## Trophic interactions decouple soil carbon temperature response from that of microbial decomposers

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#### Abstract

Soil organic carbon (SOC) stocks represent a large component of the global carbon cycle that is sensitive to warming. Modeling and empirical studies often assume that temperature responses of microbial physiological functions and extracellular enzymatic reactions are predictive of ecosystem-scale SOC decomposition responses to warming. However, temperature-dependent soil trophic interactions such as predation of microbial decomposers by other organisms have not yet been incorporated into quantitative SOC models. Here, we incorporated a microbial predator into a tri-trophic population ecology model and a global-scale predictive SOC model to determine how predation would affect soil community population dynamics and temperature sensitivity of SOC stocks. Predators increased SOC stocks and their dependence on substrate input rates. Top-down controls of predators on microbial biomass caused SOC warming responses to diverge from microbial temperature responses, with warming-induced SOC losses reduced or reversed when predators were more temperature-sensitive. Our results suggest that higher trophic levels can reduce the sensitivity of SOC to warming, and that differences in temperature sensitivity across trophic levels may be a key determinant of SOC warming responses.

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19	
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- 50

## 52 Introduction

53 Understanding how rapid global climate change may impact the structure and dynamics of food 54 webs and associated ecosystem-level processes and services is a pressing but challenging issue in 55 ecology. An important but often overlooked component of ecological dynamics lies beneath the ground in 56 the form of soil food webs. Soils represent the largest cycling terrestrial carbon (C) pool on earth [1]. 57 While soil organic carbon (SOC) stocks are thought to be vulnerable to warming [2], projected responses 58 of SOC stocks to climate change are highly uncertain [3,4] and measured responses of SOC to warming 59 have been inconclusive [5,6]. Recent work explicitly incorporating biological processes into SOC models 60 [7] highlights important mechanisms and related uncertainties in SOC cycling, including differences in 61 microbial carbon use efficiency (CUE) and its temperature sensitivity [8,9], rhizosphere priming effects 62 [10], microbial dormancy [11,12], and density-dependent microbial biomass turnover [13]. Microbial 63 processes are thus increasingly recognized as a major determinant of SOC stocks and are now being 64 incorporated into global-scale studies of climate change impacts on soil C stocks [3,10,14,15], facilitating 65 the incorporation of these processes into earth system model (ESM) projections of terrestrial C cycle 66 responses to global climate change. 67 SOC models using explicit microbial processes have also produced seemingly unrealistic results 68 like oscillations in SOC stocks and insensitivity to carbon input rates [16]. While model structures can 69 mitigate these issues [10,13,17], variations in assumptions and parameterizations can drive wide 70 differences in projected responses to ecosystem perturbations [6]. At the same time, measurements of 71 microbial physiological and phylogenetic traits can be used to directly constrain model parameters 72 [8,18,19]. Recent reviews have suggested that incorporating metagenomics information into microbial-73 explicit soil decomposition model parameterizations could improve model projections of SOC responses 74 to changing environmental conditions [20-22]. To date, however, microbial-explicit SOC models have 75 focused on the role of a single category of living organisms in the soil: microbial decomposers [7]. Such 76 models, along with laboratory and field measurements of microbial physiological traits, however, may not 77 completely reflect ecosystem dynamics if they ignore interactions with other components of the soil food web.

78 79

80 The role of trophic interactions

81 While microbial-explicit SOC models have yielded important insights about decomposition 82 processes, other important mechanisms, such as trophic interactions between microbes and other 83 organisms in the soil food web, have so far been excluded [23–27]. Food web structure can drive 84 ecosystem dynamics in both terrestrial and aquatic systems [28]. Moreover, trophic interactions are 85 temperature-dependent through physiological responses [29–31], changes in animal movement [32], and 86 other trait responses to temperature [33–35]. For example, predation pressure on eel sea grass beds varies 87 with temperature along latitudinal gradients [36], climate influences predator-prey ratios in bromeliad 88 communities [37] and warming increases the strength of plant-herbivore interactions [38]. Trophic 89 interactions can also alter SOC decomposition: the presence of microbe-eating isopods changes SOC 90 responses to global change [39], grazing on microbes by organisms at higher trophic levels impacts 91 microbial growth patterns [40], litter decomposition and C utilization vary with soil faunal community 92 complexity [41], and interactions between predatory spiders and fungivorous Collembola change with 93 warming to reduce litter decomposition [42]. Together, these results suggest important but largely 94 overlooked interactions between warming, trophic interactions and SOC responses. Food web structure

- and dynamics are susceptible to changes in temperature [43–45], but understanding of how food webs
- 96 mediate the effects of temperature on decomposition, and the integration of these principles into SOC

97 models, have so far been limited [23,46].

98 Integrating trophic interactions into SOC models is challenging due to the complexity of soil food 99 webs and the difficulty of obtaining measurements that can constrain model parameters [47]. However, 100 recent studies using microbial-explicit SOC models have demonstrated that biological interactions can be 101 integrated into tractable models and can drive important differences in projected outcomes compared to 102 models that treat biological processes implicitly [7,23,46]. To address these issues, and as a first step 103 toward integrating food web interactions into quantitative SOC models, we developed two models of soil 104 trophic interactions including SOC, microbial decomposers, and predators that feed on microbes. First, 105 we modified a population ecology predator-prey model to demonstrate conceptually how soil microbe 106 predators may determine SOC responses to temperature. Second, we modified a state-of-the-art, 107 quantitative SOC cycling model - the Carbon Organisms Rhizosphere and Protection in the Soil Environment (CORPSE) model [10] – to show how incorporating microbe predators into simulated soil 108 109 food webs impacts SOC projections under warming across gradients of climate and ecosystem 110 productivity at a global scale. Given the premise that loss of SOC in response to warming is accelerated 111 by microbial growth and SOC assimilation, we test the hypothesis that the presence of a higher trophic 112 level that consumes microbial decomposers weakens the connection between the temperature sensitivity 113 of microbial substrate consumption and the temperature sensitivity of SOC stocks. In addition, we 114 evaluate the importance of local adaptation and differences in temperature sensitivity across trophic-levels 115 in determining latitudinal patterns of these trophic interactions and their effects on SOC stocks.

## 116 Methods:

117

- 118 Trophic-chain food web models
- 119 The simplest approach to modeling SOC decomposition only considers carbon stock (*C*) naturally
- 120 decaying over time at a temperature-dependent first-order rate k (Fig 1A) while being replenished at a
- 121 constant rate *I* (Supplementary Information, eq S1). While global land surface models such as those used
- 122 in the Climate Model Intercomparison Project Phase 5 (CMIP5) comparison predominantly use multiple-
- 123 pool versions of this approach [48], studies [7] have suggested that model fidelity can be improved by
- 124 explicitly simulating microbial biomass as the driver of decomposition (Fig 1B). We model the microbial
- 125 effect on carbon as a classic type-II functional response, where the SOC decomposition rate depends on
- 126 microbial biomass and carbon stocks (*M* and *C*, respectively), as well as on two parameters controlling
- 127 the feeding process, the microbial attack rate ( $\alpha$ ) and handling time  $\eta$  [49,50]. Conversion of carbon into
- microbial biomass is determined by a conversion efficiency parameter ( $\varepsilon$ ), and microbes die naturally at a per-capita rate  $d_M$  (SI, eqs S2 and S3). Microbial attack rates are temperature-dependent, following an
- 130 Arrhenius function of the form:

$$\begin{vmatrix} 131 & \alpha(T) = V e^{-\frac{E_a}{k_b} \left(\frac{1}{T} - \frac{1}{T_0}\right)}, \tag{1}$$

132

where V is a pre-exponential rate constant (units of inverse time),  $k_b$  is the Boltzmann constant (8.62x10<sup>-5</sup> electron-volts per degree Kelvin, eV K<sup>-1</sup>), T is the temperature at which the process occurs (in K),  $T_0$  is a reference temperature (K), and  $E_a$  is the activation energy of the process (in eV), which is a measure of its temperature dependence [30,32,51].

137

138 To incorporate the effects of a microbial predator, we added a third trophic level, *P*, that preys on the

microbial biomass, *M*, also following a type II functional response with an attack rate following the same
 temperature response as that of microbial biomass (Eq. 1). This microbe-predator model (Fig 1C) makes

140 temperature response as that of microbial biomass (Eq. 1). This microbe-predator model ( 141 similar assumptions as the microbial model, and can thus be written as:

142  
143 
$$\frac{dC}{dt} = I - \frac{\alpha_1(T)CM}{1 + \alpha_1(T)\eta_1 C}$$
(2)

145 
$$\frac{dM}{dt} = \varepsilon_1 \frac{\alpha_1(T)CM}{1 + \alpha_1(T)\eta_1 C} - \frac{\alpha_2(T)MP}{1 + \alpha_2(T)\eta_2 M}$$
(3)

147 
$$\frac{dP}{dt} = \varepsilon_2 \frac{\alpha_2(T)MP}{1 + \alpha_2(T)\eta_2 M} - d_P P$$
(4)

148

144

146

For both microbe and microbe-predator models, steady-state solutions were found analytically. We
determined solutions across a range of substrate inputs and temperatures and further analyzed model
behavior using Wolfram Mathematica 11 (code available at <a href="https://github.com/JPGibert/Microbial\_munchers">https://github.com/JPGibert/Microbial\_munchers</a>).
Parameter values used in our analyses are shown in Table S1 and were chosen so that equilibrium

153 biomass in all non-warmed scenarios showed a regular biomass pyramid (C > M > P).

154 155

### 156 *Quantitative SOC models*

While the modeling approach described above illustrates the dynamical effects of an additional 157 trophic level on microbe populations and SOC concentrations (Fig 1A), it was not designed to 158 159 quantitatively reproduce observed SOC stocks or organismal biomass in soils, or to represent key 160 mechanisms in soil biogeochemical cycling such as stabilization of SOC through physico-chemical 161 interactions with minerals [52]. To incorporate the trophic interactions identified in the food web models into a quantitative SOC framework, we implemented a predator trophic level in the Carbon Organisms 162 163 Rhizosphere and Protection in the Soil Environment (CORPSE) model, which includes SOC and 164 microbial decomposer pools and has been previously applied and validated against measurements at both 165 ecosystem and global scales [3,10,53]. Here, we refer to the modified model as CORPSE-Pred. CORPSE-Pred differs from the food web model in key aspects. First, CORPSE-Pred divides substrate C into 166 167 multiple types representing simple, complex, and microbial-biomass-derived compounds. Second, 168 microbial and predator populations in CORPSE-Pred are constrained not to decline below a minimum 169 value, preventing their complete eradication. Third, decomposition and predation kinetics in CORPSE-170 Pred are calculated using the ratio of microbe to SOC carbon, or the ratio of predator to microbe carbon, 171 rather than the absolute stocks or concentrations of those factors (an equivalent formulation in the 172 predator-prey models would be to include ratio-dependent foraging rates or interference competition). 173 Under these assumptions, changes in carbon stocks, C, over time can be calculated as:

175 
$$\frac{dC_i}{dt} = I_i - V_i e^{-\frac{E_{a_i}}{k_b}(\frac{1}{T} - \frac{1}{T_0})} \times \theta^a (1 - \theta)^b k_\theta \times C_i \frac{M}{M + k_M C},$$
(5)

- 177 where  $C_i$  is substrate carbon of type *i* (representing chemical classes with different decomposition rates
- and microbial CUEs),  $I_i$  is input rate of each substrate type,  $\theta$  is volumetric soil water content as a fraction
- 179 of saturation, *a* and *b* control moisture sensitivity of decomposition,  $k_{\theta}$  is a normalization constant for
- 180 moisture sensitivity, M is microbial biomass, and  $k_M$  controls the relationship between microbial biomass

181 and decomposition rate. The temperature dependence of the interaction between C and the microbes was

182 modeled using Eq. 1 but with substrate-specific parameters, where  $V_i$  is the maximum microbial

183 decomposition rate of substrate type *i*, and *Ea<sub>i</sub>* is the activation energy for decomposition of each

substrate type. Inputs (*I*) include a fraction (60%) of microbial and predator death (excluding microbial
biomass loss from predation). The rate of change of the microbial biomass, *M*, can be modeled by:

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187 188

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$$\frac{dM}{dt} = \sum_{i} \left( \left[ V_{i} e^{-\frac{E_{a_{i}}}{k_{b}} \left(\frac{1}{T} - \frac{1}{T_{0}}\right)} \times \theta^{a} \left(1 - \theta\right)^{b} k_{\theta} \times C_{i} \frac{M}{M + k_{M} C} \right] \times \varepsilon_{i} \right) - \left( M - M_{min} \sum_{i} C_{i} \right) \cdot d_{M} - V_{P} e^{-\frac{E_{a_{P}}}{k_{b}} \left(\frac{1}{T} - \frac{1}{T_{0}}\right)} \cdot M \frac{P}{P + k_{P} M}, \tag{6}$$

189 where  $\varepsilon_i$  is microbial carbon use efficiency associated with each substrate type,  $B_{M,min}$  is the minimum 190 microbial biomass (expressed as a fraction of total substrate C),  $d_M$  is the background death rate for 191 microbial biomass,  $V_P$  is maximum predation rate,  $Ea_P$  is the activation energy parameter for predation, 192 and  $k_P$  is a parameter controlling the relationship between predation and predator biomass. Finally, the 193 rate of change of predator biomass can be modeled as:

$$\frac{dP}{dt} = \varepsilon_P \left[ V_P e^{-\frac{E_{a_P}}{k_b} (\frac{1}{T} - \frac{1}{T_0})} \times M \frac{P}{P + k_P M} \right] - (P - P_{min} M) \cdot d_P, \tag{7}$$

195 where  $\varepsilon_P$  is carbon use efficiency of predators,  $P_{min}$  is minimum predator biomass, and  $d_P$  is death rate of 196 predators. CORPSE-Pred also includes protected SOC stocks that are inaccessible to decomposition. We 197 do not show the equations for protected SOC here for brevity (see SI for full model equations including 198 those related to protected SOC).

199 We drove global SOC simulations using 10 years of monthly-average net primary production 200 (NPP), soil temperature, and soil moisture from previous global simulations using the Geophysical Fluid 201 Dynamics Laboratory (GFDL) global land model LM3 [54,55]. NPP was assumed to be equivalent to 202 total carbon inputs to soil (thereby assuming plant biomass was at approximate steady state). 203 Meteorological forcing for the LM3 simulations used a gridded historical climate dataset over years 1958-204 1967 [56], which were repeated to drive simulations of any length. We numerically integrated the 205 CORPSE-Pred model for 750 years to equilibrate all pools, then conducted control simulations and 206 warming simulations with temperatures increased by 2 °C.

207 We conducted CORPSE-Pred simulations using two alternative assumptions concerning local 208 temperature adaptation of predator physiology. With local adaptation,  $T_{\theta}$  for predators was set to the 209 control simulation mean annual temperature of each grid cell. With globally constant base temperature,  $T_{\theta}$ 210 for predators in each grid cell was equal to the mean global temperature (13 °C).

CORPSE-Pred simulations used parameter values from previous CORPSE simulations [10,57] where possible. Values of new parameters associated with predation-related processes were chosen to reproduce the same approximate global patterns under steady-state conditions but could not be further constrained due to the paucity of measurements directly comparable to model trophic levels. Parameters and values are shown in Table S2. Simulations were conducted at a five-day time step using an implementation of the model in python. Scripts, model code, forcing data, and model output are available

- 217 at the <u>aforementioned github repository</u>.
- 218

#### 219 *Characterization of SOC temperature responses*

CE (1 1)

To compare the temperature response of SOC stocks with the temperature dependence of microbe and predator growth rates, we used changes in SOC stocks under warming to calculate an equivalent SOC temperature sensitivity ( $CE_a$ ) in the same units as the temperature-dependence parameters in our models (Ea), following an approach previously used to estimate equivalent Q<sub>10</sub> values [58]. SOC temperature dependence can be approximated as:

 $SOC_T = SOC_{T_0} e$ 

$$SOC_T = SOC_{T_0} e^{-\frac{Cr_0}{k_b} \left(\frac{1}{T} - \frac{1}{T_0}\right)},\tag{8}$$

where  $SOC_T$  and  $SOC_{T_0}$  are carbon stocks at temperatures *T* and *T*<sub>0</sub> respectively. This relationship can be solved for  $CE_a$ :

228 
$$CE_a = k_B \ln\left(\frac{SOC_T}{SOC_{T_0}}\right) \left(\frac{1}{\frac{1}{T} - \frac{1}{T_0}}\right).$$
(9)

 $CE_a$  represents the temperature sensitivity that would result in a given ratio of SOC stocks at steady state under two different temperatures. Assuming SOC stocks have approached a steady state following any temperature perturbation,  $CE_a$  values can be compared across simulations with different assumptions to quantify differences in SOC temperature responses.

234 **Results**:

#### 235 Trophic-chain food web models

The population-based microbial model illustrated the fundamental impact of a third trophic level on SOC dynamics. A two-level model, including only substrate and microbial decomposers, reproduced dynamics shown in previous microbial decomposition models [16]: steady-state SOC was independent of substrate input rates (*I*) while microbial biomass increased with *I* (Figure 2a). Warming reduced SOC concentration but did not affect microbial biomass. Adding a third trophic level fundamentally changed SOC dynamics (Figure 2b). With predators, SOC increased at an accelerating rate with greater *I* while microbial biomass was constant with respect to *I*. Predator biomass did not persist below a minimal *I*. Warming decreased

- 243 SOC stocks while increasing microbial and predator biomasses.
- 244

SOC warming sensitivity varied with the relative temperature-dependence of microbes and their predators  $(E_a, Figure 2c)$ . When microbes were more temperature-sensitive than their predators, warming depleted

SOC. Above a critical predator  $E_a$ , reduction of microbial biomass due to increased predation drove

248 accumulation rather than loss of SOC under warming. The strength of this effect depended on substrate

- 249 input rate, such that an increase in substrate inputs led to a larger effect of differences in temperature
- 250 dependence across trophic levels (SI Fig S1).
- 251

252 When the two models (with and without predation) were directly compared, the temperature sensitivity of

- 253 SOC stocks in the presence of predators ( $CE_a$ ) decreased compared to that of a model without predators,
- suggesting a weaker temperature dependence of SOC stocks in the presence of predators (Fig 2d). The
- 255 difference in SOC temperature sensitivities between the two and three-level models was itself temperature
- 256 dependent and increased with warming. The magnitude of the reduction in SOC temperature sensitivity

- due to predators was determined by the relative temperature sensitivity of microbes and predators:
   increasing predator Ea reduced the temperature sensitivity of SOC when predators were present (Fig 2d).
- 259

### 260 Quantitative global SOC model

261 We used global simulations with the CORPSE-Pred model to investigate how predator activity 262 would alter SOC responses to warming across gradients of climate and ecosystem productivity. CORPSE-Pred reproduces the key aspects of top-down control of microbial populations via predation predicted in 263 the population-based approach (Fig. S2) as well as the effects of variable temperature sensitivities across 264 trophic levels (Fig. S3) suggesting a fundamental level of agreement between both modeling approaches 265 despite differences in model structure and assumptions. However, the structure of CORPSE-Pred 266 facilitated simulations across large gradients of mean annual temperature and C inputs, allowing the 267 investigation of microbe-predator interactions on SOC stocks across climate gradients, and facilitating 268 269 comparison of alternative assumptions regarding local adaptation of predator populations.

270

### 271 Predator effects across latitudes

272 Variation in predator biomass across latitudes depended on alternative assumptions of local 273 adaptation. With locally-adapted predator  $T_0$ , predator populations were significant across tropical, temperate, and boreal climate zones (Figure 3a). These larger populations led to significant top-down 274 275 control on microbial populations, reducing microbial biomass by 10-20% in the tropics and by over 50% 276 in higher latitudes (Figure 3b) relative to simulations without predators. By contrast, a globally constant 277  $T_{0}$  led to higher predator populations in the tropics and lower populations in high latitudes (Figure 3c). 278 Under this assumption, top-down control on microbial biomass was enhanced in the tropics and much 279 weaker in high latitudes (Figure 3d).

280 With no predators, SOC temperature sensitivity ( $CE_a$ ) varied moderately across latitude, with higher values (around 0.6 eV) in high latitudes and lower values (around 0.3 eV) in the tropics (Figure 281 4a). This variation was most likely due to the effect of protected C stocks that were not directly 282 283 responsive to warming but still exchanged C with unprotected SOC pools. Predators lowered  $CE_{a}$ 284 globally, indicating weaker temperature responses due to top-down control on microbial biomass. In the tropics,  $CE_a$  was reduced to about 0.2 eV with both locally-adapted and global constant predator  $T_0$ . With 285 globally constant predator  $T_0$ ,  $CE_a$  was reduced by about the same amount in high latitudes (Fig. 4c). 286 287 However, with locally adapted predator  $T_0$ ,  $CE_a$  in high latitudes was more strongly reduced, reaching negative values across northern areas that indicated a reversed temperature dependence with SOC stocks 288 289 increasing under warming (Fig. 4b). Negative  $CE_a$  values occurred in desert regions with globally 290 constant  $T_0$ , but SOC stocks were low in those regions under all conditions.

## 292 Discussion

#### 293 Implications for SOC stocks and warming responses

Both the population-based and the quantitative modeling approaches suggested that higher trophic levels
and their temperature dependence can strongly affect SOC stocks and their warming responses.
Introducing a third trophic level in food web models also caused SOC to become dependent on the rate of
substrate inputs, thus resolving a known flaw of some microbial-explicit SOC model formulations
[16,17]. Our results thus suggest that top-down control of microbial biomass by predators can address this
structural issue with a mechanistic justification.

300 In both population-based and quantitative models, microbial predators increased equilibrium SOC 301 stocks by reducing the abundance of decomposers. Models that lack explicit representation of top-down 302 controls may incorporate their effects implicitly into other parameter values such as microbial biomass 303 turnover rates or SOC pool decomposition rate constants. However, explicitly representing top-down 304 control on microbial biomass facilitates examination of key parameter values across climates and 305 ecosystems, allows for better mechanistic understanding of underlying processes, and draws a clearer link 306 between model parameters and empirical estimates of biological processes. Our results further suggest 307 that laboratory measurements of microbial biomass turnover rates in the absence of predators could 308 underestimate microbial mortality relative to field conditions. Furthermore, the divergence of SOC temperature response ( $CE_a$ ) from microbial temperature response as a function of predator traits in our 309 310 results suggests that temperature response measurements of microbial physiology and enzymatic reaction 311 rates may not be directly applicable to SOC decomposition rates.

312 Our results further suggest that not only the structure of the food web, but differences in the 313 temperature dependence of species across trophic levels can determine the integrated response of the soil 314 system to changes in temperature. As predators became more sensitive to temperature, SOC losses under 315 warming weakened. Under some circumstances an increase in top-down control under warming could 316 overwhelm increases in microbial substrate consumption rates and increase SOC stocks with warming. In 317 a recent meta-analysis [6], 47% of soil warming manipulations observed increases in SOC rather than 318 losses. Previous explanations for these unexpected results have included changes in soil moisture [59], 319 increases in plant C inputs [60], and shifts in microbial physiology [8,61]. Our results suggest that 320 increasing SOC under warming could also be explained by enhanced top-down control by microbial 321 predators that increase their activity under warmer temperatures. Alternately, predators with low or 322 negative thermal sensitivities could accelerate SOC losses under warming due to weakening of top-down 323 control on microbial biomass. Our results also corroborate recent empirical studies indicating that 324 temperature dependence of upper trophic levels could cascade down the soil food web, ultimately 325 affecting soil respiration [39,42,62]. These results highlight the need to hone our understanding of how species respond to warming across soil trophic levels, instead of focusing only on the microbial 326 327 decomposer component.

A significant challenge for this model structure is parameterization of processes related to trophic interactions [47]. Many important parameters in the models were poorly constrained in these simulations, including predator growth rates and CUE. Even parameters for which there is strong empirical evidence, such as thermal sensitivities, can vary substantially across organisms [63]. The high sensitivity of SOC temperature responses to the presence and traits of predators suggests that developing observational constraints for these parameters should be a priority in soil organic matter research. This said, note that 334 while our two modeling approaches share some core structural assumptions (two or three trophic levels,

density-independent substrate inputs), they also incorporate substantially different assumptions (e.g.,

ratio-dependent predation vs ratio-independent predation, existence of multiple C types vs only one type

- of C) and have different parameterizations. Given these important differences, the level of congruence
- between the results of the two modeling approaches suggests that these qualitative results may apply
- broadly.

### 340 Global patterns of soil food web structure

341 Our results suggest that differential thermal sensitivities could drive differences in soil food web structure at different latitudes, depending on whether predator temperature traits are adapted to local 342 343 climate. Top-down control on microbial populations was strongest in the tropics under globally-constant 344 predator traits, while local temperature adaptation strengthened top-down control in colder regions. When 345 predators were not adapted to local conditions, cold temperatures at high latitudes prevented predators 346 from adopting a significant role. These results suggest that soil food web and decomposition responses to 347 warming may be highly dependent on a combination of climate and local adaptation [64]. Because 348 predator sensitivity to temperature mediates the response of the system to warming, food webs in different 349 latitudes with different fauna or trophic structures are likely to have different warming responses.

350 Understanding differences in temperature sensitivity across trophic levels is thus crucial for 351 projecting SOC responses to warming, given that temperature sensitivities are known to vary broadly 352 across taxa, trophic levels, and habitats [63] and to differ among predators and their prey [63,65]. 353 Temperature sensitivities are strongly correlated with body size [43], which could lead to different 354 community responses depending on the size structure of trophic levels. For example, the predator trophic 355 level in our model formulations could represent organisms like nematodes and amoebae, which, being 356 larger than their bacterial and fungal prey, could suffer greater metabolic penalties from warming and thus 357 realize lower biomass gains even with increasing consumption rates [43,66]. Alternately, top-down 358 control could be exercised by viruses or phages, which are physically smaller and biochemically simpler 359 than bacteria and fungi and, thus, might have very different thermal responses than larger organisms. A 360 more sophisticated version of our modeling approach could include multiple organismal types at each 361 trophic level, including decomposers with different traits (e.g., bacteria and fungi) and different types of 362 predators with different traits and temperature sensitivities (e.g., phages, amoebae, nematodes, and 363 microarthropods). Such a model might be more directly comparable with observations of soil biological

364 communities but would introduce more difficult-to-constrain parameters.

### 365 Conclusions

366 Using two complementary modeling approaches, we show that the presence of a microbial 367 predator decouples SOC temperature response from that of microbial decomposers by exerting top-down control on the latter. Our results suggest that SOC stocks are sensitive to food web structure, particularly 368 369 the presence or absence of microbial predators, and that temperature sensitivity of decomposition is likely 370 to be reduced by the presence of higher trophic levels. This effect ultimately depends on the relative 371 temperature dependence of the microbial communities and their predators, which can lead to different 372 responses across latitudes. This implies that measurements of temperature sensitivities should be 373 understood in the context of broader trophic interactions before they can be directly applied to soil C 374 decomposition and soil respiration parameters. Variations in temperature sensitivity across trophic levels

- in soil food webs are therefore an important and underappreciated uncertainty in our predictive
- 376 understanding of SOC dynamics and global change responses across climate zones and latitudes.
- 377

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551 Figures



Figure 1: Diagram of three approaches to SOC modeling. A first-order model has only one trophic level (SOC). A
 microbial model adds a second trophic level, and a microbe-predator model includes a third trophic level. Transfers
 from one level to the next are mediated by temperature and population of adjacent trophic levels.





Figure 2: Equilibrium densities of substrate (C), microbes (M), and predators (P) of population-based microbial (a) and microbe-predator (b) models over a range of substrate input rates and two temperatures. Dashed lines show

and microbe-predator (b) models over a range of substrate input rates and two temperatures. Dashed lines show simulations at 20 °C and solid lines show simulations at 25 °C. (c) Effect of relative microbial and predator

505 simulations at 20°C and solid lines show simulations at 25°C. (c) Effect of relative interoblat and predator 566 temperature sensitivities on equilibrium SOC response to warming (relative to 20 °C). ΔEa is the difference between

567 microbial and predator Ea parameters in electron-volts. (d) Difference in the temperature sensitivity of SOC between

over ambient), for differences in temperature sensitivities between predators and microbes (blue-color coded).

a three-level model (with predators) and a two-level model (without predators) at different levels of warming (as  $\Delta T$ 

568 569





Figure 3: Predator biomass distribution and impacts on microbial biomass at steady state. Panels a and b show

573 simulations with locally-adapted predator  $T_0$ , and panels c and d show simulations with constant global  $T_0$ . Panels a

and c show total simulated predator biomass carbon, and panels b and d show the percent difference in microbial

575 biomass expressed as a fraction of total SOC compared to control simulations.



579 Figure 4: *CE<sub>a</sub>* of unprotected SOC stocks under alternative assumptions of predator traits. (a): CORPSE model

580 without predators. (b): Predators with  $T_{\theta}$  equal to mean annual temperature in each grid cell, representing local 581 adaptation. (c): Predators with a single global  $T_{\theta}$  equal to global mean temperature.

# 583 Supplemental Material

#### 585 First order and Microbial models

587 The simplest approach to modeling SOC decomposition only considers carbon stock (*C*) naturally 588 decaying over time at a temperature-dependent first-order rate k (Fig 1A) while being replenished at a 589 constant rate *I*:

$$591 \qquad \frac{dC}{dt} = I - k(T)C \tag{S1}$$

593 Here, we model the microbial effect on carbon as a classic type-II predator functional response, where the 594 SOC decomposition rate depends on microbial biomass and carbon stocks (M and C, respectively), as 595 well as on two parameters controlling the feeding process, the microbial attack rate ( $\alpha$ ) and handling time 596 n [1.2]. We further assume that the conversion of carbon into microbial biomass is determined by a 597 conversion efficiency parameter ( $\varepsilon$ ), that carbon stocks are replenished at a constant rate I, determined by substrate input levels, and that microbes die naturally at a per-capita rate  $d_M$ . For simplicity, we assume 598 599 that microbial deaths do not feed back into the SOC pool, but such a scenario can be taken into account 600 by slightly altering substrate input levels. Together, the model calculates the rates of change of C stocks and M biomass over time through the following system of differential equations: 601

$$603 \qquad \frac{dC}{dt} = I - \frac{\alpha(T)CM}{1 + \alpha(T)nC}$$
(S2)

$$604 \qquad \frac{dM}{dt} = \varepsilon \frac{\alpha(T)CM}{1+\alpha(T)\eta C} - d_M M \tag{S3}$$

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590

We further modified this model by assuming, for simplicity, that microbial attack rates, but no other model parameters, are temperature-dependent, following an Arrhenius function of the form:

608 
$$\alpha(T) = V e^{-\frac{k_a}{k_b} \left(\frac{1}{T} - \frac{1}{T_0}\right)},$$
 (S4)  
609

610 where *V* is a pre-exponential rate constant (units of inverse time),  $k_b$  is the Boltzmann constant (8.62x10<sup>-5</sup> 611 electron-volts per degree Kelvin, eV K<sup>-1</sup>), *T* is the temperature at which the process occurs (in K),  $T_0$  is a 612 reference temperature (K), and  $E_a$  is the activation energy of the process (in eV), which is a measure of its 613 temperature dependence [3–5].

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#### 617 CORPSE-Pred Model Equations

618

619 The soil carbon model is an adaptation of the Carbon Organisms Rhizosphere and Protection in the Soil

Environment (CORPSE) model (Sulman et al, 2014), modified to allow tracking of carbon isotopes.

621 Organic matter is divided into three chemically-defined forms, which can be either protected or 622 unprotected. Protected organic matter is inaccessible to microbial decomposition through chemical

623 sorption to mineral surfaces or occlusion within micro-aggregates. Unprotected organic matter can be

added as litter or root exudate inputs, decomposed by microbial action, or protected:

$$\begin{array}{l}
625 \\
626 \\
627 \\
\end{array} \underbrace{}^{dC_{U,i}}_{dt} = I_{C,i} - D_i + T_M + T_P - \frac{dC_{P,i}}{dt} \\
(1)
\end{array}$$

where  $C_{U,i}$  is unprotected C;  $I_{C,i}$  is external inputs of C (including litter deposition and root exudation);  $D_{i,j}$  is decomposition rate;  $T_M$  is microbial necromass production;  $T_P$  is predator necromass production; and  $\frac{dC_{P,i}}{dt}$  is net transfer of C to or from the protected state. *i* refers to chemically-defined types, which can be chemically simple plant-derived material (representing compounds like glucose or amino acids that are readily decomposed), chemically resistant (representing compounds like lignin or complex microbiallyproduced chemicals), or readily decomposable microbial and predator necromass.

Protected C is formed from unprotected organic matter and converted back to unprotected form at first-order rates:

637

$$638 \qquad \frac{dC_{P,i}}{dt} = C_{U,i} \cdot \gamma_i - \frac{C_{P,i}}{\tau_{C_P}}$$

$$639 \qquad (2)$$

640 The decomposition flux is controlled by microbial biomass ( $B_M$ ), temperature (T), and volumetric soil 641 water content ( $\theta$ ):

643 
$$D_i = V_{max,i}(T) \cdot \left(\frac{\theta}{\theta_{sat}}\right)^a \left(1 - \frac{\theta}{\theta_{sat}}\right)^b \cdot C_i \frac{M/C_i}{M/C_i + k_M}$$
(3)

644 645

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642

646 where  $\theta_{sat}$  is the saturation level of  $\theta$ . Note that decomposition rate is controlled by the ratio of total 647 microbial biomass carbon (summed over isotope fractions) to substrate carbon (also summed over isotope 648 fractions) on a substrate-specific basis. The maximum decomposition rate is controlled by the Arrhenius 649 relationship, which describes the temperature dependence of enzymatic reactions:

651 
$$V_{max,i}(T) = V_{max,ref,i} \times \exp\left(-\frac{E_{a,i}}{RT}\right)$$
 (4)  
652

653 where  $V_{max,ref,i}$  is a maximum decomposition rate specific to each chemically-defined organic matter 654 type,  $E_{a,i}$  is activation energy for each organic matter type, and R is the ideal gas constant (8.31 J K<sup>-1</sup> mol<sup>-</sup> 655 <sup>1</sup>). 656

Microbial growth is supported by uptake of decomposed organic matter, and biomass is lost through
turnover at a fixed rate:

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$$\begin{array}{l} 660 \quad \frac{dB_M}{dt} = \sum_i (D_i CUE_i) - \max(M - M_{min} \cdot \sum_i C_{U,i}, 0) \, d_M - p \\ 661 \end{array}$$
(5)

662 Where  $M_{min}$  is minimum microbial biomass expressed as a fraction of total unprotected C and p is 663 predation rate. Turnover is divided into maintenance respiration, which is converted directly to CO<sub>2</sub>, and 664 necromass production. The division between maintenance and respiration and necromass production is 665 controlled by a parameter  $\epsilon_t$ :

667 
$$R_{maint} = \max(M - M_{min} \cdot \sum_{i} C_{U,i}, 0) d_M (1 - \epsilon_t)$$
(6)

669 
$$T_{M,j} = \max\left(M - M_{min} \cdot \sum_{i} C_{U,i}, 0\right) d_M\left(\epsilon_t\right)$$
(7)

671 Predation rate is similar to decomposition rate, but controlled by predator biomass and, for simplicity,672 assumed to be independent of soil moisture:

674 
$$p = V_{max,P}(T)M \frac{P/M}{P/M+k_P}$$
 (8)  
675

676 
$$V_{max,P}(T) = V_{max,ref,P} \times \exp\left(-\frac{E_{a,P}}{RT}\right)$$
  
677 (9)

And predator growth and turnover are similar to their microbial counterparts, but depending on microbial
 biomass rather than substrate C:

$$681 \qquad \frac{dP}{dt} = p \cdot CUE_P - \max\left(P - P_{min} \cdot M, 0\right) d_P \tag{10}$$

$$682$$

683 Where  $CUE_P$  is predator carbon use efficiency,  $P_{min}$  is minimum predator biomass as a fraction of 684 microbial biomass, and  $\tau_P$  is turnover time of predator biomass. As with microbes, predator biomass 685 turnover is divided into necromass production and maintenance respiration:

$$R_{maint,P} = \max\left(P - P_{min} \cdot M, 0\right) d_P \left(1 - \epsilon_{t,P}\right)$$

$$\tag{11}$$

$$\begin{array}{l} 689 \quad T_P = \max\left(P - P_{min} \cdot M, 0\right) d_P\left(\epsilon_{t,P}\right) \\ 690 \end{array} \tag{12}$$

691 Total CO<sub>2</sub> production rate is the sum of maintenance respiration and respiration derived from
 692 decomposition processes:

$$\begin{array}{l}
694 \quad \frac{dCO_2}{dt} = R_{maint} + R_{maint,P} + \sum_i ((1 - CUE_i)D_i) + (1 - CUE_P \cdot p) \\
695 \\
696 \end{array} \tag{13}$$

697

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### 713 Model parameters

Parameter	Description	Value	Units
$\eta_1$	Microbial handling time	0.04	Time
$\eta_2$	Predator handling time	0.04	Time
ε1	Microbial conversion efficiency	0.4	Unitless
ε <sub>2</sub>	Predator conversion efficiency	0.2	Unitless
$d_M$	Microbial death rate	1.0	Time <sup>-1</sup>
$d_P$	Predator death rate	0.8	Time <sup>-1</sup>
$V_{I}$	Microbial attack rate	0.22	Time <sup>-1</sup>
$V_2$	Predator attack rate	0.22	Time <sup>-1</sup>
Ea <sub>1</sub>	Microbial activation energy	0.65	eV
Ea <sub>2</sub>	Predator activation energy	0.65	eV
$T_0$	Reference temperature	15	°C

Table S1: Parameter values for the population-based models used in Figure 2.

715

716 Table S2: CORPSE-Pred parameters

Parameter	Description	Value	Units
$V_{l}$	Max decomposition rate for simple C	9.0	year <sup>-1</sup>
$V_2$	Max decomposition rate for complex C	0.25	year <sup>-1</sup>
$V_3$	Max decomposition rate for necromass C	4.5	year <sup>-1</sup>
$Ea_1$	Activation energy for simple C	0.052	eV
$Ea_2$	Activation energy for complex C	0.31	eV
Ea <sub>3</sub>	Activation energy for necromass C	0.052	eV
$k_M$	Microbial decomposition saturation parameter	0.1	g microbial C g substrate C <sup>-1</sup>

a	Moisture sensitivity parameter	1.5	Unitless
b	Moisture sensitivity parameter	0.6	Unitless
M <sub>min</sub>	Minimum microbial biomass	0.001	g microbial C g substrate C <sup>-1</sup>
$d_M$	Microbial death rate	4.0	year <sup>-1</sup>
ε <sub>1</sub>	Microbial conversion efficiency for simple C	0.6	Unitless
ε <sub>2</sub>	Microbial conversion efficiency for complex C	0.05	Unitless
83	Microbial conversion efficiency for necromass C	0.6	Unitless
$\gamma_1$	Protection rate of simple C	0.3	year <sup>-1</sup>
$\gamma_2$	Protection rate of complex C	0.001	year <sup>-1</sup>
$\gamma_3$	Protection rate of necromass C	1.5	year <sup>-1</sup>
$ au_{C_P}$	Turnover time of protected C	75	years
$V_P$	Max predation rate	4.0	year <sup>-1</sup>
Ea <sub>P</sub>	Predator activation energy	0.31	eV
$P_{min}$	Minimum predator C	0.001	g predator C g microbial C <sup>-1</sup>
$d_P$	Predator death rate	2.0	year <sup>-1</sup>
Eр	Predator conversion efficiency	0.5	Unitless
k <sub>P</sub>	Predation saturation parameter	0.5	g predator C g microbial C <sup>-1</sup>



727 Figure S1: Change in steady-state SOC stock under 4°C warming as a function of predator Ea, for three

728 different substrate input rates using the population-based model.



731

Figure S2: Model pools as a function of substrate input using CORPSE-Pred. These plots are comparable

- to Fig. 2 in the main text. Microbial and predator pools are shown separately from SOC for better
- visibility due to the large differences in stock magnitudes.





Figure S3: (a) Effect of relative microbial and predator temperature sensitivities on equilibrium SOC
 response to warming, using CORPSE-Pred model. Dashed lines show simulations without predators. This

figure is comparable to Fig. 2c in the main text. (b) Data from the top panel expressed as *CEa*. Dashed

739 lines show simulations without predators, and dotted red line shows the actual *Ea* parameter value of the

slow-cycling component of unprotected SOC.