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# 1 **Managing uncertainty in soil carbon feedbacks to climate change**

2

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18

19 **Planetary warming may be exacerbated if it accelerates loss of soil carbon to the**

20 **atmosphere. This carbon cycle-climate feedback is included in climate projections. Yet**

21 **despite ancillary data supporting a positive feedback, there is limited evidence for soil**

22 **carbon loss under warming. The low confidence engendered in feedback projections is**

23 **reduced further by the common representation in models of an outdated knowledge of soil**

24 **carbon turnover. ‘Model-knowledge integration’ – representing in models an advanced**

25 **understanding of soil carbon stabilisation – is the first step to build confidence. This will**  
26 **inform experiments that further increase confidence by resolving competing mechanisms**  
27 **that most influence projected soil carbon stocks. Improving feedback projections is an**  
28 **imperative for establishing greenhouse gas emission targets that limit climate change.**

29  
30 Hundreds of studies have shown effects of warming on soil carbon (C) dynamics<sup>1,2</sup>. Much of this  
31 empirical research has been motivated by the possibility that climate warming will stimulate  
32 biologically mediated decomposition of soil C to CO<sub>2</sub><sup>3-7</sup>. Enhanced rates of soil C decomposition  
33 may reduce the capacity of the land to act as a CO<sub>2</sub> sink, so that a greater proportion of  
34 anthropogenic CO<sub>2</sub> emissions remain in the atmosphere<sup>8-10</sup>. The magnitude of this so-called  
35 ‘carbon-climate feedback’ is therefore critical for estimating the allowable greenhouse gas  
36 emissions that are compatible with climate targets<sup>10</sup>. The soil is the largest store of C (~1,500-  
37 2,400 Pg) in the terrestrial biosphere, containing more than double the C of the atmosphere<sup>11-13</sup>.  
38 Hence, loss of even a small proportion of this store may result in higher atmospheric CO<sub>2</sub>  
39 concentrations and consequently additional planetary warming<sup>8,14</sup>.

40 Despite the wealth of research into warming effects on soil C dynamics, there is no  
41 consensus on the magnitude of warming-induced reductions in soil C stocks<sup>1,14,15</sup>. The low  
42 confidence in the projected range of soil C losses arises in part from an empirical focus on the  
43 responses of soil C decomposition rates to warming, rather than the direct measurement of  
44 changes in total soil C stocks. Confidence in projected losses is further eroded because emerging  
45 ideas<sup>2,16</sup> about how soil C is formed and stabilised are not commonly represented in the soil  
46 biogeochemical models used for climate change projections<sup>17-19</sup>. Instead, the assumptions in  
47 these models about the mechanisms underlying soil C responses to warming are largely

48 similar<sup>11,14,20,21</sup> and often conflict with emerging understanding<sup>16,22,23</sup>. These assumptions  
49 underlie Earth System Model (ESM) projections of soil C losses through climate warming<sup>9,24</sup>.

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

58 In this paper, we distinguish the meaning of ‘uncertainty’ from ‘confidence’. Many forms  
59 of uncertainty exist when modelling climate change and associated biosphere feedbacks<sup>28</sup>, but  
60 they do not equally contribute to the confidence one has that projected changes will occur<sup>29</sup>. We  
61 focus on the major uncertainties underpinning low confidence in projections of soil C stock  
62 responses to warming. Three primary areas of empirical uncertainty exist: the paucity of direct  
63 observations of warming effects on soil C stocks, the potential for organism responses to  
64 warming to alter short-term biogeochemical responses, and dramatically changing ideas about  
65 how soil C formation and stabilisation are regulated. The major modelling uncertainty is  
66 associated with representing common and out-dated ideas about soil C turnover in the soil sub-  
67 models of the ESMs. We demonstrate the importance of instead representing different ideas in  
68 ESMs – i.e. ‘structural uncertainties’ – that capture emerging concepts of soil C stabilisation. We  
69 conclude by proposing ways forward for empiricists and modellers to improve confidence in  
70 projected soil C-climate feedbacks.

71

## 72 **Empirical uncertainties**

### 73 **Evidence for carbon loss**

74 Empirical research into soil C stock responses to warming has primarily focused on  
75 decomposition (Fig. 1). There is compelling evidence from observational studies across climate  
76 gradients, and both laboratory and field warming experiments, that decomposition rates respond  
77 positively to warming (but see<sup>15</sup>), at least in the short-term (<1 to ~10 years)<sup>1,2,30</sup>. These  
78 increases in decomposition of soil C to CO<sub>2</sub> occur with plants present or absent, suggesting that  
79 warming accelerates C loss from soils primarily by stimulating the activities of microbes<sup>31</sup>. This  
80 microbial mechanism underlies the C-cycle pathway in the ESMs through which soil C is  
81 redistributed to the atmosphere as climate warms.

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

93 studies reporting positive decomposition responses to warming provide weak, indirect support  
94 for the existence of a positive land C-climate feedback<sup>1,5,6</sup>.

95         The lack of direct evidence for reductions in soil C stocks may, in part, reflect a signal-to-  
96 noise issue. Soil C varies markedly at nanometre to metre scales in amount, chemistry, and the  
97 physical setting where it is found<sup>33,34</sup>. These attributes can protect soil C from microbial  
98 decomposition, meaning that a large proportion of the C in a given soil will respond slowly, if at  
99 all, to warming<sup>1</sup>. Looking for a small change in a large, spatially variable stock makes it difficult  
100 to quantify effects of warming on total soil C (Fig. 1). For example, the statistical power to detect  
101 a change in total soil C stocks at a site is typically far below that recommended, demanding  
102 higher replication than generally used<sup>35</sup>. The use of techniques, such as isotopes and  
103 fractionations, to track and quantify C turnover in soil pools that are differently vulnerable, does  
104 offer a solution for detecting a signal from among the noise<sup>36-39</sup>. However, the issues with using  
105 such techniques to infer change in stock sizes echoes those for decomposition; environmental  
106 change can alter the sizes of individual C pools or fluxes without altering the total stock<sup>40</sup>.

107         The difficulties involved in detecting changes in the total size of soil C stocks likely  
108 encouraged the use of indirect measurements, such as decomposition rates, to understand  
109 warming effects. However, demonstrating definitively that soil C stocks will be reduced under  
110 warming requires a large number of sites, long time scales (>20 years), and ecosystem (versus  
111 soil only) experimental warming. Such long-term network data will not be available in the near  
112 term<sup>41</sup> but even collation of soil C stocks in existing field studies would be a step forward. We  
113 know of only five, published field-warming studies that measured soil C directly under  
114 experimental warming plots for timescales >10 years, and they did not consistently show  
115 reductions in soil C<sup>2,42</sup>. Furthermore, of the 34 studies that have compared soil C dynamics in

116 control versus experimental warming plots<sup>2,42</sup> – over both the short and longer-term – only six  
117 measured stocks. The remainder measured soil C concentrations but these do not account for  
118 potential changes in soil bulk density, which could markedly affect stock sizes<sup>43,44</sup>. A key  
119 challenge then is determining how best to improve confidence in projected soil C-climate  
120 feedbacks in lieu of the fact that there is limited direct data on the effects of ecosystem warming  
121 on total soil C stocks.

122

### 123 **Organisms modify direct warming effects**

124 Knowing how to best represent organismal responses to climate change in biogeochemical  
125 models is a significant challenge<sup>45</sup>. Initial effects of chronic disturbance on an ecosystem are  
126 often transient because the organisms, whose activities mediate biogeochemical processes such  
127 as decomposition, first respond physiologically and second through changes in abundance (Fig.  
128 2)<sup>46</sup>. Two decades of experimental summer warming of arctic tundra, for example, gradually  
129 increased the dominance of woody plants, altering plant community architecture. The altered  
130 plant community mitigated direct summer warming of the soils but caused indirect warming in  
131 the winter. These longer-term consequences stimulated plant C inputs at depth, increasing both  
132 the activity of the soil microbes and soil C storage, despite the fact that initial warming was  
133 considered to promote soil C loss<sup>42</sup>.

134 Soil microbial communities and controls on their activities also shift as temperatures  
135 change, altering their collective responses to warming in the shorter- versus longer-term<sup>4,5,47-50</sup>.  
136 Substantive debate exists as to whether these shifts will influence soil C decomposition  
137 rates<sup>5,46,47,51</sup>. Adding to this uncertainty, new efforts to incorporate soil microbial processes in

138 biogeochemical models reveal that the manner in which they are represented means that  
139 simulated acclimation to warming can alternatively exacerbate or mitigate soil C losses<sup>4,52,53</sup>.

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

149

#### 150 **Changing ideas on soil carbon stabilisation**

151 Low temperature is considered to be one of the dominant forces protecting soil C from  
152 decomposition<sup>55</sup>. In permafrost soils (those that are  $\leq 0^{\circ}\text{C}$  for  $>2$  years) decomposition proceeds  
153 slowly because of limited availability of liquid water<sup>56,57</sup>. As liquid water becomes available,  
154 microbial decomposition of soil C initially proceeds slowly because cool temperatures directly  
155 limit activity<sup>58</sup>. Warming then releases temperature limitation on the catalytic activities of  
156 intracellular and extracellular microbial enzymes, accelerating decomposition of soil C to  $\text{CO}_2$ .  
157 The land C-climate feedback in ESMs is primarily based on the assumption of this fundamental  
158 biochemical response<sup>59</sup>. But a paradigmatic shift in our understanding of how soil C is  
159 stabilised<sup>60</sup> casts doubt on whether such cellular processes can be directly scaled to biosphere-  
160 atmosphere interactions driving the C cycle.



161 Microorganisms have been considered the primary agents of soil C decomposition for  
162 over a century. They are now also recognised, somewhat paradoxically, as dominant agents of  
163 soil C formation (Fig. 3)<sup>16,23,61</sup>. As much as 80% of the soil C in mineral soils that is protected  
164 from decomposition through physico-chemical mechanisms, exists in the form of microbial  
165 necromass and products<sup>62</sup>, and the proportion may be higher at depth<sup>63</sup>. Soil microbes therefore  
166 convert large fractions of plant-C inputs to CO<sub>2</sub> and a smaller fraction into stable soil C<sup>36</sup>. The  
167 process has been likened to a microbial funnel, whereby microorganisms consume unprotected C  
168 and a portion that passes through is converted into decomposition-resistant forms<sup>36,50,64</sup>. This  
169 dual role for microbes raises the possibility that warming could accelerate the decomposition and  
170 stabilisation of soil C, shifting stocks toward proportionally more protected forms of C which are  
171 less sensitive to warming (Fig. 3)<sup>65</sup>.

172 The emerging paradigm of soil C formation emphasises microbial growth efficiencies  
173 and mineral-matrix interactions as dominant forces stabilising soil C<sup>16,23,66,67</sup>. Structural plant  
174 compounds such as lignin, previously considered resistant to microbial decomposition<sup>66,68</sup>,  
175 represent a poor quality substrate for microbial growth. Physiological inefficiencies involved in  
176 growing on poor substrates result in more plant C being respired to CO<sub>2</sub> instead of being  
177 transformed to microbial biomass<sup>4</sup>. Under this paradigm, most stable C in mineral soils is  
178 produced via microbial uptake of primarily metabolic plant matter inputs, which microbes  
179 rapidly decompose and convert to biomass efficiently (Fig. 3)<sup>23,69</sup>. The dominant pathway for  
180 these inputs may be via plant roots and their associated mycorrhizal fungi<sup>70,71</sup>. If this paradigm is  
181 applicable across multiple ecosystems, it could help explain why increased inputs of structural  
182 plant C to soils, from aboveground litter sources, may not translate to higher soil C stocks<sup>40,72</sup>.

183           Once microbial products are formed, interactions with mineral soil surfaces, such as  
184 clays, are required to protect them from decomposition<sup>22,34</sup>. Hence, even in wet tropical  
185 rainforests, large stores of soil C can be found in aerobic, mineral soils where decomposition  
186 should otherwise be rapid<sup>12</sup>. The most vulnerable pools of soil C to warming are likely those in  
187 organic-rich soils, such as wetlands and in permafrost, where the lack of oxygen and liquid  
188 water, respectively, slow microbial decomposition. In such systems much of the soil C has not  
189 passed through the microbial funnel, but exists as relatively undecomposed plant material<sup>16</sup>. With  
190 warming, C in these soils will increasingly pass through the funnel, resulting in a major fraction  
191 being decomposed to CO<sub>2</sub> and a small fraction becoming microbial products available for “re-  
192 stabilisation”. Yet wetland and permafrost soils are poorly represented in ESM simulations of  
193 land C-climate feedbacks (but see<sup>73</sup>) and there is little data available to estimate the likely  
194 magnitude of their response to climate change<sup>11,58,74</sup>. Given that permafrost contains as much C  
195 as all non-permafrost soils combined<sup>13</sup>, such limitations must be addressed given the potential  
196 importance of their responses in dictating the magnitude of land C-climate feedbacks<sup>73</sup>.

197

## 198 **Uncertainties in modelling**

### 199 **Model structure**

200 The soil sub-models in ESMs represent soil C responses to warming in a common manner. Soil  
201 C decomposition to CO<sub>2</sub> follows a single first-order response curve, similar to half-life plots for  
202 radioactive decay, where the time taken for a constant fraction of soil C to decompose decreases  
203 with warming<sup>21,27,75,76</sup>. The mechanism then assumes that climate warming increases the short  
204 and long-term potential for microbes to decompose soil C to CO<sub>2</sub><sup>8-10</sup>, presupposing a positive C-  
205 climate feedback<sup>14</sup>.

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

219 Differences among soil sub-model projections instead result largely from parameter  
220 uncertainty. Values for parameters such as the “decay constant” for soil C, contribute to a six-  
221 fold difference in the simulated global stock of contemporary soil C<sup>27</sup>. Differences in the  
222 simulated stocks carry forward and translate to substantial among-model variation in the strength  
223 of C-climate feedback projections<sup>26,54,79</sup>. Efforts to refine parameter estimates may reduce  
224 among-model variation<sup>80</sup> but will not improve confidence in projected soil C stock responses to  
225 warming<sup>26,81</sup>. These improvements will only come through representing the new ideas about the  
226 mechanisms regulating soil C turnover.

227 Representing structural uncertainty in soil processes in the ESMs has the potential to  
228 drastically change projected terrestrial C cycle feedbacks. For example, beyond warming the

229 CO<sub>2</sub> fertilization effect is a dominant biogeochemical feedback in ESMs<sup>9</sup>. Increasingly, model  
230 structures represent the fact that the rate of soil nitrogen (N) supply can strongly constrain plant  
231 growth responses to elevated atmospheric CO<sub>2</sub><sup>82</sup>. In general, representing coupled C-N  
232 biogeochemistry dampens the CO<sub>2</sub> fertilization effect on plant productivity and reduces  
233 terrestrial C storage<sup>83,84</sup>. Given the complexity of representing global C and N cycles, inclusion  
234 of terrestrial N dynamics may increase C cycle uncertainty, but should build confidence in model  
235 projections. Similarly, recent efforts to represent structural uncertainty in soil C responses to  
236 warming in soil biogeochemical models<sup>19,85-87</sup> suggest that divergent projections of the C-climate  
237 feedback will be observed if these efforts are integrated into CMIP exercises. We argue that such  
238 initiatives are necessary to represent the true uncertainty associated with projecting terrestrial  
239 biogeochemical responses to climate change.

240

#### 241 **Advances in soil biogeochemical models**

242 Many of the ESMs simulate soil processes by using some of the most widely applied, soil  
243 biogeochemical models<sup>27</sup>. These ‘conventional’ soil models assume that decomposition of soil C  
244 to CO<sub>2</sub> is a product of microbial activity, but that microbes do not regulate the rate of soil C  
245 turnover<sup>88</sup>. Instead, the control on turnover is exerted by factors such as the chemistry of  
246 different soil C compounds<sup>60</sup>. These conventional models therefore explicitly represent controls  
247 on microbial activity, but the microbes themselves are considered ‘implicit’ to the dynamics.  
248 Recent major advances in understanding soil C dynamics have come about in the broader context  
249 of soil biogeochemical models (as opposed to the narrow subset of these models used in the  
250 ESMs) by representing explicitly how microbial physiology, biomass and enzyme kinetics  
251 respond to warming<sup>27,48,65</sup>.

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

265           Another ‘implicit’ assumption of most conventional soil models is that the rate of soil C  
266 formation (as opposed to decomposition) is regulated by microbial growth efficiencies, with  
267 higher efficiencies leading to higher formation rates<sup>89</sup>. Warming-induced reductions in growth  
268 efficiencies then exacerbate, rather than mitigate as estimated by microbial-explicit models,  
269 losses of soil C stocks<sup>4</sup>. Although microbial growth efficiencies are assumed to be invariant in  
270 most conventional models (an assumption that is under debate<sup>4,90</sup>), the example demonstrates  
271 that even slight structural differences in how soil C turnover is represented can translate to a  
272 broad spread in the projected magnitude of soil C losses. Until such structural uncertainties are  
273 represented in ESM soil sub-models, we cannot know whether the spread in the projected  
274 magnitude of the C-climate feedback is reflective of our contemporary conceptual understanding

275 of soil C turnover. As such there is low confidence in the current ESM projections of the C-  
276 climate feedback and the resulting constraints on allowable greenhouse gas emissions<sup>14,74</sup>.

277

## 278 **Addressing uncertainties to build confidence**

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

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

298

299 **Represent structural uncertainty**

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

314 Empiricists have two distinct roles to play in these model intracomparison projects. The  
315 first is to work with modellers to develop structural representations that best reflect the  
316 competing conceptualisations of soil C turnover. We refer to this approach as ‘model-knowledge  
317 integration’ to distinguish it from the now ubiquitous model-data synthesis efforts, which have  
318 failed to redress the low confidence in soil C-climate feedbacks. Model-knowledge integration  
319 will likely involve synthesising hundreds of published mathematical and conceptual soil models  
320 into broad classifications<sup>94</sup>, and summarising the general processes (and ideally their associated

321 equations) that need to be represented in models<sup>17</sup>. This methodology shows awareness of the  
322 human and computational costs related to representing structural uncertainty in climate models,  
323 which demands that only the most plausible sets of mechanisms are compared.

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

335

### 336 **Refine parameter estimates**

337 Once structural uncertainty is represented and reduced, the aim to lessen the spread in the  
338 projected magnitude of the C-climate feedback by refining parameter estimates<sup>26,79,81</sup> will be of  
339 great value. The current ensemble of ESMs vary markedly in the assumed values of soil  
340 parameters, such as the sensitivity of decay constants to warming<sup>27</sup>. Similarly, variation in even  
341 the parameter value of a single physiological process in the microbial-explicit models, can mean  
342 the difference between large versus no losses of soil C stocks under warming<sup>52</sup>. Notably, soil C  
343 stocks are sensitive to a huge range of processes in these microbial models, including community



344 composition, enzyme activities, carbon use efficiency, microbial turnover, and mineral surface  
345 interactions<sup>19,48,65,95,96</sup>. Parameter values for these processes tend to be poorly constrained by  
346 observations<sup>39,56,80,90,94</sup>. Hence, modellers can provide critical guidance to empiricists by  
347 identifying processes where modelled soil C stocks are strongly sensitive to the assumed  
348 parameter value. Such guidance will allow empiricists to focus on identifying the plausible range  
349 of values observed in nature and how these values depend on environmental conditions<sup>57,97</sup>.

350

### 351 **Consider spatially-explicit processes**

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

367 single structural representation of soil biogeochemistry will be effective at simulating soil C  
368 turnover under warming across diverse landscapes.

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

381

### 382 **Establish long-term warming experiments**

383 Achieving real-world confidence in model projections may ultimately demand direct  
384 observations of soil C stock responses to climate change<sup>26</sup>. Even once theoretical advances in  
385 understanding soil C turnover are widely represented and refined in ESMs, there will likely  
386 remain the expectation that projections should be compared to observations. Long-term field  
387 ecosystem warming studies are therefore required that, given the expectation that dominant  
388 controls on soil C turnover change with space<sup>16</sup>, are organised into networks that facilitate  
389 adoption of standard approaches for robust comparison among studies<sup>41</sup>. Experimental field

390 studies are not without limitations. Imposed step-changes in temperature may not elicit the same  
391 responses as the observed chronic rise in temperatures. In addition, the few existing long-term  
392 studies exemplify how even a detailed understanding of the processes governing the formation  
393 and decomposition of different soil C fractions, may not permit accurate inferences about how  
394 the soil C stock will respond in the longer term<sup>42</sup>. For example, organismal responses can lead to  
395 surprises that modify direct effects of warming, meaning that anticipated losses of soil C stocks  
396 may not necessarily occur<sup>30,42</sup>. Such long-term studies are arguably too few<sup>2</sup> to benchmark model  
397 projections against with any real confidence.

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

412 demand a longer-term view of the value they offer in terms of improving confidence in the  
413 effectiveness of greenhouse gas emission targets.

414

## 415 **Conclusions**

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

425

## 426 **References**

- 427 1 Conant, R. T. *et al.* Temperature and soil organic matter decomposition rates – synthesis  
428 of current knowledge and a way forward. *Global Change Biol* **17**, 3392-3404 (2011).
- 429 2 Lu, M. *et al.* Responses of ecosystem carbon cycle to experimental warming: a meta-  
430 analysis. *Ecology* **94**, 726-738 (2013).
- 431 3 Dorrepaal, E. *et al.* Carbon respiration from subsurface peat accelerated by climate  
432 warming in the subarctic. *Nature* **460**, 616-619 (2013).
- 433 4 Frey, S. D., Lee, J., Melillo, J. M. & Six, J. The temperature response of soil microbial  
434 efficiency and its feedback to climate. *Nat Clim Change* **3**, 395-398 (2013).

- 435 5 Karhu, K. *et al.* Temperature sensitivity of soil respiration rates enhanced by microbial  
436 community response. *Nature* **513**, 81-84 (2014).
- 437 6 Melillo, J. M. *et al.* Soil warming, carbon-nitrogen interactions, and forest carbon  
438 budgets. *P Natl Acad Sci USA* **108**, 9508-9512 (2011).
- 439 7 Zhou, J. *et al.* Microbial mediation of carbon-cycle feedbacks to climate warming. *Nat*  
440 *Clim Change* **2**, 106-110 (2012).
- 441 8 Friedlingstein, P. *et al.* Uncertainties in CMIP5 climate projections due to carbon cycle  
442 feedbacks. *J Climate* **27**, 511-526 (2014).
- 443 9 Arora, V. K. *et al.* Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth  
444 System Models. *J Climate* **26**, 5289-5314 (2013).
- 445 10 Jones, C. *et al.* Twenty-first-century compatible CO<sub>2</sub> emissions and airborne fraction  
446 simulated by CMIP5 Earth system models under four representative concentration  
447 pathways. *J Climate* **26**, 4398-4413 (2013). **This study laid out the idea of ‘allowable**  
448 **emissions’, highlighting the importance of terrestrial carbon cycle uncertainty in**  
449 **projecting allowable greenhouse gas emissions that are compatible with specified**  
450 **climate targets.**
- 451 11 Ciais, P. *et al.* in *Climate Change 2013: The Physical Science Basis. Contribution of*  
452 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on*  
453 *Climate Change* (eds Stocker, T.F. *et al.*) 465-570 (Cambridge Univ. Press, 2013).
- 454 12 Jobbágy, E. G. & Jackson, R. B. The vertical distribution of soil organic carbon and its  
455 relation to climate and vegetation. *Ecol App* **10**, 423-436 (2000).
- 456 13 Tarnocai, C. *et al.* Soil organic carbon pools in the northern circumpolar permafrost  
457 region. *Global Biogeochem Cy* **23**, GB2023 (2009).

- 458 14 Denman, K. L. *et al.* in *Climate Change 2007: The Physical Science Basis. Contribution*  
459 *of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on*  
460 *Climate Change* (eds Solomon, S. *et al.*) 499-587 (Cambridge Univ. Press, 2007).
- 461 15 Giardina, C. P., Litton, C. M., Crow, S. E. & Asner, G. P. Warming-related increases in  
462 soil CO<sub>2</sub> efflux are explained by increased below-ground carbon flux. *Nat Clim Change*  
463 **4**, 822-827 (2014). **This study across an elevational gradient in a tropical forest,**  
464 **showed that the positive relationship between temperature and soil respiration rates**  
465 **occurred not through expected direct warming effects on soil C decomposition but**  
466 **because of higher plant C inputs belowground.**
- 467 16 Schmidt, M. W. I. *et al.* Persistence of soil organic matter as an ecosystem property.  
468 *Nature* **478**, 49-56 (2011).
- 469 17 Davidson, D. A., Savage, K. E. & Finzi, A. C. A big-microsite framework for soil carbon  
470 modeling. *Global Change Biol* **20**, 3610-3620 (2014). **This opinion piece proposed a**  
471 **modular model structure to represent the complexity of processes influencing soil C**  
472 **turnover, bringing representations of soil C turnover in line with those of**  
473 **photosynthesis in ecosystem and global models.**
- 474 18 Wieder, W. R., Grandy, A. S., Kallenbach, C. M. & Bonan, G. B. Integrating microbial  
475 physiology and physio-chemical principles in soils with the M**I**crobial-M**I**neral Carbon  
476 Stabilization (MIMICS) model. *Biogeosciences* **11**, 1147-1185 (2014).
- 477 19 Wieder, W. R., Bonan, G. B. & Allison, S. D. Global soil carbon projections are  
478 improved by modelling microbial processes. *Nat Clim Change* **3**, 909-912 (2013).
- 479 20 Jenkinson, D. S., Adams, D. E. & Wild, A. Model estimates of CO<sub>2</sub> emissions from soil  
480 in response to global warming. *Nature* **351**, 304-306 (1991).

- 481 21 Todd-Brown, K. E. O., Hopkins, F. M., Kivlin, S. N., Talbot, J. M. & Allison, S. D. A  
482 framework for representing microbial decomposition in coupled climate models.  
483 *Biogeochemistry* **109**, 19-33 (2012).
- 484 22 Castellano, M. J., Mueller, K. E., Olk, D. C., Sawyer, J. E. & Six, J. Integrating plant  
485 litter quality, soil organic matter stabilization, and the carbon saturation concept. *Global*  
486 *Change Biol* **21**, 3200-3209 (2015). **This opinion laid out a new conceptual model that**  
487 **integrates advances in understanding of how microbial physiology controls soil C**  
488 **cycling, with established physico-chemical principles that dictate whether**  
489 **physiological responses influence soil C stocks.**
- 490 23 Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Deneff, K. & Paul, E. The Microbial  
491 Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition  
492 with soil organic matter stabilization: do labile plant inputs form stable soil organic  
493 matter? *Global Change Biol* **19**, 988-995 (2013).
- 494 24 Friedlingstein, P. *et al.* Climate-carbon cycle feedback analysis: Results from the C<sup>4</sup>MIP  
495 model intercomparison. *J Climate* **19**, 3337-3353 (2006).
- 496 25 Cox, P. M. *et al.* Sensitivity of tropical carbon to climate change constrained by carbon  
497 dioxide variability. *Nature* **494**, 341-344 (2013).
- 498 26 Exbrayat, J.-F., Pitman, A. J. & Abramowitz, G. Response of microbial decomposition to  
499 spin-up explains CMIP5 soil carbon range until 2100. *Geosci Model Dev* **7**, 3481-3504  
500 (2014).
- 501 27 Todd-Brown, K. E. O. *et al.* Causes of variation in soil carbon simulations from CMIP5  
502 Earth system models and comparison with observations. *Biogeosciences* **10**, 1717-1736  
503 (2013).

504 28 Hawkins, E. & Sutton, R. The potential to narrow uncertainty in regional climate  
505 predictions. *Bull Amer Meteor Soc* **90**, 1095-1107 (2009). **This study identified sources**  
506 **of uncertainty in physical climate projections, revealing that at decadal timescales**  
507 **model uncertainty is a dominant uncertainty source at regional and global scales,**  
508 **highlighting the large gains in certainty possible by refining climate models.**

509 29 Knutti, R. & Sedláček, J. Robustness and uncertainties in the new CMIP5 climate model  
510 projections. *Nat Clim Change* **3**, 369-373 (2013). **This study showed that model spread**  
511 **(i.e. uncertainty) in physical-based climate projections changed little from the fourth**  
512 **to fifth assessment report of the IPCC, yet the authors argued that confidence in**  
513 **these projections should be substantially greater given major advances in**  
514 **representing mechanistic understanding.**

515 30 Melillo, J. M. *et al.* Soil warming and carbon-cycle feedbacks to the climate system.  
516 *Science* **298**, 2173-2176 (2002).

517 31 Kirschbaum, M. U. F. The temperature dependence of organic-matter decomposition—  
518 still a topic of debate. *Soil Biol Biochem* **38**, 2510-2518 (2006).

519 32 Torn, M. S., Vitousek, P. M. & Trumbore, S. E. The influence of nutrient availability on  
520 soil organic matter turnover estimated by incubations and radiocarbon modeling.  
521 *Ecosystems* **8**, 352-372 (2005).

522 33 Lehmann, J. *et al.* Spatial complexity of soil organic matter forms at nanometre scales.  
523 *Nat Geosci* **1**, 238-242 (2008).

524 34 Vogel, C. *et al.* Submicron structures provide preferential spots for carbon and nitrogen  
525 sequestration in soils. *Nat Comm* **5**, 2947 (2014). **This empirical study showed that**  
526 **decomposition of plant C inputs into more stable soil C fractions occurred**



527 **preferentially via association with mineral surfaces already clustered with organic**  
528 **matter, changing ideas about how soil clay content relates to the potential of soils to**  
529 **sequester C.**

530 35 Strickland, M. S., DeVore, J. L., Maerz, J. C. & Bradford, M. A. Grass invasion of a  
531 hardwood forest is associated with declines in belowground carbon pools. *Global Change*  
532 *Biol* **16**, 1338-1350 (2010).

533 36 Bradford, M. A., Keiser, A. D., Davies, C. A., Mersmann, C. A. & Strickland, M. S.  
534 Empirical evidence that soil carbon formation from plant inputs is positively related to  
535 microbial growth. *Biogeochemistry* **113**, 271-281 (2013).

536 37 Clemmensen, K. E. *et al.* Roots and associated fungi drive long-term carbon  
537 sequestration in boreal forest. *Science* **339**, 1615-1618 (2013).

538 38 Keiluweit, M. *et al.* Mineral protection of soil carbon counteracted by root exudates. *Nat*  
539 *Clim Change* **5**, 588–595 (2015). **This empirical study showed that plant-root inputs**  
540 **could directly liberate soil C from protective associations with minerals, bypassing**  
541 **the presumed direct microbial role in decomposing this ‘stable’ soil C fraction.**

542 39 Liang, C. & Balser, T. C. Warming and nitrogen deposition lessen microbial residue  
543 contribution to soil carbon pool. *Nat Comm* **3**, 1222 (2012).

544 40 Neff, J. C. *et al.* Variable effects of nitrogen additions on the stability and turnover of soil  
545 carbon. *Nature* **419**, 915-917 (2002).

546 41 Torn, M. S. *et al.* A call for international soil experiment networks for studying,  
547 predicting, and managing global change impacts. *SOIL* **1**, 575-582 (2015).

548 42 Sistla, S. A. *et al.* Long-term warming restructures Arctic tundra without changing net  
549 soil carbon storage. *Nature* **497**, 615-618 (2013).

550 43 Gifford, R. M. & Roderick, M. L. Soil carbon stocks and bulk density: spatial or  
551 cumulative mass coordinates as a basis of expression? *Global Change Biol* **9**, 1507-1514  
552 (2003). **This study showed how conventional soil sampling procedures might fail to**  
553 **measure real changes in soil C stocks with time, and the authors proposed that a**  
554 **mass-dependent method be broadly adopted to address these issues.**

555 44 Hopkins, D. W. *et al.* Soil organic carbon contents in long-term experimental grassland  
556 plots in the UK (Palace Leas and Park Grass) have *not* changed consistently in recent  
557 decades. *Global Change Biol* **15**, 1739-1754 (2009).

558 45 Schmitz, O. J. *et al.* Animating the carbon cycle. *Ecosystems* **17**, 344-359 (2014).

559 46 Reich, P. B. The carbon dioxide exchange. *Science* **329**, 774-775 (2010).

560 47 Bradford, M. A. *et al.* Thermal adaptation of soil microbial respiration to elevated  
561 temperature. *Ecol Lett* **11**, 1316-1327 (2008).

562 48 Hagerty, S. B. *et al.* Accelerated microbial turnover but constant growth efficiency with  
563 warming in soil. *Nat Clim Change* **4**, 903-906 (2014).

564 49 Crowther, T. W. & Bradford, M. A. Thermal acclimation in widespread heterotrophic soil  
565 microbes. *Ecol Lett* **16**, 469-477 (2013).

566 50 Crowther, T. W. *et al.* Biotic interactions mediate soil microbial feedbacks to climate  
567 change. *P Natl Acad Sci USA* **112**, 7033–7038 (2015).

568 51 Mahecha, M. D. *et al.* Global convergence in the temperature sensitivity of respiration at  
569 ecosystem level. *Science* **329**, 838-840 (2010).

570 52 Allison, S. D., Wallenstein, M. D. & Bradford, M. A. Soil-carbon response to warming  
571 dependent on microbial physiology. *Nat Geosci* **3**, 336-340 (2010).

572 53 Allison, S. D. Modeling adaptation of carbon use efficiency in microbial communities.  
573 *Front Microbiol* **5**, e571 (2014).

574 54 Todd-Brown, K. E. O. *et al.* Changes in soil organic carbon storage predicted by Earth  
575 system models during the 21st century. *Biogeosciences* **11**, 2341-2356 (2014).

576 55 Davidson, E. A. & Janssens, I. A. Temperature sensitivity of soil carbon decomposition  
577 and feedbacks to climate change. *Nature* **440**, 165-173 (2006).

578 56 Carvalhais, N. *et al.* Global covariation of carbon turnover times with climate in  
579 terrestrial ecosystems. *Nature* **514**, 213-217 (2014).

580 57 Davidson, E. A., Samanta, S., Caramori, S. S. & Savage, K. The Dual Arrhenius and  
581 Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to  
582 seasonal time scales. *Global Change Biol* **18**, 371-384 (2012).

583 58 Schuur, E. A. G. *et al.* Climate change and the permafrost carbon feedback. *Nature* **520**,  
584 171-179 (2015).

585 59 Bradford, M. A. Thermal adaptation of decomposer communities in warming soils. *Front*  
586 *Microbiol* **4**, e333 (2013).

587 60 Lehmann, J. & Kleber, M. The contentious nature of soil organic matter. *Nature* **528**, 60-  
588 68 (2015).

589 61 Miltner, A., Bombach, P., Schmidt-Brücken, B. & Kästner, M. SOM genesis: microbial  
590 biomass as a significant source. *Biogeochemistry* **111**, 41-55 (2012).

591 62 Liang, C. & Balser, T. C. Microbial production of recalcitrant organic matter in global  
592 soils: implications for productivity and climate policy. *Nat Rev Microbiol* **9**, 75-77  
593 (2010).

- 594 63 Ahrens, B., Braakhekke, M. C., Guggenberger, G., Schrumpf, M. & Reichstein, M.  
595 Contribution of sorption, DOC transport and microbial interactions to the  $^{14}\text{C}$  age of a  
596 soil organic carbon profile: Insights from a calibrated process model. *Soil Biol Biochem*  
597 **88**, 390-402 (2015).
- 598 64 Grandy, A. S. & Neff, J. C. Molecular C dynamics downstream: The biochemical  
599 decomposition sequence and its impact on soil organic matter structure and function. *Sci*  
600 *Total Environ* **404**, 297-307 (2008).
- 601 65 Tang, J. & Riley, W. J. Weaker soil carbon–climate feedbacks resulting from microbial  
602 and abiotic interactions. *Nat Clim Change* **5**, 56-60 (2015). **This study showed that use**  
603 **of a dynamic, as opposed to the conventional static, model structure to represent**  
604 **spatiotemporal dependencies in temperature, microbial and mineral surface**  
605 **interactions, predicted weaker but more variable soil C-climate feedbacks.**
- 606 66 Dungait, J. A. J., Hopkins, D. W., Gregory, A. S. & Whitmore, A. P. Soil organic matter  
607 turnover is governed by accessibility not recalcitrance. *Global Change Biol* **18**, 1781-  
608 1796 (2012).
- 609 67 Doetterl, S. *et al.* Soil carbon storage controlled by interactions between geochemistry  
610 and climate. *Nature Geosci* **8**, 780-783 (2015).
- 611 68 Marschner, B. *et al.* How relevant is recalcitrance for the stabilization of organic matter  
612 in soils? *J Plant Nutr Soil Sc* **171**, 91-110 (2008).
- 613 69 Crowther, T. W. *et al.* Environmental stress response limits microbial necromass  
614 contributions to soil organic carbon. *Soil Biol Biochem* **85**, 153-161 (2015).
- 615 70 Högberg, P. & Read, D. J. Towards a more plant physiological perspective on soil  
616 ecology. *Trends Ecol Evol* **21**, 548-554 (2006).

617 71 van Hees, P. A. W., Jones, D. L., Finlay, R., Godbold, D. L. & Lundström, U. S. The  
618 carbon we do not see—the impact of low molecular weight compounds on carbon  
619 dynamics and respiration in forest soils: a review. *Soil Biol Biochem* **37**, 1-13 (2005).

620 72 Pittelkow, C. M. *et al.* Productivity limits and potentials of the principles of conservation  
621 agriculture. *Nature* **517**, 365-368 (2015).

622 73 Koven, C. D., Lawrence, D. M. & Riley, W. J. Permafrost carbon—climate feedback is  
623 sensitive to deep soil carbon decomposability but not deep soil nitrogen dynamics. *P Natl*  
624 *Acad Sci USA* **112**, 3752–3757 (2015).

625 74 Collins, M. *et al.* in *Climate Change 2013: The Physical Science Basis. Contribution of*  
626 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on*  
627 *Climate Change* (eds Stocker, T.F. *et al.*) 1029-1136 (Cambridge Univ. Press, 2013).

628 75 Sierra, C. A., Müller, M. & Trumbore, S. E. Models of soil organic matter  
629 decomposition: the SoilR package, version 1.0. *Geosci Model Dev Discuss* **5**, 1045-1060  
630 (2012).

631 76 Xia, J., Luo, Y., Wang, Y.-P. & Hararuk, O. Traceable components of terrestrial carbon  
632 storage capacity in biogeochemical models. *Global Change Biol* **19**, 2104-2116 (2013).

633 77 Flato, G. *et al.* in *Climate Change 2013: The Physical Science Basis. Contribution of*  
634 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on*  
635 *Climate Change* (eds Stocker, T.F. *et al.*) 741-866 (Cambridge Univ. Press, 2013).

636 78 Stocker, T. F. *et al.* in *Climate Change 2013: The Physical Science Basis. Contribution of*  
637 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on*  
638 *Climate Change* (eds Stocker, T.F. *et al.*) 33-115 (Cambridge Univ. Press, 2013).

639 79 Wenzel, S., Cox, P. M., Eyring, V. & Friedlingstein, P. Emergent constraints on climate-  
640 carbon cycle feedbacks in the CMIP5 Earth system models. *J Geophys Res* **119**, 794-807  
641 (2014).

642 80 Luo, Y. *et al.* Towards more realistic projections of soil carbon dynamics by Earth  
643 System Models. *Global Biogeochem Cy* **29**, doi:10.1002/2015GB005239 (2015).

644 81 Luo, Y., Keenan, T. F. & Smith, M. Predictability of the terrestrial carbon cycle. *Global*  
645 *Change Biol* **21**, 1737–1751 (2015).

646 82 Reich, P. B. *et al.* Nitrogen limitation constrains sustainability of ecosystem response to  
647 CO<sub>2</sub>. *Nature* **440**, 922-925 (2006).

648 83 Wieder, W. R., Cleveland, C. C., Smith, W. K. & Todd-Brown, K. Future productivity  
649 and carbon storage limited by terrestrial nutrient availability. *Nat Geosci* **8**, 441-444  
650 (2015).

651 84 Zhang, Q., Wang, Y. P., Mearns, R. J., Pitman, A. J. & Dai, Y. J. Nitrogen and  
652 phosphorous limitations significantly reduce future allowable CO<sub>2</sub> emissions. *Geophys*  
653 *Res Lett* **41**, 632-637 (2014).

654 85 Hararuk, O., Smith, M. J. & Luo, Y. Microbial models with data-driven parameters  
655 predict stronger soil carbon responses to climate change. *Global Change Biol* **21**, 2439–  
656 2453 (2015).

657 86 Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E. & Pacala, S. W. Microbe-  
658 driven turnover offsets mineral-mediated storage of soil carbon under elevated CO<sub>2</sub>. *Nat*  
659 *Clim Change* **4**, 1099–1102 (2014).

660 87 Wieder, W. R., Grandy, A. S., Kallenbach, C. M., Taylor, P. G. & Bonan, G. B.  
661 Representing life in the Earth system with soil microbial functional traits in the MIMICS  
662 model. *Geosci Model Dev Discuss* **8**, 2011-2052 (2015).

663 88 Parton, W. J., Schimel, D. S., Cole, C. V. & Ojima, D. S. Analysis of factors controlling  
664 soil organic matter levels in Great Plains grasslands. *Soil Sci Soc Am J* **51**, 1173-1179  
665 (1987).

666 89 Bonan, G. B., Hartman, M. D., Parton, W. J. & Wieder, W. R. Evaluating litter  
667 decomposition in earth system models with long-term litterbag experiments: an example  
668 using the Community Land Model version 4 (CLM4). *Global Change Biol* **19**, 957-974  
669 (2013).

670 90 Sinsabaugh, R. L., Manzoni, S., Moorhead, D. L. & Richter, A. Carbon use efficiency of  
671 microbial communities: stoichiometry, methodology and modelling. *Ecol Lett* **16**, 930-  
672 939 (2013).

673 91 Burd, A. B. *et al.* Terrestrial and marine perspectives on modeling organic matter  
674 degradation pathways. *Global Change Biol* **22**, 121-136 (2016).

675 92 Grant, R. F., Humphreys, E. R. & Lafleur, P. M. Ecosystem CO<sub>2</sub> and CH<sub>4</sub> exchange in a  
676 mixed tundra and a fen within a hydrologically diverse Arctic landscape: 1. Modeling  
677 versus measurements. *JGR-Biogeosciences* **120**, 1366-1387 (2015).

678 93 Jones, C. *et al.* Global climate change and soil carbon stocks; predictions from two  
679 contrasting models for the turnover of organic carbon in soil. *Global Change Biol* **11**,  
680 154-166 (2005).

681 94 Manzoni, S. & Porporato, A. Soil carbon and nitrogen mineralization: Theory and models  
682 across scales. *Soil Biol Biochem* **41**, 1355-1379 (2009).

- 683 95 German, D. P., Marcelo, K. R. B., Stone, M. M. & Allison, S. D. The Michaelis-Menten  
684 kinetics of soil extracellular enzymes in response to temperature: a cross-latitudinal  
685 study. *Global Change Biol* **18**, 1468-1479 (2012).
- 686 96 Tucker, C. L., Bell, J., Pendall, E. & Ogle, K. Does declining carbon-use efficiency  
687 explain thermal acclimation of soil respiration with warming? *Global Change Biol* **19**,  
688 252-263 (2013).
- 689 97 Suseela, V., Conant, R. T., Wallenstein, M. D. & Dukes, J. S. Effects of soil moisture on  
690 the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field  
691 climate change experiment. *Global Change Biol* **18**, 336-348 (2012).
- 692 98 Shipley, B., Lechowicz, M. J., Wright, I. & Reich, P. B. Fundamental trade-offs  
693 generating the worldwide leaf economics spectrum. *Ecology* **87**, 535-541 (2006).
- 694 99 Manning, P. *et al.* Simple measures of climate, soil properties and plant traits predict  
695 national-scale grassland soil carbon stocks. *J Appl Ecol* **52**, 1188-1196 (2015).
- 696 100 Averill, C., Turner, B. L. & Finzi, A. C. Plant–decomposer competition for nitrogen  
697 increases soil carbon storage in ecto- and ericoid-mycorrhizal ecosystems. *Nature* **505**,  
698 543-545 (2014).

699

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701

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713

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717

718 **Figure 1 Soil C stocks are the net result of outputs and inputs of plant C but most warming**  
719 **research focuses only on outputs, making stock responses highly uncertain.** Warming-  
720 induced outputs (red arrows) in the schematic are represented as CO<sub>2</sub> fluxes, reflecting the  
721 assumption in ESMs that the land C-climate feedback occurs through warming stimulating the  
722 activities of soil microorganisms that decompose soil C. Losses of soil C do occur through other  
723 pathways (lateral transport and soil erosion), but warming effects on these losses are not well  
724 characterised. Instead, the majority of warming studies focus on decomposition of soil C to CO<sub>2</sub>.  
725 Despite strong warming effects on decomposition, there are very few observed reductions in soil  
726 C stocks. This paucity of data reflects the fact that there has been far less research (depicted by  
727 thickness of flux arrow lines) into how warming affects soil C formation through plant inputs  
728 (green down arrows) versus its effects on decomposition. It also reflects the signal-to-noise

729 issues in detecting a change in soil C stocks, given marked local variation (horizontally as well  
730 as with depth) in soil C stocks and the fact only a proportion of this C is likely sensitive to  
731 warming-induced losses.

732

733 **Figure 2 Timescale of organismal responses to warming, with the potential that initial**  
734 **increases in microbial activity are exacerbated or mitigated through physiological,**  
735 **population and community level responses as the warming perturbation continues.**

736 Modelled land C-climate feedbacks rely on warming-mediated increases in the potential  
737 activities of microbial enzymes, which catalyse the decomposition of soil C, being maintained in  
738 the longer term. Yet, physiological acclimation and turnover in populations and communities –  
739 both aboveground and belowground (represented as plants and soil microbes, respectively) –  
740 may modify the assumed translation of this initial cell-level warming response directly to  
741 changes in soil C stocks. How the responses at intermediate levels of biological organisation  
742 modify this translation becomes increasingly uncertain with time, given the large and diverse  
743 array of interactions that can occur to re-structure communities.

744

745 **Figure 3 The dual role of soil microbes as the agents of both soil C decomposition and**  
746 **stabilisation.** A new conceptualisation of how soil C is formed and stabilised emphasises that  
747 plant-C inputs on which microbes grow most efficiently result in larger protected stocks of soil  
748 C. Warming-induced increases in decomposition rates may then cause more unprotected (i.e.  
749 more warming sensitive) soil C to be converted into stable pools, ultimately mitigating the  
750 presumed land C-climate feedback because accelerated decomposition rates are balanced by  
751 elevated formation rates. The grey-hatched arrow depicts this theoretical shunt of soil C from

752 more to less temperature-sensitive pools under warming via the microbial funnel into microbial  
753 product-mineral complexes.

754

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

# Atmospheric

Plant carbon inputs

CO<sub>2</sub>

Respiration

Atmospheric CO<sub>2</sub>  
(from microbial respiration)

Erosion losses

Aboveground

Belowground

Microbial and plant

Soil warming experiment

soil carbon content

Lateral transport of dissolved carbon

1 m

high

low

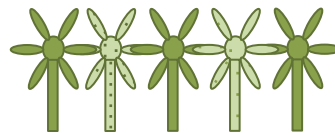
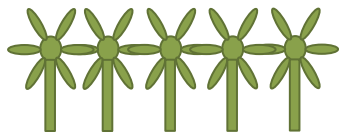
*Certainty in temperature response of plants and microbes*



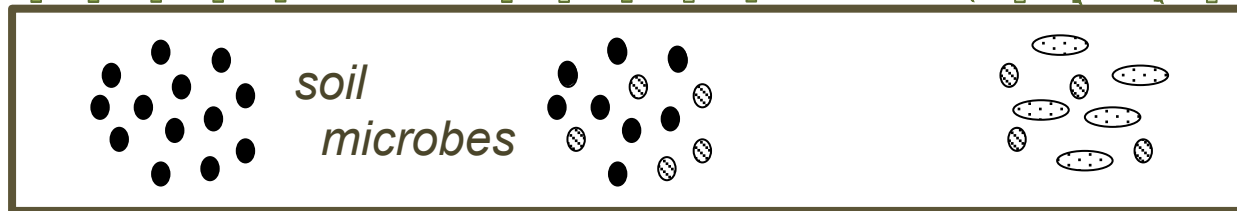
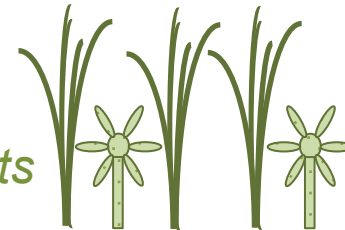
Physiological adjustment

Population turnover

Community turnover



*plants*



*Certainty in temperature response of soil carbon stock*

