1 **Evidence for large microbial-mediated losses of soil carbon under anthropogenic**

2 **warming**

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29   **Anthropogenic warming is expected to accelerate global soil organic carbon (SOC)**

30   **losses via microbial decomposition, yet there is still no consensus on the loss**

31   **magnitude. In this Perspective, we argue that despite the mechanistic uncertainty**

32   **underlying these losses, there is confidence that a strong, positive land carbon-**

33   **climate feedback can be expected. Two major lines of evidence support net global**

34   **SOC losses with warming via increases in soil microbial metabolic activity: the**

35   **increase in soil respiration with temperature and the accumulation of SOC in low**

36   **mean annual temperature (MAT) regions. Warming-induced SOC losses are likely**

37   **to be of a magnitude relevant for emission negotiations, and necessitate more**

38   **aggressive emission reduction targets to limit climate change to 1.5ºC by 2100. We**

39   **suggest microbial community−temperature interactions, and how they are**

40   **influenced by substrate availability, are promising research areas to improve the**

41   **accuracy and precision of the magnitude estimates of projected SOC losses.**

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44   The top two meters of soils store over 2,200 – 2,500 Pg of organic carbon (C)[1,2],

45   representing the largest biologically-active C pool in terrestrial ecosystems[3]. The size of

46   this C reservoir is annually balanced because large C losses to the atmosphere through

47   soil respiration (defined as the combined flux of autotrophic and heterotrophic

48   respiratory CO_2 from the soil to the atmosphere) are offset by C gains to the soil from

49   plant photosynthesis[4] (**Fig. 1**). Ongoing climate change, however, is perturbing this

50   balance and, given the size of the soil organic carbon (SOC) pool, even relatively small

51   SOC losses could represent a substantial contribution to the build-up of atmospheric

52   CO_2 (Ref[5]).

53   Anthropogenic climate change is expected to accelerate SOC losses via the

54   microbial decomposition of soil organic matter, representing a positive land C-climate

55   feedback[6]. This feedback has received considerable research attention in the past

56   decades, and is represented in the coupled climate−C cycle models of the

57   Intergovernmental Panel on Climate Change (IPCC)[7]. Yet, given considerable

58   uncertainties about the dynamics of organic matter processing in a warming climate,

59   there appears to be no consensus on the magnitude of this feedback over the rest of this

60   century (whether it will equate to small or large net soil C losses to the atmosphere)[8,9].

61   The lack of agreement about the magnitude of net SOC losses represents a major source

62   of uncertainty in projecting climate warming[5]. Further, it means the potential for SOC

63   losses under warming are not factored into climate policy negotiations, which raises

64   questions about whether agreed emission reductions are likely to translate to climate

65   targets.

66   This scientific uncertainty is deeply influenced by two fundamental discussions

67   about the temperature sensitivity of soil C fluxes into (plant C inputs) and from (soil

68   respiration) the soil[10]. The first discussion about C inputs is based on a large body of

69   literature that suggests that the land C sink is increasing because of greater plant

70   productivity in response to human-induced warming[11,12]. This effect is thought to be

71   particularly strong in cold regions, where warmer temperatures increase nitrogen (N)

72   availability via enhanced soil organic matter decomposition, alleviating N limitation for

73   plant growth[12,13]. However, soil respiration is more affected by elevated temperatures

74   than photosynthetic rates[4,14], and new evidence suggests that the land C sink via

75   enhanced plant growth might be slowing down[15]. In fact, a global time-series analysis of

76   soil heterotrophic respiration and net primary production indicates that Earth greening

77   cannot compensate for warming-induced increases in soil respiration[16]. Furthermore,

78   most of the uncertainty around the magnitude of SOC losses with warming is rooted in

79   uncertainty about microbial decomposition mechanisms, as opposed to debates about

80   soil N availability and associated plant growth, particularly when considering SOC

81   losses from cold regions[8,17].

82   In the second discussion, results from long-term warming experiments have

83   shown diverse, sometimes contradictory, responses of soil respiration to rising

84   temperatures. Some experiments indicate overall SOC losses with warming[18–21],

85   whereas others have found that soil respiration returns to pre-warming levels after a few

86   years of elevated temperatures[22,23]. The latter dynamic has been taken to suggest a

87   potential attenuation of the land carbon-climate feedback, which could be driven by the

88   depletion of labile C sources and/or changes in the temperature dependence for

89   microbial process rates (through physiological adjustments, evolutionary adaptation

90   and/or species turnover, see Box 1 for an explanation of the concepts used here to

91   describe the microbial−temperature relationship)[9,24–28]. Debate about the relative role of

92   N availability, plant growth, substrate depletion and changes in microbial temperature

93   dependence in shaping warming effects on SOC stocks generates mechanistic

94   uncertainty about the projected magnitude of SOC losses with warming. This

95   mechanistic uncertainty can also undermine the perceived scientific basis and resulting

96   confidence in the positive direction (SOC loss) and substantive magnitude of the land

97   C-climate feedback.

98   In this Perspective, we evaluate how changes in microbial communities, their

99   physiology and their substrate use will affect land C cycle feedbacks to climate change

100   (Fig. 1). We highlight that there is credible scientific confidence supporting the

101   likelihood of a strong, positive land C-climate feedback through microbially-mediated

102   decomposition of the particulate SOC that has accumulated in colder regions[29,30]. Based

103   on evidence from global-scale observational and empirical studies on soil respiration,

104   and a global analysis of SOC density as a function of MAT, we assert that there should

105   be high confidence in the expectation that there will be large net losses of SOC to the

106   atmosphere. The necessary research and discussion about the magnitude of SOC losses

107   under warming should not distract us from the strong consensus that overall soil

108   respiratory losses will increase markedly in a warming world. Finally, we emphasize

109   microbial−temperature relationships and microbial−substrate availability interactions as

110   two research areas that must be addressed to improve the accuracy and precision of the

111   magnitude estimates of SOC losses with warming (Fig. 1).

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113 **[H1] Positive land C-climate feedback**

114   Two lines of evidence support a self-reinforcing soil C feedback to the climate system.

115   First, soil respiration increases with temperature across global gradients. Furthermore,

116   field experiments show that warming can modify microbial physiology and resource

117   availability, but these effects do not alter the temperature sensitivity of soil respiration

118   across systems[31,32]. Instead, the temperature sensitivity remains at least equivalent to

119   that observed in control plots even after a few years of simulated warming[5,31,32]. Second,

120   SOC accumulates at high latitudes, and is inversely correlated with mean annual

121   temperature (MAT) at a global scale[33].

122   **[H2] Soil respiration increases with temperature.** Since the seminal review by Raich

123   & Schlesinger in 1992[34], which suggested that soil respiration will increase with rising

124   temperatures in a positive feedback loop, the number of field studies measuring soil

125   respiration rates has increased dramatically. Currently, at least 10,366 global

126   observations from studies published between 1961 and 2017 have been gathered in the

127   largest soil respiration database (SRDB) available to date[35]. MAT consistently emerges

128   as the dominant control over soil respiration in this database[5]. Most importantly, when

129   looking at the temperature sensitivity of soil respiration, Q_{10} remained high (between

130   2.6 and 3.3) across the temperature range considered[36]. These findings meant that a

131   simulated global temperature increase of 2°C translated to a 10 Pg C increase in SOC

132   loss to the atmosphere[5,36], representing a 17% increase in global annual soil respiration

133   based on estimations from the IPCC[7]. Together with many studies published since[37,38],

134   the patterns from the SRDB database suggest there is strong empirical evidence that

135   higher temperatures generally increase SOC losses via microbial respiration.

136   The patterns from the SRDB database are, however, spatial and there are

137   limitations to using spatial observations to make temporal inferences[5,36]. Yet, two

138   quantitative literature reviews that compared field warming scenarios (imposed by

139   open-top chambers, infrared heaters and soil cables) with control plots at ambient

140   temperature also support the idea that warmer temperatures will not significantly

141   dampen the temperature sensitivity of soil respiration. In the first review[31], 2°C

142   warming increased soil respiration by 12% across 50 globally distributed experiments

143   within a MAT range of −18.1 to 19.6ºC.

144   In the second review[32], the effects of warming on the temperature sensitivity of

145   soil respiration were evaluated across nine global biomes, and whether warming-

146   induced increases in soil respiration are dampened by microbial temperature

147   dependence were assessed. There were no significant differences in the temperature

148   sensitivity of soil respiration for eight of the nine biomes, with all biomes except deserts

149   showing consistent increases in respiratory losses under warmer conditions relative to

150   the controls[32]. Importantly, in the eight biomes the shape of the relationship between

151   temperature sensitivity of soil respiration and soil temperature changed across the

152   temperature range evaluated (0−40ºC), following a unimodal response. Specifically, the

153   temperature sensitivity increased with temperature up to ~25ºC, and then started to

154   decrease. This pattern suggests that in regions where soil temperature is usually below

155   25ºC (such as in colder regions at higher latitudes), the sensitivity of soil respiration to

156   warming will be higher than in warmer regions at lower latitudes where soil temperature

157   is more frequently above 25ºC. In contrast, the temperature sensitivity of soil respiration

158   in deserts was significantly lower in warmed than in control plots after the 25ºC

159   threshold was surpassed. Overall, observational studies across global MAT gradients

160   and meta-analyses of field warming experiments consistently support the expectation

161   that warming increases soil respiration, with the strongest and most consistent effects in

162   colder climates.

163   The major limitation of these data for understanding the magnitude of the land

164   C-climate feedback is that soil respiration might be a poor surrogate for resolving how

165   soil C stocks are responding to warming[5]. Instead, warming-induced changes in soil

166 respiration could simply be a product of altered C input rates to the soil and/or labile C

167 pool sizes[5], thereby only reflecting altered turnover of very recent soil C^{14} without any

168 changes in total SOC stocks. Yet even in experiments where soil respiration attenuates

169 in response to longer-term warming, microbial activity remains strongly temperature

170 sensitive[19,21,32,39]. As such, under experimental warming soil biota have a continued

171 capacity to mineralize SOC at greater rates under higher temperatures and hence release

172 CO_2 from the soil C pool. Determining how temperature affects the balance between C

173 inputs and outputs to and from SOC stocks is key to dramatically increasing the

174 accuracy and precision of future projections of the land C-climate feedback. To do that,

175 data on the response of soil C stocks to warming is necessary.

176

177 **[H2] Soil C accumulates in regions with low mean annual temperature.** Given the

178 challenges of using soil respiration data to infer how SOC stocks respond to warming,

179 confidence in a positive land C-climate feedback relies on a second line of evidence. In

180 the absence of extensive temporal data for soil C change, spatial patterns of SOC

181 storage across the globe provide this additional (albeit correlative) evidence.

182 Specifically, the balance of C between respiratory losses and photosynthetic gains to an

183 ecosystem largely determines the total SOC storage over the long term in any given

184 region. By regulating the physiology of organisms, temperature consistently emerges as

185 one of the strongest predictors of this balance[4]. As such, SOC accumulates in cold

186 regions such as the Arctic and Subarctic[33,40], where C inputs exceed outputs because

187 soil respiration is more temperature sensitive, and hence more constrained, than

188 photosynthesis[4,14,41]. This mechanism suggests a clear latitudinal pattern of SOC storage

189 across the globe, as represented in Crowther et al. (2019)[33].

190   SOC stock spatial patterns suggest a strong temperature signal (visualized here

191   with SOC density as a function of MAT; Fig. 2). Importantly, the latitudinal pattern of

192   SOC storage matches MAT, with lower storage in warmer regions. Although cold

193   regions have relatively slow C input rates to the soil, the rate of respiratory C release

194   through soil respiration is even lower[33]. Therefore, the long residence time of C in low

195   MAT soils at high latitudes led to the accumulation of huge soil C stocks over

196   thousands of years[42,43] (an estimated 1,113 tonnes SOC ha^{-1} in boreal forests and

197   tundra; Fig. 2). In contrast, both photosynthetic activity of plants and respiratory activity

198   of soil organisms are high in warm and moist regions[44], which has led to relatively

199   small SOC stocks in the tropics (281 tonnes SOC ha^{-1} in tropical forests; Fig. 2). These

200   patterns emerge despite the fact SOC also accumulates in anaerobic waterlogged

201   ecosystems such as tropical peatlands and wetlands, and in pools of mineral-associated

202   SOC in better-drained soils[33].

203   The difference in C inputs versus outputs therefore drives a clear MAT trend in

204   soil C, with massive SOC stocks in high latitude and altitude cold regions[33,40] (Fig. 2).

205   Of course, MAT does not directly determine organismal physiology, but it is indicative

206   of the extremes in temperature and variation between those extremes that drive

207   microbial activity. It could ultimately be the duration of the thawed period that is the

208   most meaningful climate variable in governing the specific activity levels of

209   decomposer organisms in higher latitude regions. Yet, the strong correlation between

210   MAT and other climate variables (minimum temperature, maximum temperature and

211   temperature seasonality) at a global scale means that the associations between

212   temperature and SOC stocks are apparent across a range of climate variables (Fig. 2).

213　　　　These patterns (Fig. 2) are supportive but not conclusive evidence of the

214　　sensitivity of SOC stock responses to warming because spatial patterns are not

215　　necessarily predictive of temporal responses. We also acknowledge the evidence is

216　　observational, and hence it is possible that other mechanisms might be driving the

217　　pattern. Further, recent ^{14}C-dating evidence suggests that global soil C stocks are on

218　　average $4,830 \pm 1,730$ years old (with permafrost SOC ranging from 2,800 at 0−30 cm

219　　to 15,000 yr mean age at 30−100 cm)[43], which is much older than the decadal to

220　　centennial age typically assumed through the turnover rates used in soil biogeochemical

221　　models[45]. If SOC turnover rates are slower than estimated from soil models, the

222　　magnitude of a positive land carbon-climate feedback might be lower than anticipated

223　　from spatial patterns. Yet that temperature consistently emerges as the strongest

224　　predictor of SOC stocks fits with the mechanistic understanding of the physiological

225　　responses of organisms to warming. Overall, it seems probable that colder temperatures

226　　are likely to be a primary driver of the large SOC stocks found in high-latitude and

227　　altitude regions, although other abiotic factors such as soil drainage[42] or lateral C export

228　　during thawing[46] could also play an important role. Nevertheless, if colder conditions

229　　drive the accumulation of C in soil, it seems highly plausible that warming those regions

230　　is likely to reverse this effect.

231　　　　Indeed, there is evidence that the rate of SOC release might be high when cold-

232　　region soils warm. First, extensive research highlights that the temperature sensitivity of

233　　SOC stocks is three-times higher in cold than in warm regions[32,47–49]. Annual cycles of

234　　freeze and thaw, and the vertical development of active layer soils could explain some

235　　of this high temperature sensitivity, and sub-annually frozen soils could represent an

236　　extreme example in terms of the effects of temperature on C storage[47]. However,

237 reductions in soil C storage with warming are observed both above and below 0°C,

238 including in regions in which soils rarely freeze (Fig. 2). Second, a global network of

239 field warming experiments − with direct measures of SOC − suggested that about 30 Pg

240 of topsoil C could be released to the atmosphere for one degree of warming by 2050,

241 based on 2016 estimates[6]. Such warming-induced SOC losses represent 12-17% of the

242 amount of CO_2 emitted from human-related activities over this time, highlighting the

243 importance of cold conditions for trapping C in the soil when addressing biosphere-

244 atmosphere feedbacks. Third, a recent model comparison suggests that, regardless of

245 how SOC responses to warming are represented mechanistically, the response of cold

246 regions predominantly determines the magnitude of net, global C change under various

247 warming scenarios[8].

248   Spatial observations, experimental field warming studies, and many modelling

249 studies converge to suggest that regions with the largest SOC stocks, for instance those

250 with low MAT (Fig. 2), are likely to drive large net global losses of soil C under

251 warming. These findings are primarily based on the hypothesis that temperature

252 limitations on SOC decomposition are being alleviated with climate warming. This

253 alleviation will result in larger soil respiratory losses that cannot be compensated by

254 warming-induced increases in net primary production[16], and hence will translate to net

255 losses of SOC stocks[14,47]. Such outcomes could be especially dramatic in the Arctic and

256 Subarctic, because these regions are warming at about two times the global rate[50].

257   A growing body of evidence suggests that the huge SOC stocks in cold regions

258 support a larger abundance of soil organisms. Specifically, the size of the SOC stock is

259 a prominent predictor of soil microbial[51,52] and animal[53] abundances. The highest

260 abundances of these soil biota are therefore found in high-latitude, organic-rich soils.

261   Yet, the metabolic activity of soil biota (including fungi, bacteria, archaea, and

262   invertebrate animals) is low under cold conditions[54], which explains why C

263   accumulation in cold (high latitude) areas is likely to have occurred in the first place.

264   However, as these regions warm with ongoing climate change, the metabolic activity of

265   these organisms should increase[24], enhancing their potential to mineralize soil C. Given

266   the immense abundances of these organisms in cold regions relative to warmer

267   regions[51,53], even slight increases in their metabolic activity could markedly accelerate C

268   losses, highlighting the need to consider decomposer abundance as a factor influencing

269   future SOC stocks[52,55].

270

[H1] Magnitude of the feedback

272   Previous work has discussed the empirical (longer-term field studies, measurements of

273   soil C stocks at deeper soil layers, more studies in tropical and dryland ecosystems,

274   incorporating emerging views on mineral-associated SOC) and modelling (representing

275   structural uncertainties and microbial-explicit processes) efforts required to robustly

276   assess the effects of warming on SOC stocks[6,9,56]. Further, given the centrality of soil

277   microbes and their collective metabolic activities to soil respiration and hence

278   decomposition rates of soil C compounds, a number of previous studies have recently

279   reviewed the consequences of microbial responses to warming for SOC turnover and

280   storage[57–59]. In this section, we focus on the need for an improved understanding of

281   microbial−temperature relationships and microbial−substrate availability−temperature

282   interactions. The nature of these relationships has high potential to dictate the

283 magnitude of net SOC losses under warming, and hence are important to constrain in

284 order to make accurate and precise estimates of the magnitude of estimated SOC losses.

285

286 **[H2] Alternative metrics for microbial−temperature relationships.** There is

287 compelling evidence suggesting that there will be marked changes in microbial

288 activity−temperature relationships in response to warmer temperatures.

289 For instance, warming-induced changes in microbial metabolism can decrease, not

290 affect, or increase temperature sensitivies of soil heterotrophic respiration[24,26,60–62];

291 these phenomena that cannot be represented with the Arrhenius response depicted in the

292 Q_{10} coefficient (Box 1). However, the coupled climate−C models of the IPCC represent

293 a monotonic increase in soil microbial respiration with warmer temperatures based on

294 Q_{10} coefficients[56,63]. To improve the representation of microbial processes in soil

295 biogeochemical models, the complex interaction between climate and the structure,

296 function and physiology of soil microbial communities must be captured[9,28].

297 Microbial physiology-temperature relationships reveal potentially contrasting

298 responses to warming for different microbial parameters such as respiration versus

299 growth[28,64]. These contrasting responses mean that net SOC losses might occur under

300 warming because of respiration, even if microbial biomass production increases and

301 provides a source of microbial necromass and secondary compounds for greater

302 formation of persistent soil C pools[65]. Such possibilities depend on the response of the

303 carbon-use efficiency (CUE, Box 1) of soil microbial communities to warming.

304 CUE is an emergent physiological variable of multiple anabolic and catabolic

305 processes[66], making its interpretation complicated. The influence of these contrasting

306 properties could explain why soil incubations in the laboratory suggest that microbial

13

307   CUE is unresponsive[67], reduced[68] or increased[69] by greater temperatures. Further, given

308   the methodological challenges in measuring CUE *in situ*, field assessments of how

309   microbial CUE responds to experimental warming are rare. The single study to date has

310   investigated how field-experimental warming changes microbial CUE, based on

311   estimates of substrate-use efficiency. It was found that although CUE declined with

312   increased temperatures in the laboratory, long-term field warming had a minor if any

313   impact on the temperature response of CUE[70]. These results were consistent with CUE

314   responses to natural geothermal warming of soil[67]. More field warming experiments

315   measuring microbial CUE across a wide range of environmental conditions are required

316   to improve our understanding of the CUE−temperature relationship, and its

317   consequences for the magnitude of projected SOC losses as the direct effect of

318   warming.

319   Given the shortcomings of the Q_{10} coefficient for understanding microbial

320   metabolic responses to sustained warming, and the paucity of field data for CUE

321   responses, there is a need to explore additional metrics. For instance, the

322   Macromolecular Rate Theory (Box 1) allows the calculation of temperature response

323   traits such as the maximum activity or the maximum temperature sensitivity of soil

324   heterotrophic respiration[71]. In particular, the minimum temperature index (T_{min}; Fig. 3a)

325   of the Square Root Model[72] appears to be ecologically-meaningful for understanding

326   soil C responses to warming (Box 1). T_{min} is the theoretical minimal temperature for

327   growth or activity, but also one of the key variables that define microbial−temperature

328   relationships[73], along with the optimal temperature and maximal temperature. The T_{min}

329   index is estimated to be 0.3°C higher per 1°C increase in soil temperature[72,74] as soil

330   microbial growth and CUE are expected to adapt to the selection pressure under climate

331   warning[75], resulting in a more warm-adapted microbial community.

332   Empirical support for warm-adapted communities comes from studies of

333   bacterial growth, which has been shown to adapt to field experimental warming[76] and

334   across gradients of MAT[74]. A shift in T_{min} of soil bacterial growth across a wide

335   gradient of increasing temperatures (Fig. 3a) also results in higher Q_{10} (Fig. 3b),

336   indicating higher temperature sensitivity of soil heterotrophic respiration in warm- than

337   in cold-adapted microbial communities (low T_{min} curves). The Macromolecular Rate

338   Theory and the Square Root Model have yet to be extended to global scales. To do so,

339   field and laboratory studies performed across different biomes and ecosystems that

340   measure microbial physiology at multiple temperatures within a range that is

341   biologically relevant are needed. Regardless, both are promising frameworks to move

342   beyond the use of a constant Q_{10} coefficient across the entire temperature range (Box 1).

343   Indeed, these new models allow the calculation of alternative metrics that better

344   represent the temperature sensitivity of a suite of microbial traits, which is fundamental

345   for determining the absolute magnitude of net SOC losses under warming.

346

347   **[H2] Addressing microbial−temperature relationships in soil C models**. The soil

348   sub-models typically used in the projections of Earth System Models include several

349   assumptions about how microbes influence SOC dynamics. For instance, conventional

350   SOC models such as Century[45] (Daycent) and RothC[77] assume that SOC losses to the

351   atmosphere through microbial respiration are a product of microbial activity, but that

352   microbial communities do not regulate soil C dynamics independently of other factors,

353   such as temperature. Specifically, soil microbial responses to temperature are

354 represented in these models as a first-order process (Fig. 3c), whereby the respired CO_2

355 is proportional to the SOC stock. The implicit representation of microbial processes in

356 SOC models can lead to marked differences between field observations and model

357 predictions of respiration rates[9,78], generating low confidence in model abilities to

358 project the magnitude of the land C-climate feedback[56].

359   Emerging empirical evidence suggests that a suite of microbial responses to

360 thermal regimes occur that deviate from the first-order representation in models[9,21,24,70].

361 Notably, the compensatory thermal response of soil heterotrophic respiration (Box 1)

362 emerges across major biomes when other driving factors, such as substrate depletion

363 and changes in microbial biomass, are controlled for[61,62]. Physiological traits such as

364 CUE and enzyme kinetics likely underlie these compensatory thermal patterns (Box 1).

365 To explicitly represent these traits in SOC models, innovative modelling efforts assume

366 particular microbial physiology−temperature relationships[25,28,79]. For instance, CUE is

367 typically represented as decreasing as climate becomes warmer in microbial-explicit

368 models [25,80]. However, recent large-scale field observations across contrasting

369 temperature regimes suggest that the opposite relationship could occur[69,81] (although it

370 is worth noting that CUE was inferred and not directly measured in these studies). The

371 lack of consensus about how microbial processes will respond to warming highlights

372 the need to represent multiple competing assumptions of microbial metabolic response

373 in models. These representations then need to be tested against field observations

374 gathered over a wide range of environmental conditions in order to refine the

375 representation of microbial processes.

376   This approach has been attempted in two studies exploring how effectively

377 different microbial−temperature representations recreate large-spatial scale empirical

378   observations, using model–data integration and database cross-validation. In the first

379   study[82], positive and negative relationships between CUE and MAT were simulated in

380   both first-order (Fig. 3c) and microbial-explicit (Fig. 3d) SOC models. The model

381   predictions were then compared with the microbial respiration rates (per unit microbial

382   biomass) observed in independent, controlled laboratory incubations of 110 soils from

383   global drylands[62] and 22 soils from boreal to tropical biomes[61]. The microbial-explicit

384   models assuming a positive CUE−MAT relationship best predicted the observations,

385   suggesting that the compensatory thermal response of soil microbial respiration[61,62] was

386   associated with higher CUE under warmer climates.

387   In the second study[83], observations from two independent field datasets from

388   global croplands[52,81] were most consistent with positive, empirical relationships

389   between CUE and MAT. When represented in a microbial-explicit SOC model, this

390   positive relationship best predicted the compensatory response of soil metabolic

391   quotient (decreased respiration rate per unit of biomass with MAT) that was empirically

392   observed. However, the SOC models[82,83] were run at a very fine temporal resolution (10

393   h), matching the short-term laboratory incubations conducted to measure soil microbial

394   respiration at different temperatures in the two empirical studies[61,62]. Only respiration

395   outcomes were queried because SOC stock changes are not detectable at such short time

396   scales. It therefore remains unclear how the observed respiratory responses to warmer

397   temperatures translate to changes in SOC stocks.

398   Here, we incorporated positive and negative relationships between physiological

399   attributes of soil microbial communities, such as CUE, and MAT into these SOC

400   models to demonstrate the potential for such microbial information to make testable

401   predictions about SOC stock responses to warming (Fig. 3c-h). The implications of

402   these assumptions in both first-order and microbial-explicit SOC models were then

403   tested on long-term (30 years) soil microbial respiration and SOC stocks (Fig. 3e-f;

404   more details on the SOC modelling in the Supplementary Materials). The sign of the

405   hypothesized CUE−MAT relationship generated opposite responses of mass-specific

406   soil respiration and SOC stocks to variation in MAT (Fig. 3e-f). Unfortunately, such

407   simulated results cannot be validated with 30-year soil incubations, as these studies

408   have not been conducted. However, it has been demonstrated[82] that a positive

409   CUE−MAT relationship is more likely to represent the microbial temperature sensitivity

410   patterns observed across space for soils from different biomes[61,62].

411   Invoking this positive relationship, both the first-order and microbial-explicit

412   model representations reproduced the expected decrease in respiration rates per unit

413   microbial biomass expected under compensatory thermal responses (Fig. 3e). In

414   contrast, the negative CUE−MAT relationship led to model predictions of increased

415   respiration rates per unit biomass, a pattern inconsistent with empirical observations

416   (Fig. 3f). Notably, the implications for SOC stocks were markedly different even when

417   the first-order and microbial-explicit models predicted qualitatively similar respiration

418   patterns. Specifically, in the first-order model with a positive CUE-MAT relationship,

419   SOC stocks slightly increased with MAT, whereas they decreased with increasing MAT

420   in the microbial-explicit model (Fig. 3g). As such, only the latitudinal pattern in SOC

421   stocks – (increasing stocks with decreasing MAT) was generated by the microbial-

422   explicit model when a positive temperature-CUE relationship was assumed (Fig. 3g).

423   Presumably, the mechanism explaining this pattern was because the microbial-explicit

424   model permitted the microbial pool to feedback to SOC decomposition[25] as in Fig. 3d.

425   Therefore, higher CUE led to higher microbial biomass and SOC consumption, and

426 thereby lower SOC stocks with elevated MAT. The advantage then of microbial-explicit

427 model structures is that they provide an effective way to test how microbial metabolic

428 shifts under warming might influence soil C dynamics.

429   A negative CUE−MAT relationship (for which there is limited field support[52,81–

430 83]) fails to recreate the observed MAT by soil C pattern generated by large SOC stocks

431 in cold regions (Fig. 2). Indeed, the microbial-explicit model indicated SOC gains with

432 increasing temperature (Fig. 3h). Notably, the first-order model did create the pattern of

433 lower SOC stocks with elevated MAT (Fig. 2 and 3h), but it failed to capture the

434 expected respiration pattern (Fig. 3g).

435   Given the lack of empirical data or consensus on decadal responses of SOC

436 stocks to warming, the evaluation of competing microbial−temperature relationships

437 against spatial field data appears to be an effective tool for building near-term

438 confidence in model projections of SOC stocks under a warmer climate. A positive

439 CUE-MAT relationship recreates both expected respiratory responses and the global

440 SOC-MAT patterning when represented in models that explicitly consider microbes as

441 controls (Figs. 2 and 3e,g). In short, the model-data integration most consistent with

442 large-spatial scale field observations suggests a positive land C-climate feedback.

443

444 **[H2] Microbial−substrate availability−temperature interactions.** When addressing

445 the relationship between soil microbial metabolism and temperature, it is important to

446 consider the interplay with other environmental factors. Long-term storage of C in

447 mineral soils is strongly controlled by physicochemical mechanisms that control the

448 accessibility of SOC to decomposers[84]. For example, occlusion in aggregates and the

449 formation of organo-mineral interactions are critical in preventing microbial

450   degradation of SOC. The resulting low accessibility to microbes of a substantial

451   proportion of the SOC pool could help explain why rates of decomposition decline with

452   warming even when only a small proportion of SOC has been released[19,23]. The

453   depletion of small pools of readily-decomposable and unprotected SOC can result in

454   subsequent declines in microbial biomass and activity[67,74,85], reducing SOC losses with

455   warming over time[67].

456   Incubated samples from a grassland warming experiment at common

457   temperatures provided evidence for the role of substrate depletion in reducing fluxes[85].

458   Lower respiration rates were observed in samples from warmed plots, and differences

459   between control and warmed cores increased over time. These observations suggest that

460   substrate loss, rather than changes in microbial thermal dependence, was the dominant

461   mechanism explaining the lower fluxes from warmed soils. Furthermore, when

462   physicochemical persistence mechanisms were disrupted by homogenizing the soil with

463   sieving, differences between warmed and control samples were largely eliminated —

464   the warming-induced reduction in unprotected SOC was swamped by the release of

465   aggregate-associated C following the disturbance of the soil structure.

466   Although the depletion of available soil organic matter should translate into

467   reduced SOC losses under prolonged warming, losses are often still observed after

468   several years of elevated temperatures[19,67,86,87]. Recent evidence suggests that this

469   discrepancy could be the result of shifts in the soil microbial community (Fig. 4), which

470   are associated with accelerated decomposition of SOC components that were less

471   biochemically available at lower temperatures. For example, the response of the enzyme

472   lignase—which is involved in the degradation of biochemically recalcitrant SOC—to

473   warming was positively correlated with changes in soil respiration[88]. In long-term

474 warming experiments, there was a higher stimulation of microbial genes related to the

475 degradation of labile SOC compounds in warmed plots[21]. However, an increase in

476 microbial genes related to the decomposition of recalcitrant SOC was found after four

477 years of warming in the same grassland experiment[87].

478   Warming studies that evaluate microbial functional information provide strong

479 evidence that as the relative availabilities of different SOC pools change under

480 warming, there is selection for microbes that specialize on more biochemically

481 recalcitrant C. This selection drives shifts in microbial community composition and

482 function (Fig. 4). As such, interactions between substrate supply, complexity and

483 warming appear to result in the development of microbial communities capable of

484 utilising a broader range of substrates[21,70,87]. Whether these shifts are related to

485 microbial communities responding to the loss of readily decomposable SOC, or to a

486 relaxation of the thermal constraints for the decomposition of complex C compounds, is

487 unknown.

488   The magnitude of SOC losses resulting from these microbial community shifts

489 will likely depend on additional mechanisms. For example, substrate complexity affects

490 microbial growth rates and physiological variables such as CUE[89], so the magnitude of

491 losses will likely depend on whether these responses enhance or mitigate increases in

492 microbial activity under warming. One field warming study suggests these responses

493 might enhance activity[85]. Specifically, when warming was periodically switched off,

494 carbon fluxes remained elevated in previously warmed plots for extended time periods

495 (days to weeks) during the cold season. These observations indicate that the changes in

496 microbial community function with warming had long-term impacts on activity that

497 could not be explained by the direct effects of temperature alone.

498   Shifts in soil microbial communities that expedite C mineralization rates might

499   be restricted to unprotected SOC pools, given mounting evidence that biochemical

500   recalcitrance is unlikely to explain the long-term persistence of mineral-associated

501   SOC[90]. However, SOC persistence might be influenced by interactions between

502   biochemical recalcitrance and mineral-association. Thus, warming effects are likely also

503   to extend to the large global pools of mineral-associated SOC[65]. Nevertheless, the extent

504   to which physicochemical persistence mechanisms are temperature sensitive, and the

505   amounts of SOC that could be released on timescales relevant to 21st century climate

506   change remain controversial. Indeed, these mechanisms and values could vary between

507   soil types depending on the affinity of the mineral surfaces for the organic matter[14].

508   For example, in many cold regions, much of the SOC seems to be in particulate

509   forms[29,30], which are not associated with mineral surfaces and might remain accessible

510   to microbes. Unlike mineral-associated SOC, increases in particulate forms of SOC do

511   not appear to asymptote as total SOC increases[91], presumably because they are not

512   dependent on a finite availability of mineral-surfaces to associate with. Therefore, it

513   seems likely that large SOC losses under warming in cold regions will likely result from

514   how shifts in microbial communities under warming affect their functional effects on

515   the decomposition rate of particulate SOC pools. At the same time, the extent to which

516   mineral protection is found across soils in colder regions is little understood. Overall,

517   microbial−substrate availability−temperature interactions demand immediate research

518   to better constrain how microbial community responses to temperature-induced changes

519   in SOC influence C loss from warmed soils (Box 2).

520

[H1] Broader implications

The sensitivity of SOC decomposition rates to warming remains a strong point of academic disagreement[6,92]. New evidence is constantly emerging that supports expectations ranging from minimal to large losses of SOC to the atmospheric CO_2 pool[43]. Yet scientists are typically trained to present more conservative estimates of change, even when higher estimates are equally, if not more, plausible. The academic uncertainty around the sensitivity of SOC decomposition rates to warming generates low confidence in the magnitude of the land C-climate feedback, meaning it is omitted from consideration during negotiations on emissions. However, there is an academic responsibility to weigh the evidence and not tend toward overly conservative projections as the default, because the reality is that academic debates around the magnitude of change—including for SOC—can have substantive societal consequences. Inclusion of the land C-climate feedback in climate negotiations would, if it is substantive, require aggressive emission reductions to meet climate change targets.

We believe that there is reasonable scientific confidence that SOC losses caused by microbial-mediated decomposition under warming are likely to be of a magnitude relevant for emission negotiations. Although long-term warming might partially dampen microbial activity via changes in substrate availability or physiology, there is no evidence as yet to suggest that these mechanisms would override or preclude net losses of SOC under warming. Instead, evidence that microbial communities might shift their substrate-use patterns to more rapidly decompose more biochemically-recalcitrant particulate forms of SOC suggests that long-term warming could actually amplify microbial activity (Fig. 4). Overall, the pattern of increasing soil C stocks in regions with lower MAT and the positive response of soil respiration to temperature both

545 plausibly support the notion that warming is likely to substantially reduce the global soil

546 C stock. That lower MAT regions are warming most rapidly, raises the possibility that

547 the most vulnerable, large SOC stocks will respond most in the near term to ongoing

548 climate warming.

549 We acknowledge that the role of variables such as soil moisture and plant

550 production, which can regulate the responses of the soil microbial community and thus

551 alter warming-induced changes in soil respiration and SOC[9,20,93,94], are not considered

552 here. The assessment of these and other factors will help to strengthen confidence in the

553 magnitude of the land C-climate feedback, and we suggest a roadmap for future

554 research and synthesis (Box 2). Still, latitudinal patterns in SOC stocks are simulated

555 through data-model integration and cross-validation of broad scale, field observational

556 and experimental patterns in microbial physiological processes such as CUE under

557 different thermal regimes. Thus, it is both academically and societally important to

558 examine shifts in microbial activities under warming, to help rapidly build a robust,

559 inferential basis on which to estimate the magnitude of C cycle-climate feedbacks with

560 reasonable confidence.

561 Even if the exact magnitude is unknown, the positive relationship between soil

562 respiration and temperature, and SOC accumulation in low MAT regions, together build

563 compelling evidence for an expectation of substantive net losses of SOC under

564 warming. Therefore, we suggest that there is enough confidence in a positive land C-

565 climate feedback to warrant its inclusion in the setting of greenhouse gas emission

566 allowances to meet stated climate targets.

567

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Author Contributions

P.G.P. and M.A.B. conceived the idea for the paper. TWC, J.R., JvDH and J.Y. conducted the analyses. The paper was drafted by P.G.P., T.W.C., M.D., I.P.H, S.R., R.R., J.R. and M.A.B., and all authors contributed to the final version.

Competing interests
The authors declare no competing interests.

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Related links

The SRDB database: https://github.com/bpbond/srdb

The SoilGrids database: https://soilgrids.org/

The CHELSA database: https://chelsa-climate.org/

843 **[b1] Box 1. Terms and concepts used to describe the microbial-temperature**

844 **relationship.**

845 **[bH1] Carbon-use efficiency**

846 The microbial carbon use efficiency (CUE) is an emergent physiological variable
847 describing the fraction of C that is retained by microbes relative to the total C
848 assimilated[66–68,95]. It is a critical variable to constrain in order to understand the
849 microbial feedback to climate warming, as it defines the first bifurcation of the flow of
850 C consumed by decomposer microorganisms, leading either to immediate C loss back to
851 the atmosphere as CO_2 or C storage as soil organic matter via microbial biomass
852 formation[64,65,70].

853 **[bH1] Temperature sensitivity (Q_{10})**

854 The Q_{10} is defined as the factor by which the rate increases with a 10°C rise in
855 temperature, that is, it describes changes in relative reaction rates[14,48]. Arrhenius first
856 proposed how biochemical reaction rates depend on temperature following equation (1),
857 where k is a biological rate, A is a constant, Ea is the activation energy for the studied
858 reaction, R is the universal gas constant and T is temperature[4]. Most soil C models
859 follow the Arrhenius model and assume a constant Q_{10} of soil respiration (Q_{10} = 2-3)[4,14].
860 However, it is now widely recognized that the Q_{10} is not constant with temperature, and
861 that it increases towards lower temperatures and grows complex when temperatures
862 approach the optimum for growth[49].

863   (1) $\ln(k) = \ln A - Ea/RT$

864 **[bH1] The macromolecular rate theory**

865 Biological reactions are typically mediated by macromolecules such as enzymes, which
866 have large heat capacities (C_p). Changes in the heat capacity leads to a marked
867 temperature dependence of the activation energy. Hence, the Arrhenius model
868 established for biochemical reactions might not match expectations from biological
869 reactions. The macromolecular rate theory develops the Arrhenius model in equation
870 (2), where $T0$ is the reference temperature, k_B is Boltzmann's constant, h is Planck's
871 constant, H is enthalpy, and S is entropy. This representation includes the temperature
872 dependence of Q_{10} (Ref[71]).

873   (2) $\ln(k) = \ln(k_B T / h) - [\Delta H_{T0} + \Delta C_p(T - T_0)] / RT + [\Delta S_{T0} + \Delta C_p(\ln T - \ln T_0)]/R$

874 **[bH1] The square-root model**

875 This model effectively captures the increasing Q_{10} towards lower temperatures, and the
876 derived parameters can yield easily interpretable information characterizing microbial
877 trait distributions with temperature. This model follows equation (3), where A is the
878 activity rate at temperature T, T_{min} is the lower temperature limit, b is a constant
879 describing the rate of decline when temperatures exceed T_{opt}, and T_{max} is the higher
880 temperature limit. The square-root model was originally developed in food
881 microbiology[73], and has been applied in different ecosystems[72,74–76].

882   (3) $\sqrt{k} = a\,(T\text{-}T_{min})\,(1\text{-}e^{b(T\text{-}Tmax)})$

[bH1] Changes in the temperature dependence: enhancing and compensatory thermal responses

The changes in the microbial temperature dependence through physiological adjustments, evolutionary adaptation and/or species turnover can be defined as the subsequent adjustment in the rate of respiration to compensate for an initial change in temperature. Both enhancing and compensatory thermal responses of soil microbial communities to warming have been found[24,62,66]. In enhancing responses, the Q_{10} of soil heterotrophic respiration will increase, whereas compensatory responses will dampen the Q_{10} and/or absolute rates.

[bH1] Substrate depletion

Labile soil C compounds can be disproportionally used by microbes under elevated temperatures, decreasing their relative abundance. The depletion of these substrates with warming can result in subsequent declines in microbial biomass and activity, reducing C losses via lower soil heterotrophic respiration over time, as found in long-term field studies[19,22,23].

910 **Box 2. Roadmap to build confidence in the magnitude of the land carbon-climate**
911 **feedback.**

912 Research needs (in italics) and suggested approaches are listed.

913 [bH1] **SOC in cold regions**

914 *[bH2] Quantify how much of the large SOC stock in cold regions is in particulate versus*
915 *mineral-associated forms.* Develop a comprehensive field-database for high latitude and altitude
916 sites using standardized protocols and consistent separation schemes of soil organic matter
917 fractions

918 *[bH2] Determine how the high abundance of soil decomposers influences SOC mineralization*
919 *rates with warming in cold regions.* Explore soil decomposer abundance in estimates of
920 warming effects on SOC stocks using microbial-explicit biogeochemical models and
921 observations across gradients in soil microbial biomass

922 [bH1] **SOC modelling**

923 *[bH2] Integrate complex microbial-temperature relationships into SOC models that go beyond*
924 *the use of a constant Q10 coefficient.* Test the Macromolecular Rate Theory and the Square-
925 Root Model across wide environmental conditions, with a particular focus in cold regions.

926 *[bH2] Explore through SOC modelling the sensitivity of model projections to the opposite*
927 *findings in the literature regarding microbial-temperature relationships.* Represent multiple
928 competing assumptions of microbial metabolic response to temperature in first-order and
929 microbial-explicit SOC models, and refine the largest structural and parameter sensitivities
930 among models

931 [bH1] **SOC stocks and warming**

932 *[bH2] Determine the extent to which soil microbial communities respond to changes in SOC*
933 *complexity with warming, and what the outcomes are for SOC stocks.* Develop microbial
934 functional information using -omics and other advanced technologies in concert with SOC
935 physicochemical characterizations, to develop robust structure-function relationships between
936 microbial communities and SOC turnover.

937 *[bH2] Quantify how factors such as moisture and plant inputs shape the responses of soil*
938 *microbial communities and SOC to warming.* Monitor these factors in observational studies
939 capturing wide environmental variation, and include them in multi-factor global change
940 experiments, to develop microbial functional and SOC fraction data for modelling.
941
942 [bH1] **Communication**

943 *[bH2] Ascertain what information on SOC responses under warming is most useful to and*
944 *needed by climate policy audiences.* Use co-production approaches to engage soil scientists and
945 ecologists with climate policy makers in a manner that efficiently and productively discerns the
946 information the policy makers need.

947 *[H2] Resolve how soil scientists and ecologists should present information on SOC responses*
948 *under warming to climate policy audiences, especially in terms of uncertainty and variance.*
949 Collaborate with social scientists working in areas such as communication, political philosophy,

950 epistemology and ethics to evaluate the most effective ways that soil scientists and ecologists
951 can present uncertainty to climate policy makers.

952

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955 **Figure captions**

956 **Figure 1. Microbial control of soil organic carbon losses to the atmosphere with**

957 **anthropogenic warming.** Soil heterotrophic respiration (Rh) increases with warming,

958 which accelerates the loss of carbon from the soil organic carbon (SOC) stock to the

959 atmosphere (depicted by the thick red arrow under a warming climate vs. thinner grey

960 arrow representing the current climate). The diagram focuses on Rh because the

961 evidence points to it being a major loss pathway of SOC under warming (the smaller red

962 circle within the grey circle) from soils in cold regions. Research in microbial

963 physiology and substrate use can improve the accuracy and precision of the magnitude

964 estimates of SOC losses with warming via Rh (red boxes). Other factors also vary with

965 temperature and can shape the responses of soil microbial communities and SOC to

966 warming, such as plant-C inputs to the soil (photosynthesis (Ps), leaf litter, root

967 exudates and root debris), autotrophic respiration (Ra) and associations of the soil

968 organic matter with soil minerals.

969

970 **Figure 2. SOC stocks are negatively correlated with temperature at the global**

971 **scale.** Soil organic carbon (SOC) stocks (tonnes C ha^{-1}) generally show a negative trend

972 with mean annual temperature (MAT). MAT is a general parameter reflecting broad

patterns of climate differences, but it is not likely to be the variable that directly relates

to organismal physiology, as it will be differences in temperature ranges, the minimum

or the maximum temperatures that ultimately limit activity levels. Using MAT in the

representation accounts for regional differences in the SOC stocks pattern that are

driven by colder conditions at higher altitudes. Indeed, several mountain ranges located

at mid-latitudes, such as the Rocky Mountains, Andes, Pyrenees, Caucasus or

Himalayas, have high SOC stocks[33]. Soil data from SoilGrids (ref.[40]) and climate

datafrom CHELSA[95]. The use of C stock per unit area (i.e. density) in this figure allows

a more comparable assessment of soil C storage in relation to thermal climate, because

the amount of land area differs by latitude[96]. Depth bars are stacked along the 0-200 cm

soil profile, and represent mean values of tonnes C ha^{-1} per 0.1°C bins across 100,000

random mapped points. Although the same data were used to develop each figure panel,

the binning groups different sets of observations together, which results, for example, in

lower maximal SOC stocks when the minimum temperature of the coldest month is

compared with MAT. Cumulative values to 2-m depth of >2000 tonnes C ha^{-1} are likely

an artefact of poor data on soil bulk density in organic-rich, high-latitude soils in global

soil mapping products.

Figure 3. Exploring the microbial−temperature relationship to improve estimates

of SOC losses. These relationships need to be explored in empirical studies and soil

organic carbon (SOC) models to improve the accuracy and precision of the magnitude

of losses with warming. a| Temperature relationship of square-root transformed bacterial

growth derived from a minimum temperature (T_{min}) in a cold and a warm climate.

Arrows indicate the competitive advantage of thermal adaptation at low vs. high

997 temperatures. b| Warm-adapted temperature relationships (high T_{min} curves) have higher

998 sensitivity of soil respiration (Q_{10}) than cold-adapted temperature relationships (low T_{min}

999 curves). c| First-order linear model with SOC, dissolved organic carbon (DOC), and

1000 microbial biomass carbon (MBC) pools. d| Four pool microbial-explicit model with

1001 enzymatic (ENZ) decomposition of SOC and subsequent assimilation (uptake) of DOC

1002 by microbes. Solid and dashed arrows represent C fluxes and controls, respectively. e|

1003 Long-term (30 years) simulated effects of mean annual temperature (MAT) on soil

1004 microbial respiration rates with first-order versus microbial-explicit models assuming

1005 positive microbial carbon use efficiency (CUE)−MAT relationship (modelling details in

1006 Supplementary Materials). f| MAT effects on respiration assuming negative CUE-MAT.

1007 g| MAT effects on SOC stocks assuming positive CUE-MAT. h| MAT effects on SOC

1008 stocks assuming negative CUE-MAT. Soil respiration was measured as mass-specific

1009 rates, to account for changes in microbial biomass. The relative changes (%) of both

1010 variables as compared to equilibrium values at 20°C (the black line) are provided to

1011 facilitate comparisons between models. The scenario in (e) and (g) with the microbial-

1012 explicit model is consistent with the global SOC-MAT relationship shown in Fig. 2 and

1013 with large-scale field experiments evaluating microbial physiological responses to

1014 spatial variation in MAT[32]. This scenario suggests that prolonged warming is likely to

1015 lead to net losses of the global SOC stock.

1016

1017 **Figure 4. Changes in the interactions between microbes and substrate availability**

1018 **under warming.** Changes in these interactions can determine the magnitude of net soil

1019 organic carbon (SOC) losses. A steep decline in SOC response to initial warming is

1020 commonly found via the reduction in the availability of readily-decomposable SOC for

1021 microbial growth and activity. However, instead of translating to stabilization of the

1022 SOC pool, C losses can continue under long-term warming as a consequence of

1023 multiple mechanisms which alter the capacity of microbial communities to decompose

1024 complex and persistent SOC components.

1025

1026 **TOC summary:**

1027 Degradation of soil organic carbon is expected to accelerate with increasing global
1028 temperatures, but the magnitude of change is controversial. This Perspective discusses
1029 evidence supporting a large loss of soil organic carbon and its broader significance.

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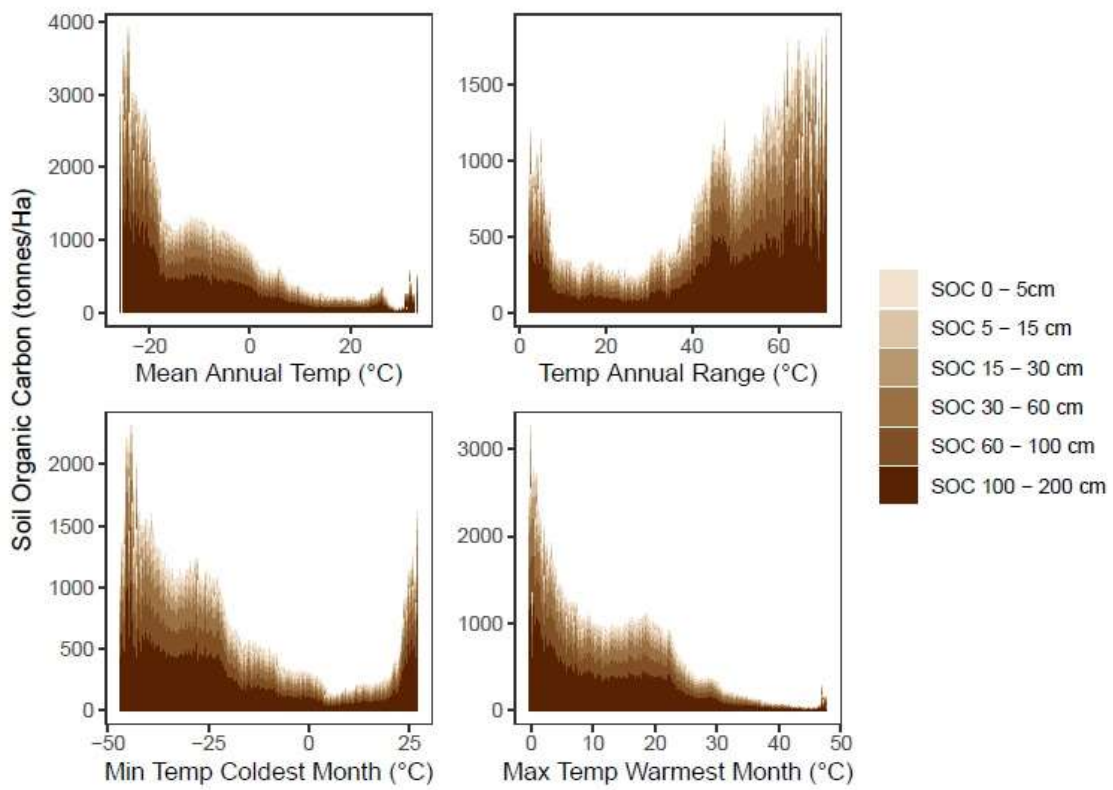
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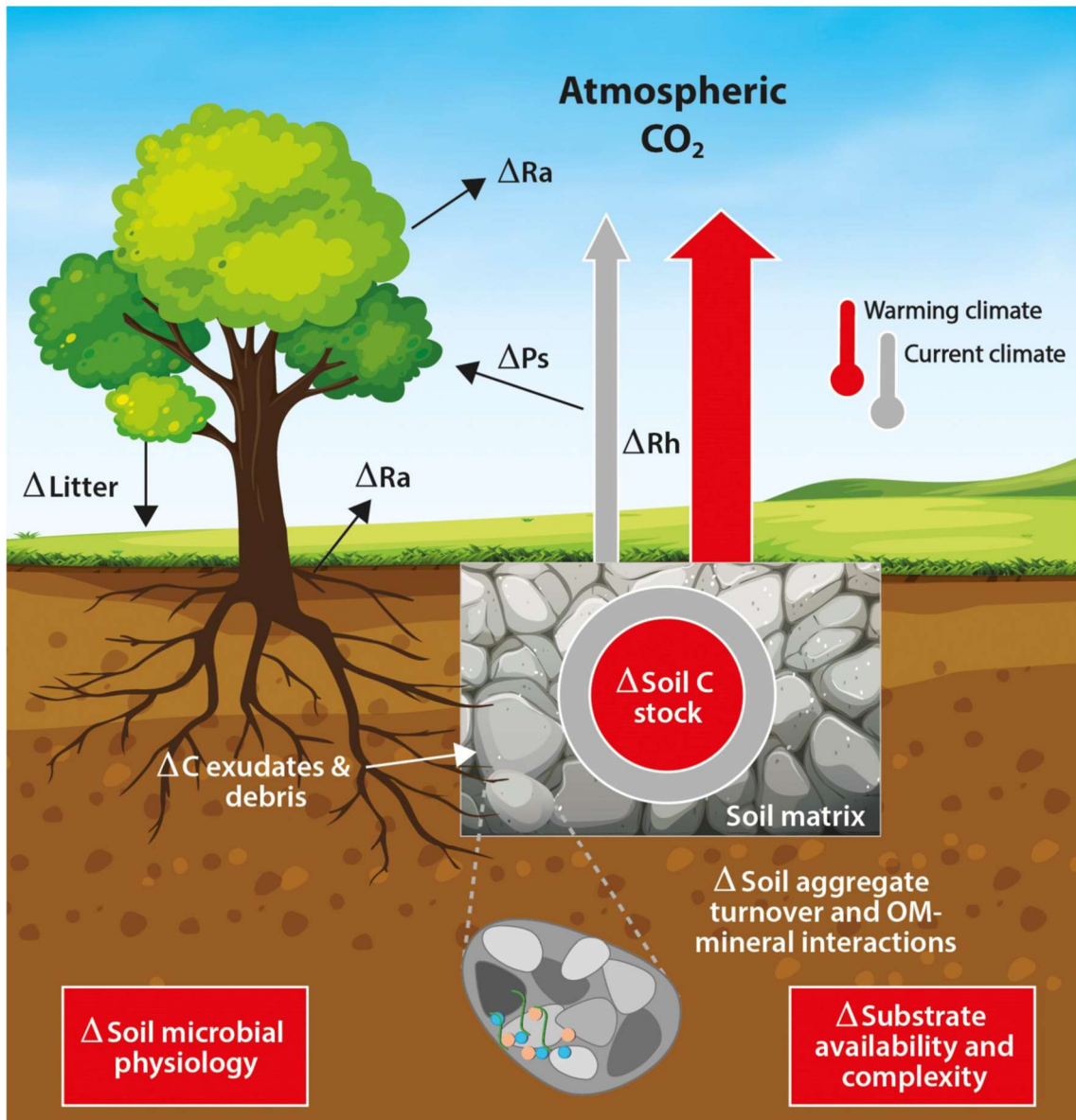
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1044 **Figure 1**

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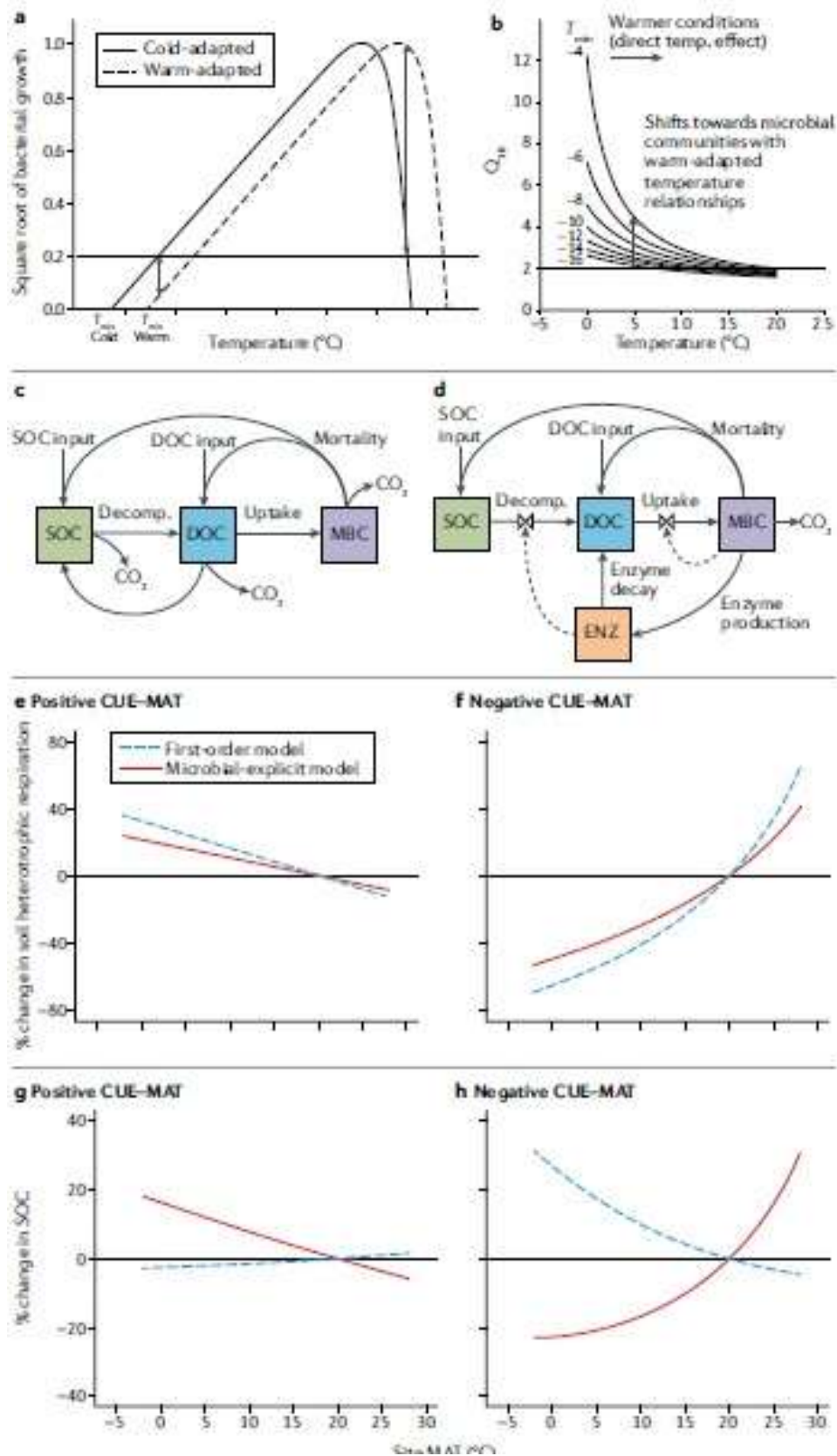
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Figure 2

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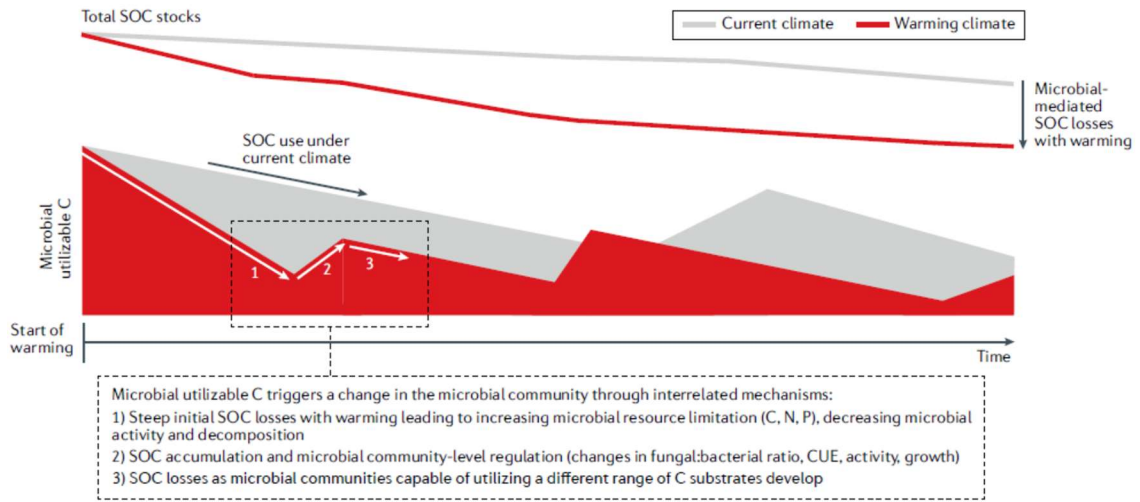1058

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Figure 3

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Figure 4

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