

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

2

3 Mark A. Bradford^{1,2}, William R. Wieder^{3,4}, Gordon B. Bonan³, Noah Fierer^{5,6}, Peter A.
4 Raymond¹ & Thomas W. Crowther^{1,2}

5

6 ¹School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, USA

7 ²Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), 6700 AB
8 Wageningen, The Netherlands

9 ³Climate and Global Dynamics Laboratory, National Center for Atmospheric Research, Boulder, CO
10 80307, USA

11 ⁴Institute for Arctic and Alpine Research, University of Colorado, Boulder, CO, 80309, USA

12 ⁵Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, 80309, USA

13 ⁶Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO
14 80309, USA

15

16 **Email addresses:** mark.bradford@yale.edu; wwieder@ucar.edu; bonan@ucar.edu;
17 noah.fierer@colorado.edu; peter.raymond@yale.edu; t.crowther@nioo.knaw.nl

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23 **reduced further by the common representation in models of an outdated knowledge of soil**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^{1,2}. 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 CO₂³⁻⁷. Enhanced rates of soil C decomposition
33 may reduce the capacity of the land to act as a CO₂ sink, so that a greater proportion of
34 anthropogenic CO₂ emissions remain in the atmosphere⁸⁻¹⁰. 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 targets¹⁰. 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 atmosphere¹¹⁻¹³.
38 Hence, loss of even a small proportion of this store may result in higher atmospheric CO₂
39 concentrations and consequently additional planetary warming^{8,14}.

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^{1,14,15}. 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^{2,16} about how soil C is formed and stabilised are not commonly represented in the soil
46 biogeochemical models used for climate change projections¹⁷⁻¹⁹. Instead, the assumptions in
47 these models about the mechanisms underlying soil C responses to warming are largely

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

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 trajectories¹¹. The
52 ESM projections of warming-induced soil C losses range from minimal, to a third of the stock
53 lost by 2100^{8,9,25}. 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^{26,27}.
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 feedbacks²⁸, but
60 they do not equally contribute to the confidence one has that projected changes will occur²⁹. 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 see¹⁵), at least in the short-term (<1 to ~10 years)^{1,2,30}. These
78 increases in decomposition of soil C to CO₂ occur with plants present or absent, suggesting that
79 warming accelerates C loss from soils primarily by stimulating the activities of microbes³¹. 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 stocks¹⁵ 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 ESMs²⁷. Yet expectations for reductions in soil C under warming are still primarily driven
88 by empirical data of accelerated decomposition rates¹, despite little evidence that decomposition
89 responses can be used to infer responses in soil C stocks^{1,32}. In a synthesis of field data, for
90 example, the mean effect size of warming on decomposition rates was statistically significant
91 and strongly positive². 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^{1,5,6}.

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^{33,34}. 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 warming¹. 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 used³⁵. 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 noise³⁶⁻³⁹. 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 stock⁴⁰.

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 term⁴¹ 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^{2,42}. Furthermore, of the 34 studies that have compared soil C dynamics in

116 control versus experimental warming plots^{2,42} – 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^{43,44}. 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 challenge⁴⁵. 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)⁴⁶. 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 loss⁴².

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^{4,5,47-50}.
136 Substantive debate exists as to whether these shifts will influence soil C decomposition
137 rates^{5,46,47,51}. 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^{4,52,53}.

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 season⁴². 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^{11,54}. 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 decomposition⁵⁵. 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^{56,57}. As liquid water becomes available,
154 microbial decomposition of soil C initially proceeds slowly because cool temperatures directly
155 limit activity⁵⁸. Warming then releases temperature limitation on the catalytic activities of
156 intracellular and extracellular microbial enzymes, accelerating decomposition of soil C to CO_2 .
157 The land C-climate feedback in ESMs is primarily based on the assumption of this fundamental
158 biochemical response⁵⁹. But a paradigmatic shift in our understanding of how soil C is
159 stabilised⁶⁰ 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)^{16,23,61}. 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 products⁶², and the proportion may be higher at depth⁶³. Soil microbes therefore
166 convert large fractions of plant-C inputs to CO₂ and a smaller fraction into stable soil C³⁶. 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^{36,50,64}. 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)⁶⁵.

172 The emerging paradigm of soil C formation emphasises microbial growth efficiencies
173 and mineral-matrix interactions as dominant forces stabilising soil C^{16,23,66,67}. Structural plant
174 compounds such as lignin, previously considered resistant to microbial decomposition^{66,68},
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 CO₂ instead of being
177 transformed to microbial biomass⁴. 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)^{23,69}. The dominant pathway for
180 these inputs may be via plant roots and their associated mycorrhizal fungi^{70,71}. 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^{40,72}.

183 Once microbial products are formed, interactions with mineral soil surfaces, such as
184 clays, are required to protect them from decomposition^{22,34}. 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 rapid¹². 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 material¹⁶. With
190 warming, C in these soils will increasingly pass through the funnel, resulting in a major fraction
191 being decomposed to CO₂ 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 see⁷³) and there is little data available to estimate the likely
194 magnitude of their response to climate change^{11,58,74}. Given that permafrost contains as much C
195 as all non-permafrost soils combined¹³, such limitations must be addressed given the potential
196 importance of their responses in dictating the magnitude of land C-climate feedbacks⁷³.

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 CO₂ 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^{21,27,75,76}. The mechanism then assumes that climate warming increases the short
204 and long-term potential for microbes to decompose soil C to CO₂⁸⁻¹⁰, presupposing a positive C-
205 climate feedback¹⁴.

206 This representation of soil C turnover in ESMs has remained essentially unchanged for
207 two decades^{20,21}. 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^{29,77,78}. 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^{28,29,74,78}. A
211 similar principle has been applied to C cycle projections in ESMs^{9,11,14,24} 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 reports⁷⁸. 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^{28,29,77}. 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^{8-10,74} is not the consequence of structural uncertainty^{26,54}.

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 C²⁷. Differences in the
222 simulated stocks carry forward and translate to substantial among-model variation in the strength
223 of C-climate feedback projections^{26,54,79}. Efforts to refine parameter estimates may reduce
224 among-model variation⁸⁰ but will not improve confidence in projected soil C stock responses to
225 warming^{26,81}. 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 CO₂ fertilization effect is a dominant biogeochemical feedback in ESMs⁹. 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 CO₂⁸². In general, representing coupled C-N
232 biogeochemistry dampens the CO₂ fertilization effect on plant productivity and reduces
233 terrestrial C storage^{83,84}. 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^{19,85-87} 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 models²⁷. These ‘conventional’ soil models assume that decomposition of soil C
244 to CO₂ is a product of microbial activity, but that microbes do not regulate the rate of soil C
245 turnover⁸⁸. Instead, the control on turnover is exerted by factors such as the chemistry of
246 different soil C compounds⁶⁰. 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^{27,48,65}.

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 sensitive⁵². 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 efficiencies⁵⁹, 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 biomass⁵². 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^{19,85-87}.

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 rates⁸⁹. Warming-induced reductions in growth
268 efficiencies then exacerbate, rather than mitigate as estimated by microbial-explicit models,
269 losses of soil C stocks⁴. Although microbial growth efficiencies are assumed to be invariant in
270 most conventional models (an assumption that is under debate^{4,90}), 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^{14,74}.

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 community⁹¹.

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 projections²⁹. 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^{48,52,63,65,92} 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 ensembles²⁸.
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^{19,93}. 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 classifications⁹⁴, and summarising the general processes (and ideally their associated

321 equations) that need to be represented in models¹⁷. 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^{16,22,23,60}, 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^{34,37,38,40},
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^{26,79,81} 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 warming²⁷. 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 warming⁵². 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^{19,48,65,95,96}. Parameter values for these processes tend to be poorly constrained by
346 observations^{39,56,80,90,94}. 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^{57,97}.

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-occur⁹⁸.
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^{65,73}. For example, the recent focus on the role of microbial-mineral surface interactions
360 in soil C stabilisation²³, combined with a move away from ideas of inherent chemical
361 recalcitrance of plant inputs^{16,66,68}, may fail to represent soil C turnover in organic soils where
362 mineral surfaces are not abundant^{22,99}. Furthermore, there is evidence that mycorrhizal
363 associations are key arbiters of soil C stocks^{37,100}, that plants can bypass microorganisms to
364 decompose soil C³⁸, and that physico-chemical sorption/ desorption processes, and not biology,
365 may regulate soil C turnover¹. 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 considered⁹⁴. 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 factors⁹⁹.
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 change²⁶. 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 space¹⁶, are organised into networks that facilitate
389 adoption of standard approaches for robust comparison among studies⁴¹. 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 term⁴². 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^{30,42}. Such long-term studies are arguably too few² to benchmark model
397 projections against with any real confidence.

398 To be of most value for determining allowable CO₂ 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 approaches³⁶⁻³⁹ 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^{43,44}. 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 CO₂ 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 CO₂ 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 MIcrobial-MIneral 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 CO₂ 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 C⁴MIP
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}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 CO₂. *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 CO₂ 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 CO₂. *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 CO₂ and CH₄ 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

700 Correspondence and requests for materials should be addressed to Mark A. Bradford.

701

702 **Acknowledgements** The work was supported by grants from the U.S. National Science
703 Foundation (DEB-1021098 and DEB-1457614) and The Royal Netherlands Academy of Arts
704 and Sciences (Visiting Professors Programme) to M.A.B. The Yale Climate and Energy Institute,
705 and a Marie Skłodowska Curie Fellowship, supported T.W.C. W.R.W. was supported by grants

706 from the U.S. Department of Agriculture (NIFA 2015-67003-23485) and U.S. Department of
707 Energy (TES DE-SC0014374). Thanks to Wim van der Putten and Fiona Cotter for comments
708 on an earlier draft of this script.

709

710 **Author Contributions** M.A.B. conceived the overall idea for this manuscript and together with
711 T.W.C. synthesised empirical and with W.R.W. modelling knowledge. M.A.B., W.R.W., G.B.B.,
712 N.F., P.A.W. and T.W.C. then co-developed the ideas and written material.

713

714 **Author Information** Reprints and permissions information is available at
715 www.nature.com/reprints. The authors declare no competing financial interests. Readers are
716 welcome to comment on the online version of the paper.

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 CO₂ 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 CO₂.
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

CO₂

Respiration

Atmospheric CO₂
(from microbial respiration)

Erosion losses

Aboveground

Belowground

Microbial and plant

Soil warming experiment

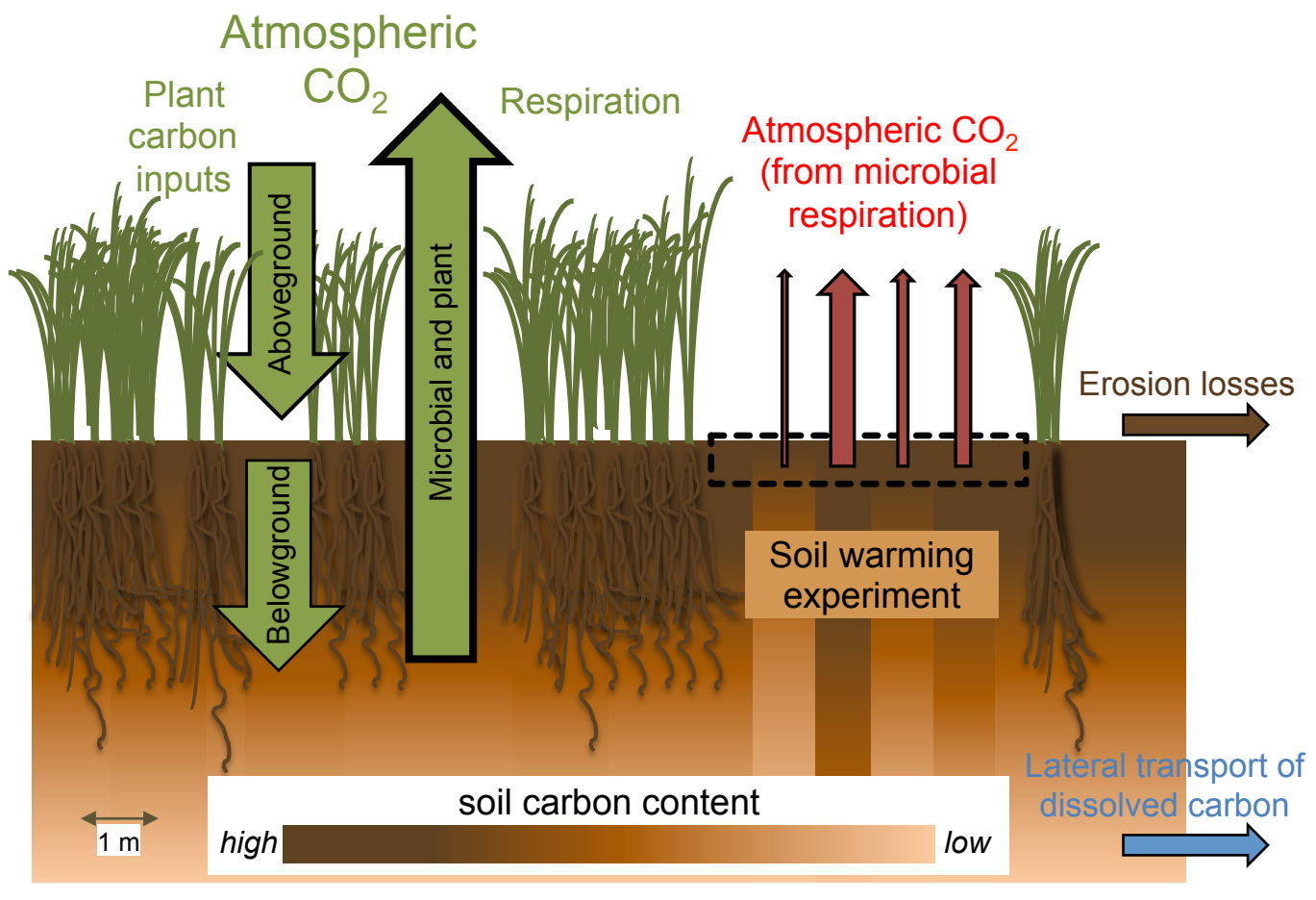
soil carbon content

high

low

Lateral transport of dissolved carbon

1 m



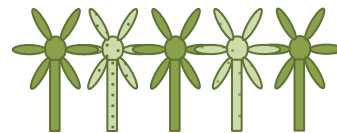
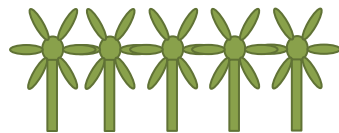
Certainty in temperature response of plants and microbes



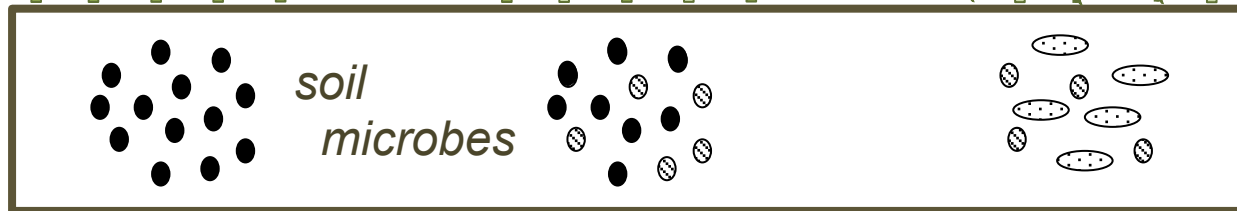
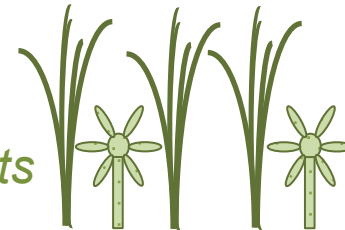
Physiological adjustment

Population turnover

Community turnover



plants



Certainty in temperature response of soil carbon stock

