- 1 We thank the Associate Editor and two referees for their providing constructive comments to this
- 2 manuscript. Below we detail how we have revised the manuscript following their suggestions.
- 3 1. The problem of more degrees of freedom with more details models is equifinality: several
- 4 combinations of parameters match the data similarly well. That needs to be incorporated in
- 5 forward simulations, which usually become more uncertain with equifinality.
- 6 *Response: Thanks for the comments. To address the impacts of "equifinality" on our*
- 7 quantifications associated with parameters, we have conducted ensemble simulations for both
- 8 20th and 21st centuries with respect to uncertain parameters. These ensemble simulations shall
- 9 cover the "equifinality" set of parameters in our model. In other words, these simulations shall
- 10 *have included the "equifinality" impacts. We presented the simulations results in Figure 11 and*
- 11 Figure 12 in this revision.
- 12 2. Fig 3: It is not clearly stated, how many parameters were calibrated and Fig. 3 is barely
- readable because of display quality. Are there only 3 out of the 6 sites displayed?
- *Response: Thanks for the comments. We have revised Figure 3. Now six sites are shown andthe figure shall be more readable.*
- 16 3. Cost function (17): Why did you not consider uncertainty of observed NEE? Usually, you
- 17 need this to determine, which parameter sets are viable. If you have larger NEE confidence
- 18 bounds, also more different parameter sets will generate predictions that are still compatible with
- 19 the calibration NEE. For my main concern above it is important to keep also the slightly less
- 20 optimal but compatible parameter sets.
- 21 *Response: The error or uncertainty of the NEE data we used have not been provided by field*
- 22 *experimentalists. Thus, in this study, the model parameters are only constrained by the observed*
- 23 magnitudes and temporal variabilities of NEE at those sites.
- 24
- 25
- 26

1 2	Microbial dormancy and its impacts on Arctic terrestrial ecosystem carbon budget
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47 Abstract

48	A large amount of soil carbon in the Arctic terrestrial ecosystems could be emitted as
49	greenhouse gases in a warming future. However, lacking detailed microbial processes such
50	as microbial dormancy in current biogeochemistry models might have biased the
51	quantification of the regional carbon dynamics. Here the effect of microbial dormancy was
52	incorporated into a biogeochemistry model to improve the quantification for the last and
53	this century. Compared with the previous model without considering the microbial
54	dormancy, the new model estimated the regional soils stored 75.9 Pg more C in the
55	terrestrial ecosystems during the last century, and will store 50.4 Pg and 125.2 Pg more C
56	under the RCP 8.5 and RCP 2.6 scenarios, respectively, in this century. This study
57	highlights the importance of the representation of microbial dormancy in earth system
58	models to adequately quantify the carbon dynamics in the Arctic.
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76 **1. Introduction**

The land ecosystems in northern high latitudes (>45 ° N) occupy 22% of the global 77 78 surface and store over 40% of the global soil organic carbon (SOC) (McGuire & Hobbie, 1997; 79 Melillo et al., 1993; Tarnocai et al., 2009; Hugelius et al., 2014). During the past decades, a 80 greening accompanying a warming in the region has been documented (Zhou et al., 2001; Lloyd 81 et al., 2002; Stow et al., 2004; Callaghan et al., 2005; Tape et al., 2006). The regional carbon 82 dynamics are expected to loom large in the global carbon cycle and exert large feedbacks to the 83 global climate system (McGuire et al., 2009; Davidson & Janssens, 2006; Bond-Lamberty & 84 Thomson, 2010).

85 To date, numerous ecosystem models have been developed to project the feedbacks between terrestrial ecosystem carbon cycling and climate (Raich et al., 1991; Zhuang et al., 86 87 2001, 2002, 2015; Parton et al., 1993; Knorr et al., 2005; Running & Coughlan, 1988), but they 88 can bias their quantifications due to missing detailed microbial mechanisms in these models 89 (Schmidt et al., 2011; Todd-Brown et al., 2013; Conant et al., 2011; Treseder et al., 2011). 90 Microorganisms play a central role in decomposition of litter and soil organic carbon, which 91 further governs the global carbon cycling and climate change (Xu et al., 2014; Treseder et al., 92 2011; Wang et al., 2015). An emerging field of research has begun to incorporate microbial 93 ecology into existing process-based models to remedy the to represent decomposition in ways 94 that include important microbial processes that were previously ignored inadequate representation 95 of soil decomposition process (Zha & Zhuang, 2018; Schimel & Weintraub, 2003; Allison et al., 96 2010; German et al., 2012). These microbial-based models tend to better reproduce field and 97 satellite observations than traditional ones that treat soil decomposition as a first-order decay 98 process without considering microbial activities (Treseder et al., 2011; Wieder et al., 2013;

99 Todd-Brown et al., 2011; Lawrence et al., 2009; Moorhead et al., 2006). However, some vital 100 microbial traits such as microbial dormancy and community shifts are still rarely explicitly 101 considered in large-scale ecosystem models (Wieder et al., 2015), and this may introduce notable 102 uncertainties (Graham et al., 2014, 2016; Wang et al., 2015; Bouskill et al., 2012; Kaiser et al., 103 2014). 104 Dormancy is broadly recognized as a strategy for microorganisms to cope with periodical 105 environmental stresses (Harder & Dijkhuizen, 1983). When environmental conditions are 106 unfavorable for growth, microbes switch to a dormant state, which is a reversible state of low to 107 zero metabolic activity (Stolpovsky et al., 2011; Lennon & Jones, 2011). In this state, 108 biogeochemical processes such as soil decomposition are slow (Blagodatskaya et al., 2013). At 109 any given time, there is only a fraction of-, likely below 50%, of metabolically active microbes in 110 natural soils number of microbes, likely below 50% of live microbes, in natural soils (Wang et 111 al., 2015; Stolpovsky et al., 2011). Soil decomposition and nutrient cycling mainly depend on 112 these active microbes because only active ones can consume organic matter and replicate 113 themselves (Wang et al., 2015; Blagodatskaya et al., 2014). To date, most existing 114 biogeochemistry models use total rather than active microbial biomass as an indicator of 115 microbial activities (Wieder et al., 2015)used total microbial biomass as indicator of microbial 116 activities, rather than the active portion of microbial biomass, which could bias the estimates of 117 soil decomposition and ecosystem carbon budget (Hagerty et al., 2014; He et al., 2015). 118 Especially, the Arctic terrestrial ecosystems are nitrogen-limited, neglecting microbial dormancy 119 will lead to incorrect estimates of nitrogen availability through soil decomposition, failing to 120 capture nitrogen feedbacks to carbon dynamics (Wang et al., 2015; Stolpovsky et al., 2011; 121 Thullner et al., 2005). Furthermore, the Arctic Besides, it is also important because of has

- 122 experienced a the marked seasonality of (i.e. active ity and /dormant eymicrobial cycles) and the
- above-global-average warming, happening in those latitudes (which might could have increased
- 124 <u>the proportion of active microbes in soils</u>) (He et al., 2015). Thus, incorporating dormancy
- 125 effects will improve model realism to and show the important role of microbial dormancy
- 126 provide a better<u>in-provide a better the</u>projection of the Arctic carbon dynamics.
- 127 This study incorporated the effects of microbial dormancy trait into an extant process-
- based biogeochemistry model (MIC-TEM) (Zha & Zhuang, 2018; He et al., 2015). The dormant
- and active microbial physiology has been considered explicitly in the new version of model
- 130 (MIC-TEM-dormancy). The revised model was parameterized, validated, and then applied to
- 131 evaluate the carbon dynamics during the last and this centuries in the Arctic terrestrial
- ecosystems (north 45 <u>P</u>N above). <u>By comparing the results of MIC-TEM-dormancy and MIC-</u>
- 133 <u>TEM, we can show that incorporating microbial dormancy may produce a much different</u>
- 134 <u>prediction in historical and future carbon budget.</u>
- 135 and demonstrate the essential role of microbial dormancy.
- 136
- **137 2. Methods**
- 138 **2.1 Overview**

Due to the importance of microbial dormancy, some recent work has been done to consider the metabolic activation and deactivation of microbes in soil and its effects on soil carbon (C) dynamics and climate feedbacks (Wang et al., 2015; Salazar et al., 2018). For example, Wang et al., (2015) has incorporated transformation processes between active and dormant states to developed two versions of MEND, that is, MEND with and without dormancy. The two versions of the model have been applied to quantify model the carbon decomposition in of laboratory 145 incubations of four soils. Salazar et al. (-2018) have also taken ook-microbial dormancy into 146 account to compare their predictions of microbial biomass and soil heterotrophic respiration (R_H) 147 under simulated cycles of stressful (dryness) and favorable (wet pulses) conditions. Our study 148 extend those modeling studies to the whole Arctic region by developing a more detailed 149 biogeochemistry model considering the dormancy impacts. In- Below, this paper, fFirst, we first 150 describe how we developed the new model (MIC-TEM-dormancy) by incorporating the 151 microbial dormancy trait into an existing microbial-based biogeochemistry model (MIC-TEM). 152 Second, we discuss how conduct the parameterization and validation of MIC-TEM-dormancy 153 model were conducted using observed net ecosystem exchange data, and heterotrophic respiration 154 data at representative sites have been shown. Third, we presented how applyied the model was applied to to-northern high latitudes (above 45 ° N) for the 20th and 21st centuries and discussed 155 156 to demonstrate the dormancy effects on regional carbon budget.

157

158 **2.2 Model description.**

159 A non-dormancy version of biogeochemistry model (MIC-TEM) has been developed by 160 incorporating a microbial module (Allison et al., 2010) into an extant large-scale biogeochemical 161 model (TEM) to explicitly (Zhuang et al., 2001, 2002, 2003) consider the effects of microbial 162 dynamics and enzyme kinetics on carbon dynamics (Zha & Zhuang, 2018). Here we further 163 advanced the MIC-TEM by incorporating algorithms that describe the effects of microbial 164 dormancy dynamics based on He et al. (2015). Different from He et al. (2015), in which 165 microbial module was driven with existing data of carbon stocks and fluxes, our study 166 incorporated the microbial module into an extant MIC-TEM that simulates carbon data 167 dynamically. This coupling enables us to extrapolate our model to whole northern high-latitudes

168 region, rather than only for temperate forest region in He et al. (2015). In our new model (MIC-TEM-dormancy), microbial biomass pool was divided into two fractions, including the dormant 169 170 and active microbial biomass pools. The two microbial biomass pools and the reversible 171 transition between them have been considered explicitly in the new model (Figure 1), which was 172 ignored in MIC-TEM (Figure 1). 173 In previous MIC-TEM, heterotrophic respiration (R_H) is calculated as: 174 $R_{\rm H}$ =ASSIM*(1-CUE) (1)175 Where ASSIM and CUE represent microbial assimilation and carbon use efficiency, respectively. 176 For detailed carbon dynamics in MIC-TEM, see Zha & Zhuang (2018). Here we revised MIC-TEM by incorporating microbial dormancy dynamics according to 177 178 He et al. (2015). In the new model (MIC-TEM-dormancy), the soil heterotrophic respiration R_H is comprised of three parts: the maintenance respiration from the active and dormant microorganisms 179 180 and the CO₂ production through the process of microbial assimilation (He et al., 2015): $R_{\rm H} = m_{\rm R} Q_{10 \rm mic}^{\frac{\rm temp-15}{10}} B_{\rm a} + \beta m_{\rm R} Q_{10 \rm mic}^{\frac{\rm temp-15}{10}} B_{\rm d} + CO_2$ 181 (2) 182 where the first two terms are maintenance respiration from the active and dormant 183 microorganisms, respectively. The last term is the CO_2 produced during the process of microbial assimilation. 184 185 For first two terms, Ba and Bd represents the active and dormant microbial biomass pool, 186 respectively. The parameter m_R denotes the specific maintenance rate at active state (h⁻¹), and β 187 is the ratio of dormant maintenance rate to active maintenance rate. Thus, βm_R denotes the 188 maximum specific maintenance rate at dormant state. Temperature sensitivity was expressed as the Q_{10} function $(Q_{10}^{\frac{\text{temp-15}}{10}})$, where temp is soil temperature at top 20 cm (units: °C). 189

For the third term, the CO₂ produced through microbial assimilation is calculated as in He et al.
(2015) and Allison et al. (2010):

$$CO_2 = ASSIM^*(1-Y_g)$$
(3)

193 Where ASSIM represents the variable of microbial assimilation and the parameter Y_g represents 194 carbon use efficiency. Microbial assimilation (ASSIM) is calculated as in He et al. (2015):

195
$$ASSIM = \frac{1}{Y_g} \frac{\Phi}{\alpha} m_R Q_{10enz}^{\frac{temp-15}{10}} Ba \left(\frac{CN_{soil}}{CN_{mic}}\right)^{0.6}$$
(4)

Here parameter α is <u>called the maintenance</u> weight (h⁻¹), CN_{soil} and CN_{mic} denotes the C:N ratio<u>s</u> of soil and that of microbial biomass to consider substrate quality. Besides, Φ is <u>the called substrate</u> saturation level and defined as in He et al. (2015) and Wang et al. (2014):

199
$$\Phi = \frac{S}{K_s + S}$$
(5)

Where K_s is the half saturation constant for substrate uptake as indicated by the Michaelis–Menten kinetic, and S is soluble C substrates that are directly accessible for microbial assimilation (Wang et al., 2014). Here we quantified concentration of soluble C substrates that are directly accessible for microbial assimilation by using conceptual framework from Davidson et al. (2012):

204

$$= \text{Soluble C} * D_{\text{lig}} * \theta^3 \tag{6}$$

205 The term 'Soluble C' denotes the state variable of soluble carbon pool. D_{liq} is the diffusion 206 coefficient of the substrate in the liquid phase, and is formulated as:

207
$$D_{liq} = 1/(1-BD/PD)^3$$
 (7).

S

208 <u>Where BD</u> is the bulk density and PD is the soil particle density. θ is the volumetric soil moisture. 209 Different from MIC-TEM, the transitions between active and dormant microbial biomass are 210 included in MIC-TEM-dormancy. We used $B_{a\rightarrow d}$ and $B_{d\rightarrow a}$ denotes the transition from the active 211 to dormant microbe and from the dormant to active microbe, respectively (He et al., 2015; Wang 212 et al., 2014):

$$B_{a \to d} = (1 - \Phi) m_R Q_{10 \text{mic}}^{\frac{\text{temp} - 15}{10}} B_a$$
 (87)

214
$$B_{d\to a} = \Phi m_R Q_{10mic}^{\frac{temp-15}{10}} B_d$$
 (98)

Where $B_{a \rightarrow d}$ and $B_{d \rightarrow a}$ denote the transition from the active to dormant microbe and from the 215 dormant to active microbe, respectively (He et al., 2015; Wang et al., 2014). 216

Thus, dDormancy rate is affected by active and dormant biomass, substrate availability (B_a, B_d), 217

soil temperature (temp) and soil moisture (
$$\theta$$
 in Φ).

219 The active microbial biomass (B_a) is modeled as (He et al., 2015; Wang et al., 2014):

220
$$\frac{dBa}{dt} = ASSIM * Y_g - m_R Q_{10mic}^{\frac{temp-15}{10}} B_a - B_{a \to d} + B_{d \to a} - DEATH - EPROD$$
 (109)

221 Where DEATH and EPROD denotes microbial biomass death and enzyme production, which are modeled as proportional to active microbial biomass with constant rates r_{death} and r_{EnzProd} (Allison 222 223 et al., 2010):

DEATH =
$$r_{death} * Ba$$
 (110)

225

213

$$EPROD = r_{EnzProd} * Ba$$
 (124)

Where r_{death} and r_{EnzProd} are the rate constants of microbial death and enzyme production, 226 respectively. 227

228 The dormant microbial biomass (B_d) is modeled as (He et al., 2015; Wang et al., 2014):

229
$$\frac{dB_{d}}{dt} = -\beta m_{R} Q_{10mic}^{\frac{temp-15}{10}} B_{d} + B_{a \to d} - B_{d \to a}$$
(132)

230 The Soluble C pool is modeled as (He et al., 2015; Allison et al., 2010):

231
$$\frac{d \text{ Soluble C}}{dt} = \text{DECAY} - \text{ASSIM} + \text{ELOSS} + \text{DEATH} \quad (143)$$

(1<u>2</u>+)

233 represents the loss of enzyme. 234 DECAY is regulated by enzyme biomass (ENZ), soil organic carbon (SOC), soil temperature, and 235 substrate quality (He et al., 2015): $DECAY = V_{max} * Q_{10enz}^{\frac{temp-15}{10}} * ENZ * \frac{SOC}{Km_{uptake} + SOC} * (120 - CN_{soil})$ 236 (1<u>5</u>4) Where V_{max} is the maximum SOC decay rate, Km_{uptake} is half saturation constant for enzymatic 237 238 decay. 239 ELOSS is modeled as a first-order process (Allison et al., 2010) to represent enzyme turnover: 240 $ELOSS = r_{encloss} * ENZ$ (1<u>6</u>5) 241 Where $r_{enzloss}$ is the rate constant of enzyme loss. 242 The soil organic carbon pool (SOC) is modeled as: $\frac{dSOC}{dt}$ = Litterfall – DECAY 243 (1<u>7</u>6) 244 Where Litterfall is estimated as a function of vegetation carbon (Zhuang et al., 2010). 245 Last, enzyme pool (ENZ) is modeled as: $\frac{dENZ}{dt}$ =EPROD-ELOSS 246 (1<u>8</u>7) 247 With the modification of microbial carbon dynamics by considering microbial life-history trait, 248 soil decomposition is changed since it is controlled by microbes. When microbial dormancy is 249 considered, the number of active microbes that participate in soil decomposition is much less than 250 that we considered beforedifferent. The changes in soil decomposition directly influence the 251 amount of soil respiration, and further influence soil nitrogen (N) mineralization that determines 252 soil N availability for plants, affecting gross primary production (GPP). Since both GPP and soil

Where DECAY represents the enzymatic decay of soil organic carbon (SOC), and ELOSS

respiration (R_H) can be affected by microbial dormancy, net ecosystem production (NEP) will also
 be affected.

255

256 **2.3 Model parameterization and validation**

The detailed description of parameters that are related to microbial dormancy can be found 257 258 in He et al. (2015) (Table 1). Here we calibrated the MIC-TEM-dormancy at six representative sites with gap-filled monthly net ecosystem productivity (NEP, gCm⁻²mon⁻¹) data in northern high 259 260 latitudes (Table 2). Site-level climatic data and soil texture data were organized for driving model. 261 All sites information can be found on AmeriFlux network (Davidson et al., 2000). The results for model parameterization were presented in Figure 2. We conducted the parameterization using a 262 263 global optimization algorithm known as SCE-UA (Shuffled complex evolution) method (Duan et 264 al., 1994). An ensemble of 50 independent sets of parameters were performed based on prior ranges 265 from literature (Table 1) to minimize the difference between the monthly simulated and measured 266 NEP at the chosen sites. The cost function of the minimization is:

267

$$Obj = \sum_{i=1}^{k} (NEP_{obs,i} - NEP_{sim,i})^2$$
(17)

Where NEP_{obs,i} and NEP_{sim,i} are the observed and simulated NEP, respectively. k is the number of data pairs for comparison. Except for the parameters of microbial dormancy, other parameters are derived directly from MIC-TEM (Zha & Zhuang, 2018). The optimized parameters were used for model validation and regional simulations.

For model validation, we chose another six sites that containing monthly NEP data from AmeriFlux network (Table 3). Moreover, we also conducted site-level validations with monthly soil respiration data from AmeriFlux network and Fluxnet dataset. The site information was provided in Table 4. For these sites, we assumed 50% of soil respiration was heterotrophic 276 respiration (R_H) for forest (Hanson et al., 2000), 60% and 70% of that was R_H for grassland (Wang 277 et al., 2009) and tundra (Billings et al., 1977). Because there is a -of-limited ations in the amount 278 of available RH datathere is a limited amount of measured data of heterotrophic respiration, we 279 could not conduct a regional validation for all pixels in northern high latitudes. Instead, we 280 extracted 61 sites providing data of average annual heterotrophic respiration from ORNL global 281 Soil Respiration Dataset (https://daac.ornl.gov/SOILS/guides/SRDB V4.html, Bond-Lamberty et 282 al., 2018) for model validation. The site-level observed average annual $R_{\rm H}$ was used to compare 283 with simulated annual R_H by MIC-TEM-dormancy and MIC-TEM. The new model (MIC-TEM-284 dormancy) was run at monthly time step to keep consistent with the time step of MIC-TEM. Although microbial dynamics occur at fine temporal scales (Tang & Riley, 2014), we can still 285 286 quantify the cumulative impacts of microbial dynamics on carbon and nitrogen cycling at monthly 287 time by not changing the model structure.

288

289 **2.4 Spatial extrapolation**

For historical simulations during the 20th century, two sets of regional simulations using 290 291 MIC-TEM-dormancy and MIC-TEM at a spatial resolution of 0.5° latitude $\times 0.5^{\circ}$ longitude were 292 conducted. Our model simulation contains two parts: spin-up and transient simulation. A typical spin-up was conducted to get the model to a steady state for each spatial location, which will be 293 294 used as initial conditions for transient simulations (McGuire et al., 1992). During spin-up 295 procedure, cyclic forcing data was used to force the model run, and repeated continuously until 296 dynamic equilibrium was achieved at which the modeled state variables show a cyclic pattern or 297 become constant. Specifically, this study used the monthly historical climate data from 1900 to 298 1940 to repeatedly drive the model for the spin-up. Before spin-up procedure, the model was

299 initialized with default built-in carbon stocks (Raich et al., 1991). During transient simulations, 300 the calibrated ecosystem-specific parameters were used for regional simulations. The previous 301 dynamic equilibrium was used as initial value for transient simulation. The historical climatic 302 forcing data, including the monthly air temperature, precipitation, cloudiness, and atmospheric 303 CO₂ concentrations, were organized from the Climatic Research Unit (CRU TS3.1) from the 304 University of East Anglia (Harris et al., 2014). We also used gGridded data of soil texture (Zhuang 305 et al., 2003), elevation (Zhuang et al., 2015), and potential natural vegetation (Melillo et al., 1993) 306 from literatures were also used. In our model, we assumed that soil texture, elevation, and potential 307 natural vegetation data only vary spatially, not vary over time (Zhuang et al., 2015).

In addition, regional simulations over the 21st century were conducted under two 308 309 Intergovernmental Panel on Climate Change (IPCC) climate scenarios (RCP 2.6 and RCP 8.5). 310 The future climatic forcing data under these two climate change scenarios were derived from the 311 HadGEM2-ESmodel, which CMIP5project213 (https://esgfis а member of node.llnl.gov/search/cmip5/). Then the regional estimations were obtained by summing up the 312 gridded outputs for our study region. The positive simulated NEP represents a CO₂ sink from the 313 atmosphere to terrestrial ecosystems, while a negative value represents a source of CO₂ from 314 315 terrestrial ecosystems to the atmosphere.

316 <u>2.5 Parameter equifinality effects uncertainty</u>

Our previous studies using TEM has demonstrated that equifinality derived from site-level
 parameterization will affect the uncertainty in the estimation of regional carbon dynamics (Tang
 and Zhuang, 2008, 2009). Here equifinality refers to that a number of sets of parameters result in
 model simulations that all match the data similarly well. To quantify this e-effect on our simulation
 uncertainty, parameter uncertainty in our model, we conducted ensemble regional simulations with

- 322 <u>50 sets of parameters for both historical and future studies. The 50 sets of parameters were obtained</u>
 323 <u>according to the method in Tang and Zhuang (2008).</u>
- 324 **3. Results**

325 **3.1 Inversed Model Parameters and model validation**

326 Using SCE-UA ensemble method, 50 independent sets of parameters were converged to 327 minimize the objective function. Then the optimized parameters are calculated as the mean of these 328 50 sets of inversed parameters. The boxplot of parameter posterior distributions reflects different 329 ecosystem properties at these sites (Figure 3). For instance, growth yieldearbon use efficiency 330 (CUE) was <u>much</u> higher in tundra types than in forests, meaning microorganisms in environment with higher energy limitation tend to enhance the efficiency of energy transportation. Besides, 331 332 alpha, the maintenance weight, was also<u>much</u> higher in tundra types than in forests. FThe opposite 333 can be seen from the plot for parameter beta, the ratio of dormant maintenance rate to specific 334 maintenance rate for active biomass in tundra types is lower than that it in forest types. Other 335 microbial related parameters did not differentiate much among different vegetation types.

336 After parameterization, the MIC-TEM-dormancy was validated with monthly NEP data for six representative ecosystems, and the comparisons between monthly observed NEP and 337 338 simulated NEP were presented in Figure 4. With the optimized parameters, the dormancy-based 339 model was used to reproduce NEP to compare with the measured NEP (Table 5). The statistical analysis shows that R² ranges from 0.67 for Atqasuk to 0.93 for Bartlett Experimental Forest 340 341 (Table 5). Generally, our new model performs better for forest ecosystems than for tundra 342 ecosystems. Compared with MIC-TEM, which is no dormancy-based, dormancy model performs 343 better for alpine tundra, temperate coniferous forest, and grassland. For other sites, bothtwo 344 models show similar performance (Table 5). Besides, aAnother set of sites with monthly soil

345 respiration data were selected to evaluate validate the ability of the estimated ing R_H of our 346 modelconduct model validation. The comparisons between monthly observed R_H and simulated $R_{\rm H}$ from two contrasting models were conducted (Figure 5). MIC-TEM-dormancy has higher R^2 347 348 and lower root mean square error (RMSE) (Table 6). Sixty-one sites with average annual $R_{\rm H}$ in 349 northern high-latitude regions were used to further evaluate the new model performance. The dormancy model has lower intercept and slope with R² of 0.45, while R² of MIC-TEM is 0.3 350 351 (Figure 6). These analyses indicate that new model is more realistic in representing heterotrophic 352 respiration ($R_{\rm H}$) by considering microbial dormancy. This difference in $R_{\rm H}$ further affects soil 353 available nitrogen dynamics, influencing nitrogen uptake by plants, the rate of photosynthesis 354 and NPP (Zhuang et al., 2015; Zha et al., 2018; Thullner et al., 2005).

355

356 **3.2 Regional carbon dynamics during the 20th century**

357 Regional extrapolation with both models estimated a regional carbon sink but with different 358 magnitudes (Figure 7c). Here positive values of NEP represent sinks of CO₂ into terrestrial 359 ecosystems, while negative values represent sources of CO₂ to the atmosphere. With optimized 360 parameters, MIC-TEM estimated a regional carbon sink of 77.6 Pg with the interannual standard deviation of 0.21 Pg C yr⁻¹ during the 20th century. However, MIC-TEM-dormancy nearly doubles 361 the sink at 153.5 Pg with the interannual standard deviation of 0.12 Pg C yr⁻¹ during the last 362 363 century, which estimates 75.9 Pg more carbon sink than MIC-TEM does but with less interannual 364 variation (Figure 7c). At the end of the century, MIC-TEM estimated that NEP reaches 1.0 Pg C yr⁻¹ in comparison with MIC-TEM-dormancy estimates of 1.5 Pg C yr⁻¹ (Figure 7c). Both models 365 366 simulated similar trends for regional NPP, R_H and NEP (Figure 7). Generally, they show an 367 increasing trend in the 20th century except a slight decrease during the 1960s (Figure 7).

368 Meanwhile, with optimized parameters, MIC-TEM-dormancy estimated NPP and R_H at 7.94 Pg C yr⁻¹ and 6.4 Pg C yr⁻¹, which are 5.8% and 16.3% less than the estimations from MIC-TEM, 369 370 respectively (Figures 7a and 7b). This pronounced difference of NEP between two models comes 371 from the disparity between the simulated NPP and R_H with them since NEP is calculated as the 372 difference between NPP and R_H. Without considering dormancy, MIC-TEM estimates more active 373 microbial biomass since it assumes the whole microbial biomass pool will participate in soil 374 decomposition. The fact is only active part of microbial biomass can affect decompose organic 375 matter decompositionwork for soil decomposition, meaning MIC-TEM overestimates R_H. On the other hand, ooverestimation of R_H can induce higher nitrogen uptake by plants, which will 376 accelerate rate of photosynthesis and further enhance NPP projection. Although MIC-TEM 377 378 estimates higher NPP and R_H than MIC-TEM-dormancy does, NEP estimated from MIC-TEM is 379 actually lower.

380 The average annual seasonal patterns of NPP, R_H and NEP during the 1990s were also 381 organized from regional simulations with two models (Figure 8). Temporally, both two-models 382 projected higher NPP and R_H in summer than in winter (Figures 8a and 8b) due to higher soil 383 temperature and moisture (McGuire et al., 1992). Setting the R_H projection from MIC-TEM as a 384 baseline, MIC-TEM-dormancy averagely projected 33% less R_H in summer (May to September), 385 and 30% more in winter (other months)MIC-TEM produced less R_H in winter but higher R_H in 386 summer than MIC-TEM-dormancy (Figure 8b), which indicates that without dormancy, model 387 tends to estimate lower soil respiration compared to dormancy model due to ignorance of 388 dormant respiration in winter but estimate higher soil respiration due to higher estimation of 389 active biomass in summer. In the meantime, seasonal cycle of NPP with MIC-TEM-dormancy 390 shows a relative flattening pattern compared with MIC-TEM, which is similar to seasonal cycle

391 of R_H (Figure 8a). This is because higher R_H-can cause higher NPP due to the reasons we have 392 mentioned above. Though R_H and NPP show the similar seasonal patterns, NEP can still show 393 different pattern since it's the difference between NPP and R_H. Here seasonal cycles of NEP with 394 models are close to each other (Figure 8c), but dormancy model projected slightly higher NEP in 395 summer. Besides, setting the R_H projection from MIC-TEM as baseline, MIC-TEM-dormancy 396 averagely projected 33% less R_H in summer (May to September), and 30% more in winter (other months). This suggested that relative difference of R_H between two models in summer was 397 398 higher than in winter.

399 3.3 Regional carbon dynamics during the 21st century

400 Under the RCP 8.5 scenario, both models estimated the region acts as a carbon sink (Figure 401 9). The MIC-TEM-dormancy predictedesd a net-C accumulation sequestration of 129.9 Pg by 402 the end of this century. that the sink is 129.9 Pg with the interannual standard deviation of 0.13 Pg C yr⁻¹, whereas MIC-TEM estimates <u>a net-C accumulation sequestration of 79.5 Pg the sink is</u> 403 79.5 Pg with the interannual standard deviation of 0.37 Pg C yr⁻¹ during the 21st century (Figure 404 9). Thus, MIC-TEM-dormancy estimates an increase of 50.4 Pg regional carbon sequestration 405 406 relative to MIC-TEM, but with less interannual variation (Figure 9). Under this scenario, bBoth 407 models predict similar temporal trends for NEP, namely increasing from the 2000s and then 408 decreasing from the 2070s onward (Figure 9). MIC-TEM-dormancy predicts that carbon sink reaches 1.36 Pg C yr⁻¹ in the 2090s, which is 0.26 Pg C yr⁻¹ more than projection of MIC-TEM. 409 Moreover, MIC-TEM-dormancy estimated NPP and R_H at 10.2 Pg C yr⁻¹ and 8.9 Pg C yr⁻¹, 410 which are 1.3 Pg C yr⁻¹ and 1.8 Pg C yr⁻¹ less than the estimations from MIC-TEM, respectively 411

412 (Figure 9).

413	Under the RCP 2.6 scenario, the cumulative NEP from two models diverged by 125.2 Pg C
414	by 2100. The trajectory of inter-annual NEP estimated with the two models also diverged. The
415	MIC-TEM predicted the region fluctuates between carbon sinks and sources, and totally acts as a
416	carbon source of 1.6 Pg C with the interannual standard deviation of 0.24 Pg C yr ⁻¹ during the
417	21 st century. In contrast, MIC-TEM-dormancy projected the region acts as a carbon sink of 123.6
418	Pg C with <u>anthe</u> interannual standard deviation of 0.1 Pg C yr ⁻¹ (Figure 9). MIC-TEM-dormancy
419	estimates NPP and R_H at 9.9 Pg C yr ⁻¹ and 8.7 Pg C yr ⁻¹ , which are 0.5 Pg C yr ⁻¹ and 1.7 Pg C yr ⁻¹
420	¹ less than the estimations from MIC-TEM, respectively (Figure 9). Moreover, simulations under
421	the two contrasting climate scenarios (RCP 2.6 and RCP 8.5) exhibit a large difference of 81.1
422	Pg C of cumulative NEP during the 21st century by MIC-TEM, but only 6.3 Pg C of that by
423	MIC-TEM-dormancy. This difference indicates microbes provide a resistant response to climate
424	change due to dormancy to some extent (Treseder et al., 2011).
425	The average annual seasonal patterns of NPP, $R_{\rm H}$ and NEP during the 2990s by two models were
426	also presented (Figure 10). MIC-TEM-dormancy estimated higher $R_{\rm H}$ in winter, but lower $R_{\rm H}$ in
427	summer under both future scenarios (Figure 10). <u>NPP is the same in winter with or without</u>
428	dormancy, and in the late summer is higher with than that without dormancy (i.e. opposite to
429	RH), especially in the RCP 8.5 scenario. Similar seasonal cycle pattern appears for NPP
430	projection. The combined flattening patterns of NPP and R_H result in different patterns for NEP.
431	Under the RCP 2.6 scenario, MIC-TEM-dormancy predicts higher NEP from June to October,
432	but lower NEP from January to April compared-similar NEP in other months to MIC-TEM
433	(Figure 10). Under the RCP 8.5 scenario, MIC-TEM-dormancy predicts higher NEP from June
434	to September, but much lower NEP in other months than MIC-TEM (Figure 10).
1	

435 <u>3.4 Regional uncertainty considering equifinality effects Ensemble simulations</u> during for
 436 20th and 21st centuries

- The ensemble simulations for the 20^{th} century is shown in Figure 11. Given the 437 438 uncertainty in parameters, MIC-TEM-dormancy predicted that the regional cumulative carbon 439 ranges from a carbon loss of 28.2 Pg to a carbon sink of 362.1 Pg by different ensemble 440 members, with a mean of 71.2 ± 54.8 Pg (Figure 11). For the 21^{st} century, MIC-TEM-dormancy 441 predicted that the region acts from a carbon source of 49.3 Pg C to a carbon sink of 296.5 Pg C, with a mean of 112.7±116.5 Pg under the RCP 2.6 scenario (Figure 12). Under the RCP 8.5 442 443 scenario, MIC-TEM-dormancy predicted that the region acts from a carbon source of 27.1 Pg C 444 to a carbon sink of 401.3 Pg C, with a mean of 143.1±162.5 Pg (Figure 12). 445 4. Discussion Soils are the largest carbon repository in the terrestrial biosphere and hold 2.5 times more 446 447 carbon than the atmosphere (Frey et al., 2013; Schlesinger & Andrews, 2000). Especially, a 448 significant portion of soil organic carbon currently stored in northern high latitudes region 449 (Tarnocai et al., 2009). Besides, the magnitude of the warming in these regions is larger, almost 450 twice, that of the global average climate over this region has warmed in recent decades (Serreze 451 & Francis, 2006) and the changing climate is expected to alter the carbon cycle through 452 influencing the activities of microorganisms in controlling soil decomposition (Manzoni et al., 453 2012; Melillo et al., 2011). Therefore, explicit consideration of microbial traits and functions in 454 large-scale biogeochemistry models is necessary for better quantification of carbon-climate 455 feedbacks (Thullner et al., 2005; Wang et al., 2015). Our regional simulations with two
- 456 contrasting models (MIC-TEM, MIC-TEM-dormancy) indicate the region was a carbon sink in
- 457 past decades, which is consistent with results from other process-based models (White et al.,

458 2000; Houghton et al., 2007; McGuire et al., 2009; Schimel, 2013). However, the magnitudes of 459 this sink are quite different in two models. Moreover, MIC-TEM-dormancy predicts the sink will 460 decrease under both RCP 8.5 and RCP 2.6 scenarios during the 21st century, while MIC-TEM 461 projects that the sink will increase under the RCP 8.5 but change to carbon source under the RCP 462 2.6 scenario. Estimations based on models without dormancy could fit observations of R_H as well 463 as estimations with dormancy, but at the cost of underestimating microbial biomass (Wang et al., 464 2014). Differences in predicted $R_{\rm H}$ with and without dormancy increase with temperature and 465 with the length of the dry periods between wetting events (Salazar et al., 2018). The large 466 difference in two models suggests the importance of incorporating microbial dormancy effects. The large bias between dormancy and non-dormancy models mainly comes from two parts. 467 468 First, many-most important microbial activities such as soil organic carbon decomposition and 469 nutrient cycling largely depend on the active fraction of microbial communities, not total 470 microbial biomass (Wang et al., 2014; Blagodatsky et al., 2000). However, only a small part 471 (about 0.1-2%, seldom exceed 5%) of the total soil microbial biomass is recognized to be active 472 under natural conditions (Blagodatsky et al., 2011; Werf & Verstraete, 1987). Thus, dormancy 473 could be a prominent feature in soil systems (Wang et al., 2014). Without considering dormancy, 474 the "effective" microbial biomass for soil decomposition could be overestimated, resulting in 475 overestimation of heterotrophic respiration (He et al., 2015). Our regional estimate of R_H is 6.4 Pg C yr⁺ during the 20th century by MIC-TEM-dormancy, while 7.7 Pg C yr⁺ by MIC-TEM. No 476 dormancy model simulated 20.3% higher respiration than dormancy model. For future 477 simulations, MIC-TEM-dormancy predicted 8.7 Pg C yr⁻¹ and 9.0 Pg C yr⁻¹ of R_H under RCP 2.6 478 and RCP 8.5 scenarios during the 21st century, respectively. Nevertheless, no dormancy model 479 480 simulated 19.5% and 21.2% higher respiration than dormancy model under RCP 2.6 and RCP 8.5 481 scenarios, respectively. He et al. (2015) predicted total soil R_H of all temperate forests (25°N-50°N) from the dormancy model amounted to 7.28 Pg C yr⁻¹ and 8.83 Pg C yr⁻¹ from a no-482 483 dormancy model, which is 21.3% higher than the dormancy model. Although their study region 484 and simulation period are different from our study, the results can still be comparable. Both 485 studies indicated that the magnitude of R_H and proportion from no-dormancy model are higher 486 than dormancy models. Second, high soil respiration stimulates N mineralization in soils 487 (Zhuang et al., 2001, 2002), making more nutrients for photosynthesis of plants (Raich et al., 488 1991; McGuire et al., 1995). Therefore, NPP will be higher due to the N enrichment from higher 489 R_H. However, how NEP will change is still unclear. Our regional estimate of NEP during the 20th century by MIC-TEM-dormancy is 1.54 Pg C yr⁻¹, and is 0.78 Pg C yr⁻¹ by MIC-TEM. Our 490 estimates of the northern extratropical NEP in the 1980s (1.61 Pg C yr⁻¹ with MIC-TEM-491 dormancy and 0.84 Pg C yr⁻¹ with MIC-TEM) are within ranges (0.6 to 2.3 PgC yr⁻¹) reported in 492 the literature for northern regions (Schimel et al., (2001). reported that a range of estimates of the 493 northern extratropical NEP is from 0.6 to 2.3 PgC yr⁴ in the 1980s. In comparison with our 494 estimates of 1.61 Pg C yr⁴ with MIC-TEM-dormancy and 0.84 Pg C yr⁴ with MIC-TEM, our 495 496 regional estimates of NEP are in reasonable range. Moreover, our predicted time trajectory trend 497 of NEP in the 21st century under the RCP 2.6 scenario is very similar to the finding of White et 498 al. (2000), indicating that NEP increases from the 2000s to the 2070s, and then decreases in the 499 2090s. Moreover, future simulations under two contrasting climate scenarios (RCP 2.6 and RCP 500 8.5) exhibit a large difference of 81.1 Pg C of cumulative NEP during the 21st century by MIC-TEM, but only 6.3 Pg C of that by MIC-TEM-dormancy. This difference indicates microbes 501 502 provide a resistant response to climate change due to dormancy to some extent (Treseder et al., 503 2011).

504 Although our dormancy model can project reasonable carbon fluxes and indicate the 505 importance of incorporating microbial dormancy when compared with MIC-TEMno dormancy 506 model (MIC TEM; Zha & Zhuang et al., 2018), there are some other microbial traits have not yet 507 been considered in our model. For instance, one vital common evolutionary trait of microbe is 508 the community shift (Wang et al., 2015) with changing environment, including warming, N 509 fertilization and precipitation (Treseder et al., 2011; Frey et al., 2013; Allison et al., 2009; Evans 510 & Wallenstein, 2011). Community shift will influence microbial physiology, temperature 511 sensitivity and growth rates (Classen et al., 2015), which will further affect the rate of soil 512 decomposition and other carbon dynamics (Treseder et al., 2011; Schimel & Schaeffer, 2012; 513 Todd-Brown et al., 2011). Moreover, microbial acclimation is another important trait to affect 514 soil decomposition. Recent studies have found the capacity of the microbial community to 515 maintain the warming-induced elevated respiration could decrease over time because of 516 acclimation (Melillo et al. 1993; Todd-Brown et al., 2011). This mechanism of adaption to a new 517 temperature regime shall be factored into future soil decomposition analysis. Besides, microbial 518 community composition was ignored in our model. We didn't separate among functional 519 microbial groups, but gather microbes into one "box". However, microbial community 520 composition could influence ecosystem functioning, and their variance in responses to 521 environmental conditions could alter the prediction of the rates of decomposition of organic 522 material (Balser et al. 2002; Fierer et al. 2007). Especially, some narrowly-distributed functions 523 can be more sensitive to microbial community composition, and these might benefit most from 524 explicit consideration of distinguishing functional groups in ecosystem models (McGuire & 525 Treseder, 2010; Schimel 1995). Thus, functional dissimilarity in microbial communities can be 526 considered in next step for model development (Strickland et al., 2009; Moorhead et al., 2006).

Moreover, microbial acclimation, a mechanism of adaption to a new temperature regime, is
 another important trait to affect soil decomposition. Recent studies have found that the warming induced elevated respiration of the microbial community could decrease over time because of
 acclimation (Melillo et al. 1993; Todd-Brown et al., 2011). This mechanism shall be factored
 into future soil decomposition analysis.

532 Except for <u>model limitations mentioned above model limitations</u>, additional 533 uncertainties may come from inadequate model parameterization and model assumptions. For 534 example, a critical microbial parameter, carbon use efficiency (CUE), is a primary control to soil 535 CO₂ efflux. Higher CUE indicates more microbial growth and more carbon uptake by plants, 536 while lower CUE indicates higher soil decomposition (Manzoni et al., 2012). Theoretical and 537 empirical studies have suggested that CUE depends on both temperature and substrate quality 538 (Frey et al., 2013) and decreases as temperature increases and nutrient availability decreases 539 (Manzoni et al., 2012). Our study considered the CUE sensitivity to temperature, but not nutrient 540 availability. On the other hand, some model assumptions can also cause uncertainties. For 541 example, we assumed that vegetation will not change during the transient simulation. However, 542 over the past few decades in northern high latitudes, temperature increases have led to vegetation 543 shift from one type to another (Hansen et al., 2006; White et al., 2000). The vegetation changes 544 will affect carbon cycling in these ecosystems.

545

546 **5.** Conclusions

547 This study incorporated microbial dormancy into a detailed microbial-based soil
548 decomposition biogeochemistry model to examine the fate of large Arctic soil carbon under
549 changing climate conditions. Regional simulations using MIC-TEM-dormancy indicated that,

over the 20th century, the region is a carbon sink of 153.5 Pg. This sink could decrease to 129.9 550 551 Pg under the RCP 8.5 scenario or 123.6 Pg under the RCP 2.6 scenario during the 21st century. 552 Whether considering microbial dormancy or not can cause large differences in soil 553 decomposition estimation between two models. Meanwhile, due to available nitrogen affected by 554 soil decomposition, net primary production is consequently influenced in these two centuries. 555 The combined changes in soil decomposition and net primary production led to large differences 556 in carbon budget estimation between two models. Compared with MIC-TEM, MIC-TEM-557 dormancy projected 75.9 Pg more C stored in the terrestrial ecosystems over the last century, 558 50.4 Pg and 125.2 Pg more C under the RCP 8.5 and RCP 2.6 scenarios, respectively. This study 559 highlights the importance of the representation of microbial dormancy in earth system models in 560 order to adequately quantify the carbon dynamics in northern high latitudes.

561

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574 **References:**

- 575 Allison, E. H., Perry, A. L., Badjeck, M.-C., Neil Adger, W., Brown, K., Conway, D., Halls, A.
- 576 S., Pilling, G. M., Reynolds, J. D., Andrew, N. L., and Dulvy, N. K.: Vulnerability of national
- economies to the impacts of climate change on fisheries, Fish and Fisheries, 10, 173-196,
 10.1111/j.1467-2979.2008.00310.x, 2009.
- 579 Allison, S. D., Wallenstein, M. D., and Bradford, M. A.: Soil-carbon response to warming
- dependent on microbial physiology, Nature Geoscience, 3, 336-340, 10.1038/ngeo846, 2010.
- 581 Balser, T. C., Kinzig, A. P., and Firestone, M. K.: Linking soil microbial communities and
- 582 ecosystem functioning, The functional consequences of biodiversity: Empirical progress and
- theoretical extensions, 265-293, 2002.
- 584 Blagodatskaya, E., and Kuzyakov, Y.: Active microorganisms in soil: Critical review of
- estimation criteria and approaches, Soil Biology and Biochemistry, 67, 192-211,
- 586 10.1016/j.soilbio.2013.08.024, 2013.
- 587 Blagodatskaya, E., Khomyakov, N., Myachina, O., Bogomolova, I., Blagodatsky, S., and
- 588 Kuzyakov, Y.: Microbial interactions affect sources of priming induced by cellulose, Soil
- 589 Biology and Biochemistry, 74, 39-49, 10.1016/j.soilbio.2014.02.017, 2014.
- 590 Blagodatsky, S., Grote, R., Kiese, R., Werner, C., and Butterbach-Bahl, K.: Modelling of
- 591 microbial carbon and nitrogen turnover in soil with special emphasis on N-trace gases emission,
- 592 Plant and soil, 346, 297-330, 10.1007/s11104-011-0821-z, 2011.
- 593 Blagodatsky, S. A., Heinemeyer, O., and Richter, J.: Estimating the active and total soil
- microbial biomass by kinetic respiration analysis, Biol Fertil Soils, 32, 73-81, 2000.
- 595 Bond-Lamberty, B., and Thomson, A.: Temperature-associated increases in the global soil
- respiration record, Nature, 464, 579-582, 10.1038/nature08930, 2010.
- 597 Bond-Lamberty, B., Bailey, V. L., Chen, M., Gough, C. M., and Vargas, R.: Globally rising soil
- heterotrophic respiration over recent decades, Nature, 560, 80-83, 10.1038/s41586-018-0358-x,
 2018.
- 600 Bouskill, N. J., Tang, J., Riley, W. J., and Brodie, E. L.: Trait-based representation of biological
- nitrification: model development, testing, and predicted community composition, Frontiers in
 microbiology, 3, 364, 10.3389/fmicb.2012.00364, 2012.
- 603 Callaghan, T., Björn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., Ims, R.,
- Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., and Shaver, G.: Arctic tundra
- and polar desert ecosystems, Arctic climate impact assessment, 243-352, 2005.
- 606 Carney, K. M., and Matson, P. A.: The influence of tropical plant diversity and composition on
- 607 soil microbial communities, Microbial ecology, 52, 226-238, 10.1007/s00248-006-9115-z, 2006.
- 608 Chmlelewrki, R. A. N., and Frank, J. F.: Formation of viable but nonculturable Salmonella
- during starvation in chemically defined solutions, Letters in Applied Microbiology, 20, 380-384,1995.
- 611 Classen, A. T., Sundqvist, M. K., Henning, J. A., Newman, G. S., Moore, J. A. M., Cregger, M.
- A., Moorhead, L. C., and Patterson, C. M.: Direct and indirect effects of climate change on soil
- 613 microbial and soil microbial-plant interactions: What lies ahead?, Ecosphere, 6, art130,
- 614 10.1890/es15-00217.1, 2015.
- 615 Conant, R. T., Ryan, M. G., Ågren, G. I., Birge, H. E., Davidson, E. A., Eliasson, P. E., Evans, S.
- E., Frey, S. D., Giardina, C. P., Hopkins, F. M., Hyvönen, R., Kirschbaum, M. U. F., Lavallee, J.
- 617 M., Leifeld, J., Parton, W. J., Megan Steinweg, J., Wallenstein, M. D., Martin Wetterstedt, J. Å.,
- and Bradford, M. A.: Temperature and soil organic matter decomposition rates synthesis of

- 619 current knowledge and a way forward, Global change biology, 17, 3392-3404, 10.1111/j.1365-
- 620 2486.2011.02496.x, 2011.
- 621 Coursolle, C., Margolis, H. A., Barr, A. G., Black, T. A., Amiro, B. D., McCaughey, J. H.,
- 622 Flanagan, L. B., Lafleur, P. M., Roulet, N. T., Bourque, C. P. A., Arain, M. A., Wofsy, S. C.,
- 623 Dunn, A., Morgenstern, K., Orchansky, A. L., Bernier, P. Y., Chen, J. M., Kidston, J., Saigusa,
- 624 N., and Hedstrom, N.: Late-summer carbon fluxes from Canadian forests and peatlands along an
- east–west continental transect, Canadian Journal of Forest Research, 36, 783-800, 10.1139/x05-
- **626** 270, 2006.
- 627 Davidson, E. A., Trumbore, S. E., and Amundson, R.: Biogeochemistry: soil warming and
- 628 organic carbon content, Nature, 408, 2000.
- Davidson, E. A., and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and
 feedbacks to climate change, Nature, 440, 165-173, 10.1038/nature04514, 2006.
- 631 Davidson, E. A., Janssens, I. A., and Luo, Y.: On the variability of respiration in terrestrial
- ecosystems: moving beyond Q10, Global change biology, 12, 154-164, 10.1111/j.1365-
- 632 ecosystems: moving beyond Q10, Global change biology, 12, 154-164, 10.1111/j.1365-
- 633 2486.2005.01065.x, 2006.
- 634 Davidson, E. A., Samanta, S., Caramori, S. S., and Savage, K.: The Dual Arrhenius and
- 635 Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to seasonal
- time scales, Global change biology, 18, 371-384, 10.1111/j.1365-2486.2011.02546.x, 2012.
- 637 Duan, Q., Sorooshian, S., and Gupta, V. K.: Optimal use of the SCE-UA global optimization
- method for calibrating watershed models, Journal of Hydrology, 158, 265-284, 1994.
- 639 Evans, S. E., and Wallenstein, M. D.: Soil microbial community response to drying and
- rewetting stress: does historical precipitation regime matter?, Biogeochemistry, 109, 101-116,
- 641 10.1007/s10533-011-9638-3, 2011.
- 642 Fierer, N., Morse, J. L., Berthrong, S. T., Bernhardt, E. S., and Jackson, R. B.: Environmental
- 643 controls on the landscape scale biogeography of stream bacterial communities, Ecology, 88, 2162-2173-2007
- 6442162-2173, 2007.
- 645 Frey, S. D., Lee, J., Melillo, J. M., and Six, J.: The temperature response of soil microbial
- 646 efficiency and its feedback to climate, Nature Climate Change, 3, 395-398,
- 647 10.1038/nclimate1796, 2013.
- 648 Gangsheng Wang, M. A. M., Lianhong Gu, Christopher W. Schadt: Representation of Dormant
- and Active Microbial Dynamics for Ecosystem Modeling, Public Library of Science, 9,
 10.1371/journal.pone.0089252.g001, 2014.
- 651 German, D. P., Marcelo, K. R. B., Stone, M. M., and Allison, S. D.: The Michaelis-Menten
- 652 kinetics of soil extracellular enzymes in response to temperature: a cross-latitudinal study,
- 653 Global change biology, 18, 1468-1479, 10.1111/j.1365-2486.2011.02615.x, 2012.
- 654 Gilmanov, T. G., Tieszen, L. L., Wylie, B. K., Flanagan, L. B., Frank, A. B., Haferkamp, M. R.,
- Meyers, T. P., and Morgan, J. A.: Integration of CO2flux and remotely-sensed data for primary
- 656 production and ecosystem respiration analyses in the Northern Great Plains: potential for
- quantitative spatial extrapolation, Global Ecology and Biogeography, 14, 271-292,
- 658 10.1111/j.1466-822X.2005.00151.x, 2005.
- 659 Gough, C. M., Hardiman, B. S., Nave, L. E., Bohrer, G., Maurer, K. D., Vogel, C. S.,
- 660 Nadelhoffer, K. J., and Curtis, P. S.: Sustained carbon uptake and storage following moderate
- disturbancein a Great Lakes forest, Ecological Applications, 23, 1202-1215, 2013.
- Goulden, M. L., Winston, G. C., McMillan, A. M. S., Litvak, M. E., Read, E. L., Rocha, A. V.,
- and Rob Elliot, J.: An eddy covariance mesonet to measure the effect of forest age on

- land?atmosphere exchange, Global change biology, 12, 2146-2162, 10.1111/j.1365-
- 665 2486.2006.01251.x, 2006.
- 666 Graham, E. B., Wieder, W. R., Leff, J. W., Weintraub, S. R., Townsend, A. R., Cleveland, C. C.,
- 667 Philippot, L., and Nemergut, D. R.: Do we need to understand microbial communities to predict
- 668 ecosystem function? A comparison of statistical models of nitrogen cycling processes, Soil
- 669 Biology and Biochemistry, 68, 279-282, 10.1016/j.soilbio.2013.08.023, 2014.
- 670 Graham, E. B., Knelman, J. E., Schindlbacher, A., Siciliano, S., Breulmann, M., Yannarell, A.,
- 671 Beman, J. M., Abell, G., Philippot, L., Prosser, J., Foulquier, A., Yuste, J. C., Glanville, H. C.,
- Jones, D. L., Angel, R., Salminen, J., Newton, R. J., Burgmann, H., Ingram, L. J., Hamer, U.,
- 673 Siljanen, H. M., Peltoniemi, K., Potthast, K., Baneras, L., Hartmann, M., Banerjee, S., Yu, R. Q.,
- 674 Nogaro, G., Richter, A., Koranda, M., Castle, S. C., Goberna, M., Song, B., Chatterjee, A.,
- 675 Nunes, O. C., Lopes, A. R., Cao, Y., Kaisermann, A., Hallin, S., Strickland, M. S., Garcia-
- 676 Pausas, J., Barba, J., Kang, H., Isobe, K., Papaspyrou, S., Pastorelli, R., Lagomarsino, A.,
- 677 Lindstrom, E. S., Basiliko, N., and Nemergut, D. R.: Microbes as Engines of Ecosystem
- 678 Function: When Does Community Structure Enhance Predictions of Ecosystem Processes?,
- 679 Frontiers in microbiology, 7, 214, 10.3389/fmicb.2016.00214, 2016.
- 680 Griffis, T. J., Lee, X., Baker, J. M., Billmark, K., Schultz, N., Erickson, M., Zhang, X.,
- 681 Fassbinder, J., Xiao, W., and Hu, N.: Oxygen isotope composition of evapotranspiration and its
- relation to C4photosynthetic discrimination, Journal of Geophysical Research, 116,
- 683 10.1029/2010jg001514, 2011.
- Hagerty, S. B., van Groenigen, K. J., Allison, S. D., Hungate, B. A., Schwartz, E., Koch, G. W.,
- 685 Kolka, R. K., and Dijkstra, P.: Accelerated microbial turnover but constant growth efficiency
- with warming in soil, Nature Climate Change, 4, 903-906, 10.1038/nclimate2361, 2014.
- Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D. W., and Medina-Elizade, M.: Global
- temperature change, Proceedings of the National Academy of Sciences of the United States of
 America, 103, 14288-14293, 10.1073/pnas.0606291103, 2006.
- Harder, w., and Dijkhuizen, L.: Physiological responses to nutrient limitation, Annual Review ofMicrobiology, 37, 1983.
- Harris, I., Jones, P. D., Osborn, T. J., and Lister, D. H.: Updated high-resolution grids of monthly
- climatic observations the CRU TS3.10 Dataset, International Journal of Climatology, 34, 623642, 10.1002/joc.3711, 2014.
- He, Y., Yang, J., Zhuang, Q., Harden, J. W., McGuire, A. D., Liu, Y., Wang, G., and Gu, L.:
- 696 Incorporating microbial dormancy dynamics into soil decomposition models to improve
- 697 quantification of soil carbon dynamics of northern temperate forests, Journal of Geophysical
- 698 Research: Biogeosciences, 120, 2596-2611, 10.1002/2015jg003130, 2015.
- Hiller, R. V., McFadden, J. P., and Kljun, N.: Interpreting CO2 Fluxes Over a Suburban Lawn:
- 700 The Influence of Traffic Emissions, Boundary-Layer Meteorology, 138, 215-230,
- 701 10.1007/s10546-010-9558-0, 2010.
- Houghton, R. A.: Balancing the Global Carbon Budget, Annual Review of Earth and Planetary
- 703 Sciences, 35, 313-347, 10.1146/annurev.earth.35.031306.140057, 2007.
- Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A. G., Ping, C. L.,
- 705 Schirrmeister, L., Grosse, G., Michaelson, G. J., Koven, C. D., amp, apos, Donnell, J. A.,
- 706 Elberling, B., Mishra, U., Camill, P., Yu, Z., Palmtag, J., and Kuhry, P.: Estimated stocks of
- circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps,
- 708 Biogeosciences, 11, 6573-6593, 10.5194/bg-11-6573-2014, 2014.

- 709 Jenkins, J. P., Richardson, A. D., Braswell, B. H., Ollinger, S. V., Hollinger, D. Y., and Smith,
- 710 M. L.: Refining light-use efficiency calculations for a deciduous forest canopy using
- 711 simultaneous tower-based carbon flux and radiometric measurements, Agricultural and Forest
- 712 Meteorology, 143, 64-79, 10.1016/j.agrformet.2006.11.008, 2007.
- Kaiser, C., Franklin, O., Dieckmann, U., and Richter, A.: Microbial community dynamics 713
- 714 alleviate stoichiometric constraints during litter decay, Ecology letters, 17, 680-690,
- 715 10.1111/ele.12269, 2014.
- 716 Knorr, W., Prentice, I. C., House, J. I., and Holland, E. A.: Long-term sensitivity of soil carbon
- 717 turnover to warming, Nature, 433, 2005.
- 718 Lawrence, C. R., Neff, J. C., and Schimel, J. P.: Does adding microbial mechanisms of
- 719 decomposition improve soil organic matter models? A comparison of four models using data
- 720 from a pulsed rewetting experiment, Soil Biology and Biochemistry, 41, 1923-1934,
- 721 10.1016/j.soilbio.2009.06.016, 2009.
- 722 Lennon, J. T., and Jones, S. E.: Microbial seed banks: the ecological and evolutionary
- implications of dormancy, Nature reviews. Microbiology, 9, 119-130, 10.1038/nrmicro2504, 723
- 724 2011.
- 725 Lloyd, A. H., Rupp, T. S., Fastie, C. L., and Starfield, A. M.: Patterns and dynamics of treeline
- 726 advance on the Seward Peninsula, Alaska, Journal of Geophysical Research, 108,
- 727 10.1029/2001jd000852, 2002.
- 728 Manzoni, S., Taylor, P., Richter, A., Porporato, A., and Agren, G. I.: Environmental and
- 729 stoichiometric controls on microbial carbon-use efficiency in soils, The New phytologist, 196,
- 730 79-91, 10.1111/j.1469-8137.2012.04225.x, 2012.
- 731 McEwing, K. R., Fisher, J. P., and Zona, D.: Environmental and vegetation controls on the
- spatial variability of CH4 emission from wet-sedge and tussock tundra ecosystems in the Arctic, 732
- Plant and soil, 388, 37-52, 10.1007/s11104-014-2377-1, 2015. 733
- 734 McGuire, A. D., Melillo, J. M., Joyce, L. A., Kicklighter, D. W., Grace, A. L., III, B. M., and
- 735 Vorosmarty, C. J.: Interactions between carbon and nitrogen dynamics in estimating net primary
- 736 productivity for potential vegetation in North America, Global Biogeochemical Cycles, 6, 101-
- 737 124, 1992.
- 738 McGuire, A. D., Melillo, J. M., Kicklighter, D. W., and Joyce, L. A.: Equilibrium responses of
- 739 soil carbon to climate change: Empirical and process-based estimates, Journal of Biogeography,
- 740 22, 785-796, 1995.
- 741 McGuire, A. D., and Hobbie, J. E.: Global climate change and the equilibrium responses of
- 742 carbon storage in arctic and subarctic regions, In Modeling the Arctic system: A workshop report
- 743 on the state of modeling in the Arctic System Science program, 53-54, 1997.
- 744 McGuire, A. D., Anderson, L. G., Christensen, T. R., Dallimore, S., Guo, L., Hayes, D. J.,
- Heimann, M., Lorenson, T. D., Macdonald, R. W., and Roulet, N.: Sensitivity of the carbon 745
- 746 cycle in the Arctic to climate change, Ecological Monographs, 79, 523-555, 2009.
- 747 McGuire, K. L., and Treseder, K. K.: Microbial communities and their relevance for ecosystem
- 748 models: Decomposition as a case study, Soil Biology and Biochemistry, 42, 529-535,
- 749 10.1016/j.soilbio.2009.11.016, 2010.
- Me´tris, A., Gerrard, A. M., Cumming, R. H., Weigner, P., and Paca, J.: Modelling shock 750
- 751 loadings and starvation in the biofiltration of toluene and xylene, Journal of Chemical
- Technology and Biotechnology, 76, 565-572, 2001. 752
- 753 Melillo, J. M., McGuire, A. D., Kicklighter, D. W., III, B. M., Vorosmarty, C. J., and Schloss, A.
- L.: Global climate change and terrestrial net primary production, Nature, 363, 1993. 754

- 755 Melillo, J. M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., Burrows, E., Bowles, F.,
- 756 Smith, R., Scott, L., Vario, C., Hill, T., Burton, A., Zhou, Y.-M., and Tang, J.: Soil warming,
- carbon nitrogen interactions, and forest carbon budgets, PNAS, 108, 9508-9512, 2011.
- 758 Merbold, L., Kutsch, W. L., Corradi, C., Kolle, O., Rebmann, C., Stoy, P. C., Zimov, S. A., and
- 759 Schulze, E. D.: Artificial drainage and associated carbon fluxes (CO2/CH4) in a tundra
- 760 ecosystem, Global change biology, 15, 2599-2614, 10.1111/j.1365-2486.2009.01962.x, 2009.
- 761 Moorhead, D. L., and Sinsabaugh, R. L.: A theoretical model of litter decay and microbial
- interaction, Ecological Monographs, 76, 151-174, 2006.
- 763 Oechel, W. C., Laskowski, C. A., Burba, G., Gioli, B., and Kalhori, A. A. M.: Annual patterns
- and budget of CO2flux in an Arctic tussock tundra ecosystem, Journal of Geophysical Research:
- 765 Biogeosciences, 119, 323-339, 10.1002/2013jg002431, 2014.
- 766 P.J. Hanson, N. T. E., C.T. Garten, J.A. Andrews: Separating root and soil microbial
- 767 contributions to soil respiration: A review of methods and observations, Biogeochemistry, 48,768 115-146, 2000.
- 769 Parton, W. J., Scurlock, J. M. O., Ojima, D. S., Gilmanov, T. G., Scholes, R. J., Schimel, D. S.,
- 770 Kirchner, T., Menaut, J. C., Seastedt, T., Moya, E. G., Kamnalrut, A., and Kinyamario, J. I.:
- 771 Observations and modeling of biomass and soil organic matter dynamics for the grassland biome
- worldwide, Global Biogeochemical Cycles, 7, 785-809, 1993.
- 773 Raich, J. W., Rastetter, E. B., Melillo, J. M., Kicklighter, D. W., Steudler, P. A., Peterson, B. J.,
- Grace, A. L., III, B. M., and Vorosmarty, C. J.: Potential net primary productivity in South
- America: application of a global model, Ecological Applications, 1, 399-429, 1991.
- 776 Richardson, A. D., Jenkins, J. P., Braswell, B. H., Hollinger, D. Y., Ollinger, S. V., and Smith,
- 777 M. L.: Use of digital webcam images to track spring green-up in a deciduous broadleaf forest,
- 778 Oecologia, 152, 323-334, 10.1007/s00442-006-0657-z, 2007.
- 779 Running, S. W., and Coughlan, J. C.: A general model of forest ecosystem processes for regional
- applications I. Hydrologic balance, canopy gas exchange and primary production processes.,
- 781 Ecological Modelling, 42, 125-154, 1988.
- Schimel, D. S.: Terrestrial ecosystems and the carbon cycle, Global change biology, 1, 77-91,1995.
- Schimel, D. S., House, J. I., Hibbard, K. A., Bousquet, P., Ciais, P., Peylin, P., Braswell, B. H.,
- Apps, M. J., Baker, D., Bondeau, A., Canadell, J., Churkina, G., Cramer, W., Denning, A. S.,
- Field, C. B., Friedlingstein, P., Goodale, C., Heimann, M., Houghton, R. A., Melillo, J. M., III,
- 787 B. M., Murdiyarso, D., Noble, I., Pacala, S. W., Prentice, I. C., Raupach, M. R., Rayner, P. J.,
- 788 Scholes, R. J., Steffen, W. L., and Wirth, C.: Recent patterns and mechanisms of carbon
- exchange by terrestrial ecosystems, Nature, 414, 2001.
- 790 Schimel, J.: Microbes and global carbon, Nature Climate Change, 3, 867-868,
- 791 10.1038/nclimate2015, 2013.
- 792 Schimel, J. P., and Weintraub, M. N.: The implications of exoenzyme activity on microbial
- carbon and nitrogen limitation in soil: a theoretical model, Soil Biology and Biochemistry, 35,
- 794 549-563, 10.1016/s0038-0717(03)00015-4, 2003.
- Schimel, J. P., and Schaeffer, S. M.: Microbial control over carbon cycling in soil, Frontiers in
- 796 microbiology, 3, 348, 10.3389/fmicb.2012.00348, 2012.
- 797 Schlesinger, W. H., and Andrews, J. A.: Soil respiration and the global carbon cycle,
- 798 Biogeochemistry, 48, 7-20, 2000.
- 799 Schmidt, M. W., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber,
- 800 M., Kogel-Knabner, I., Lehmann, J., Manning, D. A., Nannipieri, P., Rasse, D. P., Weiner, S.,

- and Trumbore, S. E.: Persistence of soil organic matter as an ecosystem property, Nature, 478,
- **802** 49-56, 10.1038/nature10386, 2011.
- Serreze, M. C., and Francis, J. A.: The Arctic on the fast track of change, Weather, 61, 65-69,
 2006.
- 805 Stolpovsky, K., Martinez-Lavanchy, P., Heipieper, H. J., Van Cappellen, P., and Thullner, M.:
- Incorporating dormancy in dynamic microbial community models, Ecological Modelling, 222,
 3092-3102, 10.1016/j.ecolmodel.2011.07.006, 2011.
- 808 Stow, D. A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S.,
- 809 Racine, C., Sturm, M., Tape, K., Hinzman, L., Yoshikawa, K., Tweedie, C., Noyle, B.,
- 810 Silapaswan, C., Douglas, D., Griffith, B., Jia, G., Epstein, H., Walker, D., Daeschner, S.,
- 811 Petersen, A., Zhou, L., and Myneni, R.: Remote sensing of vegetation and land-cover change in
- 812 Arctic Tundra Ecosystems, Remote Sensing of Environment, 89, 281-308,
- 813 10.1016/j.rse.2003.10.018, 2004.
- 814 Strickland, M. S., Lauber, C., Fierer, N., and Bradford, M. A.: Testing the functional
- significance of microbial community composition, Ecology, 90, 441-451, 2009.
- 816 Tang, J., Q. Zhuang (2009) A global sensitivity analysis and Bayesian inference framework for
- 817 <u>improving the parameter estimation and prediction of a process-based Terrestrial Ecosystem</u>
- 818 <u>Model J. Geophys. Res., 114, D15303, doi:10.1029/2009JD011724., 2009.</u>
- 819 <u>Tang, J., Q. Zhuang (2008) Equifinality in parameterization of process-based biogeochemistry</u>
- models: A significant uncertainty source to the estimation of regional carbon dynamics J.
 Geophys. Res., 113, G04010, doi:10.1029/2008JG000757, 2008.
- 822 Tang, J., and Riley, W. J.: Weaker soil carbon–climate feedbacks resulting from microbial and
- abiotic interactions, Nature Climate Change, 5, 56-60, 10.1038/nclimate2438, 2014.
- 824 Tape, K. E. N., Sturm, M., and Racine, C.: The evidence for shrub expansion in Northern Alaska
- and the Pan-Arctic, Global change biology, 12, 686-702, 10.1111/j.1365-2486.2006.01128.x,
 2006.
- 827 Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., and Zimov, S.: Soil
- 828 organic carbon pools in the northern circumpolar permafrost region, Global Biogeochemical
- 829 Cycles, 23, n/a-n/a, 10.1029/2008gb003327, 2009.
- 830 Thullner, M., Van Cappellen, P., and Regnier, P.: Modeling the impact of microbial activity on
- redox dynamics in porous media, Geochimica et Cosmochimica Acta, 69, 5005-5019,
- 832 10.1016/j.gca.2005.04.026, 2005.
- 833 Todd-Brown, K. E. O., Hopkins, F. M., Kivlin, S. N., Talbot, J. M., and Allison, S. D.: A
- 834 framework for representing microbial decomposition in coupled climate models,
- Biogeochemistry, 109, 19-33, 10.1007/s10533-011-9635-6, 2011.
- 836 Todd-Brown, K. E. O., Randerson, J. T., Post, W. M., Hoffman, F. M., Tarnocai, C., Schuur, E.
- A. G., and Allison, S. D.: Causes of variation in soil carbon simulations from CMIP5 Earth
- system models and comparison with observations, Biogeosciences, 10, 1717-1736, 10.5194/bg-
- 839 10-1717-2013, 2013.
- 840 Treseder, K. K., Balser, T. C., Bradford, M. A., Brodie, E. L., Dubinsky, E. A., Eviner, V. T.,
- 841 Hofmockel, K. S., Lennon, J. T., Levine, U. Y., MacGregor, B. J., Pett-Ridge, J., and Waldrop,
- 842 M. P.: Integrating microbial ecology into ecosystem models: challenges and priorities,
- 843 Biogeochemistry, 109, 7-18, 10.1007/s10533-011-9636-5, 2011.
- 844 W. D. Billings, K. M. P., G. R. Shaver, A. W. Trent: Root Growth, Respiration, and Carbon
- 845 Dioxide Evolution in an Arctic Tundra Soil, Arctic and Alpine Research, 9, 129-137,
- 846 10.1080/00040851.1977.12003908, 1977.

- 847 Wang, G., M. A. M., Lianhong Gu, Christopher W. Schadt: Representation of Dormant and
- Active Microbial Dynamics for Ecosystem Modeling, Public Library of Science, 9,
- 849 <u>10.1371/journal.pone.0089252.g001, 2014.</u>
- 850 Wang, G., Jagadamma, S., Mayes, M. A., Schadt, C. W., Steinweg, J. M., Gu, L., and Post, W.
- 851 M.: Microbial dormancy improves development and experimental validation of ecosystem
- model, The ISME journal, 9, 226-237, 10.1038/ismej.2014.120, 2015.
- 853 Wang Wei, F. J., T. Oikawa: Contribution of Root and Microbial Respiration to Soil CO2 Efflux
- and Their Environmental Controls in a Humid Temperate Grassland of Japan, Pedosphere, 19,
 31-39, 2009.
- 856 Werf, H. V. d., and Verstraete, W.: Estimation of active soil microbial biomass by mathematical
- analysis of respiration curves: relation to conventional estimation of total biomass, Soil Biologyand Biochemistry, 19, 267-271, 1987.
- White, A., Cannell, M. G. R., and Friend, A. D.: The high-latitude terrestrial carbon sink: amodel analysis Global change biology, 6, 227-245, 2000.
- 861 Wieder, W. R., Bonan, G. B., and Allison, S. D.: Global soil carbon projections are improved by
- modelling microbial processes, Nature Climate Change, 3, 909-912, 10.1038/nclimate1951,
- 863 2013.
- Xu, X., Schimel, J. P., Thornton, P. E., Song, X., Yuan, F., and Goswami, S.: Substrate and
- environmental controls on microbial assimilation of soil organic carbon: a framework for Earth
 system models, Ecology letters, 17, 547-555, 10.1111/ele.12254, 2014.
- 867 Zha, J., and Zhuang, Q.: Microbial decomposition processes and vulnerable arctic soil organic
- 868 carbon in the 21st century, Biogeosciences, 15, 5621-5634, 10.5194/bg-15-5621-2018, 2018a.
- 869 Zha, J., and Zhuang, Q.: Microbial decomposition processes and vulnerable Arctic soil organic
- arbon in the 21st century, Biogeosciences Discussions, 1-34, 10.5194/bg-2018-241, 2018b.
- 271 Zhou, L., Tucker, C. J., Kaufmann, R. K., Slayback, D., Shabanov, N. V., and Myneni, R. B.:
- 872 Variations in northern vegetation activity inferred from satellite data of vegetation index during
- 1981 to 1999, Journal of Geophysical Research: Atmospheres, 106, 20069-20083,
- 874 10.1029/2000jd000115, 2001.
- 875 Zhuang, Q., Romanovsky, V. E., and McGuire, A. D.: Incorporation of a permafrost model into a
- 876 large-scale ecosystem model: Evaluation of temporal and spatial scaling issues in simulating soil
- thermal dynamics, Journal of Geophysical Research: Atmospheres, 106, 33649-33670,
- 878 10.1029/2001jd900151, 2001.
- 879 Zhuang, Q., McGuire, A. D., O'Neill, K. P., Harden, J. W., Romanovsky, V. E., and Yarie, J.:
- 880 Modeling soil thermal and carbon dynamics of a fire chronosequence in interior Alaska, Journal
- of Geophysical Research, 108, 10.1029/2001jd001244, 2002.
- Zhuang, Q., He, J., Lu, Y., Ji, L., Xiao, J., and Luo, T.: Carbon dynamics of terrestrial
- 883 ecosystems on the Tibetan Plateau during the 20th century: an analysis with a process-based
- biogeochemical model, Global Ecology and Biogeography, 19, 649-662, 10.1111/j.1466-
- 885 8238.2010.00559.x, 2010.
- Zhuang, Q., Zhu, X., He, Y., Prigent, C., Melillo, J. M., David McGuire, A., Prinn, R. G., and
- 887 Kicklighter, D. W.: Influence of changes in wetland inundation extent on net fluxes of carbon
- dioxide and methane in northern high latitudes from 1993 to 2004, Environmental Research
- Letters, 10, 095009, 10.1088/1748-9326/10/9/095009, 2015.
- 890 Zhuang, Q., McGuire, A. D., Melillo, J. M., Clein, J. S., Dargaville, R. J., Kicklighter, D. W.,
- 891 Myneni, R. B., Dong, J., Romanovsky, V. E., Harden, J., and Hobbie, J. E.: Carbon cycling in
- 892 extratropical terrestrial ecosystems of the Northern Hemisphere during the 20th century: a

- 893 modeling analysis of the influences of soil thermal dynamics, Tellus B: Chemical and Physical
- 894 Meteorology, 55, 751-776, 10.3402/tellusb.v55i3.16368, 2016.
- 895
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- 897 898
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- 907 Figure 1. Framework of the dormancy model: microbial biomass is split into two parts, active908 microbial biomass and dormant microbial biomass (shown in the green dashed circle).
- 909 Maintenance respiration from these two parts, and the CO₂ production through microbial
- 910 assimilation contributes to heterotrophic respiration. The model was revised based on Zha &
- 911 Zhuang (2018).
- 912



913 914 Figure 2. Comparison between observed and simulated NEP (gC m⁻²mon⁻¹) at: (a) Ivotuk (alpine

tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate 915

coniferous forest), (d) Univ. of Mich. Biological Station (Temperate deciduous forest), (e) 916

KUOM Turfgrass Field (Grassland), and (f) Atqasuk (Wet tundra). Note: scales are different. 917

918 Error bars represent standard errors among daily measure data in one month.



Figure 3. Boxplot of parameter posterior distribution that are obtained after ensemble inverse
 modeling for MIC-TEM-dormancy all six sites: US-Ivo: Ivotuk (alpine tundra), CA-NS3: UCI-

924 1964 burn site (boreal forest), US-Ho1: Howland Forest (temperate coniferous forest), US-UMB:

- 925 Univ. of Mich. Biological Station (temperate deciduous forest), US-KUT: KUOM Turfgrass
- 926 Field (grassland), US-Atq: Atqasuk (wet tundra).
- 927





928 929 Figure 4. Comparison between observed and simulated NEP (gC m⁻²mon⁻¹) at: (a) Ivotuk (alpine

930 tundra), (b) UCI-1964 burn site (boreal forest), (c) Howland Forest (main tower) (temperate coniferous forest), (d) Bartlett Experimental Forest (Temperate deciduous forest), (e) Brookings 931

932 (Grassland), and (f) Atqasuk (Wet tundra). Note: scales are different.



934 935 Figure 5. Comparison between observed and simulated R_H (gC m⁻²mon⁻¹) at: (a) US-EML (alpine

- tundra), (b) CA-SJ2 (boreal forest), (c) US-Ho2 (temperate coniferous forest), (d) US-UMB 936
- (Temperate deciduous forest), (e) US-Ro4 (Grassland), and (f) RU-Che (Wet tundra). Note: 937
- 938 scales are different.



940 Figure 6. Linear regression between simulated and observed annual R_H (gC m⁻²yr⁻¹) for: (a) MIC-TEM-dormancy, and (b) MIC-TEM.



Figure 7. Simulated annual net primary production (NPP, top panel), heterotrophic respiration (R_H,
center panel) and net ecosystem production (NEP, bottom panel) during the 20th century by
dormancy model and MIC-TEM, respectively.



949 Figure 8. Annual seasonal pattern of simulated (a) net primary production (NPP, top panel), (b)

heterotrophic respiration (R_H , center panel) and (c) net ecosystem production (NEP, bottom panel) during the 1990s from dormancy model and MIC-TEM.



Figure 9. Predicted changes in carbon fluxes: (i) NPP, (ii) R_H, and (iii) NEP for all land areas north of 45 <u>o</u>N in response to transient climate change under the RCP 8.5 scenario (left panel) and RCP 2.6 scenario (right panel) with dormancy model and MIC-TEM, respectively. The decadal running mean is applied.





- Figure 10. Annual seasonal pattern of simulated net primary production (NPP, top panel), heterotrophic respiration (R_H, center panel) and net ecosystem production (NEP, bottom panel)
- during the 2090s from dormancy model and MIC-TEM under: (a) RCP 2.6 scenario (top panel) and (b) RCP 8.5 scenario (bottom panel).



Figure 11. Simulated annual net primary production (NPP, top panel), heterotrophic respiration
 (R_H, center panel) and net ecosystem production (NEP, bottom panel) by MIC-TEM-dormancy
 with ensemble of parameters.
 984



1020 Table 1. Parameters associated with detailed microbial dormancy in MIC-TEM-dormancy

parameter	unit	description	Parameter range	references
m _R	h ⁻¹	Specific maintenance rate at active state	[0.001, 0.08]	Wang et al. (2014)
Q _{10mic}	-	Temperature effects on microbial metabolic activity (rate change per 10 °C increase in temperature). Based on 0.65 eV activation energy for soils) [1.5, 3.5]	He et al. (2015)
Q10enz	-	Temperature effects on enzyme activity (rate change per 10 °C increase in temperature). Based on 6% rate increase per degree Celsius	1.79	He et al. (2015)
α	-	the ratio of m_R to the sum of maximum specific growth rate	[0.01, 0.5]	Wang et al. (2014)
β	-	Ratio of dormant microbial maintenance rate to m _R	[0.0005, 0.005]	Wang et al. (2014)
Yg	-	carbon use efficiency	[0.3, 0.7]	He et al. (2015)
Ks	mgC cm ⁻²	Half-saturation constant for directly accessible substrate	[0.01, 10]	Wang et al. (2014)
Kmuptake	mgC cm ⁻²	Half-saturation constant for enzymatic decay of SOC	[200, 1000]	He et al. (2015)
r _{death}	h ⁻¹	Potential rate of microbial death	$[2e^{-4}, 2e^{-3}]$	Allison et al. (2010)
r _{EnzProd}	h ⁻¹	Enzyme production rate of microbe	[1e ⁻⁴ , 8e ⁻⁴]	He et al. (2015)
r _{enzloss}	h ⁻¹	Enzyme loss rate	[0.0005, 0.002]	Allison et al. (2010)
V _{max}	$mgC cm^{-2} h^{-1}$	Maximum SOC decay rate	$[1e^{-4}, 5e^{-3}]$	He et al. (2015)

Site Name	Location (Longitude (degrees) /Latitude (degrees))	Elevation (m)	Vegetation type	Description	Data range	Citations
Univ. of Mich. Biological Station	84.71W 45.56 N	234	Temperate deciduous forest	Located within a protected forest owned by the University of Michigan. Mean annual temperature is 5.83° C with mean annual precipitation of 803mm	01/2005- 12/2006	Gough et al. (2013)
Howland Forest (main tower)	68.74W 45.20N	60	Temperate coniferous forest	Closed coniferous forest, minimal disturbance.	01/2004- 12/2004	Davidson et al. (2006)
UCI-1964 burn site	98.38W 55.91N	260	Boreal forest	Located in a continental boreal forest, dominated by black spruce trees, within the BOREAS northern study area in central Manitoba, Canada.	01/2004- 10/2005	Goulden et al. (2006)
KUOM Turfgrass Field	93.19W 45.0N	301	Grassland	A low-maintenance lawn consisting of cool-season turfgrasses.	01/2006- 12/2008	Hiller et al. (2011)
Atqasuk	157.41W 70.47N	15	Wet tundra	100 km south of Barrow, Alaska. Variety of moist-wet coastal sedge tundra, and moist-tussock tundra surfaces in the more well-drained upland.	01/2005- 12/2006	Oechel et al. (2014);
Ivotuk	155.75W 68.49N	568	Alpine tundra	300 km south of Barrow and is located at the foothill of the Brooks Range and is classified as tussock sedge, dwarf-shrub, moss tundra.	01/2004- 12/2004	McEwing et al. (2015)

1025 Table 2. Site description and measured NEP data used to calibrate MIC-TEM-dormancy

1031 Table 3. Site description and measured NEP data used to validate MIC-TEM-dormancy

Site Name	Location	Elevation	Vegetation	Description	Data range	Citations
	(Longitude	(m)	type			
	(degrees)					
	(degrees))					
Bartlett	71.29W/	272	Temperate	Located within the White Mountains National Forest in north-central	01/2005-	Jenkins et al. (2007);
Experimental Forest	44.06N		deciduous forest	New Hampshire, USA, with mean annual temperature of 5.61 °C and mean annual precipitation of 1246mm.	12/2006	Richardson et al. (2007);
Howland Forest (main tower)	68.74W/ 45.20N	60	Temperate coniferous forest	Closed coniferous forest, minimal disturbance.	01/2003- 12/2003	Davidson et al. (2006)
UCI-1964 burn site	98.38W/ 55.91N	260	Boreal forest	Located in a continental boreal forest, dominated by black spruce trees, within the BOREAS northern study area in central Manitoba, Canada.	01/2002- 12/2003	Goulden et al. (2006)
Brookings	96.84W/ 44.35N	510	Grassland	Located in a private pasture, belonging to the Northern Great Plains Rangelands, the grassland is representative of many in the north central United States, with seasonal winter conditions and a wet growing season.	01/2005- 12/2006	Gilmanov et al. (2005)
Atqasuk	157.41W/ 70.47N	15	Wet tundra	100 km south of Barrow, Alaska. Variety of moist-wet coastal sedge tundra, and moist-tussock tundra surfaces in the more well-drained upland.	01/2003- 12/2004	Oechel et al. (2014);
Ivotuk	155.75W/ 68.49N	568	Alpine tundra	300 km south of Barrow and is located at the foothill of the Brooks Range and is classified as tussock sedge, dwarf-shrub, moss tundra.	01/2005- 12/2005	McEwing et al. (2015)

1035						
1036	Site	Location	Elevation	Vegetation type	Data range	Citations
1037		(Longitude (degrees)	(m)			
1038		/Latitude (degrees))			0.1.10.0.00	
1020	US-EML	149.25W/	700	Alpine tundra	01/2009-	Belshe et al. (2012)
1059		63.88N			12/2013	
1040						
1041	CA-SJ2	104.65W/	580	Boreal forest	01/2004-	Coursolle et al. (2006)
1042		53.95N			12/2008	
1042						
1045	US-Ho2	68.75W/	91	Temperate coniferous	01/2000-	Davidson et al. (2006)
1044		45.21N		forest	12/2004	
1045						
	US-UMB	84.71W/	234	Temperate deciduous	01/2005-	Gough et al. (2013)
		45.56N		forest	12/2006	8
	US-Ro4	93.07W/	274	Grasslands	01/2016-	Griffis et al. (2011)
		44.68N			12/2017	
	RU-Che	161.34E/	6	Wet tundra	01/2002-	Merbold et al. (2009)
		68.61N			12/2005	

Table 4. Site description and measured R_H data used to validate MIC-TEM-dormancy model

1047			•					
1048	Site Name	Vegetation type	Models	Intercept	Slope	R-square	Adjusted R-square p-value	
1049	Inotal	Alpine tundre	MIC-TEM	0.85	0.83	0.70	0.67	< 0.001
1050	IVOLUK	Alpine tunura	Dormancy	-0.51	1.09	0.75	0.73	< 0.001
1051								
1052	UCI 1064 burn site	Boreal forest	MIC-TEM	0.18	1.03	0.912	0.9080	< 0.001
1053	UCI-1704 Dufii Site	Doreal lorest	Dormancy	-0.21	0.96	0.90	0.894	< 0.001
1054								
1055	Howland Forest	Temperate	MIC-TEM	7.29	0.72	0.85	0.83	< 0.001
1056	(main tower)	coniferous forest	Dormancy	0.27	1.05	0.89	0.88	< 0.001
1057								
1058	Bartlett Experimental	Temperate	MIC-TEM	-6.05	0.91	0.944	0.941	< 0.001
1059	Forest	deciduous forest	Dormancy	-2.34	1.13	0.93	0.924	< 0.001
1060								
1061	Brookings	Grassland	MIC-TEM	3.05	0.71	0.84	0.83	< 0.001
1062	Dioonings	Crubblund	Dormancy	0.17	0.95	0.90	0.898	< 0.001
	Atgasuk	Wet tundra	MIC-TEM	7.22	1.85	0.71	0.70	< 0.001
			Dormancy	0.19	0.82	0.67	0.66	< 0.001

1046 Table 5. Model validation statistics for Dormancy model and MIC-TEM at six sites with NEP data

1063Table 6. Model validation statistics for Dormancy model and MIC-TEM at six sites with R_H data1064

Site ID	Vegetation type	Models	Intercept	Slope	R-square	Adjusted R-square	RMSE	p-value
US-EML	Alpine tundra	MIC-TEM	2.90	0.91	0.79	0.78	3.55	< 0.001
		Dormancy	1.81	0.74	0.87	0.85	2.69	< 0.001
CA-SJ2	Boreal forest	MIC-TEM	7.59	1.12	0.84	0.83	9.8	< 0.001
		Dormancy	2.6	0.74	0.86	0.85	3.97	< 0.001
US-Ho2	Temperate coniferous	MIC-TEM	4.07	0.89	0.86	0.84	12.39	< 0.001
	forest	Dormancy	6.59	0.71	0.91	0.89	11.83	< 0.001
US-UMB	Temperate deciduous	MIC-TEM	-4.73	1.32	0.81	0.8	20.05	< 0.001
	forest	Dormancy	13.6	0.67	0.85	0.84	12.94	< 0.001
US-Ro4	Grassland	MIC-TEM	9.34	0.87	0.81	0.79	11.25	< 0.001
		Dormancy	4.81	0.65	0.86	0.84	9.21	< 0.001
RU-Che	Wet tundra	MIC-TEM	2.5	0.67	0.72	0.71	6.24	< 0.001
		Dormancy	1.96	0.77	0.81	0.79	5.95	< 0.001