is temperature in Kelvin, and A is the theoretical decomposition rate at $E_a = 0$. This therefore provides a methodology for how to calculate pool decomposition rates based on theoretical considerations from thermodynamics. We used this methodology to modify the standard Q_{10} model temperature sensitivity (k_{mod}) while retaining the shape of the temperature response:

$$k_{\mathrm{mod}} = k_{Q_{10}} e^{\frac{-E_a}{RT}}. \tag{2}$$

Standard model approximations of $k(T)$ are based on data from experiments on quickly decomposing SOC pools. However, Knorr et al. (2005) argued that the decomposition of slowly decaying SOC is more sensitive to temperature than decomposition in the quickly decaying pools common to most experiments. Therefore, we modified the Arrhenius model term in Eq. (2) to be dependent on the turnover time characteristic of each soil and litter pool, expressed as the difference between the activation energy of the pool and a standard activation energy (E_{astd}). The sign convention was chosen such that the temperature sensitivity of k increases with pool turnover time, as used by Knorr et al. (2005):

$$k_{\mathrm{mod}} = k_{Q_{10}} e^{\frac{(E_a - E_{\mathrm{astd}})}{RT}}. \tag{3}$$

Table 1. Values for the parameters used in the calculation of the temperature sensitivity of decomposition rates for this study (Eq. 4). Turnover times for all carbon pools are from Thornton and Rosenbloom (2005) and are the same as those used in CLM4. Activation energies are computed using the linear fit given by Knorr et al. (2005) in their Fig. 2. A least-squares, best-fit Q_{10} coefficient is given for each of the modified decomposition rates, $k_{\mathrm{mod}}(T)$.

Carbon pool	Turnover time ($T = 25\,°C$) [days]	Activation energy [J mol^{-1}]	Q_{10} coefficient for K_{mod}
Soil 1	21.4	39 882	1.50
Soil 2	107.1	46 736	1.66
Soil 3	1071.4	56 543	1.93
Soil 4	15 000.0	67 783	2.27
Litter 1	2.1	30 075	1.29
Litter 2	21.4	39 882	1.50
Litter 3	107.1	46 736	1.66
K_{frag}	1500.0	57 976.0	1.97

To be consistent with the conclusions of Knorr et al. (2005) as mentioned above, we use the activation energy of the fastest decomposing soil pool as the standard in this expression. Activation energy was calculated for each C pool using the turnover times from Thornton and Rosenbloom (2005), also used in CLM4, and a linear fit to empirical activation energy data given by Knorr et al. (2005) (Table 1).

In addition, we modified the term in the exponent from Eq. (3) to equal zero when the pool temperature equals 15 °C, or roughly the global average temperature, by multiplying by the factor $(T - T_{15})/T_{15}$, where T_{15} is $T = 15\,°C$. This ensured that the temperature response of the model was the same for k_{mod} and $k_{Q_{10}}$ at this temperature.

$$k_{\mathrm{mod}} = k_{Q_{10}} e^{\frac{(e_a - E_{\mathrm{astd}})(T - T_{15})}{RT T_{15}}} \tag{4}$$

We computed new decomposition rates for all C pools and temperatures using Eq. (4) and fitted a new Q_{10} coefficient to the temperature sensitivity of k_{mod} for each pool (Table 1, Fig. 1). The quickly decomposing soil 1 pool was used as the standard and was kept unchanged. The values of Q_{10} increase up to 2.27 in the more slowly decomposing pools (Table 1).

2.2.2 Priming effect

Plants add C to the soil, broadly in proportion to their growth rate. In the standard model, meaning that everything else being equal, the C content in soils will increase with increasing plant biomass production. However, there is evidence that input of fresh C can increase the decomposition rate of the C that is already there, through the priming effect (Kuzyakov, 2010). To account for priming of native SOM, we used data from a laboratory incubation experiment (Garcia-Pausas and Paterson, 2011). This experiment used ^{13}C-enriched glucose
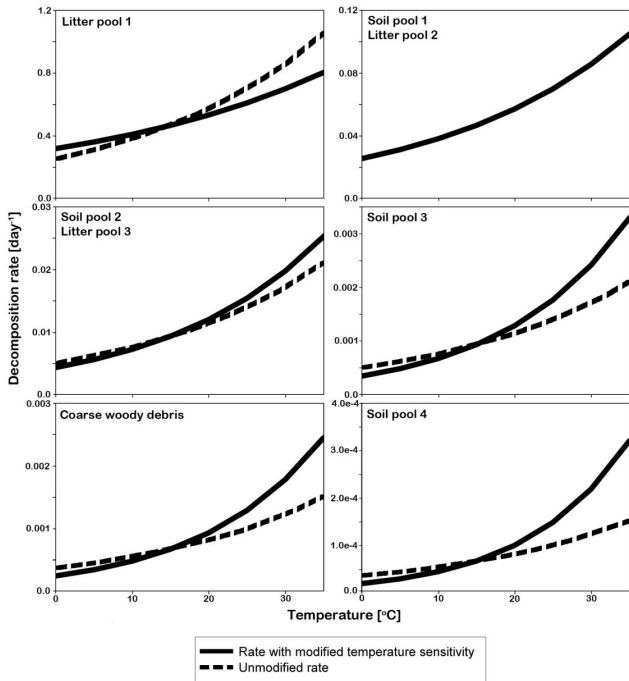
Figure 1. Decomposition rate (k) as a function of temperature in the standard Q_{10} model (unmodified rate) and the modified model given by Eq. (4). The rates are plotted for all model carbon pools, indicated in the top left of each panel.
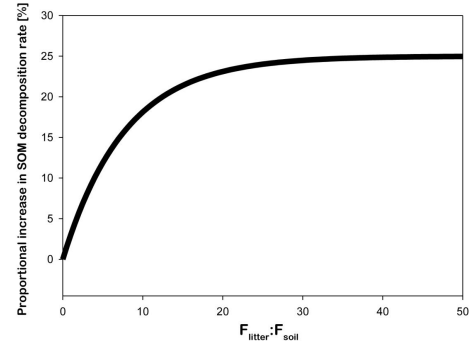

Figure 2. Plot of the proportional increase in decomposition rate of all soil pools, given as percentages, due to priming from an influx of C from the litter pools, computed from Eq. (5). The changes in rates are plotted as a function of the ratio of the sum of the unmodified potential C loss fluxes from all litter pools, F_{litter}, to the sum of the unmodified potential C loss fluxes from all soil pools, F_{soil}.

as a surrogate for plant-derived inputs allowing the mineralisation of native SOM to be quantified by isotopic mass balance (partitioning SOM-derived CO_2 efflux from that derived from the added glucose). They found that the SOM-derived CO_2-C efflux from soils increased by roughly 25 % with the addition of the glucose. Here we modified the SOM decomposition scheme in CLM to account for up to a 25 % increase in decomposition rate from an input of C from the litter pools.

CLM calculates a potential C flux from each soil and litter pool that occurs if N is not limiting. We expressed priming as a function of the ratio between the potential C loss flux from all litter pools (F_{litter}) and potential C loss flux from all soil pools (F_{soil}) before priming had been introduced. Priming can then be represented as a proportional increase in the decomposition rate of each soil pool that grows with an increase in the ratio of F_{litter} to F_{soil} and reaches a maximum at a proportional increase in soil decomposition rate of 25 %, following the results of Garcia-Pausas and Paterson (2011). This relation was described with a continuous function that asymptotes to the maximum proportional increase in decomposition rate (25 %) and is added to the potential C flux from decomposition of SOM (C_p):

$$C_{p\text{-mod}} = C_p \cdot \left[1 + a \cdot \left(1 - e^{(-b \cdot F_{litter}/F_{soil})} \right) \right], \quad (5)$$

where a and b are constants, here $a = 0.25$ (maximum proportional increase) and $b = 0.1291$, and $C_{p\text{-mod}}$ is the modified potential C flux from decomposition. The parameter b was fitted such that the function nears the maximum proportional increase, $a = 0.25$, for a ratio of F_{litter} to F_{soil} that corresponds roughly to the ratio of C added through the glucose treatments to the soil C efflux in the experiments of Garcia-Pausas and Paterson (2011). Here we assume that the effect of increasing the amount of added substrate levels off near the highest glucose concentration added in their experiments. The behaviour of this function for a range of $F_{litter} : F_{soil}$ values is shown in Fig. 2. Further experiments have shown that the priming effect does saturate at high substrate addition rates, but sometimes at rates much higher than the maximum used here (Paterson and Sim, 2013). Therefore, the representation of the magnitude of priming effects can be considered conservative. These coefficients are only valid for an initial assessment of the global effects of including priming. If priming were to be permanently included in the model, a more thorough calibration, including interactions with environmental variables, would be required.

2.3 Simulation protocol

We tested the sensitivity of global C stocks to these changes in the decomposition rates in CLM experiments using the standard, unmodified model (referred to as ES), the model including the modified temperature sensitivity of decomposition (referred to as ET), and the model including the modified priming effect on decomposition (referred to as EP). Initially, equilibrium simulations were performed with CLM for ES, ET, and EP to assess the impacts of the modified decomposition treatments on steady-state model C stocks. For these equilibrium simulations we used present-day land cover (Hurtt et al., 2006), atmospheric CO_2 concentration, and N and aerosol deposition. The terrestrial biosphere was

forced from the atmosphere by prescribed temperature, precipitation, solar radiation, wind, specific humidity and air pressure, and data for this analysis were taken from the reanalysis by Qian et al. (2006). A 25-year period (1972–2004) from the re-analysis was cycled throughout the CLM equilibrium simulations. The cycling was continued until the total global drift in net ecosystem C exchange was less than $0.05\,\mathrm{PgC\,year^{-1}}$ averaged over a 25-year atmospheric forcing cycle. This "spin-up" procedure required approximately 1000 model years for all cases. The model was simulated at $1.9°$ latitude by $2.5°$ longitude horizontal grid spacing and a time step of 30 min.

Additional simulations were carried out with the modified and unmodified SOC model versions to explore how the different models predict future changes in SOC. These simulations were initialised from the final state of the corresponding equilibrium runs, but used transient atmospheric CO_2 and meteorological forcing. Output from the ECHAM5/MPI-OM (Max Planck Institute Ocean Model) CMIP3 (Coupled Model Intercomparison Project phase 3) runs (Roeckner et al., 2006) based on the SRES (Special Report on Emission Scenarios) A1B greenhouse gas projection (Nakicenovic et al., 2000) was used to define future climate anomalies (for the period 2000–2100, relative to the 1948–1972 mean) for the quantities used in the atmospheric forcing (listed above). The climate anomalies are applied to a repeating 25-year cycle of atmospheric reanalysis (from the years 1948–1972) to create the atmospheric forcing data sets. With this method we retain observed diurnal, seasonal and interannual climate variability into the future even as it is scaled to the predicted future climate trends (Kloster et al., 2012; Ward et al., 2012). Transient atmospheric CO_2 concentrations also follow the SRES A1B scenario for the years 2000–2100. In this scenario, CO_2 concentrations increase through the 21st century, exceeding 700 ppm (parts per million) by the year 2100. Global N deposition distributions from the year 2000 (Lamarque et al., 2005) were used throughout for all simulations.

2.4 Soil data

Soil data from the ISRIC-WISE (International Soil Reference and Information Centre - World Inventory of Soil Emission Potentials) $0.5°$ data set (Batjes, 2005) were used to compare against output from the simulations. The model generates SOC as a stock in each grid cell, while the ISRIC-WISE data set gives SOC as a percentage of soil mass in each map unit within a grid cell. Therefore we converted the observed data to SOC stocks with the following expression:

$$C_s = d \cdot 10 \cdot \left(1 - \frac{g}{100}\right) \cdot b \cdot \frac{C_p}{100}, \quad (6)$$

where C_s are SOC stocks $(\mathrm{kg\,m^{-2}})$, d is thickness of soil layer (cm), g is gravel content (%) b is bulk density $(\mathrm{g\,cm^{-3}})$ and C_p is SOC content (%) from the ISRIC-WISE data set.
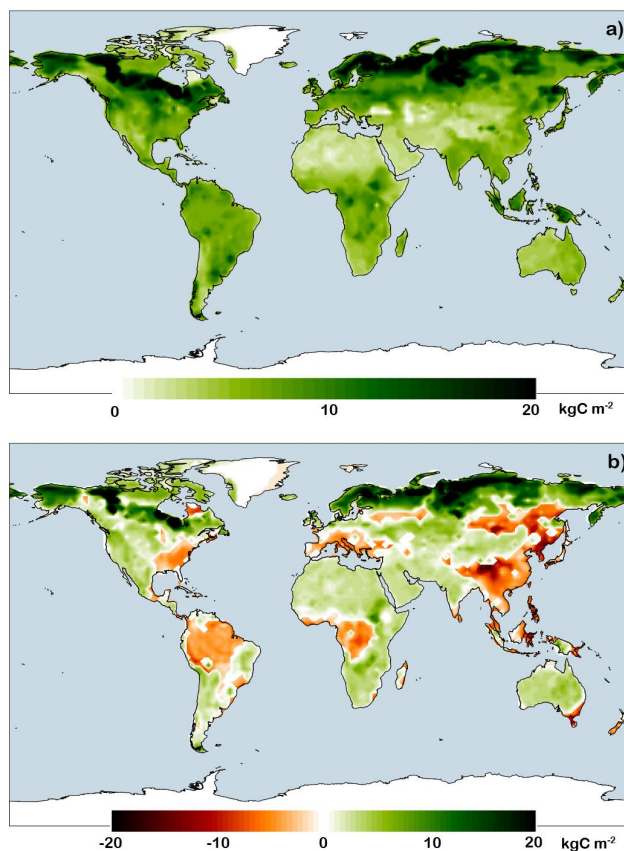

Figure 3. Soil carbon from the ISRIC-WISE data set **(a)** and the difference between this and simulated SOC with the standard (unmodified) CLM at equilibrium (OBS − ES) **(b)**. Data from the ISRIC-WISE data set were recalculated for stocks in the top 1 m and a weighted average over map units was produced. A full description of the calculation method is given in the text.

The calculation was done separately for the two soil layers in the ISRIC-WISE data set (0–0.3 and 0.3–1 m). The SOC content of both layers is summed, and a weighted average of C_s over the map units was calculated based on fractional area covered by each map unit.

3 Results and discussion

The unmodified CLM predicts about 26 % less SOC than estimated from the ISRIC-WISE data set (the ISRIC-WISE data set is abbreviated as "OBS" in the tables and figures) (Table 2). It should be noted that the data set only has SOC in the top 1 m, so that real SOC storage and underprediction is even higher. The main reason for the underprediction is that the model is unable to predict the very high SOC contents in northern latitudes (Fig. 3). This is unsurprising as the model does not include effects of waterlogging, low pH and permafrost on SOC dynamics. However, the model also underpredicts slightly in many other areas. Exceptions are tropical
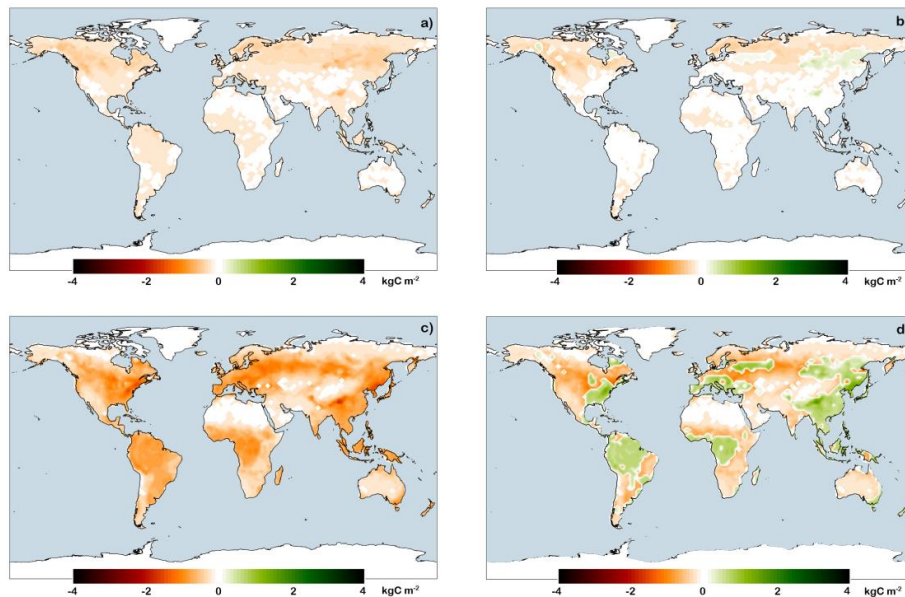
Figure 4. Difference in SOC at equilibrium between ET and ES (ET − ES) **(a)**, between EP and ES (EP − ES) **(c)**, and the change in error in SOC predictions with respect to the observations due to the modified temperature sensitivity (|OBS − ES|) − (|OBS − ET|) **(b)**, and due to adding priming (|OBS − ES| − |OBS − EP|) **(d)**. Positive values in **(b)** and **(d)** indicate the modification to the model's improved prediction of SOC compared to the observations.

Table 2. Total SOC storage estimated from the ISRIC-WISE data set in the top 1 m, using the Eq. (6) unit conversion, in comparison to those calculated with CLM at equilibrium (unmodified) and with each of the modifications described in the text.

	OBS	ES	ET	EP
Total soil organic carbon (Pg)	967.9	712.7	707.1	666.0
Proportion (% of OBS)	100	74	73	69

rainforests in Amazonia and Africa and temperate forests in Asia and eastern United States where the model overpredicts SOC (Fig. 3). These are all high-productivity regions, which suggests that plant productivity is a stronger determinant of SOC in the model than in reality (overall r^2 between net primary productivity (NPP) and the magnitude of the model's overprediction of SOC compared to the observed is 0.56). It is also important to note that the standard model does not account for influences of soil texture and structure, which are strong determinants of stabilisation of SOC by constraining the access of decomposers to SOM (Lutzow et al., 2006; Dungait et al., 2012). This will account for some of the unexplained variability in the distribution of SOC.

Including temperature and priming modifications did not dramatically alter predictions of total global SOC, but did affect the predicted distribution (Table 2, Fig. 4). The results do not include litter pools, but the difference in litter pools between the various versions of the model was negligible (data not shown) as is to be expected as the modifications

introduced act on SOC pools but not directly on litter pools. While the standard model has been calibrated to reproduce global SOC stocks, the lack of explicit representation of soil processes may limit their capacity to capture spatial variability in these stocks. That is, setting standard model functions to represent global means can reproduce global SOC stocks, but without further modification may not improve prediction of geographical variation. Such spatial variability would be expected where soil and environmental factors affect the relative importance of SOC-accrual and SOC-loss processes, causing deviation from mean responses on a global scale. In addition, analogously to predicting geographic variation in SOC, modelling impacts of environmental change on global SOC stocks may require more explicit representation of soil processes, as factors such as CO_2 fertilisation, N addition through deposition and/or fertilisation and temperature rise may directly affect the balance of these soil processes.

SOC decreased at most grid points for ET relative to ES, especially in the high latitudes of the Northern Hemisphere (Fig. 4a). However, the magnitude of the decrease was small, never exceeding $1 \, \text{kgC m}^{-2}$ at any location, compared to the difference in SOC between the ES results and OBS, which falls between 5 and $20 \, \text{kgC m}^{-2}$ at many locations (Fig. 3). This comparison is made even clearer in Fig. 4b, which shows how the difference between the model and observations changes when the modified temperature sensitivity is included in the simulation.

Including the simple priming effect also reduced global SOC (Table 2, Fig. 4c) by a higher magnitude compared to
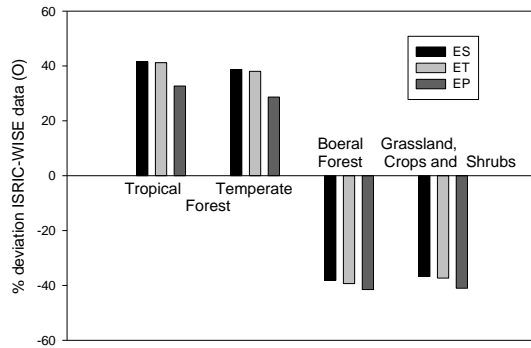
Figure 5. Deviation from ISRIC-WISE data (OBS) for the ES and the two modifications, ET and EP, grouped by ecoregions.

Table 3. Predicted total carbon in pools at the end of the future simulation (year 2100) and percentage increase in each carbon pool over the simulation period.

	ES	ET	EP
Ecosystem carbon (Pg)	1862.3 7.4 %	1853.7 7.5 %	1803.6 6.7 %
Vegetation carbon (Pg)	1058.9 16.9 %	1055.5 17.0 %	1030.9 13.4 %
Soil organic carbon (Pg)	684.6 −3.9 %	680.2 −3.8 %	657.5 −1.3 %

the reduction from the modified temperature sensitivity. The global decrease results from the representation of priming in EP for which C turnover could only decrease or remain unchanged. Importantly, the land areas where the priming had the greatest effect on SOC were those with high NPP (tropical and temperate forest). These are the same regions where the standard model over-predicted SOC relative to measured data to the greatest extent (Figs. 3, 4d). Including a priming effect improved predictions in these areas by 20–25 %, but predictions got worse in lower productivity ecosystems such as grasslands, shrubs, and boreal forests (by 1–9 %) (Fig. 5). While underprediction in lower productivity regions can be explained by waterlogging and permafrost, overprediction in high-productivity regions can be resolved by better mechanistic predictions of turnover and its dependence on productivity. We suggest that including a priming effect is a credible and mechanistically sound way to improve these predictions in high-productivity regions.

The conservative assumption used here was that the maximum change in C turnover from input of plant-derived C is 25 %. Although our results indicate where priming effects may be expected to have the greatest impact, the magnitude and geographic variation in these effects may be greater, as changes in SOC turnover of up to 300 % have been reported (Zhu and Cheng, 2011). Further work should focus on parameterising how various factors affect the strength of SOC turnover, and evaluate if this further improves predictions of SOC. For example, empirical data are emerging indicating that priming responses can be quantified as soil-specific functions of C-input rate (Paterson and Sim, 2013), are affected by composition of inputs (Ohm et al., 2007), are modified by nutrient availability (Fontaine et al., 2003; Garcia-Pausas and Paterson, 2011), change with soil depth (Fontaine et al., 2007; Salomé et al., 2010) and may vary in response to direct and indirect effects of environmental conditions on the biological processes involved (Dijkstra et al., 2010; Ghee et al., 2013; Thiessen et al., 2013). These effects are potentially complex due to interactions between environmental factors and the biological processes mediating element fluxes. For

example, plant-derived C enters soil from aboveground litter and rhizodeposition, supplying organic material of differing quality, affecting retention in soil, microbial activity and processes mediated by microbial communities (including priming). The magnitude and relative contribution of above- and belowground plant C is affected by a host of factors, including interactions between plant type, temperature and nutrient availability (Metcalfe et al., 2011). Under conditions of high nutrient availability, relative allocation of plant C to roots and mycorrhizal symbionts is reduced (Yuan and Chen, 2010; Grman and Robinson, 2013). However, whether this results in an absolute reduction in C transfer to soil is dependent on whether the reduction in relative belowground allocation outweighs the impact of increased gross plant productivity (Henry et al., 2005). These interactions, across ecosystem types, require further quantitative study to refine the representation of plant-mediated priming effects in models.

The difference in pool size between the standard and the modified runs is to a large extent maintained into the future (Fig. 6, Table 3), although the vegetation pool in EP is reduced early in the future simulation. This may be a result of smaller C stocks in the soil at equilibrium with this modification. That means that there was less N available for mineralisation, and the effect of warming on N mineralisation and availability was therefore less. The difference in pool sizes would potentially have a large effect in a fully coupled simulation, and could therefore mean a different biotic feedback to climate change than current models predict. The predictions of changes to the C cycle under global change appear to be relatively robust towards the assumptions made about SOC sensitivity to temperature, as differences in pool sizes at equilibrium were maintained (Fig. 6, Table 3).

4 Conclusions

Comparison of CLM model simulations to observations suggest an overprediction of soil C in the high-productivity regions of midlatitudes and the tropics, with too little soil C in other regions, especially the high latitudes, as noted elsewhere (e.g. Randerson et al., 2009; Thornton et al., 2009).
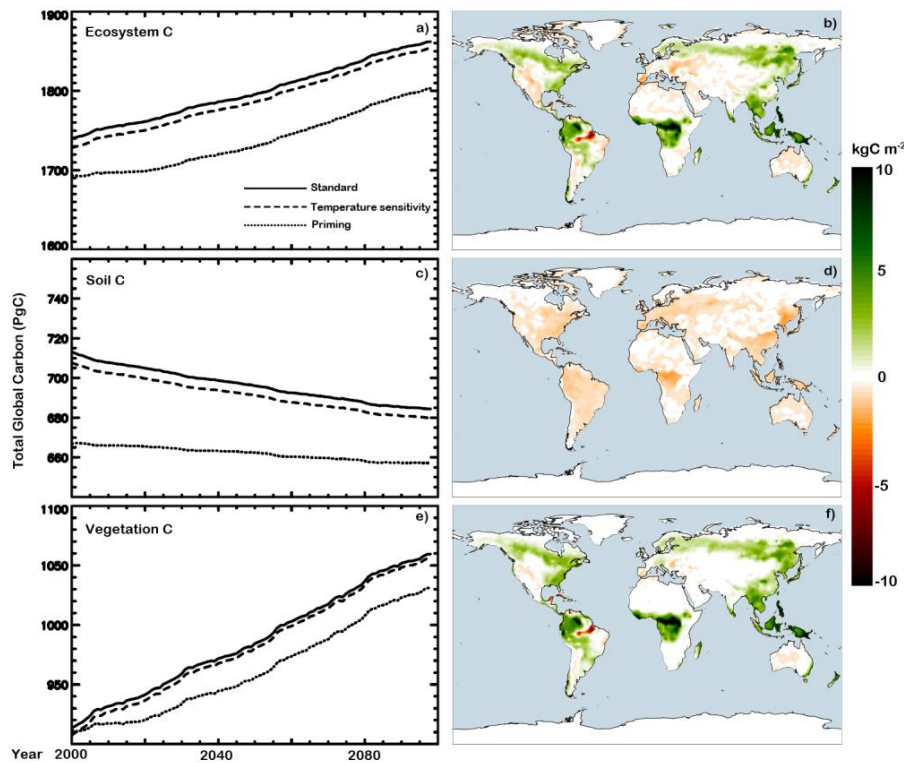
Figure 6. Predicted total global organic carbon in the entire ecosystem **(a)**, soil **(c)** and vegetation **(e)** starting from equilibrium year 2000 underpredicted climate change with ES ("standard"), ET ("temperature sensitivity") and EP ("priming"). The spatial maps show the changes between the average of the last 25 years of the equilibrium run and the average of the last 25 years of the future run (i.e. the period 2075–2099) for total ecosystem C **(b)**, soil C **(d)**, and vegetation C **(f)** using the standard model.

This differential in the soil C bias in the model can be due to multiple causes, and we explore two of these effects in this paper, temperature dependence and soil priming. We did not explore some potentially important effects specific to high latitudes such as a representation of the inhibition of biological processes in soils subject to permafrost and waterlogging.

The overprediction of C in the high-productivity areas indicated that the model underpredicts C turnover when plant input is high, and one way of improving that is to include a priming effect, which does improve the predictions of SOC distribution by 20–25 %. Further work should focus on better quantification of priming, how it depends on external factors and how it may also improve our ability to predict biotic feedback to climate change. In this paper we also explored the impact of different temperature sensitivity of C pools, but this mechanism had less of an effect in most areas.

As soil C feedbacks in earth system models are some of the most important uncertainties in future climate predictions (Huntingford et al., 2009), further work should focus on better quantification of the priming effect, how it depends on other factors and how this can improve predictions of SOC distribution even further.

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