

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

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Referee # 1, William Wieder

Beer uses a reduced complexity model to look at different formulations of a land ecosystem respiration term that uses first order vs. Michaelis-Menten kinetics (FOK and MMK, respectively). The paper reports a stronger land C uptake with the Michaelis-Menten parameterization. The manuscript is a nice, albeit unsurprising, illustration of structural uncertainty in land models and how they impact the magnitude of the terrestrial C sink and potential carbon-cycle climate sensitivities.

I like the work, but feel some additional information and clarification is needed to make the findings more straight forward to understand / interpret.

I would like to thank you for reading carefully this manuscript and for your helpful and constructive questions and suggestions that helped to improve the manuscript.

Mainly. I'm a little fuzzy about the use of the term carbon-climate feedback here, which seems analogous to the gamma term in the C4MIP literature (e.g. Arora et al 2020; typically expressed as PgC per degree Celsius). With this convention, gamma_land is typically negative (from the atmosphere perspective), reflecting less land carbon storage under warmer conditions.

The carbon-climate feedback (γ) quantifies the response of the carbon cycle to changes in physical climate and is expressed in units of carbon uptake or release per unit change in global mean temperature (PgC °C⁻¹).

Conceptually, this looks similar to the left side of Fig 1, which focuses on positive feedbacks between temperature, ecosystem respiration and atmospheric CO₂ burden. The rest of the results, however, don't share this perspective, which makes the conclusion (and title) confusing.

Thank you very much for this comment which shows that I need to explain the definition of the metrics used to quantify the carbon-climate feedback in more detail. I will add equations to the text in section 2.3 and hope this increases the clarity. Note, there was a clear mistake in the calculation of the feedback and the feedback factor before as has been noted by the other reviewer.

Confusion can occur because sometimes terms are used in short in the literature. According to the IPCC definition, a climate feedback is an interaction in which a perturbation in one climate quantity (here atmospheric CO₂ content) causes a change in a second and the change in the second quantity ultimately leads to an *additional* change in the first due to mechanisms internal to the system. In our case of biogeochemical feedbacks, the feedback is the *additional* change in CO₂ after its perturbation due to internal system mechanisms. We start with pre-industrial CO₂ content and add anthropogenic CO₂ until 2100. Then, we can measure the temporal difference as Delta_CO₂. Due to feedbacks, this difference is not pre-industrial CO₂ plus the sum of emissions ("ΔCO₂ off" in the revised manuscript), but there is a difference which we call feedback f in units of mass of C (Hansen et al., 1984; Lade et al., 2018; Zickfeld et al., 2011) In addition, one can compute the ratio of both temporal CO₂

changes, with and without feedback, which is called the feedback factor F (Zickfeld et al., 2011). This factor shows if the feedback is positive ($F > 1$) or negative ($F < 1$) and can be used to compare several biogeochemical feedbacks.

Another question that has been discussing in the literature is the response of land and ocean carbon pools to changes in CO_2 or air temperature and assuming a linear relationship $\Delta C_{\text{land}} = \beta_{\text{land}} * \Delta \text{CO}_2 + \gamma_{\text{land}} * \Delta T$ (Friedlingstein et al., 2003, 2006, Arora et al., 2020). The feedback parameters beta and gamma are sensitivities: How much is land carbon changing due to either CO_2 or T effects? Units are mass C per atmospheric concentration or mass C per temperature.

In this paper, I would like to use concentrate on the quantification of the feedback (change in atmospheric CO_2) without assuming a linear relationship of the gamma-beta approach. Therefore, the feedback factor is applied. However, because the gamma-beta approach seems to be so manifested in the literature and also is asked for by two reviewers, I have extended the manuscript and added radiatively and biogeochemically coupled simulation experiments in order to estimate these sensitivities following (Friedlingstein et al., 2006; Friedlingstein et al., 2003).

I'll try to walk through some sources of this confusion and offer suggestions on how to clarify:

- *Results (Fig 3) shows higher land C uptake and lower atmospheric burden of CO_2 with the MMK. To me this implies a reduction in strength of the temperature-respiration feedback with MMK, which allows for more land C uptake. Is this accurate?*

This is a very important question to understand the study. Fig 3 shows changes in state variables of the two model versions when assuming all feedbacks. This is to show how the system of equations work in general and how model results compare to observation-based estimates during the historical period, and how they evolve in future. This shows us the behaviour of the model, e.g. inter-annual variability is not captured, but trends do. The higher land uptake by the MMK model is due to internal carbon dynamics: the CO_2 fertilization of GPP leads to more substrate availability for respiration which leads to proportionally more respiration in the case of the linear model (FOK) while the Menten kinetics model assumes a less pronounced impact of more substrate availability and hence reduced respiration relative to the input.

- *The “terrestrial carbon-climate feedback”, Table 2, it's unclear if this is basically the size of the cumulative land sink, which is positive (i.e.; from the land perspective) and expressed as Pg C , (not Pg C/degC). Or if this is the difference in atmospheric CO_2 accumulation from the “feedback on”, ($Q_{10}=2$) vs. “feedbacks off” ($Q_{10}=1$). If it's the later, this suggests a larger atmospheric CO_2 burden from warming with the MMK approach, which is difficult to square with the results in Fig 3. Maybe the heading for this figure can be clarified?*

I hope that Tab 2 becomes clear with the advanced definition of what is the carbon-climate feedback in section 2.3 of the revised manuscript. Indeed, Tab 2 shows that the feedback is stronger for the MMK model.

- *Finally the “feedback factor” seems to be some kind of a ratio (see additional question below), maybe comparing the runs with $Q_{10}=2$ (“feedbacks on”) vs. $Q_{10}=1$*

(feedbacks off)? this may allow diagnoses of the inferred temperatures sensitivity of FOK vs. MMK respiration schemes, but it's not really clear what this metric is communicating, or where the results from the "feedbacks off" simulations come into play here?

Yes, the feedback factor is explained in detail in (Lade et al., 2018; Zickfeld et al., 2011) but I will extend the methods section using equations to make it more clear here. There is a new definition in the revised manuscript because reviewer #2 identified a mistake. The feedback factor is the ration of two changes in atmospheric CO₂ content, including specifically this feedback and without any feedback. Please, have a look in the revised methods section. This dimensionless factor can be used to compare the strength of different feedbacks and different models, and it shows whether the feedback is positive (>1) or negative (<1).

The simplest solution here may be to remove the use of "carbon-climate feedbacks" here, unless results can be presented in a way that similar to the C4MIP conventions (commonly a reduction in land C uptake per deg warming). If taking this approach, the manuscript can focus on land C sink or land C uptake from the title and throughout the manuscript to be more consistent with results presented. If taking this approach Fig 1 may not be necessary. Clarification on the 'feedback factor' (Table 3, Fig 5) would also be necessary. This may not be accurate, however, if Table 2 is actually showing the difference in atmospheric CO₂ burden from Q10=2 vs. Q10=1 experiments.

I hope to have clarified the term carbon-climate feedback (not the feedback parameter) and how it is calculated, and that I could convince you about its usefulness to understand the uncertainty of model structure for such feedback estimation. In addition, feedback parameters (sensitivities) beta and gamma has been added, too.

Minor and technical questions

Abstract (and elsewhere?) for a single author paper use "I" not "we".

Yes I can change the manuscript accordingly.

I'm not really clear how the "carbon climate feedbacks" were calculated (Table 2), or what the carbon-climate feedback factor represents (Table 3 and Fig 5)? It's the ratio of temporal changes in the land C stocks (end of 21st century pools / end of 19th century pools) Line 134? This doesn't add up when if I do the math on numbers reported in Tables 1 & 2, please clarify in methods. Maybe it's the ratio of the temporal changes in the runs with Q10=2 (feedbacks on) vs. Q10=1 (feedbacks off)? Some addition text in the method and results would help clarify these results.

See above. Methods section revised.

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Referee # 2

I would like to thank this reviewer for reading this manuscript so carefully, for all the important questions, and for identifying one important misunderstanding of the feedback analysis (see below) which all improved substantially the manuscript.

I agree to reviewer #1 that, qualitatively, the results from this study are rather foreseeable: Because the MMK model limits soil respiration when the land carbon storage grows beyond a certain amount, this model enhances the land carbon sink, whereby the remaining carbon budget gets larger, the land contribution to the carbon-concentration feedback gets more positive (there is more carbon stored per ppm CO₂ rise; – sensitivity), and the land contribution to the climate-carbon feedback gets more negative (there is more soil carbon to be respired per degree climate change; sensitivity). So the main advancement by this study would be its quantitative results (that are partly noted in the abstract). But I doubt that those numbers have any relevance (major comment 1 below) and, moreover, I don't trust these numbers (major comment 2 below). In addition, as also noted by reviewer #1, the feedback analysis is rather unclear (major comment 3 below), and – if my reconstruction of its meaning is right – the feedback metrics used are not simply a measure of the carbon-climate feedback (as intended by the author; see title) but are mixing information on this and the carbon-concentration feedback.

I agree with the reviewer that it is important to quantify the effect of a Menten kinetics formulation for the carbon-climate feedback. That is actually the aim of the study and the methods used. The numbers presented shows the order of magnitude of the effect of the different respiration formulation itself. This shows the strong need to advance our theoretical understanding of which assumptions and equations to be used at which scale. I will clarify all major and minor points raised by the reviewer below.

This study aims to quantify the effect of the respiration model formulation used on the response of the carbon cycle and climate to anthropogenic emissions and hence the carbon-climate feedback. This is an important question because different model formulations are used in the literature and parameters calibrated based on recent observations. Here, I show that different formulations of the respiration differential equation lead to different responses to emissions even when the models are fitted to recent observations.

Major 1)

I agree with the reviewer that the coupling of carbon and nutrient cycles can largely influence the response of ecosystems to climate change and hence climate feedbacks. This is also true for many other interactions within ecosystems which are not considered in this study, e.g. the coupling to the hydrological cycle: soil carbon stocks influence soil water content and hence evapotranspiration and also GPP and plant growth. This study aims to quantify the effect of the respiration model formulation used on the response of the carbon cycle and climate to anthropogenic emissions and hence on the carbon-climate feedback. For this, a simplified 0-dimensional model is used because the overall order of magnitude of the effect is of interest. To include many other important effects on the carbon cycle is interesting but out of the scope of this study, and could be still hard to be done even using a most advanced Earth System Model. For example, coupling of carbon, water and nutrient cycles and using a Menten kinetics formulation of heterotrophic respiration is represented in (Yu et al., 2020) but global simulations are still work in progress and I do not know any respective experiments using a full coupled ESM simulation.

Still, I fully agree with the reviewer that these additional ecosystem interactions are generally important for a quantification of the climate-carbon feedback and will advance the discussion section of the revised manuscript in this respect.

On the usage of either equation for respiration: This is more a scaling question than a question of biogeochemical cycles interaction. The underlying biogeochemical reactions are all enzymatic, hence at the process level we should apply a Menten kinetics model with some assumptions like the transition complex being in steady state. At the macro scale, the same model can be used when all state variables and environmental conditions are correctly integrated (Reichstein & Beer, 2008). This is for example how we operate in land surface models for estimating photosynthesis: The Farquhar model is a Menten kinetics model and we use it at the landscape scale integrating the leaf area index. However, sometimes we can simplify the Menten kinetics to a first-order model, e.g. when the amount of substrate is much smaller than the Menten parameter K . Such first-order model is the traditional model used (Andr  n & K  tterer, 1997; Parton et al., 1988) in ESMs but novel developments assume Menten kinetics now (Yu et al., 2020) This led to the research question of this paper: what is the structural uncertainty of this model formulation on future carbon cycle functions and the carbon-climate feedback even when parameters are calibrated such that recent fluxes are similar to observations? I will make sure in the revised manuscript introduction section that this rational is more clear.

Major 2)

- a) Land carbon cycle model formulation. Thank you very much for thinking in depth into this problem.

There is a misunderstanding about the respiration term in the model: This is not heterotrophic respiration but ecosystem respiration as the sum of autotrophic and heterotrophic respiration. This is clear from the second term of the equation in (Lade et al., 2018) which multiplies the decomposition rate constant with the total land carbon pool. Indeed, I was co-author of the study (Lade et al., 2018) in particular to oversee the land carbon model formulation.

For this study, I recognized this mistake in the previous formulation and made the model consistent. The first term of the equation represents GPP (CO₂ fertilization works on GPP not NPP), the second term ecosystem respiration and the last term land use emissions. That is also why the parameters needed to be adjusted in the FOK model version: the decomposition rate constant k is the ratio of GPP to total land carbon following (Carvalhais et al., 2014). Fig 2 shows that this more consistent model also compares well to observations.

- b) MMK model parameter estimation. I adjusted the two Menten parameters v_{max} and K have in order to match historical observations and FOK model results in the previous version of the manuscript. I agree with the reviewer that this calibration could have been done in a more formal way. For the revised version of the manuscript, I used a formal least-squares gradient decent method (MATLAB function `lsqnonlin`) to calibrate the two Menten kinetics parameters against observations of the land-atmosphere exchange of CO₂ for the historial period. The such slightly adjusted parameters are $v_{max}=200 \text{ PgC a}^{-1}$ and $K=1787 \text{ PgC}$. MMK model results are similar to the previous version. All results will be re-computed using these parameters and the methods section extended.

Major 3)

I would like to thank the reviewer to think about the feedback analysis in that detail and for pointing out an important previous misconception on my side. I fully agree with the reviewer to estimate the carbon-climate feedback as the difference in CO₂ change of two simulations: one switching off all feedbacks (“off”) and one having considered the feedback of interest, here the carbon-climate feedback (“on”) following the procedure explained in (Hansen et al., 1984; Zickfeld et al., 2011). With that the feedback factor is defined as $F = \Delta\text{CO}_2(\text{on}) / \Delta\text{CO}_2(\text{off})$. This way the carbon-concentration feedback does not influence the analysis of the carbon-climate feedback. The methods section is extended in order to explain the procedure and calculations in detail.

I can understand that the audience wants to compare also feedback parameters (sensitivities) beta and gamma following (Friedlingstein et al., 2006; Friedlingstein et al., 2003) and I present these numbers in the revised manuscript and extend the methods section accordingly.

After applying the adjusted concept, the feedback factors are similar and the overall conclusions do not change (table below). Beta and gamma values of the FOK model simulation assuming the high-emission pathway (SSP5-85) are at the higher end of the range of values reported in the literature (Arora et al., 2020; Friedlingstein et al., 2006; Zickfeld et al., 2011). Beta and gamma (and feedback factors) increase towards low-emission scenarios (REF) and also amplify when using the Menten kinetics model MMK (table below). I will extend the discussion section with these comparisons.

Feedback factor	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

Feedback parameters	β , PgC ppm ⁻¹ , first-order kinetics (FOK)	β , PgC ppm ⁻¹ , Michaelis-Menten kinetics (MMK)	γ , PgC K ⁻¹ , first-order kinetics (FOK)	γ , PgC 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

Minor

Title, abstract, and throughout: Whenever the author talks of respiration, heterotrophic respiration is meant (also called “soil respiration”), in contrast to autotrophic respiration. This should be made clear in the title, the abstract, and elsewhere.

As explained above, the model considers ecosystem respiration.

The Lade et al. model is missing the temperature dependence of photosynthetic production. I don't think that a quantification of the carbon-climate feedback without that temperature dependence makes sense. At least it should be made clear that the study accounts (if at all) only for part of that feedback.

On a global scale, there is no clear relation of GPP to temperature; individual plant functional types can have different low and high temperature inhibition functions (Sitch et al., 2003), but in general photosynthesis is most constrained by light, CO₂ and nutrients. The indirect effect of temperature on soil water content and hence stomatal conductivity, and the limitation of photosynthesis by light and CO₂ will override any specific increase of photosynthesis with temperature. But also at the individual scale, there is no clear relationship, see Fig 9.16 in <https://www.ehleringer.net/uploads/3/1/8/3/31835701/413.pdf> Temperature dependence of autotrophic respiration is accounted for by the model as full ecosystem respiration is considered.

Line 9 (abstract): The formulation "The epistemic uncertainty . . . is unclear" a bit weird: I guess the author wants to express that because of epistemic uncertainty there is quantitative uncertainty whose size is unclear – hence it would be the quantitative uncertainty being unclear, not the epistemic uncertainty.

I agree and update this sentence to: "The effect of the respective mathematical representations on the terrestrial carbon-climate feedback is unclear."

Lines 13-15 (abstract): This formulation is misleading: taking it literally, the author suggests to improve our understanding of the model structure of Earth system models. But I guess the author wants to emphasize that we need to improve our understanding of heterotrophic respiration to improve its representation in Earth system models.

No, it is less the understanding at the process level that is missing but more the question on how to model these processes at a landscape to global scale.

Line 28: Why "in contrast"? In contrast to what?

Words deleted. Thanks.

Line 35 (caption of Fig. 1) and line 39: Only the negative feedback may be termed "biogeochemical", the positive feedback is non-biological and mostly determined by physics (radiation in the atmosphere, temperature dependence of reaction rates); for terminology see e.g. [3].

Following IPCC AR6, chapter 5, we define biogeochemical feedbacks as feedbacks that change atmospheric greenhouse gas concentrations due to biological functions which is the case for both the carbon-concentration feedback (biological function photosynthesis) and the carbon-climate feedback (biological respiration processes), cf. Fig 1. See also (Arnell et al., 2010). In contrast, a change in vegetation cover hence albedo change as a response to CO₂ and climate would form a biogeophysical feedback mechanism.

Line 50: A better reference than (Zickfeld et al., 2011) on the methodology of separating climate-carbon feedbacks would be the original study [2] or the recent review [3].

Thank you for pointing on these references. For the original methodology of the feedback factor I will include also Hansen et al (1984). This is included into the revised version of the manuscript.

Line 85: Better: “atmospheric CO2 concentration” instead of “atmospheric carbon content”.

The model operates with the latter one, units in PgC, see methods section parameter table. But I will extend the methods section to make this more clear.

Line 106: Should this read “1850” instead of “1750”? If not: explain how the model is forced between 1750 and 1850.

We run the model during the time period 1850-2100. The model is initialized with values at 1850 and driven by emissions. Land-use change emissions were available since 1850 from the Global Carbon Project.

Line 117 (Fig. 2): Use “PgC/a” for the units noted in the ordinate labelling (as in Fig. 3).

I harmonize the text using PgC a⁻¹

Line 123: Concerning the methodology for determining climate-carbon feedbacks you cite (Zickfeld et al., 2011). Please give credit also to the inventors of this methodology [1, 2].

Done.

Line 147 and Fig. 3: You use the term “changes” with two different meanings: Your “stock changes” are rates of stock change (fluxes), while your “temperature change” refers to a difference. It would be more clear to make this transparent in the text and Figure (as you did in line 164).

Carbon fluxes are reaction rates calculated as stock change per year. Fig 3 also shows the temperature anomaly, here the difference to the pre-industrial average is meant. I will use terms “carbon flux” and “temperature anomaly” for more clarity in the revised version of the manuscript.

Lines 157-160 (caption Fig. 3): I guess the solid lines show the results for the FOK model, but this is not noted.

Thanks, added to the caption.

Lines 256 and 282: I do not see how the value of 35% – mentioned as key result of the study in the abstract – follows from the values in table 3. I guess its some kind of mean value, which would not make sense (see next comment).

Line 234 (Fig. 5): This figure doubles the information from table 3. Moreover, it is inappropriate to show these data as box plots: Box plots are meant to display major characteristics of a statistical distribution, for which it makes sense to calculate mean

value and percentiles. But the four scenarios, whose data are listed in table 3, do not form a statistical ensemble so that the results from the scenario simulations are not realizations of a random process which could be characterized by a statistical distribution.

Thank you for this clarification. I remove the boxplot, and discuss the four individual relative differences in the revised text.

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