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

Christian Beer[1, 2]

[1]Department of Earth System Sciences, Universität Hamburg, Hamburg, 20134, Germany
[2]Center for Earth System Research and Sustainability, Universität Hamburg, Hamburg, 20134, Germany

Correspondence to: Christian Beer (christian.beer@uni-hamburg.de)

Abstract.

Earth system models simplify complex terrestrial respiration processes assuming a first-order chemical reaction or assuming a Michaelis-Menten kinetics. The epistemic uncertainty related to the respective mathematical representations is unclear. Using a simplified model of biogeochemical feedbacks to climate, we show that the terrestrial carbon-climate feedback is more than 35% higher, and hence the remaining carbon budget to keep global warming below 2 °C is 89-158 Pg C higher, when assuming Michaelis-Menten kinetics instead of first-order kinetics, but these differences depend on the underlying 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.

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 et al., 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 and Taylor, 1994). This temperature sensitivity of respiration forms a 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).

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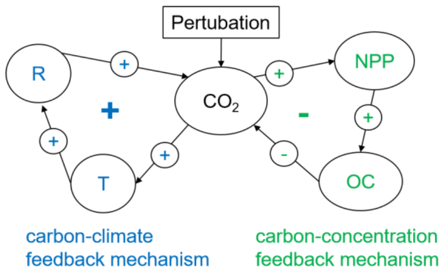

Figure 1: Feedback diagram for two main terrestrial biogeochemical feedback mechanisms. NPP: Net primary production, R: respiration, OC: land organic carbon stocks, T: global surface air temperature, CO_2: atmospheric carbon dioxide content.

These two biogeochemical feedback mechanisms have been identified as two major feedback mechanisms in the Earth system with great impact on climate (Friedlingstein et al., 2006; Arora et al., 2020). 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; Jones et al., 2023). To estimate such feedbacks, we need to run a modified version of an Earth System Model in which the direct effect of one system quantity on another is removed in a way that the feedback mechanism of question is not represented anymore. The temporal difference in atmospheric CO_2 concentration from such experiments to results of a control model run that incorporates all feedbacks is used to quantify these feedbacks (Zickfeld et al., 2011).

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),

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

using a different amount of carbon pools (Sitch et al., 2003; Brovkin et al., 2013; Tang et al., 2022), with decomposition rate constants k. However, the underlying biochemical reactions are mostly enzymatic, hence a Michaelis-Menten kinetics model should be more valid to represent the dynamics of respiration (Wieder et al., 2013; Yu et al., 2020)

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

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. 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. Such model enables a more valid aggregation from the process level (e.g. rhizosphere, aggregatusphere) to the landscape scale (Reichstein and Beer, 2008).

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

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

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

under different carbon emission scenarios? To address these questions we perform a full feedback analysis using a simplified but process-based model of global biogeochemical feedback mechanisms twice, using a first-order and a Michaelis-Menten kinetics model of respiration.

2 Methods

2.1 Simplified Carbon-Climate Feedback Model

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

A detailed description of the model can be found in (Lade et al., 2018). This model version has been revised in terms of the land carbon pool dynamics. Here, we apply two alternative model versions, one assuming a first-order kinetics of respiration (FOK), and one assuming a Michaelis-Menten kinetics of respiration (MMK). The representation of terrestrial carbon uptake by gross primary productivity is identical in both model versions. It is assumed to increase logarithmic with atmospheric carbon dioxide C_a (Equations 3 and 4, first term right-hand side). In addition, emissions due to land use change E_L are subtracted the same way in both versions, and the increase in respiration with temperature is represented by a typical Q_{10} model (Equations 3 and 4, second term right-hand side). Only the dependence of respiration to land carbon stocks differs. The FOK model assumes a first-order kinetics with a respiration rate constant estimated by pre-industrial GPP and carbon stocks, $k = \frac{GPP_0}{C_{L,0}}$ following the same principle as in (Lade et al., 2018).

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

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

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

2.2 Carbon emission scenarios

The models have been run from 1750 until 2100 forced by anthropogenic carbon dioxide emissions from fossil fuel burning and from land-use change. For this, we 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). We 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). We 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.

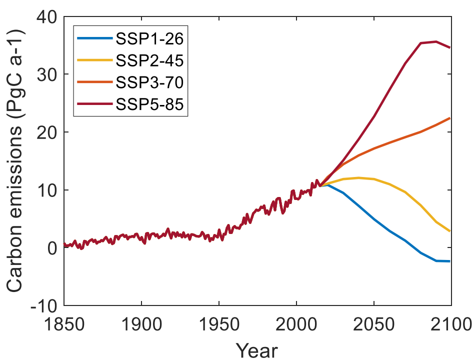

Figure 2: Total CO_2 emissions from burning fossil fuels and land-use change from combining a historical dataset with results from Integrated Assessment Models for different scenarios.

2.3 Feedback analysis and modelling protocol

We define the biogeochemical feedback following (Zickfeld et al., 2011) as the difference between two different temporal changes in atmospheric carbon dioxide content, one derived using a model including the feedback mechanism and using one neglecting such mechanism. For this, we averaged atmospheric CO_2 content during a reference period in the past (1850-1900), and one in the future (2080-2100). The difference between both periods is the carbon dioxide change. Then, we express the feedback in units of Pg C as the difference in carbon dioxide change between two distinct model runs: (i) the control model run which represents the feedback ("on") and (ii) a model run which avoids the feedback mechanism ("off"). To disable the terrestrial carbon-climate feedback mechanism we set the parameter Q (Equations 3 and 4) to 1, i.e. any change in atmospheric temperature does not affect terrestrial ecosystem respiration in this model experiment. We performed these two model runs for both

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model versions, FOK and MMK so that we can analyse the feedback separately, and then repeat all the procedure for all of the applied emission scenarios.

In addition, we calculate the feedback factor as the ratio of these temporal changes instead of the difference (Zickfeld et al., 2011; Lade et al., 2018). This measure is commonly used to compare the relative strength among various biogeochemical feedback mechanisms. It also shows if a positive or negative feedback is present.

The models run from 1850 until 2100 in a daily time step with CO_2 emission input interpolated from annual data. Parameters and pre-industrial pools and fluxes for model initialization were taken from (Lade et al., 2018) and partly adjusted (Table 1). The transient climate response to CO_2 doubling λ is set at the higher end of the range reported for CMIP6 model results (Nijsse et al., 2020; Arora et al., 2020) in order to match the observed historical temperature change. Parameters v_{max} and K_M of Equation 4 are set such that MMK model results match FOK model results for the pre-industrial period (cf. Fig. 3).

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

Name	Symbol	Value	Reference/comment
Pre-industrial soil and vegetation Carbon	$C_{L,0}$	2287 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 (Nijsse et al., 2020; Arora et al., 2020)
Respiration sensitivity parameter	Q	2	(Vaughn and Torn, 2019)
Pre-industrial GPP	GPP_0	113 Pg C / a	(Friedlingstein et al., 2023)
CO_2 sensitivity of GPP	α	0.35	Tuning parameter, (Alexandrov et al., 2003)
Max respiration rate in MMK model	v_{max}	176 Pg C / a	Tuning parameter
Substrate concentration at half of max respiration rate in MMK model	K_M	1300 Pg C	Tuning parameter

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3 Results

Model results of carbon stock changes and the surface temperature change for the historical time period are in general agreement with observations (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). This general 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.

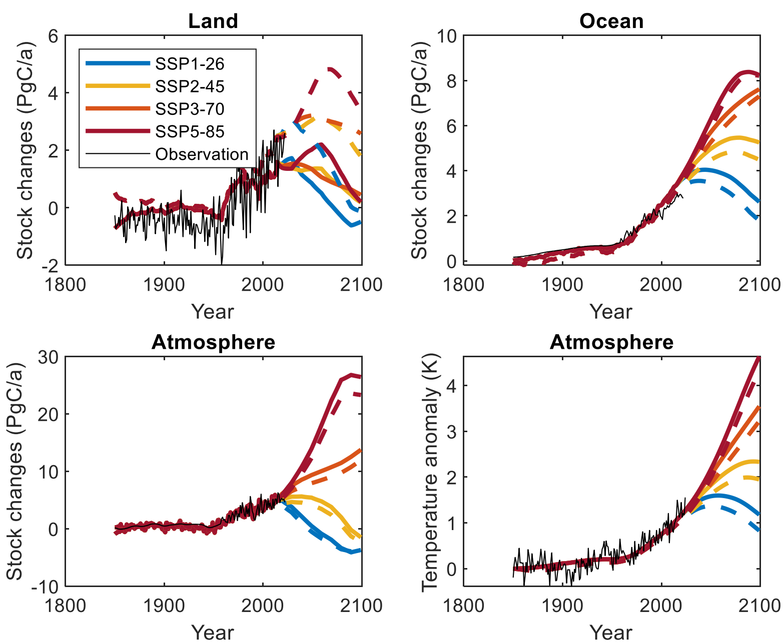

Figure 3: Simulated carbon stock changes and temperature anomaly for the different scenarios. MMK model results are displayed by dashed lines. Simulation results are compared to estimates by the Global Carbon Project or to the NOAA Global Surface Temperature record, which has been bias corrected to the 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). Our projected ocean carbon sink 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).

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However, spread of carbon cycle projections using other models is usually also very high (Canadell 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; 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 SSP1-26, the land sink starts to decrease immediately after the historical period, i.e. when emissions are reduced, and depending on the model structure is getting even negative at the second half of the century.
The projected land carbon sink in 2100 is much higher when assuming a Michaelis-Menten kinetics model for respiration (MMK) even under an equal temperature sensitivity of respiration as by the first-order kinetics model (FOK), and even when parameters are chosen to fit both model results during the historical period. In addition, the peak in the middle of the century is more pronounced when using the MMK model (Fig. 3). Hence, this difference is only due to internal carbon dynamics differences, in particular a non-linear (decreasing) change of the respiration rate with increasing substrate availability under when assuming Michaelis-Menten kinetics. This clearly demonstrates the uncertainty of land carbon sink dynamics just due to alternative assumptions and mathematical formulations of respiration processes. As a result of higher land sinks using the MMK model, ocean and atmosphere sinks are smaller and the temperature change is lower (Fig. 3). Due to the higher land C sink assuming Michaelis-Menten kinetics, also total changes in land carbon stocks are much higher, i.e. land takes up several hundred of Pg C more depending on the emission scenario.

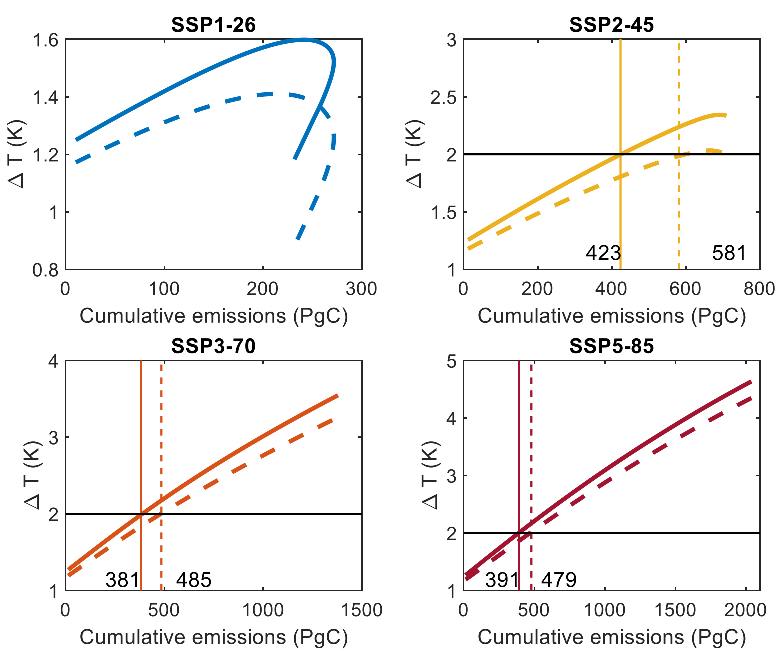

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Figure 4. Relationship between global air surface temperature difference to pre-industrial temperature and the cumulative emission of CO_2 from 2024 until 2099 for different emission scenarios and the two model simulations FOK (solid lines) and MMK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

These differences in the projected land sinks do have clear consequences for the Transient Climate Response to Cumulative Emissions of Carbon Dioxide (TCRE) and hence the remaining anthropogenic carbon budgets under different emission scenarios. Usually, there is a quasi-linear relationship between the cumulative emission and the temperature change (Fig. 4). Under reduced emissions of SSP1-26 scenario, ocean and land C uptake may remain high (blue curves in Fig. 3), leading to a hysteresis in the TCRE (Koven et al., 2023). 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 479-581 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)	relative difference (%)
SSP1-26	74	101	37
SSP2-45	163	221	36
SSP3-70	262	365	39
SSP5-85	380	534	40

Using the first-order kinetics approach of respiration (FOK), we estimate a carbon-climate feedback of 74 to 380 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 a mean feedback factor of 1.42 with a small range (Fig. 5) (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 is even 36-40% higher (Table 2, Fig. 5) depending on the underlying scenario. While the absolute feedback difference increases with the

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amount of anthropogenic carbon emissions (Table 2), the relative difference of the feedback factor decreases from 63% (SSP1-26) to 26% (SSP5-85) (Table 3).

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)	relative difference (%)
SSP1-26	1.45	2.36	63
SSP2-45	1.45	2.03	41
SSP3-70	1.4	1.82	30
SSP5-85	1.37	1.73	26

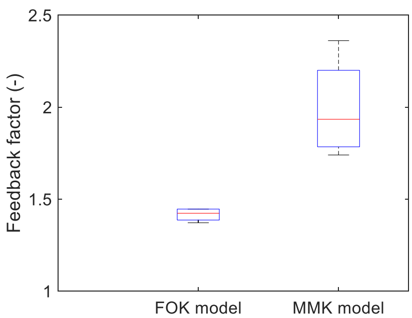

Figure 5 Distribution of the feedback factor for the two model versions FOK and MMK across emission scenarios based on the temporal change in atmospheric carbon content between 2080-2100 and 1850-1900.

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 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 similar to 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

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cumulative carbon emissions (Fig. 4). Since increasing surface temperature will lead to an additional CO_2 release from land to the atmosphere, there is the positive carbon-climate feedback mechanism (Arneth et al., 2010)and we asked the question, is there also an effect of the respiration model structure on this feedback strength?

Indeed, this feedback is more than 35 % higher when assuming Michaelis-Menten kinetics, and it is higher for strong carbon emission scenarios (Table 2). As a consequence, our results imply a 88 Pg C (SSP5-85) to 158 Pg C (SSP2-45) higher remaining anthropogenic carbon budget to keep warming below 2 °C above pre-industrial levels only because we assume an alternative model structure for respiration. These estimates are of the same order of magnitude but substantially higher than estimates of additional warming-induced C loss from permafrost-affected soils until 2100 of 10-100 Pg C (Koven et al., 2015). Other additional Earth system feedbacks currently not represented in Earth system models (section 5.5.2.2.5 in (Canadell et al., 2023)), and additional Geophysical Uncertainties like non- CO_2 forcing or emission uncertainty (Table 5.8 in (Canadell et al., 2023)) are also of the same order of magnitude .

We applied a simplified model of global biogeochemical feedback mechanisms, considering only one terrestrial carbon pool and no explicit pool of microbial biomass and microbial functions. Therefore, many specific underlying processes and interactions of ecosystem components are neglected. For example, an increase in respiration due to increasing plant productivity and carbon input to soils (priming effect, (Fontaine et al., 2007; Keuper et al., 2020)), or changing microbial community structure as a response to climate change (Glassman et al., 2018) is not considered. Nutrient limitations of vegetation productivity (Hungate et al., 2003) is only implicitly parametrized in Equations 3 and 4. In addition, climate change is expressed as a temperature change in this model and precipitation effects on carbon cycle functions (Jung et al., 2017) are not taken into account. We therefore see our results as first conservative estimates that point to the importance to communicate and address existing structural uncertainties in Earth System Models. Just by assuming an underlying Michaelis-Menten kinetics of respiration processes leads to distinct projections of future respiration and the carbon-climate feedback mechanism. These results also 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 leads to a relative difference in the carbon-climate feedback over the 21st century of more than 35%. Depending on the underlying emission scenario, that translates into a difference of the remaining carbon budget to keep global warming below 2 °C of 89 Pg C (SSP5-85) to 158 Pg C (SSP2-45). 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 will be made available via github after publication.

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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