

# Managing uncertainty in soil carbon feedbacks to climate change

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**Planetary warming may be exacerbated if it accelerates loss of soil carbon to the atmosphere. This carbon-cycle-climate feedback is included in climate projections. Yet, despite ancillary data supporting a positive feedback, there is limited evidence for soil carbon loss under warming. The low confidence engendered in feedback projections is reduced further by the common representation in models of an outdated knowledge of soil carbon turnover. 'Model-knowledge integration' — representing in models an advanced understanding of soil carbon stabilization — is the first step to build confidence. This will inform experiments that further increase confidence by resolving competing mechanisms that most influence projected soil-carbon stocks. Improving feedback projections is an imperative for establishing greenhouse gas emission targets that limit climate change.**

Hundreds of studies have shown the effects of warming on soil-carbon (C) dynamics<sup>1,2</sup>. Much of this empirical research has been motivated by the possibility that climate warming will stimulate biologically mediated decomposition of soil C to CO<sub>2</sub> (refs 3–7). Enhanced rates of soil-C decomposition may reduce the capacity of the land to act as a CO<sub>2</sub> sink, so that a greater proportion of anthropogenic CO<sub>2</sub> emissions remain in the atmosphere<sup>8–10</sup>. The magnitude of this so-called carbon-climate feedback is therefore critical for estimating the allowable greenhouse gas emissions that are compatible with climate targets<sup>10</sup>. The soil is the largest store of C (~1,500–2,400 PgC) in the terrestrial biosphere, containing more than double the C of the atmosphere<sup>11–13</sup>. Hence, loss of even a small proportion of this store may result in higher atmospheric-CO<sub>2</sub> concentrations and consequently additional planetary warming<sup>8,14</sup>.

Despite the wealth of research into warming effects on soil-C dynamics, there is no consensus on the magnitude of warming-induced reductions in soil C stocks<sup>11,14,15</sup>. The low confidence in the projected range of soil-C losses arises in part from an empirical focus on the responses of soil C decomposition rates to warming, rather than the direct measurement of changes in total soil C stocks. Confidence in projected losses is further eroded because emerging ideas<sup>2,16</sup> about how soil C is formed and stabilized are not commonly represented in the soil biogeochemical models used for climate change projections<sup>17–19</sup>. Instead, the assumptions in these models about the mechanisms underlying soil C responses to warming are largely similar<sup>11,14,20,21</sup> and often conflict with emerging understanding<sup>16,22,23</sup>. These assumptions underlie Earth system model (ESM) projections of soil C losses through climate warming<sup>9,24</sup>.

The ESMs are the most complex of the climate models, and incorporate the global C cycle to simulate how the atmosphere and biosphere interact to shape climate trajectories<sup>11</sup>. The ESM projections of warming-induced soil C losses range from minimal, to one-third of the stock lost by 2100<sup>8,9,25</sup>. The ESM characteristics generating this wide range in the projected magnitude of the feedback are well documented, involving uncertainties in the parameter values used to control the rate at which soil-C decomposes and the sensitivity of this rate to warming<sup>26,27</sup>. Reducing these parameter

uncertainties will do little to build confidence in the magnitude of the modelled feedback.

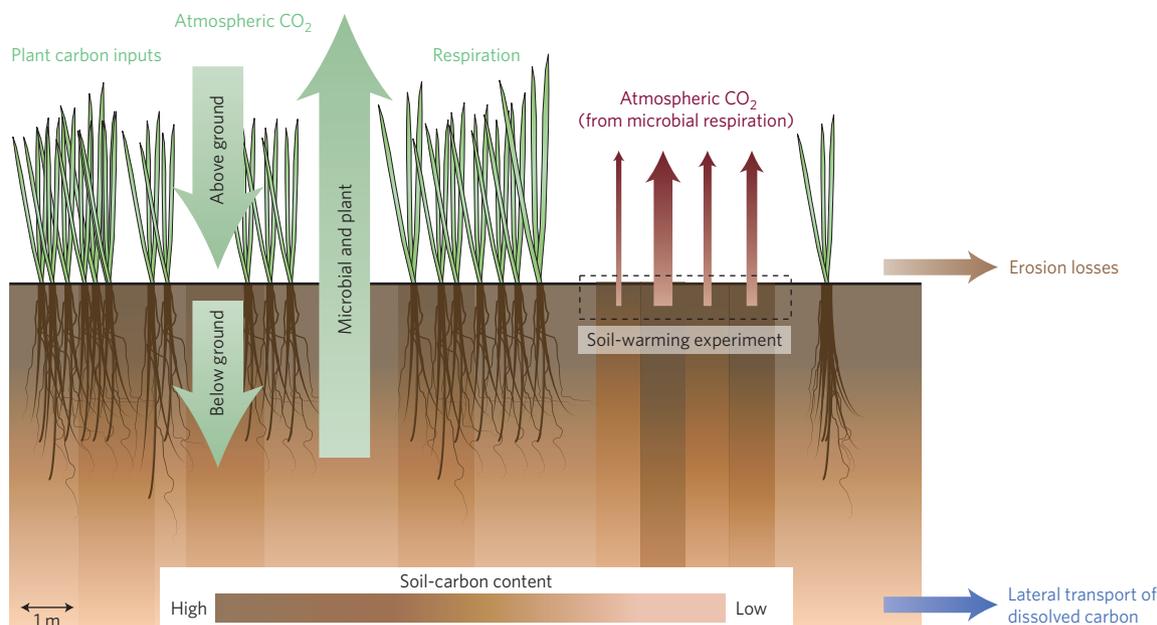
In this Review Article, we distinguish the meaning of 'uncertainty' from 'confidence'. Many forms of uncertainty exist when modelling climate change and associated biosphere feedbacks<sup>28</sup>, but they do not equally contribute to the confidence one has that projected changes will occur<sup>29</sup>. We focus on the four major uncertainties underpinning low confidence in the projections of soil C stock responses to warming. Three of these major uncertainties are empirical and the fourth is related to how soil C turnover is treated in ESMs. Specifically, the major modelling uncertainty is associated with representing common and outdated ideas about soil C turnover in the soil sub-models of the ESMs. We demonstrate the importance of instead representing different ideas in ESMs — that is, 'structural uncertainties' — that capture emerging concepts of soil C stabilization. To facilitate these efforts, we propose collaborative ways forward for empiricists and modellers to efficiently and rapidly improve confidence in projected soil-C-climate feedbacks.

## Empirical uncertainties

We begin by discussing, in turn, the three primary areas of empirical uncertainty that generate low confidence in feedback projections: (1) the paucity of direct observations of warming effects on soil C stocks; (2) the potential for organism responses to warming to alter short-term biogeochemical responses; and (3) the dramatically changing ideas about how soil C formation and stabilization are regulated.

**Evidence for carbon loss.** Empirical research into soil C stock responses to warming has primarily focused on decomposition (Fig. 1). There is compelling evidence from observational studies across climate gradients, and both laboratory and field warming experiments, that decomposition rates respond positively to warming (but see ref. 15), at least in the short-term (<1 to ~10 years)<sup>1,2,30</sup>. These increases in decomposition of soil C to CO<sub>2</sub> occur with plants present or absent, suggesting that warming accelerates C loss from soils primarily by stimulating the activities of microbes<sup>31</sup>. This

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**Figure 1 | Soil C stocks are the net result of outputs and inputs of plant C, but most warming research focuses only on outputs, making stock responses highly uncertain.** Warming-induced outputs (red arrows) in the schematic are represented as CO<sub>2</sub> fluxes, reflecting the assumption in ESMs that the land-C–climate feedback occurs through warming stimulating the activities of soil microorganisms that decompose soil C. Losses of soil C do occur through other pathways (lateral transport and soil erosion, blue and brown arrows), but warming effects on these losses are not well characterized. Instead, the majority of warming studies focus on decomposition of soil C to CO<sub>2</sub>. Despite strong warming effects on decomposition, there are very few observed reductions in soil C stocks. This paucity of data reflects the fact that there has been far less research into how warming affects soil C formation through plant inputs (downward green arrows) versus its effects on decomposition. It also reflects the signal-to-noise issues in detecting a change in soil C stocks, given marked local variation (horizontally as well as with depth) in soil C stocks and the fact only a proportion of this C is likely to be sensitive to warming-induced losses.

microbial mechanism underlies the C-cycle pathway in the ESMs through which soil C is redistributed to the atmosphere as the climate warms.

The soil C stock is not, however, just determined by microbial decomposition rates. Changes in the soil C stock are the net product of outputs (decomposition) and also inputs (soil C formation, Fig. 1). More rapid decomposition is therefore not synonymous with reductions in total soil C stocks<sup>15</sup> if coupled with similar increases in soil C formation. The idea that soil C stocks are the net outcome of inputs and outputs seems obvious and is captured by the soil sub-models in the ESMs<sup>27</sup>. Yet expectations for reductions in soil C under warming are still primarily driven by empirical data of accelerated decomposition rates<sup>1</sup>, despite little evidence that decomposition responses can be used to infer responses in soil C stocks<sup>1,32</sup>. In a synthesis of field data, for example, the mean effect size of warming on decomposition rates was statistically significant and strongly positive<sup>2</sup>. However, the same meta-analysis showed that the mean effect of warming on soil C stocks was indistinguishable from zero. Collectively, the plethora of studies reporting positive decomposition responses to warming provide weak, indirect support for the existence of a positive land-C–climate feedback<sup>1,5,6</sup>.

The lack of direct evidence for reductions in soil C stocks may, in part, reflect a signal-to-noise issue. Soil C varies markedly at nanometre to metre scales in quantity, chemistry and the physical setting where it is found<sup>33,34</sup>. These attributes can protect soil C from microbial decomposition, meaning that a large proportion of the C in a given soil will respond slowly (if at all) to warming<sup>1</sup>. Looking for a small change in a large, spatially variable stock makes it difficult to quantify the effects of warming on total soil C (Fig. 1). For example, the statistical power to detect a change in total soil C stocks at a site is typically far below that recommended, demanding higher replication than generally used<sup>35</sup>. The use of techniques (such as

isotopic labelling and soil pool fractionations) to track and quantify C turnover in soil pools that are differently vulnerable, does offer a solution for detecting a signal from among the noise<sup>36–39</sup>. However, the issues with using such techniques to infer change in stock sizes echoes those for decomposition; environmental change can alter the sizes of individual C pools or fluxes without altering the total stock<sup>40</sup>.

The difficulties involved in detecting changes in the total size of soil C stocks probably encouraged the use of indirect measurements, such as decomposition rates, to understand warming effects. However, demonstrating definitively that soil C stocks will be reduced under warming requires a large number of sites, long time scales (>20 years) and ecosystem (versus soil only) experimental warming. Such long-term network data will not be available in the short term<sup>41</sup>, but even collation of soil C stocks in existing field studies would be a step forward. So far, we know of only five published field-warming studies that measured soil C directly under experimental warming plots for timescales greater than ten years, and they did not consistently show reductions in soil C<sup>2,42</sup>. Furthermore, of the 34 studies that have compared soil C dynamics in control versus experimental warming plots<sup>2,42</sup> — over both the short- and longer-term — only six measured stocks. The remainder measured soil C concentrations but these do not account for potential changes in soil bulk density, which could markedly affect stock sizes<sup>43,44</sup>. A key challenge then, is determining how best to improve confidence in projected soil-C–climate feedbacks in lieu of the fact that there is limited direct data on the effects of ecosystem warming on total soil C stocks.

**Organisms modify direct warming effects.** Knowing how to best represent organismal responses to climate change in biogeochemical models is a significant challenge<sup>45</sup>. Initial effects of chronic disturbance on an ecosystem are often transient because the

organisms, whose activities mediate biogeochemical processes such as decomposition, first respond physiologically and second through changes in abundance (Fig. 2)<sup>46</sup>. Two decades of experimental summer warming of arctic tundra, for example, gradually increased the dominance of woody plants, altering plant community architecture. The altered plant community mitigated direct summer warming of the soils but caused indirect warming in the winter. These longer-term consequences stimulated plant C inputs at depth, increasing both the activity of the soil microbes and soil C storage, despite the fact that initial warming was considered to promote soil C loss<sup>42</sup>.

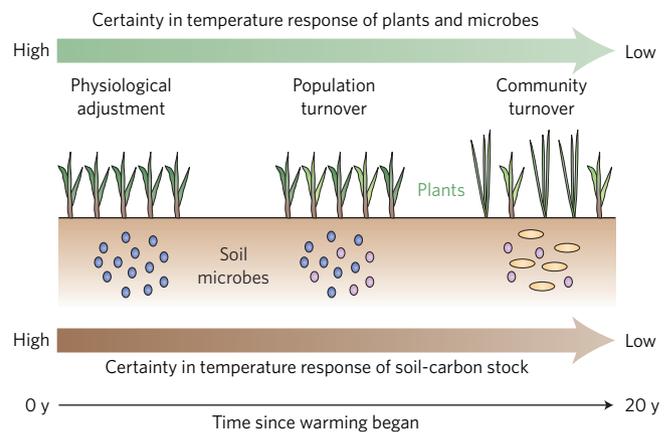
Soil microbial communities and controls on their activities also shift as temperatures change, altering their collective responses to warming in the short- versus long-term<sup>4,5,47–50</sup>. Substantive debate exists as to whether these shifts will influence soil C decomposition rates<sup>5,46,47,51</sup>. Adding to this uncertainty, new efforts to incorporate soil microbial processes in biogeochemical models reveal that the manner in which they are represented means that simulated acclimation to warming can alternatively exacerbate or mitigate soil C losses<sup>4,52,53</sup>.

Some organismal responses to warming are incorporated in ESM formulations. For example, positive responses of plant production to warming are expected in cold, high-latitude systems because higher temperatures extend the growing season<sup>42</sup>. Most ESMs then project an increase in land-C stocks at high latitudes because increased plant-C inputs to soils more than offset the increases in soil C decomposition rates<sup>11,54</sup>. Both model and empirical findings therefore highlight that warming responses of organisms influencing either soil C inputs or outputs will probably alter direct effects of warming on soil C stocks. The reality, however, is that we do not know whether the collective effects of these organismal responses under warming will amplify, dampen or scarcely influence direct warming-induced changes in the global stock of soil C.

**Changing ideas on soil carbon stabilization.** Low temperature is considered to be one of the dominant forces protecting soil C from decomposition<sup>55</sup>. In permafrost soils (those that are  $\leq 0^\circ\text{C}$  for greater than two years) decomposition proceeds slowly because of limited availability of liquid water<sup>56,57</sup>. As liquid water becomes available, microbial decomposition of soil C initially proceeds slowly because cool temperatures directly limit activity<sup>58</sup>. Warming then releases temperature limitation on the catalytic activities of intracellular and extracellular microbial enzymes, accelerating decomposition of soil C to  $\text{CO}_2$ . The land-C–climate feedback in ESMs is primarily based on the assumption of this fundamental biochemical response<sup>59</sup>. But a paradigmatic shift in our understanding of how soil C is stabilized<sup>60</sup> casts doubt on whether such cellular processes can be directly scaled to biosphere–atmosphere interactions driving the C cycle.

Microorganisms have been considered the primary agents of soil C decomposition for over a century. They are now also recognized, somewhat paradoxically, as dominant agents of soil C formation (Fig. 3)<sup>16,23,61</sup>. As much as 80% of the soil C in mineral soils that is protected from decomposition through physico-chemical mechanisms, exists in the form of microbial necromass and products<sup>62</sup>, and the proportion may be higher at depth<sup>63</sup>. Soil microbes therefore convert large fractions of plant-C inputs to  $\text{CO}_2$  and a smaller fraction into stable soil C<sup>36</sup>. The process has been likened to a microbial funnel, whereby microorganisms consume unprotected C and a portion that passes through is converted into decomposition-resistant forms<sup>36,50,64</sup>. This dual role for microbes raises the possibility that warming could accelerate the decomposition and stabilization of soil C, shifting stocks toward proportionally more protected forms of C that are less sensitive to warming (Fig. 3)<sup>65</sup>.

The emerging paradigm of soil C formation emphasizes microbial growth efficiencies and mineral-matrix interactions as dominant forces stabilizing soil C<sup>16,23,66,67</sup>. Structural plant compounds such as lignin, previously considered resistant to microbial decomposition<sup>66,68</sup>,



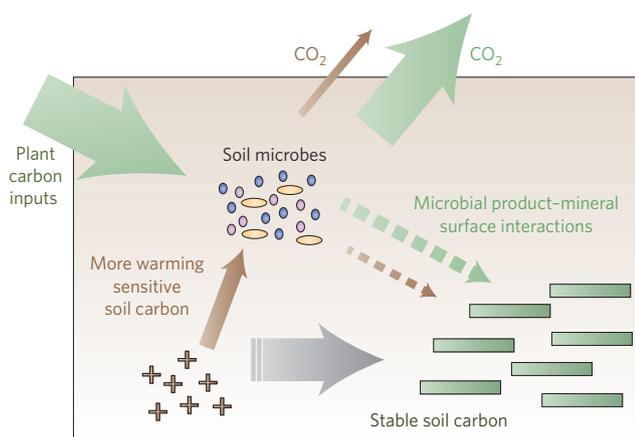
**Figure 2 | Timescale of organismal responses to warming, with the potential that initial increases in microbial activity are exacerbated or mitigated through physiological, population and community-level responses as the warming perturbation continues.** Modelled land-C–climate feedbacks rely on warming-mediated increases in the potential activities of microbial enzymes, which catalyse the decomposition of soil C, being maintained in the longer term. Yet, physiological acclimation and turnover in populations and communities — both above ground and below ground (represented as plants and soil microbes, respectively) — may modify the assumed translation of this initial cell-level warming response directly to changes in soil C stocks. How the responses at intermediate levels of biological organization modify this translation becomes increasingly uncertain with time, given the large and diverse array of interactions that can occur to restructure communities.

represent a poor-quality substrate for microbial growth. Physiological inefficiencies involved in growing on poor substrates result in more plant C being respired to  $\text{CO}_2$  instead of being transformed to microbial biomass<sup>4</sup>. Under this paradigm, most stable C in mineral soils is produced via microbial uptake of primarily metabolic plant matter inputs, which microbes rapidly decompose and convert to biomass efficiently (Fig. 3)<sup>23,69</sup>. The dominant pathway for these inputs may be via plant roots and their associated mycorrhizal fungi<sup>70,71</sup>. If this paradigm is applicable across multiple ecosystems, it could help explain why increased inputs of structural plant C to soils, from aboveground litter sources, may not translate to higher soil C stocks<sup>40,72</sup>.

Once microbial products are formed, interactions with mineral-soil surfaces, such as clays, are required to protect them from decomposition<sup>22,34</sup>. Hence, even in wet tropical rainforests, large stores of soil C can be found in aerobically respiring mineral soils where decomposition should otherwise be rapid<sup>12</sup>. The most vulnerable pools of soil C to warming are likely to be those in organic-rich soils, such as wetlands and in permafrost, where the lack of oxygen and liquid water, respectively, slow microbial decomposition. In such systems much of the soil C has not passed through the microbial funnel, but exists as relatively undecomposed plant material<sup>16</sup>. With warming, C in these soils will increasingly pass through the funnel, resulting in a major fraction being decomposed to  $\text{CO}_2$  and a small fraction becoming microbial products available for ‘restabilization’. Yet wetland and permafrost soils are poorly represented in ESM simulations of land-C–climate feedbacks (but see ref. 73) and there is little data available to estimate the likely magnitude of their response to climate change<sup>11,58,74</sup>. Given that permafrost contains as much C as all non-permafrost soils combined<sup>13</sup>, such limitations must be addressed given the potential importance of their responses in dictating the magnitude of land-C–climate feedbacks<sup>73</sup>.

### Uncertainties in modelling

The major modelling uncertainty generating low confidence in the magnitude of projected soil C losses arises because of the common



**Figure 3 | The dual role of soil microbes as the agents of both soil C decomposition and stabilization.** A new conceptualization of how soil C is formed and stabilized emphasizes that plant-C inputs on which microbes grow most efficiently result in larger protected stocks of soil C. Warming-induced increases in decomposition rates may then cause more unprotected (that is, more warming sensitive) soil C to be converted into stable pools, ultimately mitigating the presumed land-C–climate feedback because accelerated decomposition rates are balanced by elevated formation rates. The grey arrow depicts this theoretical shunt of soil C from more to less temperature-sensitive pools under warming via the microbial funnel into microbial product–mineral complexes.

and outdated assumptions about soil C turnover represented in the soil sub-models of the ESMs. We discuss these assumptions below and how new advances in soil biogeochemical modelling suggest a productive way forward.

**Model structure.** The soil sub-models in ESMs represent soil C responses to warming in a common manner. Soil-C decomposition to  $\text{CO}_2$  follows a single first-order response curve, similar to half-life plots for radioactive decay, where the time taken for a constant fraction of soil C to decompose decreases with warming<sup>21,27,75,76</sup>. The mechanism then assumes that climate warming increases the short and long-term potential for microbes to decompose soil C to  $\text{CO}_2$  (refs 8–10), presupposing a positive C–climate feedback<sup>14</sup>.

This representation of soil C turnover in ESMs has remained essentially unchanged for two decades<sup>20,21</sup>. Over the same time, advances in climate change projection have been made by representing the different mechanisms thought to underlie responses of the physical climate system to anthropogenic emissions<sup>29,77,78</sup>. For the physical climate, the spread in an ensemble of model projections with the same scenario forcing is taken as a measure of model uncertainty<sup>28,29,74,78</sup>. A similar principle has been applied to C-cycle projections in ESMs<sup>9,11,14,24</sup> but the validity of doing so is questionable. Specifically, the use of multi-model ensembles underlies the Coupled Model Intercomparison Project (CMIP), which is a hallmark of the Intergovernmental Panel on Climate Change (IPCC) assessment reports<sup>78</sup>. A key objective of the CMIP is to quantify the influence of structural uncertainty, reflected in representing different mechanisms among models, on projected climate change<sup>28,29,77</sup>. Yet, because they represent common mechanisms for soil C turnover, the broad spread among ESMs in the magnitude of projected land-C–climate feedbacks<sup>8–10,74</sup> is not the consequence of structural uncertainty<sup>26,54</sup>.

Differences among soil sub-model projections instead result largely from parameter uncertainty. Values for parameters such as the ‘decay constant’ for soil C, contribute to a sixfold difference in the simulated global stock of contemporary soil C<sup>27</sup>. Differences in the simulated stocks carry forward and translate to substantial

among-model variation in the strength of C–climate feedback projections<sup>26,54,79</sup>. Efforts to refine parameter estimates may reduce among-model variation<sup>80</sup> but will not improve confidence in projected soil C stock responses to warming<sup>26,81</sup>. These improvements will only come through representing the new ideas about the mechanisms regulating soil C turnover.

Representing structural uncertainty in soil processes in the ESMs has the potential to drastically change projected terrestrial C-cycle feedbacks. For example, beyond warming, the  $\text{CO}_2$  fertilization effect is a dominant biogeochemical feedback in ESMs<sup>9</sup>. Increasingly, model structures represent the fact that the rate of soil nitrogen (N) supply can strongly constrain plant growth responses to elevated atmospheric  $\text{CO}_2$ <sup>82</sup>. In general, representing coupled C–N biogeochemistry dampens the  $\text{CO}_2$  fertilization effect on plant productivity and reduces terrestrial C storage<sup>83,84</sup>. Given the complexity of representing global C and N cycles, inclusion of terrestrial N dynamics may increase C-cycle uncertainty, but should build confidence in model projections. Similarly, recent efforts to represent structural uncertainty in soil C responses to warming in soil biogeochemical models<sup>19,85–87</sup> suggest that divergent projections of the C–climate feedback will be observed if these efforts are integrated into CMIP exercises. We argue that such initiatives are necessary to represent the true uncertainty associated with projecting terrestrial biogeochemical responses to climate change.

**Advances in soil biogeochemical models.** Many of the ESMs simulate soil processes by using some of the most widely applied, soil biogeochemical models<sup>27</sup>. These ‘conventional’ soil models assume that decomposition of soil C to  $\text{CO}_2$  is a product of microbial activity, but that microbes do not regulate the rate of soil C turnover<sup>88</sup>. Instead, the control on turnover is exerted by factors such as the chemistry of different soil C compounds<sup>60</sup>. These conventional models therefore explicitly represent controls on microbial activity, but the microbes themselves are considered ‘implicit’ to the dynamics. Recent major advances in understanding soil C dynamics have come about in the broader context of soil biogeochemical models (as opposed to the narrow subset of these models used in the ESMs) by representing explicitly how microbial physiology, biomass and enzyme kinetics respond to warming<sup>27,48,65</sup>.

Marked reductions in the size of the soil C stock in response to 30 years of simulated warming were observed with a conventional model structure but not with a microbial-explicit structure, despite the assumption that all of the processes were temperature sensitive<sup>52</sup>. The difference in model structure was that, in the latter case, the microbial biomass controlled soil C decomposition rates via production of degradative enzymes. As microbial biomass and hence enzyme production declined over time, because warming was assumed to reduce microbial growth efficiencies<sup>59</sup>, decomposition slowed and soil C stocks were maintained. Whereas the conventional model projected that warming would reduce soil C stocks, because the first-order decay mechanism assumes soil C decomposition rates are independent of the size of the microbial biomass<sup>52</sup>. Whether the microbial-explicit models are a more accurate mechanistic representation of soil C dynamics is unknown. However, they have been shown to improve the ability of conventional soil C model structures to estimate observed spatial variation and stock sizes of global soil C, as well as their responses to environmental change<sup>19,85–87</sup>.

Another implicit assumption of most conventional soil models is that the rate of soil C formation (as opposed to decomposition) is regulated by microbial growth efficiencies, with higher efficiencies leading to higher formation rates<sup>89</sup>. Warming-induced reductions in growth efficiencies therefore exacerbate, rather than mitigate as estimated by microbial-explicit models, losses of soil C stocks<sup>4</sup>. Although microbial growth efficiencies are assumed to be invariant in most conventional models (an assumption that is under

debate<sup>4,90</sup>), the example demonstrates that even slight structural differences in how soil C turnover is represented can translate to a broad spread in the projected magnitude of soil C losses. Until such structural uncertainties are represented in ESM soil sub-models, we cannot know whether the spread in the projected magnitude of the C–climate feedback is reflective of our contemporary conceptual understanding of soil C turnover. As such there is low confidence in the current ESM projections of the C–climate feedback and the resulting constraints on allowable greenhouse gas emissions<sup>14,74</sup>.

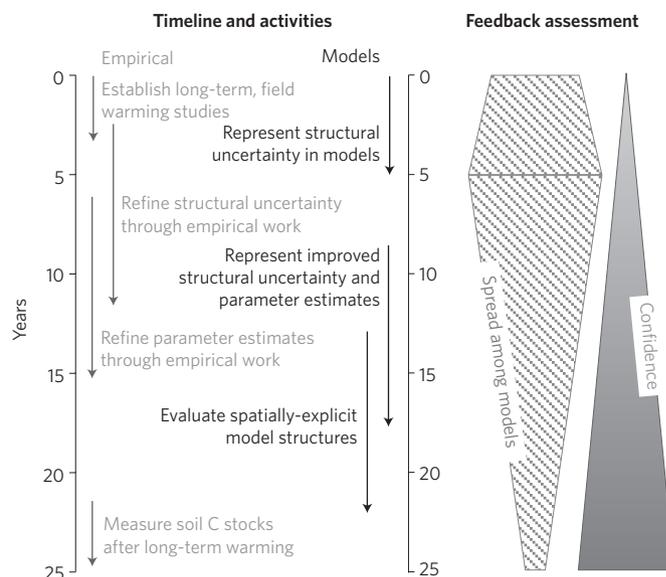
### Addressing uncertainties to build confidence

We have neither the data nor the models required to reliably determine how soil C stocks will be affected by a warmer world. These realities suggest a need for modellers and empiricists to collaborate to increase confidence in the magnitude of projected C–climate feedbacks. Such collaborations will succeed through an open discussion — of the knowledge and data gaps in soil C research — between the more geophysical-based Earth system modelling community and the more ecological-based empirical community<sup>91</sup>.

We propose four ways forward for modellers and empiricists to focus efforts on identifying and addressing critical and tangible assumptions that generate low confidence in projected soil C stock responses. The overarching idea is to induce an exchange cycle of model and empirical insights that rapidly advance mechanistic understanding of how soil C is formed, stabilized and decomposed. The expectation is that these advances in mechanistic understanding will improve confidence in soil C stock responses to warming, at timescales more attractive than those required to assemble direct field observations of soil C stock responses to long-term, chronic ecosystem warming. Importantly, the development of physical climate models shows that higher confidence in feedback projections may be achieved through better representation of mechanisms, even when this does not reduce the spread among model projections<sup>29</sup>. We suggest that the aims for soil biogeochemistry should mirror these developments, with the primary focus on representing and improving our basic understanding of soil C cycling and a secondary focus on reducing the spread among models in the magnitude of projected feedbacks (Fig. 4).

**Represent structural uncertainty.** The most important short-term goal in Earth system modelling efforts focused on the land-C–climate feedback should be to represent theoretical uncertainty in soil C decomposition and formation processes through different underlying model structures. The major advances in representing such structural uncertainty in microbial-explicit soil biogeochemical models<sup>48,52,63,65,92</sup> should facilitate rapid adoption of competing assumptions in soil sub-models embedded within ESMs. The fundamental approach should emulate standard practices in the atmospheric sciences to sample model structural uncertainty through multi-model ensembles<sup>28</sup>. The standardized protocols, however, should more narrowly compare different mechanistic representations of soil C decomposition and formation within a common modelling framework (for example, different soil biogeochemical models within the same ESM). If these intracomparison efforts are computationally too expensive at the level of complexity of ESMs, it is feasible to compare structurally distinct soil biogeochemical models within the land models that are a component of ESMs<sup>19,93</sup>. Adopting these systematic ‘intracomparisons’ will facilitate effective model evaluation and improvement at regional to global scales.

Empiricists have two distinct roles to play in these model intracomparison projects. The first is to work with modellers to develop structural representations that best reflect the competing conceptualizations of soil C turnover. We refer to this approach as model-knowledge integration to distinguish it from the now ubiquitous model-data synthesis efforts, which have failed to redress the low confidence in soil-C–climate feedbacks. Model-knowledge



**Figure 4 | Proposed activities to address low confidence in the projected magnitude of carbon-climate feedbacks.** Shown is a timeline for major initiatives that empiricists and modellers can act on to address the low confidence and wide projected spread in soil C stock responses to warming. Real-world confidence (inverted triangle) in the projected magnitude of these responses increases when different assumptions (that is, structural uncertainty) about the mechanisms governing soil C turnover are represented in models, which then guides empirical research to advance understanding of the mechanisms to which the models are most sensitive. The trajectory of change in the spread among models of the projected magnitude of the feedback is less assured and may increase when structural uncertainty is represented. To establish allowable emissions of greenhouse gases to meet specified climate targets, high confidence in widely divergent projections is superior to low confidence in a narrow range of projections, because policy can then be developed in light of the knowledge that the best available science is considered.

integration will probably involve synthesizing hundreds of published mathematical and conceptual soil models into broad classifications<sup>94</sup>, and summarizing the general processes (and ideally their associated equations) that need to be represented in models<sup>17</sup>. This methodology shows awareness of the human and computational costs related to representing structural uncertainty in climate models, which demands that only the most plausible sets of mechanisms are compared.

The second role for empiricists is to design and execute empirical studies that distinguish which of the rapidly proliferating mechanisms put forth to govern soil C formation and stabilization<sup>16,22,23,60</sup>, are most consistent with field observations of soil C turnover. The rapid growth in development and application of isotopic labelling and fractionation techniques that permit a “look inside” the soil to resolve such dynamics as root-microbial-mineral interactions<sup>34,37,38,40</sup>, highlight the potential for such approaches to refine the sets of mechanisms that must be represented in models. Empiricists can be guided in these efforts by the structural assumptions about soil C turnover to which simulated soil C stock responses are most responsive. An improved mechanistic understanding of soil C turnover can then go hand-in-hand with reductions in model structural uncertainty and, consequently, increasing confidence in the magnitude of the projected feedback (Fig. 4).

**Refine parameter estimates.** Once structural uncertainty is represented and reduced, the aim to lessen the spread in the projected magnitude of the C–climate feedback by refining parameter

estimates<sup>26,79,81</sup> will be of great value. The current ensemble of ESMs vary markedly in the assumed values of soil parameters, such as the sensitivity of decay constants to warming<sup>27</sup>. Similarly, variation in even the parameter value of a single physiological process in the microbial-explicit models, can mean the difference between large versus no losses of soil C stocks under warming<sup>52</sup>. Notably, soil C stocks are sensitive to a huge range of processes in these microbial models, including community composition, enzyme activities, carbon use efficiency, microbial turnover and mineral surface interactions<sup>19,48,65,95,96</sup>. Parameter values for these processes tend to be poorly constrained by observations<sup>39,56,80,90,94</sup>. Hence, modellers can provide critical guidance to empiricists by identifying processes where modelled soil C stocks are strongly sensitive to the assumed parameter value. Such guidance will allow empiricists to focus on identifying the plausible range of values observed in nature and how these values depend on environmental conditions<sup>57,97</sup>.

**Consider spatially explicit processes.** A guiding principle in developing climate models and ESMs has been to represent major processes, within a model, in a mathematically uniform manner across space. This principle has been effective for representing physical atmospheric processes and also biological processes such as photosynthesis, where trade-offs in the balance between leaf respiratory demands and photosynthetic rates constrain the set of mechanisms and parameter values that can co-occur<sup>98</sup>. However, soil C turnover is regulated by interacting physical and biological processes, with the relative role of each process dependent on a complex suite of environmental conditions that vary in space<sup>65,73</sup>. For example, the recent focus on the role of microbial-mineral surface interactions in soil C stabilization<sup>23</sup>, combined with a move away from ideas of inherent chemical recalcitrance of plant inputs<sup>16,66,68</sup>, may fail to represent soil C turnover in organic soils where mineral surfaces are not abundant<sup>22,99</sup>. Furthermore, there is evidence that mycorrhizal associations are key arbiters of soil C stocks<sup>37,100</sup>, that plants can bypass microorganisms to decompose soil C<sup>38</sup>, and that physico-chemical sorption/desorption processes, and not biology, may regulate soil C turnover<sup>1</sup>. Clearly there are a growing number of different and potentially important controls on soil C stocks that remain poorly understood. As such, it is possible that no single structural representation of soil biogeochemistry will be effective at simulating soil C turnover under warming across diverse landscapes.

The practical and computational costs of using different structural representations in ESMs may be infeasible, but there needs to be an appreciation that even a single model structure may need to represent dramatic shifts in the mechanisms underlying soil dynamics. As such, the spatial and temporal scales at which models are parameterized and applied must be carefully considered<sup>94</sup>. For example, effective simulation of soil C turnover may require different mechanisms to operate as the location changes from one underlain by a mineral to an organic soil. These different mechanisms may even be required for the same location, where the turnover of C in organic horizons and underlying mineral horizons are controlled by different factors<sup>99</sup>. Initial investigations of such possibilities will be best facilitated by controlled experiments that separately resolve C turnover in soil C fractions and horizons, and then test whether these dynamics are better represented by models that use a common or spatially dependent mechanistic structure to simulate the total soil C stock.

**Establish long-term warming experiments.** Achieving real-world confidence in model projections may ultimately demand direct observations of soil C stock responses to climate change<sup>26</sup>. Even once theoretical advances in understanding soil C turnover are widely represented and refined in ESMs, the expectation that projections should be compared to observations is likely to remain. Long-term field ecosystem warming studies are therefore required that, given the expectation that dominant controls on soil C turnover change

with space<sup>16</sup>, are organized into networks that facilitate adoption of standard approaches for robust comparison among studies<sup>41</sup>. Experimental field studies are not without limitations. Imposed step-changes in temperature may not elicit the same responses as the observed chronic rise in temperatures. In addition, the few existing long-term studies exemplify how even a detailed understanding of the processes governing the formation and decomposition of different soil C fractions, may not permit accurate inferences about how the soil C stock will respond in the longer term<sup>42</sup>. For example, organismal responses can lead to surprises that modify direct effects of warming, meaning that anticipated losses of soil C stocks may not necessarily occur<sup>30,42</sup>. Such long-term studies are arguably too few<sup>2</sup> to benchmark model projections against with any real confidence.

To be of most value for determining allowable CO<sub>2</sub> emissions to meet specified climate targets, field-warming experiments should be initiated now and/or existing warming experiments extended to facilitate observations of soil C stock responses. These studies must be well replicated, warm the aboveground as well as soils, and be of sufficiently long duration so that changes in soil C stocks can be reliably assessed despite the 'noise' created by the slow turnover of the total C stock and its pronounced fine-scale spatial variation in size (Fig. 1). Long durations will also permit organismal responses to manifest at multiple temporal scales (Fig. 2), increasing confidence that the observed responses might represent those of natural systems. Similarly, if such long-term studies use isotopic and fractionation approaches<sup>36–39</sup> to resolve the turnover of soil C of differing sensitivities to warming, then inferences that shorter-term responses can be used to estimate total C stock responses can be validated. If long-term studies are broadly initiated, they may need to measure soil C stocks on a mass basis, and not simply C concentrations and/or depth-dependent stocks given their inherent limitations<sup>43,44</sup>. These studies will face the usual challenge of the limited duration of grants to fund research and so will demand a longer-term view of the value they offer in terms of improving confidence in the effectiveness of greenhouse gas emission targets.

## Conclusions

Major conceptual advances across the past 20 years in understanding soil C turnover are not yet reflected in the way in which soil biogeochemistry is represented in ESMs. Evaluating these advances in ESMs will identify how this new knowledge might alter expected responses of soil C stocks to climate change. In turn, insights from the models will expedite gains in basic understanding by identifying mechanisms that must be empirically researched before we can accurately simulate soil C turnover. These activities may initially increase the spread in the projected magnitude of soil C stock responses to warming, but should systematically improve confidence in the projections by factoring conceptual uncertainties into recommendations to manage human-induced changes in climate.

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## References

- Conant, R. T. *et al.* Temperature and soil organic matter decomposition rates — synthesis of current knowledge and a way forward. *Glob. Change Biol.* **17**, 3392–3404 (2011).
- Lu, M. *et al.* Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. *Ecology* **94**, 726–738 (2013).
- Dorrepaal, E. *et al.* Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature* **460**, 616–619 (2013).
- Frey, S. D., Lee, J., Melillo, J. M. & Six, J. The temperature response of soil microbial efficiency and its feedback to climate. *Nature Clim. Change* **3**, 395–398 (2013).
- Karhu, K. *et al.* Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature* **513**, 81–84 (2014).
- Melillo, J. M. *et al.* Soil warming, carbon–nitrogen interactions, and forest carbon budgets. *Proc. Natl Acad. Sci. USA* **108**, 9508–9512 (2011).

7. Zhou, J. *et al.* Microbial mediation of carbon-cycle feedbacks to climate warming. *Nature Clim. Change* **2**, 106–110 (2012).
8. Friedlingstein, P. *et al.* Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *J. Clim.* **27**, 511–526 (2014).
9. Arora, V. K. *et al.* Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth System Models. *J. Clim.* **26**, 5289–5314 (2013).
10. Jones, C. *et al.* Twenty-first-century compatible CO<sub>2</sub> emissions and airborne fraction simulated by CMIP5 Earth system models under four representative concentration pathways. *J. Clim.* **26**, 4398–4413 (2013).  
**This study laid out the idea of ‘allowable emissions’, highlighting the importance of terrestrial carbon cycle uncertainty in projecting allowable greenhouse gas emissions that are compatible with specified climate targets.**
11. Ciais, P. *et al.* in *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. *et al.*) 465–570 (IPCC, Cambridge Univ. Press, 2013).
12. Jobbágy, E. G. & Jackson, R. B. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* **10**, 423–436 (2000).
13. Tarnocai, C. *et al.* Soil organic carbon pools in the northern circumpolar permafrost region. *Glob. Biogeochem. Cycles* **23**, GB2023 (2009).
14. Denman, K. L. *et al.* in *Climate Change 2007: The Physical Science Basis* (eds Solomon, S. *et al.*) 499–587 (IPCC, Cambridge Univ. Press, 2007).
15. Giardina, C. P., Litton, C. M., Crow, S. E. & Asner, G. P. Warming-related increases in soil CO<sub>2</sub> efflux are explained by increased below-ground carbon flux. *Nature Clim. Change* **4**, 822–827 (2014).  
**This study across an elevation gradient in a tropical forest showed that the positive relationship between temperature and soil respiration rates occurred not through expected direct warming effects on soil-C decomposition but because of higher plant C inputs belowground.**
16. Schmidt, M. W. I. *et al.* Persistence of soil organic matter as an ecosystem property. *Nature* **478**, 49–56 (2011).
17. Davidson, D. A., Savage, K. E. & Finzi, A. C. A big-microsite framework for soil carbon modeling. *Glob. Change Biol.* **20**, 3610–3620 (2014).  
**This opinion piece proposed a modular model structure to represent the complexity of processes influencing soil C turnover, bringing representations of soil C turnover in line with those of photosynthesis in ecosystem and global models.**
18. Wieder, W. R., Grandy, A. S., Kallenbach, C. M. & Bonan, G. B. Integrating microbial physiology and physio-chemical principles in soils with the Microbial-MIneral Carbon Stabilization (MIMICS) model. *Biogeosci.* **11**, 1147–1185 (2014).
19. Wieder, W. R., Bonan, G. B. & Allison, S. D. Global soil carbon projections are improved by modelling microbial processes. *Nature Clim. Change* **3**, 909–912 (2013).
20. Jenkinson, D. S., Adams, D. E. & Wild, A. Model estimates of CO<sub>2</sub> emissions from soil in response to global warming. *Nature* **351**, 304–306 (1991).
21. Todd-Brown, K. E. O., Hopkins, F. M., Kivlin, S. N., Talbot, J. M. & Allison, S. D. A framework for representing microbial decomposition in coupled climate models. *Biogeochem.* **109**, 19–33 (2012).
22. Castellano, M. J., Mueller, K. E., Olk, D. C., Sawyer, J. E. & Six, J. Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. *Glob. Change Biol.* **21**, 3200–3209 (2015).  
**This opinion laid out a new conceptual model that integrates advances in understanding of how microbial physiology controls soil C cycling, with established physico-chemical principles that dictate whether physiological responses influence soil C stocks.**
23. Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K. & Paul, E. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Glob. Change Biol.* **19**, 988–995 (2013).
24. Friedlingstein, P. *et al.* Climate-carbon cycle feedback analysis: results from the C<sup>4</sup>MIP model intercomparison. *J. Clim.* **19**, 3337–3353 (2006).
25. Cox, P. M. *et al.* Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* **494**, 341–344 (2013).
26. Exbrayat, J.-F., Pitman, A. J. & Abramowitz, G. Response of microbial decomposition to spin-up explains CMIP5 soil carbon range until 2100. *Geosci. Model Dev.* **7**, 3481–3504 (2014).
27. Todd-Brown, K. E. O. *et al.* Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosci.* **10**, 1717–1736 (2013).
28. Hawkins, E. & Sutton, R. The potential to narrow uncertainty in regional climate predictions. *Bull. Am. Meteorol. Soc.* **90**, 1095–1107 (2009).  
**This study identified sources of uncertainty in physical climate projections: revealing that at decadal timescales model uncertainty is a dominant uncertainty source at regional and global scales, and highlighting the large gains in certainty possible by refining climate models.**
29. Knutti, R. & Sedláček, J. Robustness and uncertainties in the new CMIP5 climate model projections. *Nature Clim. Change* **3**, 369–373 (2013).  
**This study showed that model spread (that is, uncertainty) in physical-based climate projections changed little from the fourth to fifth assessment report of the IPCC, yet the authors argued that confidence in these projections should be substantially greater given major advances in representing mechanistic understanding.**
30. Melillo, J. M. *et al.* Soil warming and carbon-cycle feedbacks to the climate system. *Science* **298**, 2173–2176 (2002).
31. Kirschbaum, M. U. F. The temperature dependence of organic-matter decomposition — still a topic of debate. *Soil Biol. Biochem.* **38**, 2510–2518 (2006).
32. Torn, M. S., Vitousek, P. M. & Trumbore, S. E. The influence of nutrient availability on soil organic matter turnover estimated by incubations and radiocarbon modeling. *Ecosystems* **8**, 352–372 (2005).
33. Lehmann, J. *et al.* Spatial complexity of soil organic matter forms at nanometre scales. *Nature Geosci.* **1**, 238–242 (2008).
34. Vogel, C. *et al.* Submicron structures provide preferential spots for carbon and nitrogen sequestration in soils. *Nature Commun.* **5**, 2947 (2014).  
**This empirical study showed that decomposition of plant C inputs into more stable soil C fractions occurred preferentially via association with mineral surfaces already clustered with organic matter, changing ideas about how soil clay content relates to the potential of soils to sequester C.**
35. Strickland, M. S., DeVore, J. L., Maerz, J. C. & Bradford, M. A. Grass invasion of a hardwood forest is associated with declines in belowground carbon pools. *Glob. Change Biol.* **16**, 1338–1350 (2010).
36. Bradford, M. A., Keiser, A. D., Davies, C. A., Mersmann, C. A. & Strickland, M. S. Empirical evidence that soil carbon formation from plant inputs is positively related to microbial growth. *Biogeochem.* **113**, 271–281 (2013).
37. Clemmensen, K. E. *et al.* Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* **339**, 1615–1618 (2013).
38. Keiluweit, M. *et al.* Mineral protection of soil carbon counteracted by root exudates. *Nature Clim. Change* **5**, 588–595 (2015).  
**This empirical study showed that plant-root inputs could directly liberate soil C from protective associations with minerals, bypassing the presumed direct microbial role in decomposing this ‘stable’ soil C fraction.**
39. Liang, C. & Balser, T. C. Warming and nitrogen deposition lessen microbial residue contribution to soil carbon pool. *Nature Commun.* **3**, 1222 (2012).
40. Neff, J. C. *et al.* Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature* **419**, 915–917 (2002).
41. Torn, M. S. *et al.* A call for international soil experiment networks for studying, predicting, and managing global change impacts. *SOIL* **1**, 575–582 (2015).
42. Sistla, S. A. *et al.* Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature* **497**, 615–618 (2013).
43. Gifford, R. M. & Roderick, M. L. Soil carbon stocks and bulk density: spatial or cumulative mass coordinates as a basis of expression? *Glob. Change Biol.* **9**, 1507–1514 (2003).  
**This study showed how conventional soil sampling procedures might fail to measure real changes in soil C stocks with time, and the authors proposed that a mass-dependent method be broadly adopted to address these issues.**
44. Hopkins, D. W. *et al.* Soil organic carbon contents in long-term experimental grassland plots in the UK (Palace Leas and Park Grass) have not changed consistently in recent decades. *Glob. Change Biol.* **15**, 1739–1754 (2009).
45. Schmitz, O. J. *et al.* Animating the carbon cycle. *Ecosystems* **17**, 344–359 (2014).
46. Reich, P. B. The carbon dioxide exchange. *Science* **329**, 774–775 (2010).
47. Bradford, M. A. *et al.* Thermal adaptation of soil microbial respiration to elevated temperature. *Ecol. Lett.* **11**, 1316–1327 (2008).
48. Hagerty, S. B. *et al.* Accelerated microbial turnover but constant growth efficiency with warming in soil. *Nature Clim. Change* **4**, 903–906 (2014).
49. Crowther, T. W. & Bradford, M. A. Thermal acclimation in widespread heterotrophic soil microbes. *Ecol. Lett.* **16**, 469–477 (2013).
50. Crowther, T. W. *et al.* Biotic interactions mediate soil microbial feedbacks to climate change. *Proc. Natl Acad. Sci. USA* **112**, 7033–7038 (2015).
51. Mahecha, M. D. *et al.* Global convergence in the temperature sensitivity of respiration at ecosystem level. *Science* **329**, 838–840 (2010).
52. Allison, S. D., Wallenstein, M. D. & Bradford, M. A. Soil-carbon response to warming dependent on microbial physiology. *Nature Geosci.* **3**, 336–340 (2010).
53. Allison, S. D. Modeling adaptation of carbon use efficiency in microbial communities. *Front. Microbiol.* **5**, e571 (2014).

54. Todd-Brown, K. E. O. *et al.* Changes in soil organic carbon storage predicted by Earth system models during the 21st century. *Biogeosci.* **11**, 2341–2356 (2014).
55. Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* **440**, 165–173 (2006).
56. Carvalhais, N. *et al.* Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature* **514**, 213–217 (2014).
57. Davidson, E. A., Samanta, S., Caramori, S. S. & Savage, K. The Dual Arrhenius and Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Glob. Change Biol.* **18**, 371–384 (2012).
58. Schuur, E. A. G. *et al.* Climate change and the permafrost carbon feedback. *Nature* **520**, 171–179 (2015).
59. Bradford, M. A. Thermal adaptation of decomposer communities in warming soils. *Front. Microbiol.* **4**, e333 (2013).
60. Lehmann, J. & Kleber, M. The contentious nature of soil organic matter. *Nature* **528**, 60–68 (2015).
61. Miltner, A., Bombach, P., Schmidt-Brücken, B. & Kästner, M. SOM genesis: microbial biomass as a significant source. *Biogeochem.* **111**, 41–55 (2012).
62. Liang, C. & Balser, T. C. Microbial production of recalcitrant organic matter in global soils: implications for productivity and climate policy. *Nature Rev. Microbiol.* **9**, 75–77 (2010).
63. Ahrens, B., Braakhekke, M. C., Guggenberger, G., Schruppf, M. & Reichstein, M. Contribution of sorption, DOC transport and microbial interactions to the  $^{14}\text{C}$  age of a soil organic carbon profile: insights from a calibrated process model. *Soil Biol. Biochem.* **88**, 390–402 (2015).
64. Grandy, A. S. & Neff, J. C. Molecular C dynamics downstream: the biochemical decomposition sequence and its impact on soil organic matter structure and function. *Sci. Total Environ.* **404**, 297–307 (2008).
65. Tang, J. & Riley, W. J. Weaker soil carbon–climate feedbacks resulting from microbial and abiotic interactions. *Nature Clim. Change* **5**, 56–60 (2015). **This study showed that use of a dynamic, as opposed to the conventional static, model structure to represent spatiotemporal dependencies in temperature, microbial and mineral surface interactions, predicted weaker but more variable soil-C–climate feedbacks.**
66. Dungait, J. A. J., Hopkins, D. W., Gregory, A. S. & Whitmore, A. P. Soil organic matter turnover is governed by accessibility not recalcitrance. *Glob. Change Biol.* **18**, 1781–1796 (2012).
67. Doetterl, S. *et al.* Soil carbon storage controlled by interactions between geochemistry and climate. *Nature Geosci.* **8**, 780–783 (2015).
68. Marschner, B. *et al.* How relevant is recalcitrance for the stabilization of organic matter in soils? *J. Plant. Nutr. Soil. Sci.* **171**, 91–110 (2008).
69. Crowther, T. W. *et al.* Environmental stress response limits microbial necromass contributions to soil organic carbon. *Soil Biol. Biochem.* **85**, 153–161 (2015).
70. Högberg, P. & Read, D. J. Towards a more plant physiological perspective on soil ecology. *Trends Ecol. Evol.* **21**, 548–554 (2006).
71. van Hees, P. A. W., Jones, D. L., Finlay, R., Godbold, D. L. & Lundström, U. S. The carbon we do not see: the impact of low molecular weight compounds on carbon dynamics and respiration in forest soils: a review. *Soil Biol. Biochem.* **37**, 1–13 (2005).
72. Pittelkow, C. M. *et al.* Productivity limits and potentials of the principles of conservation agriculture. *Nature* **517**, 365–368 (2015).
73. Koven, C. D., Lawrence, D. M. & Riley, W. J. Permafrost carbon–climate feedback is sensitive to deep soil carbon decomposability but not deep soil nitrogen dynamics. *Proc. Natl Acad. Sci. USA* **112**, 3752–3757 (2015).
74. Collins, M. *et al.* in *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. *et al.*) 1029–1136 (IPCC, Cambridge Univ. Press, 2013).
75. Sierra, C. A., Müller, M. & Trumbore, S. E. Models of soil organic matter decomposition: the SoilR package, version 1.0. *Geosci. Model Dev. Discuss.* **5**, 1045–1060 (2012).
76. Xia, J., Luo, Y., Wang, Y.-P. & Hararuk, O. Traceable components of terrestrial carbon storage capacity in biogeochemical models. *Glob. Change Biol.* **19**, 2104–2116 (2013).
77. Flato, G. *et al.* in *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. *et al.*) 741–866 (IPCC, Cambridge Univ. Press, 2013).
78. Stocker, T. F. *et al.* in *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. *et al.*) 33–115 (IPCC, Cambridge Univ. Press, 2013).
79. Wenzel, S., Cox, P. M., Eyring, V. & Friedlingstein, P. Emergent constraints on climate-carbon cycle feedbacks in the CMIP5 Earth system models. *J. Geophys. Res.* **119**, 794–807 (2014).
80. Luo, Y. *et al.* Towards more realistic projections of soil carbon dynamics by Earth System Models. *Glob. Biogeochem. Cycles* **29**, 40–56 (2015).
81. Luo, Y., Keenan, T. F. & Smith, M. Predictability of the terrestrial carbon cycle. *Glob. Change Biol.* **21**, 1737–1751 (2015).
82. Reich, P. B. *et al.* Nitrogen limitation constrains sustainability of ecosystem response to  $\text{CO}_2$ . *Nature* **440**, 922–925 (2006).
83. Wieder, W. R., Cleveland, C. C., Smith, W. K. & Todd-Brown, K. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nature Geosci.* **8**, 441–444 (2015).
84. Zhang, Q., Wang, Y. P., Matear, R. J., Pitman, A. J. & Dai, Y. J. Nitrogen and phosphorus limitations significantly reduce future allowable  $\text{CO}_2$  emissions. *Geophys. Res. Lett.* **41**, 632–637 (2014).
85. Hararuk, O., Smith, M. J. & Luo, Y. Microbial models with data-driven parameters predict stronger soil carbon responses to climate change. *Glob. Change Biol.* **21**, 2439–2453 (2015).
86. Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E. & Pacala, S. W. Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated  $\text{CO}_2$ . *Nature Clim. Change* **4**, 1099–1102 (2014).
87. Wieder, W. R., Grandy, A. S., Kallenbach, C. M., Taylor, P. G. & Bonan, G. B. Representing life in the Earth system with soil microbial functional traits in the MIMICS model. *Geosci. Model Dev. Discuss.* **8**, 2011–2052 (2015).
88. Parton, W. J., Schimel, D. S., Cole, C. V. & Ojima, D. S. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil. Sci. Soc. Am. J.* **51**, 1173–1179 (1987).
89. Bonan, G. B., Hartman, M. D., Parton, W. J. & Wieder, W. R. Evaluating litter decomposition in earth system models with long-term litterbag experiments: an example using the Community Land Model version 4 (CLM4). *Glob. Change Biol.* **19**, 957–974 (2013).
90. Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L. & Richter, A. Carbon use efficiency of microbial communities: stoichiometry, methodology and modelling. *Ecol. Lett.* **16**, 930–939 (2013).
91. Burd, A. B. *et al.* Terrestrial and marine perspectives on modeling organic matter degradation pathways. *Glob. Change Biol.* **22**, 121–136 (2016).
92. Grant, R. F., Humphreys, E. R. & Lafleur, P. M. Ecosystem  $\text{CO}_2$  and  $\text{CH}_4$  exchange in a mixed tundra and a fen within a hydrologically diverse Arctic landscape: 1. Modeling versus measurements. *J. Geophys. Res.-Biogeosci.* **120**, 1366–1387 (2015).
93. Jones, C. *et al.* Global climate change and soil carbon stocks: predictions from two contrasting models for the turnover of organic carbon in soil. *Glob. Change Biol.* **11**, 154–166 (2005).
94. Manzoni, S. & Porporato, A. Soil carbon and nitrogen mineralization: theory and models across scales. *Soil Biol. Biochem.* **41**, 1355–1379 (2009).
95. German, D. P., Marcelo, K. R. B., Stone, M. M. & Allison, S. D. The Michaelis-Menten kinetics of soil extracellular enzymes in response to temperature: a cross-latitude study. *Glob. Change Biol.* **18**, 1468–1479 (2012).
96. Tucker, C. L., Bell, J., Pendall, E. & Ogle, K. Does declining carbon-use efficiency explain thermal acclimation of soil respiration with warming? *Glob. Change Biol.* **19**, 252–263 (2013).
97. Suseela, V., Conant, R. T., Wallenstein, M. D. & Dukes, J. S. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Glob. Change Biol.* **18**, 336–348 (2012).
98. Shipley, B., Lechowicz, M. J., Wright, I. & Reich, P. B. Fundamental trade-offs generating the worldwide leaf economics spectrum. *Ecology* **87**, 535–541 (2006).
99. Manning, P. *et al.* Simple measures of climate, soil properties and plant traits predict national-scale grassland soil carbon stocks. *J. Appl. Ecol.* **52**, 1188–1196 (2015).
100. Averill, C., Turner, B. L. & Finzi, A. C. Plant–decomposer competition for nitrogen increases soil carbon storage in ecto- and ericoid-mycorrhizal ecosystems. *Nature* **505**, 543–545 (2014).

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## Author contributions

M.A.B. conceived the overall idea for this manuscript and together with T.W.C. synthesized empirical information, and with W.R.W. modelling knowledge. M.A.B., W.R.W., G.B.B., N.F., P.A.W. and T.W.C. then co-developed the ideas and written material.

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## Competing financial interests

The authors declare no competing financial interests.