Carbon-climate feedback higher when assuming Michaelis-Menten kinetics of respiration

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Abstract.

Earth System Models simplify complex terrestrial respiration processes assuming a first-order chemical reaction or assuming a Michaelis-Menten kinetics. The effect of the respective mathematical representation on the terrestrial carbon-climate feedback is unclear. Using a simplified model of biogeochemical feedbacks to climate, I show that the terrestrial carbon-climate feedback roughly doubles when assuming Michaelis-Menten kinetics of respiration. Consequently, the remaining carbon budget to keep global warming below 2 °C is substantially higher. The effects of the respiration formulation also depend on the underlying emission scenario. These results highlight the importance of an increased understanding of the respiration processes on a global scale for more reliably project future carbon dynamics and climate, related feedback mechanisms, and thus to estimate a valid remaining anthropogenic carbon budget using Earth System Models.

1 Introduction

The anthropogenic emission of carbon dioxide into the atmosphere since the industrialization period led to a global warming of about 1 K due to the greenhouse effect (Canadell et al., 2023). However, less than half of the anthropogenically emitted carbon remains in the atmosphere because terrestrial ecosystems and the ocean take up 34% and 25%, respectively (Friedlingstein et al., 2023). The main reasons for this strong carbon dioxide uptake in terrestrial ecosystems are biogeochemical feedbacks (Cox, Betts, Jones, Spall, & Totterdell, 2000). Increasing atmospheric carbon dioxide (CO_2) concentration leads to an enhanced photosynthesis rate, and hence to a CO_2 uptake by vegetation on land (Cramer et al., 2001; O'Sullivan et al., 2022). This carbon is stored in vegetation pools and ultimately transferred to soils by exudation, litterfall, and mortality processes, thereby increasing the soil carbon content. This is the important carbon-concentration feedback mechanism (Arneth et al., 2010) (Fig. 1) which is a negative feedback, hence responsible for the current net CO_2 sink on land that has been preventing us from an even stronger climate change. In contrast, autotrophic and heterotrophic respiration are also higher than under pre-industrial conditions (Canadell et al., 2023) due to i) higher substrate availability and ii) the positive temperature sensitivity of respiration (Lloyd & Taylor, 1994). This temperature sensitivity of respiration forms the positive carbon-climate feedback mechanism (Fig. 1): Higher CO_2 concentration leads to higher temperature, which increases respiration and hence leads to an even higher atmospheric CO_2 concentration (Arneth et al., 2010).

carbon-climate
feedback mechanism

carbon-concentration
feedback mechanism
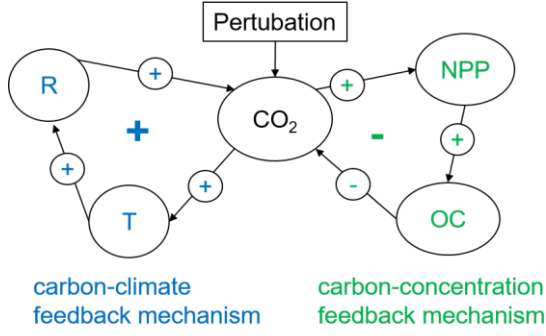
Figure 1: Feedback diagram for two main terrestrial biogeochemical feedback mechanisms. NPP: Net primary production, R: respiration, OC: land organic carbon stocks, T: global surface air temperature, CO_2: atmospheric carbon dioxide content.

These two biogeochemical feedback mechanisms have been identified as two major feedback mechanisms in the Earth system with great impact on climate (Arora et al., 2020; Friedlingstein et al., 2006). Currently, the positive carbon-climate feedback is lower than the negative carbon-concentration feedback and therefore land ecosystems act as a natural sink of CO_2 of about 3 Pg C per year (Friedlingstein et al., 2023). However, due to internal dynamics of the system, climate change, and changes in anthropogenic CO_2 emissions, the future strength of the feedback mechanisms and hence the net CO_2 exchange between land and atmosphere remains unclear. Recent accumulation of soil carbon in concert with higher future temperature and a declining increase in productivity can lead to a decreasing land sink under increasing CO_2 emissions in future (Cramer et al., 2001; C. D. Jones et al., 2023). To estimate such feedbacks, we need to run a modified version of an Earth System Model in which only one feedback mechanism is considered. The temporal difference in atmospheric CO_2 concentration from such experiments to model runs without the feedback is used to quantify these feedbacks (Hansen et al., 1984).

For the carbon-climate feedback mechanism (Fig. 1), the representation of respiration processes in Earth System Models is crucial. Several assumptions about the underlying processes and respective mathematical representations have been proposed. Land surface models usually represent respiration as a linear function (first-order kinetics) to the amount of available substrate (organic carbon, C),

$$\frac{dC}{dt} = -\text{k} \cdot \text{C} \qquad (1)$$

using several carbon pools (Brovkin et al., 2013; Sitch et al., 2003; Tang, Riley, & Zhu, 2022), with different decomposition rate constants k. In doing so, we assume that the active microbial biomass pool increases in relation to increased substrate availability. However, the underlying biochemical reactions are mostly enzymatic, hence a Michaelis-Menten kinetics model has been proposed to represent the dynamics of respiration (Wieder, Bonan, & Allison, 2013; Yu, Ahrens, Wutzler, Schrumpf, & Zaehle, 2020)

$$\frac{dC}{dt} = v_{max} \frac{C}{K_M + C} \qquad (2)$$

where v_{max} is the maximum reaction rate under infinite carbon substrate C, and K_M represents the amount of carbon at which the reaction rate is half of the maximum. In this model, we assume a constant active microbial biomass pool. The nonlinear shape of this relationship between reaction rate and substrate availability (in contrast to the linear dependency of first-order kinetics models) leads to a steep increase of the reaction rate under low substrate availability while only a moderate to negligible increase under high substrate availability. In doing so, this model implicitly represents the function of enzymes in the underlying biochemical reactions. It has been proposed, that such model enables a more valid aggregation from the process level (e.g. rhizosphere,

68 aggregatusphere) to the landscape scale (Reichstein & Beer, 2008). However, both models are great simplifications
69 of the underlying biogeochemical processes with strong assumptions. Therefore, in this study I will use both
70 equations to represent respiration and study the resulting structural uncertainty in feedbacks and remaining C
71 budgets.

72 The two approaches represented by equations 1 and 2 imply different responses of respiration to changing substrate
73 availability. Therefore, future dynamics of respiration should differ depending on the mathematical formulation.
74 Such structural model uncertainty is in particular of interest because there might be a point when the land sink
75 starts to decrease even under continuing high anthropogenic emissions(Cramer et al., 2001), or for the question on
76 how land sinks will react to decreasing or even negative anthropogenic carbon emissions.

77 Therefore, I ask three main questions in this paper: What is the effect of the respiration model structure on

78 - projections of the land carbon sink
79 - the strength of the carbon-climate feedback
80 - the remaining anthropogenic carbon budget

81 under different carbon emission scenarios? To address these questions I performed a feedback analysis using a
82 simplified but process-based model of global biogeochemical feedback mechanisms twice, using a first-order and
83 a Michaelis-Menten kinetics model of respiration. The simplified model of global biogeochemical feedback
84 mechanisms is of zero dimension (only globally aggregated pools) and neglects many detailed processes and
85 interactions between ecosystem components. Therefore, the idea is not to precisely quantify C budgets or feedback
86 but rather show qualitatively the effects of the respiration model structure on these estimates.

87 **2 Methods**

88 **2.1 Simplified Carbon-Climate Feedback Model**

89 The model has been designed to study the two major biogeochemical feedbacks to climate displayed in Fig. 1.
90 Exchanges of carbon among atmosphere, ocean and land are represented using a reduced number of carbon pools
91 without spatial details but still in a process-based way, i.e. based on a set of differential equations. For example,
92 the amount of carbon taken up by vegetation depends on the atmospheric carbon content while the amount of CO_2
93 released to the atmosphere due to respiration depends on the carbon content of the ecosystem. The model assumes
94 a global surface air temperature response to changing atmospheric carbon dioxide content using a transient climate
95 response parameter, which is lagged due to the ocean heat capacity. The model is driven by anthropogenic carbon
96 dioxide emissions to the atmosphere following several scenarios developed for the IPCC 6th assessment report.

97 A detailed description of the model can be found in (Lade et al., 2018). Here, I apply two alternative model
98 versions, one assuming a first-order kinetics of respiration (FOK), and one assuming a Michaelis-Menten kinetics
99 of respiration (MMK). The representation of terrestrial carbon uptake by gross primary productivity is identical in
100 both model versions. It is assumed to increase logarithmically with atmospheric carbon dioxide C_a (Equations 3
101 and 4, first term right-hand side). In addition, emissions due to land use change E_L are subtracted the same way in
102 both versions, and the increase in respiration with temperature is represented by a typical Q10 model (Equations 3
103 and 4, second term right-hand side). Only the dependence of respiration to land carbon stocks differs. The FOK
104 model assumes a first-order kinetics with a respiration rate constant estimated by pre-industrial GPP and carbon
105 stocks, $k = \frac{GPP_0}{C_{L,0}}$ following the same principle as in (Lade et al., 2018).

106 $\quad \frac{dC_L}{dt} = GPP_0 \left(1 + \alpha \log \frac{C_a}{C_{a,0}}\right) - Q^{\frac{\Delta T}{10}} \cdot k \cdot C_L - E_L$ (3)

107 In contrast, the MMK model represents respiration as a classical Michaelis-Menten equation with parameters v_{max}
108 and K_M:

109 $\quad \frac{dC_L}{dt} = GPP_0 \left(1 + \alpha \log \frac{C_a}{C_{a,0}}\right) - Q^{\frac{\Delta T}{10}} \cdot v_{max} \frac{C_L}{K_M + C_L} - E_L$ (4)

110 Parameters and pre-industrial pools and fluxes for model initialization were taken from (Lade et al., 2018) and
111 partly adjusted (Table 1). The transient climate response to CO_2 doubling λ is set at the higher end of the range
112 reported for CMIP6 model results (Arora et al., 2020; Nijsse, Cox, & Williamson, 2020) in order to match the
113 observed historical temperature anomaly. Parameters v_{max} and K_M of Equation 4 are optimized using a standard
114 gradient decent approach (MATLAB R 2023b function lsqnonlin) such that the difference of the modelled and
115 observation-based land carbon changes is minimized.

116 **Table 1. Value and description of parameters different from (Lade et al., 2018).**

Name	Symbol	Value	Reference/comment
Pre-industrial soil and vegetation Carbon	$C_{L,0}$	2305 Pg C	Sum of vegetation and soils carbon stocks following (Canadell et al., 2023), and C stocks of the active layer of gelisols following (Hugelius et al., 2014)
Transient climate response to CO_2 doubling (TCR)	λ (Equation 10 of (Lade et al., 2018))	2.5 K	Tuning parameter, higher end of range of CMIP6 models (Arora et al., 2020; Nijsse et al., 2020)
Respiration sensitivity parameter	Q	2	(Vaughn & Torn, 2019)
Pre-industrial GPP	GPP_0	113 Pg C a^{-1}	(Friedlingstein et al., 2023)
CO_2 sensitivity of GPP	α	0.35	Tuning parameter (Alexandrov, Oikawa, & Yamagata, 2003)
Max respiration rate in MMK model	v_{max}	200 Pg C a^{-1}	Tuning parameter
Substrate concentration at half of max respiration rate in MMK model	K_M	1787 Pg C	Tuning parameter

117

2.2 Modeling protocol

The two model versions have been run from 1850 until 2100 using a daily time step forced by anthropogenic carbon dioxide emissions from fossil fuel burning and from land-use change. For this, I combined reported historical emissions from the Global Carbon Project (Friedlingstein et al., 2023) with Shared Socioeconomic Pathways (SSP) emission scenarios from the public database of the Institute for Applied Systems Analysis (Riahi et al., 2017). I selected four widely used scenarios produced for the CMIP6 protocol (Gidden et al., 2019): SSP1-26 (optimistic scenario, reaching economic growth while retaining sustainability and reducing inequalities), SSP2-45 (including mitigation strategies), SSP3-70 (represents a future of inequality and fossil fuel dependency), and SSP5-85 (representing economic growth through strong reliance on fossil fuels). These scenarios reach a forcing of 2.6, 4.5, 7.0, and 8.5 W/m² at the end of the century and represent a huge spread of carbon emissions into the atmosphere (Fig. 2). I interpolated linearly the reported emissions at decadal scale to an annual resolution. In the combined time series (Fig. 2), historical emissions span the period 1850-2014 and scenarios continue from 2015 until 2100.
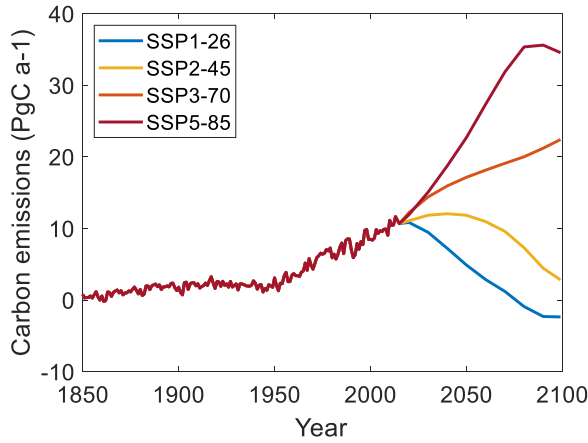
Figure 2: Total CO₂ emissions from burning fossil fuels and land-use change from combining a historical dataset with results from Integrated Assessment Models for different scenarios.

I performed model simulations for these emission scenarios and for both model versions, FOK and MMK. The results were used to evaluate the model during the historical period, and to estimate the remaining carbon budgets to keep warming below a certain threshold. For the feedback analysis, all these simulations were repeated three times. To estimate the feedback factor, I did model simulations in which only the terrestrial carbon-climate feedback is considered. The results were used to estimate the respective ΔC_A^{on} (section 2.4). For calculating the feedback sensitivities β and γ (Section 2.4), I additionally performed biogeochemically and radiatively coupled simulations following (Friedlingstein et al., 2006; Lade et al., 2018) and derived ΔC_L, ΔC_A and ΔT from these simulations. In the biogeochemically coupled simulation, I set λ to 0, hence effects of CO₂ change on temperature are excluded. In the radiatively coupled simulation, I neglected all effects of CO₂ on terrestrial or marine carbon pools. In total, that are 32 model simulations.

2.4 Feedback analysis

Atmospheric carbon content increases in time due to annual anthropogenic emissions (e_i) and internal feedback mechanisms. To estimate this carbon dioxide change when considering a terrestrial carbon-climate feedback ("on"), I averaged the atmospheric carbon content during a reference period in the future (2080-2100) and in the past (1850-1900) using the respective model simulation (section 2.3), and subtract both:

$$\Delta C_A^{on} = C_A^{future} - C_A^{past} \quad (5).$$

The respective atmospheric carbon change without considering the feedback ("off") equals the sum of emissions:

$$\Delta C_A^{off} = \sum_{i=1850}^{2100} e_i \quad (6).$$

The feedback is the difference $\Delta C_A^{on} - \Delta C_A^{off}$ and the feedback factor F is the ratio of both changes, which can be used to compare feedbacks and to identify positive (F>1) or negative feedbacks (F<1) (Cox et al., 2000; Friedlingstein, Dufresne, Cox, & Rayner, 2003; Hansen et al., 1984; Zickfeld, Eby, Matthews, Schmittner, & Weaver, 2011)

$$F = \frac{\Delta C_A^{on}}{\Delta C_A^{off}} \quad (7).$$

Sensitivities of the land carbon change to atmospheric carbon concentration (β) and temperature changes (γ) are defined following (Friedlingstein et al., 2006; Heinze et al., 2019) as

$$\Delta C_L = \beta \cdot \Delta C_A + \gamma \cdot \Delta T \quad (8).$$

I used the biogeochemically coupled simulation results to estimate β (ΔT=0), and the radiatively coupled results to estimate γ (ΔC_A=0).

3 Results

Model results of carbon fluxes and the surface temperature anomaly for the historical period are in general agreement with results by the Global Carbon Project (Friedlingstein et al., 2023) and the NOAA Global Surface Temperature record (Fig. 3), i.e. the overall historical trends are captured. The model does not represent spatial details, oversimplifies functional diversity and does not represent certain processes, such as disturbances. Therefore, the model is not able to capture the inter-annual variability of land carbon fluxes (Fig. 3). The general long-term agreement shows that major biogeochemical feedback mechanisms are correctly represented, and that initial conditions (Table 1) and model parameters (Table 1) are reasonable. Therefore, we assume that we can apply this model to study the effects of structural respiration model uncertainty on the carbon-climate feedback strength.
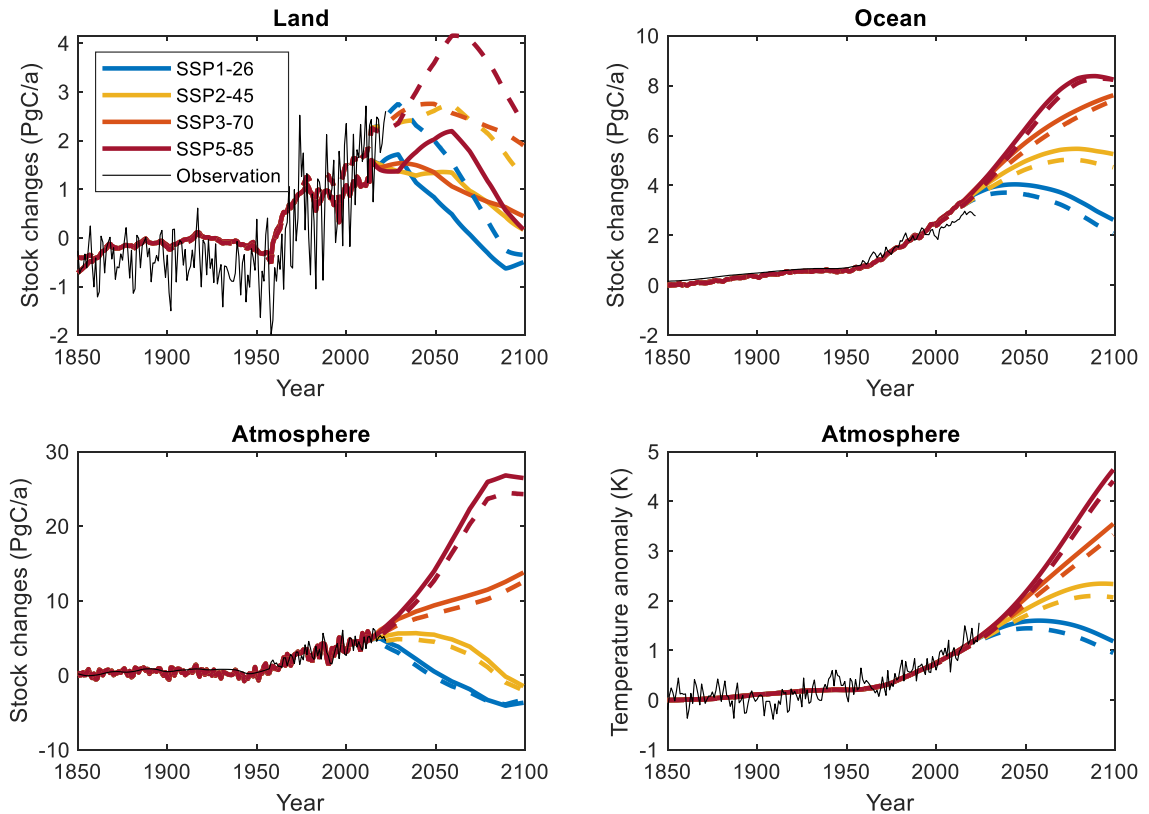
Figure 3: Simulated carbon fluxes and temperature anomaly for the different scenarios. FOK and MMK model results are displayed by solid and dashed lines, respectively. Simulation results are compared to estimates by the Global Carbon Project or to the NOAA Global Surface Temperature record, which has been bias corrected to the model results to match reference periods.

Figure 3 also shows the projections of carbon fluxes to land, ocean and atmosphere, as well as the temperature change for the two different model structures until 2100 following the different emission scenarios. Overall, these projections of the main carbon cycle fluxes and temperature change are similar to concentration-driven CMIP6 results (Canadell et al., 2023; Chris D. Jones et al., 2023). The projected ocean carbon sink in this study is substantially higher for most of the scenarios, and the land carbon sink of the model using a first-order kinetics respiration approach (FOK) is lower, but comparable with Lade et al. (2018). Otherwise, the projections of the change in atmospheric carbon stocks and the global surface temperature change are similar to studies using Earth System Models (Canadell et al., 2023). However, spread of carbon cycle projections using other models is usually also very high (Canadell et al., 2023; Chris D. Jones et al., 2023), and the uncertainty due to parameter values or initial conditions hardly quantified in these studies.

The projected land sink evolution differs depending on both, the emission scenario and the model structure applied. Under high emission scenarios, the land sink continues to rise and peaks in the middle of the century followed by a decreasing sink until 2100. This peak has been reported by DGVMs and ESMs before (Cramer et al., 2001; C. D. Jones et al., 2023) and is due to the reverse shape of the two main response functions, logarithmic productivity response to elevated CO_2 and quasi-exponential respiration response to temperature. A second reason is internal carbon dynamics: Respiration depends on the amount of land carbon stocks, which continued to increase until some maximum and therefore is the basis for a high respiration flux during the following time. For the scenario

199 SSP1-26, the land sink starts to decrease immediately after the historical period, i.e. when emissions are reduced,

200 and depending on the model structure is getting even negative at the second half of the century.

201 The projected land carbon sink in 2100 is much higher when assuming a Michaelis-Menten kinetics model for

202 respiration (MMK) even under an equal temperature sensitivity of respiration as by the first-order kinetics model

203 (FOK), and even when parameters are chosen to fit both model results during the historical period. In addition, the

204 peak in the middle of the century is more pronounced when using the MMK model (Fig. 3). Hence, this difference

205 is only due to internal carbon dynamics differences, in particular a non-linear (decreasing) change of the respiration

206 rate with increasing substrate availability under when assuming Michaelis-Menten kinetics. This clearly

207 demonstrates the uncertainty of land carbon sink dynamics just due to alternative assumptions and mathematical

208 formulations of respiration processes. As a result of higher land sinks using the MMK model, ocean and

209 atmosphere sinks are smaller and the temperature change is lower (Fig. 3). Due to the higher land C sink assuming

210 Michaelis-Menten kinetics, also total changes in land carbon stocks are much higher, i.e. land takes up several

211 hundred of Pg C more depending on the emission scenario.

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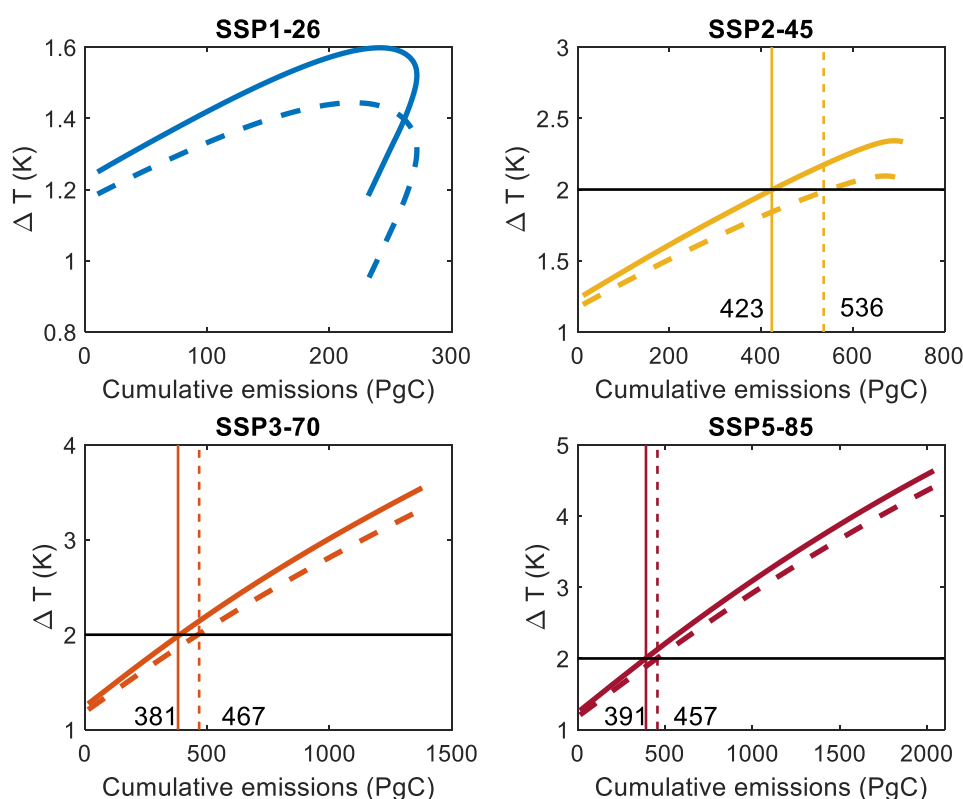
213 **Figure 4**. Relationship between global air surface temperature difference to pre-industrial temperature and the cumulative
214 emission of CO_2 from 2024 until 2099 for different emission scenarios and the two model simulations FOK (solid lines) and
215 MMK (dashed lines). Horizontal lines indicate a temperature change threshold of 2K, and vertical lines and numbers indicate
216 the respective cumulative emissions since 2024 to reach that temperature change target.

217

218 These differences in the projected land sinks do have clear consequences for the Transient Climate Response to

219 Cumulative Emissions of Carbon Dioxide (TCRE) and hence the remaining anthropogenic carbon budgets under

220 different emission scenarios. Usually, there is a quasi-linear relationship between the cumulative emission and the

221 temperature change (Fig. 4). Under reduced emissions of SSP1-26 scenario, ocean and land C uptake may remain

222 high (blue curves in Fig. 3), leading to a hysteresis in the TCRE (Charles D. Koven, Sanderson, & Swann, 2023).

223 Such hysteresis is not visible in the other scenarios (Fig. 4) because emission reductions are not strong enough

(Fig. 2). Interestingly, the relationship is less steep and more non-linear for the MMK model for all scenarios. From the TCRE the remaining carbon budget for a certain temperature threshold can be estimated (Canadell et al., 2023). In Fig. 4, the vertical lines indicate the amount of emissions since 2024 that - according to this model - can be still emitted in order to keep warming below the threshold of 2 °C warming compared to the pre-industrial situation, which is indicated by the horizontal line. We skip this analysis for scenario SSP1-26 results because the MMK model fails to reach a 2 °C increase at all (Fig. 4). For the other emission scenarios, the FOK model suggests 381 to 423 Pg C that can be emitted to the atmosphere in order to keep warming below 2 °C compared to pre-industrial temperature (Fig. 4). These estimates are slightly higher than the median remaining C budget estimated by CMIP6 experiments using ESMs of 370 Pg C (table 5.8, (Canadell et al., 2023)). Importantly, when assuming a Michaelis-Menten kinetics of respiration (MMK), the remaining C budget is higher and range between 457-536 Pg C. This is due to flatter slopes of these model results (Fig. 4).

Table 2. Terrestrial carbon-climate feedback (Pg C) for different representations of respiration in the model. Shown is the difference of model results accounting for the feedback and excluding it based on the temporal change in atmospheric carbon content between 2080-2100 and 1850-1900.

	First-order kinetics (FOK)	Michaelis-Menten kinetics (MMK)
SSP1-26	379	920
SSP2-45	423	955
SSP3-70	431	959
SSP5-85	498	1019

Using the first-order kinetics approach of respiration (FOK), I estimate a carbon-climate feedback of 379 to 498 Pg C when comparing the average CO_2 concentration of the period 2080-2100 with pre-industrial conditions, depending on the emission scenario (Table 2). This translates into feedback factors of 1.2 to 1.4 (Table 3), which are similar to previous estimates (Lade et al., 2018). Interestingly, the strength of the feedback mechanism as expressed by the feedback factor decreases with increasing carbon emissions (Table 3), i.e. the internal Earth system interactions are more important under reduced anthropogenic emissions. However, when assuming Michaelis-Menten kinetics of respiration, this carbon-climate feedback strength is higher (Table 3) depending on the underlying scenario.

Table 3. Feedback factor of the terrestrial carbon-climate feedback for different representations of respiration in the model. Shown is the difference of model results accounting for the feedback and excluding it based on the temporal change in atmospheric carbon content between 2080-2100 and 1850-1900.

	First-order kinetics (FOK)	Michaelis-Menten kinetics (MMK)
SSP1-26	1.41	2.0
SSP2-45	1.31	1.71
SSP3-70	1.23	1.52

SSP5-85	1.21	1.43

The FOK model estimates the sensitivity of the land carbon change to increasing atmospheric CO2 concentration (β, Table 4) to be 1.4 Pg C ppm^{-1} assuming the high-emission scenario SSP5-8.5. This is similar to CMIP4 model runs using the high-emission scenario SREAS A2 (Friedlingstein et al., 2006) and at the higher end of the range of CMIP6 model results without considering the N cycle in 4xCO2 experiments (Arora et al., 2020). Interestingly, the sensitivity increases towards scenarios assuming less emissions (Table 4), and the sensitivity is higher when assuming a Michaelis-Menten kinetics of respiration (Table 4). The land carbon change sensitivity to climate change (γ, Table 4) is estimated at -117 Pg C K^{-1} in this case. This is at the higher end of the range for the previously mentioned ESM results (Arora et al., 2020; Friedlingstein et al., 2006). This parameter is also more negative when assuming Michaelis-Menten kinetics or when considering a lower emission scenario (Table 4).

Table 4. Sensitivities of the land carbon change to changing atmospheric carbon dioxide (β , Pg C ppm^{-1}) and temperature (γ , Pg C K^{-1}) for different representations of respiration in the model (FOK and MMK).

	β, Pg C ppm^{-1}, first-order kinetics (FOK)	β, Pg C ppm^{-1}, Michaelis-Menten kinetics (MMK)	γ, Pg C K^{-1}, first-order kinetics (FOK)	γ, Pg C K^{-1}, Michaelis-Menten kinetics (MMK)
SSP1-26	3.4	9.8	-133	-218
SSP2-45	2.3	5.4	-125	-204
SSP3-70	1.6	3.4	-124	-198
SSP5-85	1.4	2.7	-117	-187

4 Discussion

Besides gross primary productivity, ecosystem respiration is one of the main land-atmosphere carbon exchange processes (Friedlingstein et al., 2023). The underlying biochemical processes are complex and mathematical models of simplified net reactions are usually applied in Earth System Models: Either assuming a first-order chemical reaction of carbon and oxygen to carbon dioxide and applying Equation 1, or considering the underlying enzymatic reactions and hence applying Equation 2. The epistemic uncertainty in projecting future land-atmosphere exchange of CO_2, climate and the related biogeochemical feedbacks underlying these assumptions have been addressed in this paper. Model parameters have been chosen based on literature values, and to fit published historical carbon and temperature changes (section 2.3) for the first-order kinetics approach (FOK). For the Michaelis Menten kinetics model (MMK), we selected parameter values such that results are also similar to Global Carbon Budget estimates and the FOK model during the pre-industrial period. Interestingly, effects of anthropogenic carbon emissions on future land sink dynamics differ between both model versions, with several Pg C per year higher uptake by land when assuming Michaelis-Menten kinetics for respiration (Fig. 3). Such higher land carbon uptake leads to a lower ocean carbon sink hence increasing differences between land and ocean sinks. In addition, the projected global surface temperature change until 2100 is lower in the MMK model (Fig. 3), i.e. a lower temperature change response to cumulative carbon emissions (Fig. 4). Since increasing surface temperature

284 will lead to an additional CO_2 release from land to the atmosphere, there is the positive carbon-climate feedback
285 mechanism (Arneth et al., 2010), and here I asked the question, is there also an effect of the respiration model
286 structure on this feedback strength?

287 Indeed, this feedback roughly doubles when assuming Michaelis-Menten kinetics, and it is higher for strong carbon
288 emission scenarios (Table 2). As a consequence, the model results imply a higher remaining anthropogenic carbon
289 budget to keep warming below 2 °C above pre-industrial levels of up to circa 100 Pg C but depending on the
290 emission scenario only because we assume an alternative model structure for respiration. These estimates are
291 similar to estimates of additional warming-induced C loss from permafrost-affected soils until 2100 of 10-100 Pg
292 C (C. D. Koven et al., 2015). Other additional Earth system feedbacks currently not represented in Earth system
293 models (section 5.5.2.2.5 in (Canadell et al., 2023)), and additional Geophysical Uncertainties like non- CO_2
294 forcing or emission uncertainty (Table 5.8 in (Canadell et al., 2023)) are also of the same order of magnitude. The
295 structural uncertainty in the formulation of respiration is also of the same order of magnitude as the total annual
296 gross primary production or the respiration flux (both 130 Pg C yr-1, Friedlingstein et al., 2023). Shall we assume
297 a linear or non-linear dependence of respiration on the amount of substrate? This assumption influences the internal
298 land carbon dynamics, because in the latter case respiration does not respond to higher substrate availability in the
299 same way as in the linear model. This is also visible when looking at the sensitivities of the land carbon change to
300 CO_2 change (β, Table 4) which roughly double when assuming Michaelis-Menten kinetics because the response
301 of respiration to higher substrate availability is lower.

302 I applied a simplified model of global biogeochemical feedback mechanisms, considering only one terrestrial
303 carbon pool, and hence integrating autotrophic and heterotrophic respiration,and no explicit pool of microbial
304 biomass and microbial functions. Therefore, many specific underlying processes and interactions of ecosystem
305 components are neglected. For example, an increase in heterotrophic respiration due to increasing plant
306 productivity and carbon input to soils (priming effect, (Fontaine et al., 2007; Keuper et al., 2020)), or changing
307 microbial community structure as a response to climate change (Glassman et al., 2018) is not considered. Nutrient
308 limitation of vegetation productivity (Hungate, Dukes, Shaw, Luo, & Field, 2003) is only implicitly parametrized
309 in Equations 3 and 4 through a logarithmic response function of GPP to CO_2. Hence, I do not quantify the effects
310 of nutrient availability on the carbon-climate feedback in addition to the effects of either respiration model used.
311 When assuming a MMK model, increasing CO_2 leads to higher increase in land C stocks (β, Table 4) due to lower
312 respiration. However, this mechanism can, for instance, also lock more nutrients in soil organic matter hence
313 change the response function of GPP to CO_2. When considering nutrient processes, land C change sensitivities to
314 CO_2 and temperature have been shown to be much smaller (Arora et al., 2020). In addition, climate change is
315 expressed as a temperature change in this model and precipitation effects on carbon cycle functions (Jung et al.,
316 2017) are not taken into account. Therefore, the presented results are first conservative estimates which should be
317 verified using a state-of-the-art ESM including nutrient cycles and Michaelis-Menten kinetics (Yu et al., 2020).
318 Still, the presented results point to the importance to communicate and address existing structural uncertainties in
319 Earth System Models. Just by assuming an underlying Michaelis-Menten kinetics of respiration processes leads to
320 distinct projections of future respiration and the carbon-climate feedback mechanism. These results also
321 demonstrate the need for novel research clarifying a valid process-based model structure of ecosystem respiration.

5 Conclusions

Two major gross carbon fluxes govern the recent land carbon sink, photosynthesis and respiration. While detailed process-based photosynthesis models have been developed and applied in Earth System Models, how to model respiration processes remains unclear. The model structure of respiration alone can lead to a doubling of the carbon-climate feedback estimate over the 21st century. Depending on the underlying emission scenario, that translates into a substantial difference of the remaining carbon budget to keep global warming below 2 °C of up to circa 100 Pg C depending on the emission scenario. These results show the importance of an increased understanding of the mathematical model structure of respiration processes in Earth System Models for more reliably projecting future carbon dynamics and climate, related feedback mechanisms, and hence to estimate a valid remaining anthropogenic carbon budget.

Code availability

MATLAB code of the model versions applied is available via github.

Data availability

All required data to run the model and reproduce the results is available online and open access.

Author contribution CB designed the study, wrote the computer code, downloaded and interpolated the emission data, run the models, analysed the results and wrote the manuscript.

Competing interests CB declares that he has no conflict of interest.

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References

Alexandrov, G. A., Oikawa, T., & Yamagata, Y. (2003). Climate dependence of the CO2 fertilization effect on terrestrial net primary production. *Tellus Series B-Chemical and Physical Meteorology, 55*(2), 669-675. doi:DOI 10.1034/j.1600-0889.2003.00021.x

Arneth, A., Harrison, S. P., Zaehle, S., Tsigaridis, K., Menon, S., Bartlein, P. J., . . . Vesala, T. (2010). Terrestrial biogeochemical feedbacks in the climate system. *Nature Geoscience, 3*(8), 525-532. doi:10.1038/ngeo905

Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein, P., . . . Ziehn, T. (2020). Carbon–concentration and carbon–climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences, 17*(16), 4173-4222. doi:10.5194/bg-17-4173-2020

Brovkin, V., Boysen, L., Raddatz, T., Gayler, V., Loew, A., & Claussen, M. (2013). Evaluation of vegetation cover and land-surface albedo in MPI-ESM CMIP5 simulations. *Journal of Advances in Modeling Earth Systems, 5*(1), 48-57. doi:https://doi.org/10.1029/2012MS000169

Canadell, J. G., Monteiro, P. M. S., Costa, M. H., Cotrim da Cunha, L., Cox, P. M., Eliseev, A. V., . . . Zickfeld, K. (2023). Global Carbon and Other Biogeochemical Cycles and Feedbacks. In C. Intergovernmental Panel on Climate (Ed.), *Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 673-816). Cambridge: Cambridge University Press.

365 Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., & Totterdell, I. J. (2000). Acceleration of global warming due
366   to carbon-cycle feedbacks in a coupled climate model. *Nature, 408*(6809), 184-187.
367 Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A., Brovkin, V., . . . Young-Molling, C.
368   (2001). Global response of terrestrial ecosystem structure and function to CO2 and climate change: results
369   from six dynamic global vegetation models. *Global Change Biology, 7*(4), 357-373. Retrieved from
370   http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2486.2001.00383.x/full
371 Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., & Rumpel, C. (2007). Stability of organic carbon in deep
372   soil layers controlled by fresh carbon supply. *Nature, 450*(7167), 277-U210. doi:10.1038/nature06275
373 Friedlingstein, P., Cox, P., Betts, R., Bopp, L., Von Bloh, W., Brovkin, V., . . . Zeng, N. (2006). Climate-carbon
374   cycle feedback analysis: Results from the C⁴MIP model intercomparison. *Journal of Climate, 19*(14),
375   3337-3353.
376 Friedlingstein, P., Dufresne, J. L., Cox, P. M., & Rayner, P. (2003). How positive is the feedback between climate
377   change and the carbon cycle? *Tellus B: Chemical and Physical Meteorology, 55*(2), 692-700.
378   doi:10.3402/tellusb.v55i2.16765
379 Friedlingstein, P., O'Sullivan, M., Jones, M. W., Andrew, R. M., Bakker, D. C. E., Hauck, J., . . . Zheng, B. (2023).
380   Global Carbon Budget 2023. *Earth Syst. Sci. Data, 15*(12), 5301-5369. doi:10.5194/essd-15-5301-2023
381 Gidden, M. J., Riahi, K., Smith, S. J., Fujimori, S., Luderer, G., Kriegler, E., . . . Takahashi, K. (2019). Global
382   emissions pathways under different socioeconomic scenarios for use in CMIP6: a dataset of harmonized
383   emissions trajectories through the end of the century. *Geosci. Model Dev., 12*(4), 1443-1475.
384   doi:10.5194/gmd-12-1443-2019
385 Glassman, S. I., Weihe, C., Li, J. H., Albright, M. B. N., Looby, C. I., Martiny, A. C., . . . Martiny, J. B. H. (2018).
386   Decomposition responses to climate depend on microbial community composition. *Proceedings of the*
387   *National Academy of Sciences of the United States of America, 115*(47), 11994-11999.
388   doi:10.1073/pnas.1811269115
389 Hansen, J., Lacis, A., Rind, D., Russell, G., Stone, P., Fung, I., . . . Lerner, J. (1984). Climate Sensitivity: Analysis
390   of Feedback Mechanisms. In *Climate Processes and Climate Sensitivity* (pp. 130-163).
391 Heinze, C., Eyring, V., Friedlingstein, P., Jones, C., Balkanski, Y., Collins, W., . . . Vancoppenolle, M. (2019).
392   ESD Reviews: Climate feedbacks in the Earth system and prospects for their evaluation. *Earth Syst.*
393   *Dynam., 10*(3), 379-452. doi:10.5194/esd-10-379-2019
394 Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J. W., Schuur, E. A. G., Ping, C.-L., . . . Kuhry, P. (2014).
395   Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data
396   gaps. *Biogeosciences, 11*(23), 6573-6593. doi:10.5194/bg-11-6573-2014
397 Hungate, B. A., Dukes, J. S., Shaw, M. R., Luo, Y. Q., & Field, C. B. (2003). Nitrogen and climate change. *Science,*
398   *302*(5650), 1512-1513. doi:DOI 10.1126/science.1091390
399 Jones, C. D., Ziehn, T., Anand, J., Bastos, A., Burke, E., Canadell, J. G., . . . Yun, J. (2023). RECCAP2 Future
400   Component: Consistency and Potential for Regional Assessment to Constrain Global Projections. *Agu*
401   *Advances, 4*(6), e2023AV001024. doi:https://doi.org/10.1029/2023AV001024
402 Jones, C. D., Ziehn, T., Anand, J., Bastos, A., Burke, E., Canadell, J. G., . . . Yun, J. M. (2023). RECCAP2 Future
403   Component: Consistency and Potential for Regional Assessment to Constrain Global Projections. *Agu*
404   *Advances, 4*(6). doi:ARTN e2023AV001024
405 10.1029/2023AV001024
406 Jung, M., Reichstein, M., Schwalm, C. R., Huntingford, C., Sitch, S., Ahlström, A., . . . Zeng, N. (2017).
407   Compensatory water effects link yearly global land CO
408 sink changes to temperature. *Nature, 541*(7638), 516-520. doi:10.1038/nature20780
409 Keuper, F., Wild, B., Kummu, M., Beer, C., Blume-Werry, G., Fontaine, S., . . . Dorrepaal, E. (2020). Carbon loss
410   from northern circumpolar permafrost soils amplified by rhizosphere priming. *Nature Geoscience, 13*(8),
411   560-565. doi:10.1038/s41561-020-0607-0
412 Koven, C. D., Sanderson, B. M., & Swann, A. L. S. (2023). Much of zero emissions commitment occurs before
413   reaching net zero emissions. *Environmental Research Letters, 18*(1), 014017. doi:10.1088/1748-
414   9326/acab1a
415 Koven, C. D., Schuur, E. A. G., Schädel, C., Bohn, T. J., Burke, E. J., Chen, G., . . . Turetsky, M. (2015). A
416   simplified, data-constrained approach to estimate the permafrost carbon–climate feedback. *Philosophical*
417   *Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 373*(2054),
418   20140423. doi:10.1098/rsta.2014.0423
419 Lade, S. J., Donges, J. F., Fetzer, I., Anderies, J. M., Beer, C., Cornell, S. E., . . . Steffen, W. (2018). Analytically
420   tractable climate--carbon cycle feedbacks under 21st century anthropogenic forcing. *Earth System*
421   *Dynamics, 9*(2), 507-523. Retrieved from https://www.earth-syst-dynam.net/9/507/2018
422 Lloyd, J., & Taylor, J. A. (1994). On the temperature dependence of soil respiration. *Functional Ecology, 8*, 315-
423   323.

424 Nijsse, F. J. M. M., Cox, P. M., & Williamson, M. S. (2020). Emergent constraints on transient climate response
425   (TCR) and equilibrium climate sensitivity (ECS) from historical warming in CMIP5 and CMIP6 models.
426   *Earth System Dynamics, 11*(3), 737-750. doi:10.5194/esd-11-737-2020
427 O'Sullivan, M., Friedlingstein, P., Sitch, S., Anthoni, P., Arneth, A., Arora, V. K., . . . Zaehle, S. (2022). Process-
428   oriented analysis of dominant sources of uncertainty in the land carbon sink. *NATURE*
429   *COMMUNICATIONS, 13*(1). doi:ARTN 4781
430 10.1038/s41467-022-32416-8
431 Reichstein, M., & Beer, C. (2008). Soil respiration across scales: the importance of a model--data integration
432   framework for data interpretation. *Journal of Plant Nutrition and Soil Science, 171*(3), 344-354.
433   Retrieved from http://onlinelibrary.wiley.com/doi/10.1002/jpln.200700075/full
434 Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O'Neill, B. C., Fujimori, S., . . . Tavoni, M. (2017). The
435   Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications:
436   An overview. *Global Environmental Change, 42*, 153-168.
437 Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., . . . others. (2003). Evaluation of
438   ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation
439   model. *Global Change Biology, 9*(2), 161-185. Retrieved from
440   http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2486.2003.00569.x/full
441 Tang, J., Riley, W. J., & Zhu, Q. (2022). Supporting hierarchical soil biogeochemical modeling: version 2 of the
442   Biogeochemical Transport and Reaction model (BeTR-v2). *Geosci. Model Dev., 15*(4), 1619-1632.
443   doi:10.5194/gmd-15-1619-2022
444 Vaughn, L. J. S., & Torn, M. S. (2019). C evidence that millennial and fast-cycling soil carbon are equally sensitive
445   to warming. *Nature Climate Change, 9*(6), 467-+. doi:10.1038/s41558-019-0468-y
446 Wieder, W. R., Bonan, G. B., & Allison, S. D. (2013). Global soil carbon projections are improved by modelling
447   microbial processes. *Nature Climate Change, 3*(10), 909-912. doi:10.1038/nclimate1951
448 Yu, L., Ahrens, B., Wutzler, T., Schrumpf, M., & Zaehle, S. (2020). Jena Soil Model (JSM v1.0; revision 1934):
449   a microbial soil organic carbon model integrated with nitrogen and phosphorus processes. *Geoscientific*
450   *Model Development, 13*(2), 783-803. doi:10.5194/gmd-13-783-2020
451 Zickfeld, K., Eby, M., Matthews, H. D., Schmittner, A., & Weaver, A. J. (2011). Nonlinearity of Carbon Cycle
452   Feedbacks. *Journal of Climate, 24*(16), 4255-4275. doi:https://doi.org/10.1175/2011JCLI3898.1

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