We thank both reviewers for their helpful comments. We summarize the changes we made in the revised manuscript in this document by:

1. General changes (overview)
2. Revised response reviewer 1
3. Revised response reviewer 2

Where possible and useful we refer to changes by referring to lines in the revised manuscript.

General changes

Both reviewers asked for major revision, with a strong focus on streamlining the introduction and result section and a clearer description of model limitations in the discussion section. Therefore we heavily revised these sections following the reviewers suggestions. We here summarize these changes and highlight important alterations.

Introduction

We completely revised and streamlined the introduction and here display our line of thought for the new introduction:
The introduction starts with a general overview on nutrient limitation on CO_2 fertilization and how this relates to root exudation and uncertainties in soil C sequestration. We explain that observations and model-data synthesis for FACE experiments in N-limited forests, highlight the importance of root exudation but that knowledge about microbial-mediated soil C sequestration processes, especially in P limited forests, is limited. We refine the research gap by focusing on the P limitation and EucFACE. We point to the missing link between observed GPP and heterotrophic respiration increase under eCO2, and use conclusions from previous model-data synthesis studies at this site, to highlight the need for representation of root exudation in a microbial explicit TBM. We shortly explain the general method of this study (implementation of a dynamic root exudation flux) and conclude that our model can help in disentangling underlying microbial-mediated soil C sequestration mechanisms. We explain 3 distinct mechanisms and present our research objectives according to these mechanisms.

We added a figure for the discussed mechanism. We now focus on three mechanism (line 115-135):

- microbial growth and necromass growth, including microbial CUE.
- microbial decomposition of necromass and priming
- biochemical mineralization as additional flux for nutrient acquisition.

(1) Exudates regulate gross growth of microbial biomass, which in turn influences necromass production (Fig. 1 (1)) (Cotrufo et al., 2013). The capability of microbes to transform additional C input into biomass depends on their carbon-use efficiency (CUE). Carbon-use efficiency of microbial growth has been shown to be constrained under nutrient limitations (Manzoni et al., 2012; Spohn, 2015). If microbes are not able to fulfill their stoichiometric nutrient requirement for growth, excess C will be respired as waste respiration, leading to a

decline in CUE (Schimel and Weintraub, 2003). How much of the additional C input is ultimately transferred into biomass and necromass therefore depends on microbial nutrient limitation.

(2) Under N or P limitation, microbes can stimulate the depolymerisation of nutrient rich microbial necromass to potentially acquire more N and P (Fig. 1 (2)) (van Groenigen et al., 2014; Vestergård et al., 2016; Yin et al., 2013). While this may happen proportional to growth, microbes may also change their relative investment into nutrient acquisition strategies. Either way, the additional depolymerization of microbial necromass under increased root exudation, often referred to as priming, will result in an increased respiration of old organic C and has the potential to offset the gross growth of necromass.

(3) Under strong P limitation, P can be gained through biochemical mineralization without the need to decompose necromass (Fig. 1 (3)) (Margalef et al., 2017; Turner et al., 2014; Walker and Syers, 1976). In this process, microbes use phosphatase to hydrolyze terminal phosphate groups from organic matter as inorganic PO_4 that is available for plants and microbes (McGill and Cole, 1981; Nannipieri et al., 2011). As this mechanism does not require the full depolymerization of microbial necromass it decouples microbial nutrient acquisition from C cycling and does not directly decrease C storage.

We mention association of microbial biomass with mineral surfaces in line 110 but removed it from the list of mechanisms. We are aware that this process is relevant for soil C sequestration and protects microbial biomass from decomposition. The model accounts for this and we discuss this in line 567-575 of the discussion. However the contribution of this process is beyond the scope of this study.

We further altered our research objectives, fitting to explained mechanisms (line 139-150)

With this study we aim for a first quantification of root exudation fluxes for the EucFACE experiment. We test our implementation against observations regarding allocation of additional GPP under eCO_2 in the ecosystem. We further aim to answer the following objectives:

(1) To which extent did increased root exudation under eCO_2 contribute to gross microbial growth, gross necromass production and increased heterotrophic respiration?

(2) Was priming, as a mechanism for microbial N acquisition, increased by higher root exudation under eCO_2?

(3) Was biochemical mineralization, as a mechanism for microbial P acquisition, increased by higher root exudation under eCO_2?

(4) Was net necromass production, defined as the difference between gross necromass production and decomposition, increased by higher root exudation under eCO_2?

We try to keep the structure we set with the research objectives in result and discussion.

Methods

We followed the reviewer suggestions (see reviewer replies for details). Important changes include:

- The revised manuscript starts with a section on how the model was used (prev. section 2.4, now sect. 2.1) and then continue with the model description.
- We added a new column to table 1, to clarify how available specific soil pools are for microbial processes.
- For clarity we do not further use microbial residue to refer to microbial necromass, but only use necromass. We accordingly updated figures and equations.
- removed ecosystem turnover time calculation

Results

We updated figures providing clearer x-axis and labels. We reduced the amount of displayed data and fitted it closer to research objectives:

Section 3.1 focuses on model evaluation and general plant C fluxes, as these were the original motivation behind this study. In the revised manuscript we do no longer discuss every flux in GPP allocation but focus on the important fluxes. Additional numbers are still given in the supplement.

Section 3.2 focuses on the research objectives regarding microbial-mediated C cycling:

3.2.1 aligns with research objective 1 focusing on gross microbial growth, necromass production and respiration. We altered Fig. 4 (now Fig. 5) and added gross necromass production. We reduced the numbers displayed in the text and now focus on important fluxes.

3.2.2 now has a clear focus on resource acquisition. We removed fig 5 a-c, Instead we added a new figure (Fig. 6) with a clear focus on necromass decomposition for N acquisition and biochemical mineralization for P acquisition. We made fig 5 c-e an individual figure (now Fig. 7) and completely removed figure 6 of the old manuscript. We instead add a figure about mineralization and biochemical mineralization under aCO_2 and eCO_2 to the appendix (B5, new manuscript).

3.2.3 still summarizes necromass cycling. We transferred the turnover time table into appendix (B4). We also corrected an error: *The displayed figure 7 (now 8) was wrong*. *We updated it and the corresponding numbers in the text.* The absolute flux numbers given in the supplement were already right and now also correspond with the displayed figure/text (line 449, line 451).

before:

“However, increased depolymerization under eCO_2, as result of increased priming activity and biochemical mineralization also led to increased outgoing fluxes (C: 8 %, N: 8 %, P: 30 %). “

“For C and N, the effect of eCO_2 was positive leading to a 11 gC m^{-2} yr^{-1} and 2 gN m^{-2} yr^{-1} increased net input through microbial necromass compared to ambient conditions”

after:

“However, increased depolymerization and biochemical mineralization under eCO_2 also increased outgoing fluxes (C: 9 %, N: 9 %, P: 30 %). “

“Under ambient CO_2, net necromass production in C and N was close to zero, whereas under eCO_2, net production was positive causing a 12 gC m^{-2} yr^{-1} and 2 gN m^{-2} yr^{-1} necromass increase compared to ambient conditions. “

Discussion

Due to the altered research objectives and reviewer comments, we revised our discussion:
4.1 to 4.4 follow the research objectives, with 4.1 focusing on the quantification of root exudation under ambient and elevated CO_2, 4.2 focusing on growth and respiration, 4.3 focusing on nutrient acquisitions and 4.4 focusing on net effect in necromass. All sections follow the same structure: interpretation of results, comparison with observations and possible model limitations that would refer to the discussed process.
For consistency, we altered the discussed recommendations (4.6) for further advancements in modeling and experimental work and reduced some text.
We additionally altered the conclusion following reviewer comments

Appendix

Removed sections. Added table B4 (turnover times), and figures B5 and B10 to the appendix.

Supplement

Changes numbers of tables. Added new table for new figure.

Reply to reviewer 1

This is a revised version of the already given reply. The reviewer comments are in bold, and the replies in regular font.

This manuscript presents an interesting and timely study that contributes to the overall understanding of carbon allocation and transfer via root exudates, and how these processes interact with nutrient cycling under elevated CO_2. The work highlights the importance of root exudation from a modelling perspective and provides valuable recommendations for improving the representation of root exudation, microbial dynamics, and plant-microbe interactions in global ecosystem models.

The authors implemented a dynamic root exudation module within the QUINCY-JSM model and applied it to the EucFACE experiment, a P-limited mature eucalypt forest. The goal of quantifying competing soil mechanisms that regulate carbon storage under changing root exudation fluxes at elevated CO_2 is both relevant and timely, particularly given the current uncertainties surrounding belowground carbon dynamics and their coupling to nutrient availability under future conditions. The model appears to be a meaningful advancement in simulating carbon and nutrient dynamics by explicitly incorporating exudation fluxes. Although the exudation flux is not validated, I appreciate that the authors transparently discuss model limitations and outline thoughtful directions for future development.

We thank referee 1 for taking the time to read our manuscript and acknowledge the advancements of our manuscript. We appreciate the detailed feedback, which will help us to improve the manuscript.

Major Comments

- **Focus and structure of results: The results section is very detailed, and at times it is difficult to see how each subsection directly contributes to addressing the central research aim. To improve readability and narrative coherence, I recommend focusing the main text on the findings that directly support the study's objectives and relocating more descriptive or tangential results to the supplementary information.**

  We reduced the main text of the result section, by reducing text and figures, and focused on important fluxes. We further tailored our results to the research objectives. .See General changes: Results.

Clarity of terminology: Several key terms are used inconsistently or remain insufficiently defined. For example, "C sequestration" is not clearly specified—does this refer to plant biomass, soil carbon, or both? Please clarify terminology throughout.

Where it is not clear from context (e.g. line 51, 475), we now write “soil C sequestration” (e.g. line 37, 89) and “ecosystem C sequestration” (line 577).

Introduction, structure, and research gap: The introduction would benefit from clearer structuring. Some sections are heavily process-oriented without sufficiently linking these processes to the specific research gaps the study aims to address. In particular, a clearer explanation of how belowground carbon allocation fits into the forest carbon cycle – and how it connects to NPP or GPP under elevated CO_2 - would strengthen the rationale for the study.

We completely revised the introduction, please see General changes: introduction above

Mechanisms for soil carbon sequestration: The paragraph outlining mechanisms contributing to soil carbon sequestration requires revision, as several points are unclear or insufficiently explained (see specific line comments).

see General changes: introduction above

Grammar and style: Please ensure the manuscript is carefully revised for grammar, typos, and general language clarity.

We checked for grammar, typos, and language clarity.

L28: If the study anticipated that root exudation would play a key role here, please state this explicitly, as it would help clarify the motivation behind the work.

- Jiang et al (2020) does not explicitly mention root exudation but states “our results suggest a direct connection between plant photosynthesis and belowground activity”. We revised the sentence (line 27-29):

  “ In this experiment, eCO_2 increased gross primary productivity (GPP) and soil respiration, but more than half of additional GPP under eCO_2 could not be assigned to measured biomass production or autotrophic respiration, and was likely allocated belowground..”

L35–36: This conclusion appears too weak, given the strength of the results. One key outcome seems to be that incorporating exudate C fluxes into forest C budgets under elevated CO_2 improves the precision of GPP estimates—shouldn’t this be highlighted?

- Revised (line 36):

  “Our study highlights the importance of root exudation as a key pathway in vegetation C allocation under eCO_2 and identifies microbial responses to this flux as a key modulator of soil C sequestration in nutrient limited forests, thereby guiding further research regarding plant-microbe interactions.”

L57: This sentence is incomplete and needs revision.

- We deleted this sentence and now write (line 54):

  “Under elevated CO_2 (eCO_2), plants may allocate additional C derived from increased photosynthesis to root exudation and mycorrhizae to compensate for nutrient limitations, by increasing microbial decomposition and mineralization of organic matter (Drake et al., 2011; Phillips et al., 2011; Reay et al., 2025). “

L70: Does this statement imply a shift in carbon use efficiency? Please clarify.

- We now clarify this in line 116-117:

  "The capability of microbes to transform additional C input into biomass depends on their carbon-use efficiency (CUE). Carbon-use efficiency of microbial growth has been shown to be constrained under nutrient limitations (Manzoni et al., 2012; Spohn, 2015). "

L72–77: This passage is highly speculative. As phrased, it describes a natural process; larger microbial biomass will, of course, generate more necromass. This could be more clearly integrated into point (i): exudates regulate microbial biomass, which in turn influences necromass production.

- Revised. We now describe gross growth (production) in microbial biomass and necromass as one mechanism in line 115:

  "Exudates regulate gross growth of microbial biomass, which in turn influences gross necromass production (Fig. 1 (1)) (Cotrufo et al., 2013). "

  and further describe how CUE links this process with nutrient availability.

L84–88: Is this describing a specific scenario? Please clarify how this relates to mechanisms promoting soil C sequestration.

- We describe the process of biochemical mineralization, by which microbes (and plants) are able to acquire P without depolymerisation of microbial necromass. This is especially relevant in the scenario of microbial P limitation and represents a pathway which does not exist under microbial N limitation. We now clarify this in line 128:

  "Under strong P limitation, P can be gained through biochemical mineralization without the need to decompose necromass (Fig. 1 (3)) (Margalef et al., 2017; Turner et al., 2014; Walker and Syers, 1976) "

L92: Why are FACE sites considered "low-disturbance"? Please justify or clarify this statement.

- We referred to FACE experiments as low-disturbance since after establishment, vegetation is not removed from the experiment and soil conditions are kept as close to the original conditions as possible. However, the experiment is still subject to natural disturbances by climate, and the infrastructure and its construction itself is some form of disturbance, in particular at the start of the experiment. We thank the reviewer for questioning the terminology here, and removed this sentence as it may be unnecessarily misleading at this point.

L97: Please repeat or clarify the explanation here; the meaning is currently unclear.

- We now write this statement as (line 66):

“One explanation is that plants maintained N availability under eCO_2 at Duke FACE, by promoting enhanced decomposition of soil organic matter (SOM) via increased root exudation, thereby increasing N mineralization but offsetting accumulation of C in soil pools (Drake et al., 2011; Terrer et al., 2021).”

L111–117: This seems to be methodological information and may fit better in the Methods section.

- We thank the reviewer for this observation. However, we believe that the description of our methodological approach and the study site is necessary here to to understand the research questions. We use the introduction to hint towards research gaps in plant C allocation to soils and soil C sequestration mechanism in EucFACE discovered by observational and model data-synthesis studies and now write (line 100):

“Here we aim to address the key missing link between GPP increase, plant C allocation and cycling of C, N and P in soils by implementing root exudation in the microbial-explicit, terrestrial biosphere model, QUINCY-JSM (Thum et al., 2019; Yu et al., 2020) to simulate CO_2 fertilization at EucFACE. Like in other models, previous simulations with QUINCY-JSM, showed a mismatch between simulated and observed C allocation and response of soil heterotrophic respiration to eCO_2 for EucFACE (Jiang et al., 2020). We therefore implemented root exudation in QUINCY-JSM. We assume root exudation as dynamic flux, based on plant fine root respiration and nutrient status. We use our model to investigate how root exudation affects underlying mechanisms of microbial soil C sequestration under eCO_2”

L120–122: This information requires appropriate references.

- We now write (line 82):

“At the site eCO_2 increased gross primary productivity (GPP) by 12 %, but the effect on biomass production and autotrophic respiration was comparatively small (Jiang et al., 2020). “

L122–123: Please explain “surplus” and “vegetation flux” more clearly. How do these terms connect to exudation processes and soil C sequestration?

- Revised, now (line 82):

“Notably, Jiang et al. (2020) found that more than 50 % of additional GPP under eCO_2 could not be attributed to biomass production or autotrophic respiration, in this experiment. ”

L138: Please define what is meant by “dynamic root exudation.”

- Revised, we now write (line 104):

> “We therefore implemented root exudation in QUINCY-JSM. We assume root exudation as dynamic flux, based on plant fine root respiration and nutrient status. ”

L141: The phrasing is awkward; a model cannot “decompose” something. Please rephrase.

- Revised. We now write (line 109):

> “.Therefore, we use our model to investigate three competing mechanisms that may regulate soil C sequestration response in microbial necromass to altered microbial growth and nutrient acquisition as a result of increased root exudation (Fig. 1). “

L144-157: This section reads like a procedural description, yet this is where one would expect the research aim, plus research questions or hypotheses. Please revise accordingly.

- We revised the research objectives, so that they align better with the displayed mechanisms for microbial-mediated soil C sequestration. See comment above.

L154: Is it possible to describe in this section how the model was used *for this study*, not how the model functions in general?

- We thank the reviewer for this observation. We think that a general model description is necessary and an important part of the methodology. We explain in section 2.4. model application in more detail how we used the model for this particular study. To improve readability, and to account for this concern, we moved section 2.4 (now 2.1) before the model description (now 2.2) in the revised manuscript. See general changes: methods

L172: How do the soil layers in the model correspond to actual soil horizons, especially given the podsolic profile with strong vertical heterogeneity?

- The model does not explicitly model soil horizons and cannot reproduce the strong vertical heterogeneity. However our model simulates vertical heterogeneity by explicitly calculating C,N and P dynamics on different soil layers. There are 15 soil layers reflecting to 9.5 m depth, from which 6 layers represent the top 50 cm (in manuscript defined as topsoil). In our simulations we adjusted the model by using sand, silt and clay fractions measured at the experiment. Additionally we reduced P content in lower soil layers and reduced maximum sorption capacity of organic matter to fine soil particles to adjust for the weathered soils. Furthermore even between the rings of the experiment there is strong variation.

L225: Please justify how well supported the assumption is that exudate C: N reflects the C: N of the labile soil pool.

- We thank the reviewer for this observation. This was in fact a typo and we meant to say that the exudate C:N ratio reflects the C:N ratio of the current plant labile pool. We revised the sentence as (line 235):

> “Root exudation is modelled as direct, respiration-free flux from the plant labile pool to the soil DOM pool, with a C: N stoichiometry corresponding to the current C: N ratio of the plant labile pool (Fig. 2). “

L310–313: I cannot evaluate the technical accuracy, but as written, the logic is unclear. Please check and revise for coherence.

- Revised. We clarified this by writing (line 311):

“We trace the fate of the additionally assimilated C under eCO_2, through the ecosystem. We standardize fluxes as the percentage of additional overstorey GPP for both simulations and observations. The model currently only simulates forests without understorey vegetation. To maintain comparability, we use observations from overstorey aboveground biomass production, overstorey autotrophic respiration and overstorey changes in vegetation C pools. However, for belowground fluxes, i.e., heterotrophic respiration, root respiration, root biomass production and changes in soil C pools we cannot differentiate between overstorey and understorey origin. We still standardize them as the percentage of additional overstorey GPP but are therefore likely to overestimate the observed change per additional overstorey GPP under eCO_2 in soil fluxes.”

L225: The assumption that exudates contain no P is incorrect. Several known exudates contain phosphorus. This should be reconsidered.

- We thank the reviewer for this observation. We assume that the majority of root exudates are sugars, amino-acids and carboxylates, and therefore focus on modelling C and N exudation. We revised this into (line 236):

  > “As we assume that root exudation mainly consists of carbohydrates, amino acids and carboxylates (Jones et al., 2004) we do not model exudation of P “

  and further write in the discussion (line 548):

  > “Finally, simulated microbial nutrient demand is substantially controlled by root exudation stoichiometry. In our model root exudation C to N ratio was 176 (no P exudation), whereas microbial C to N ratio was 4.3 (N: P = 4.1). Simulated C:N ratio is higher than root exudation measurements (Li et al., 2021; Su et al., 2022; Zhang et al., 2016) but ensures that modelled root exudation does not cause an extensive N loss in plants. As a consequence, increased root exudation enhanced microbial nutrient demand, and plant-microbial competition for N and P (Thurner et al., 2023). Under a root exudation stoichiometry closer to microbial stoichiometry, increased root exudation may further promote microbial growth. Microbial N supply may be less dependent on decomposition of microbial necromass, resulting in stronger decomposition of litter for C acquisition. Instead, a substantial amount of N would be stored in SOM, unavailable for plants. Root exudation C:N ratio remains a key variable in plant- microbe nutrient dynamics, but further research regarding the fate of exudate N is needed to improve model assumptions in plant C-for-N trade mechanisms (Drake et al., 2013; Rumeau et al., 2025). “

L233: Does this imply that a lower amount of root branches exude less simply because they exhibit less growth? How well does this assumption reflect empirical field observations?

- In QUINCY-JSM we do not model root branching. To a specific range less root growth might reflect an increase in plant labile C pools and may therefore result in higher exudation rates. However, ultimately, root exudation is bound to root biomass distribution across the soil profile (more precise root N content). We currently lack observations to model specific exudation rates based on different soil depth. We are aware that this is a debatable assumption and contributes to the uncertainty of the model results. Please see our response to reviewer 2 on this point. We now discuss this topic in line 566:

> “Uncertainties in C storage arise from model representation of C cycling in deep soil layers and mineral sorption of necromass. The model predicts increased soil C in deep soil layers under eCO_2, caused by increased root exudation in these soil layers. As the model assumes root exudation following root biomass distribution, eCO_2, enhances root exudation in deeper soil layers with low microbial activity (Fig. 4). As a consequence, additional labile C is adsorbed to the mineral surface and thereby sequestered. While specific exudation rate may differ with depth and function of roots, we are currently missing data to further calibrate this.”
>
> .”

L255: Please clarify what “saturation” refers to in this context.

- Agreed. We revised this to (line 266):

> “We constrained to values larger than 0.0125 () reflecting a minimal root exudation flux even at nutrient saturated conditions.”

L316: Again, how accurately does this separation represent actual soil horizons?

- See top comment.

L390: This figure and also the other figures in the manuscript would benefit from improved clarity, for example, by reducing the number of abbreviations and making the x-axis description clearer.

- We revised axes and abbreviations for all figures in the manuscript

L410: It may be worthwhile to discuss whether implementing microbial non-growth anabolism in the model would be appropriate.

- We thank the reviewer for this observation. We have explicitly decided not to implement non-growth anabolism as it is not suitable for our model. The model assumes a quasi-steady-state approximation of enzyme dynamics, to reduce complexity. This has been discussed in detail in Wutzler et al. (2022).

L646: Would using in-situ root exudates to extract plant-available P yield more realistic results than the Hedley extraction?

- We agree that artificial root systems may be more suited to evaluate the plant P availability and the direct interaction between root exudation and plant-available PO4. However it remains to be discussed if this method can actually reproduce root zone activity. We mention Hedley fractions here as they are commonly used and available.

Reply to reviewer 2

The reviewer comments are in bold, and the replies in regular font.

The authors integrated root exudation into the QUINCY-JSM model to ascertain whether it would provide a plausible mechanism for the empirical inability to measure a vegetation flux that could account for the increase in GPP under elevated CO_2 as well as explain why there was an increase in heterotrophic respiration without a concurrent increase in soil C at EUCFACE site. The core motivating idea behind this model-data synthesis paper is intriguing and the inclusion of root exudation in QUINCY-JSM is a significant model development. The model formulation of root exudation that depends upon the nutrient status of the plant presented in Figure 2 is also a simple but novel way to predict exudation fluxes in a dynamic manner. Overall, the manuscript presents a good idea, executes it in the model, and uses it to generate new hypotheses to explore to understand how elevated CO_2 impacts ecosystem carbon cycling in P limited systems. However, the manuscript needs better structure, some cleaning up of grammar and sentence structure, a culling down of the presented results to give the reader the main points in a way that is easy to follow, and some clear discussion of the limitations and assumptions of the modeling effort and how they impact the conclusions. Below I provide the major concerns followed by more detailed line by line comments.

We thank the anonymous referee for taking the time to read our manuscript, for appreciating the novelty of this work and for their detailed feedback.

- **Structure of introduction: The introduction could use some streamlining and focus. Some examples: The authors present four mechanisms to explain the fate of root exudates early in the introduction (one note here a conceptual pictorial model of this would be a great addition). Then there are three loose objectives that are presented at the end. However, these loose objectives are not tied to the four mechanisms that start off the introduction and would benefit from being clearly stated formal objectives or hypotheses. Another example is the paragraph that starts on line 120. I would split this into a simple clear description of the empirical results and then another paragraph that speaks to where models have failed in capturing these results.**
    - We thank the referee for the recommendations and revised the structure of the introduction and reformulated the research goals (see general changes: introduction)

- **Results and figures: The results section is very hard to comprehend and follow. This seems to result from the authors presenting almost all the model data in the text and figures. My recommendation is to go through and pull out the relevant model results that meet the objectives and provide evidence for which of the four proposed mechanisms is operating at the site. As a reader of the results section, I found that there were too many fluxes, too many percentage changes, and many presented that didn't inform the conclusions or the loose objectives in the introduction.**
    - We revised the result section to fit it closer to the revised objectives (see general changes: results)

- **Discussion of the model parametrization and assumptions: First, in Section 2.6, the authors provide a very brief overview of the model parameterization. One of the clear assumptions in the parameterization is that root exudation was parameterized to get the other fluxes right. What are the implications of this and can you provide more detail on how this was done.**
    - We thank the reviewer for this comment. We now clarified how the parametrization was conducted in line 293: .

      "We parameterized the model following in situ-based observations for *E. tereticornis*, taken under ambient conditions from 2013 - 2019, provided by (Jiang et al., 2024a) (Table A1). As no direct measurements of root exudation exist for this site, we calibrated and   to reproduce GPP, biomass and soil respiration for ambient conditions from 2013-2016 (Jiang et al., 2020) (Table B1). By this we limit the size of the root exudation flux. We ensured that the modelled exudation flux still responded to variations in the size and stoichiometry of the labile plant pool, i.e., that the flux was not controlled by empirical bounds of maximum exudation, implying that it is sensitive to changes in plant carbon and nutrient status induced by eCO_2."

Second, the model assumes that if you have roots they exude carbon. One big impact of this assumption is that there are exudate fluxes deep in the soil profile that lead to enhanced carbon storage at depth. At some level these deep roots are probably more important in water uptake than priming decomposition where nutrients and organic matter are scarce and more than likely are not exuding substantial amounts of carbon. Another big impact of this assumption is that with the model predicting a 33% increase in belowground production that is not matched in the empirical data that you have more roots exuding more carbon.

We thank the reviewer for this observation. We agree that the allocation of C in lower soil levels, based on the model assumption that root exudates follows root distribution, is a major uncertainty. This reflects a common model simplification that does not separate functionality of water and nutrient acquiring roots, given a lack of data to parameterise these functions and the relative contributions across soil depth. As a result of this assumption, we prescribe an exponential declining distribution of the exudation response to eCO_2, which may lead to an overestimate of the carbon input via exudation in deep soil layers. Nonetheless, we agree that this is an important point for future improvement and will add this as a point in the discussion to further elaborate on how it impacted the model results and interpretation thereof.

We mention this now in line 376 (results):

"However, the model also simulates an accumulation of C in deeper soil layers equal to 7 % of the additional C uptake, likely caused by increased root exudation in deeper soil layers. "

And discuss in more detail in line 565 (discussion):

"Uncertainties in C storage arise from model representation of C cycling in deep soil layers and mineral sorption of necromass. The model predicts increased soil C in deep soil layers under eCO_2, caused by increased root exudation in these soil layers. As the model assumes root exudation following root biomass distribution, eCO_2, enhances root exudation in deeper soil layers with low microbial activity (Fig. 4). As a consequence, additional labile C is adsorbed to the mineral surface and thereby sequestered. While specific exudation rate may differ with depth and function of roots, we are currently missing data to further calibrate this. ”

To clarify further, our model simulated a 33% increase in biomass production under eCO_2, which translated into a 13.6 % increase in annual fine root production only. This did cause an increase in total root exudation. However, our model also showed an increase in annual specific root exudation (up to 30%, mean increase over whole treatment period: 18%), such that increased root exudation is not solely attributable to increased fine root production.

We revised our manuscript and discuss annual specific root exudation rate increase (line 488):

“Elevated CO_2 also enhanced mean annual root exudation rate per unit fine root mass by 18 % (Fig. B2). “

And discuss consequences of increased BP and litter production in line 500:

“The model also simulated a 33 % increase in overstorey BP under eCO_2, which was not observed in EucFACE. In the simulation, C accumulated primarily in woody biomass and labile plant pool (Fig. B10), but this had only a minor influence on soil processes because plant litter contributed little to microbial growth in C, N and P in the treatment period (Fig. 7). Instead, root exudation dominated the additional C input and the supply to microbial growth under eCO_2. Observational studies suggest that plant P limitation suppressed plant growth under eCO_2 (Jiang et al., 2020), suggesting that the model likely underestimates P constraints or overestimates plant adaptability to P limitation.”

For clarification we also added Figure B10 to appendix

Finally, there also appear to be mechanistic assumptions in how microbial necromass is cycled in the model. The necromass appears to simply just get recycled as the microbes are using it to mine nutrients. Does the model assume that all necromass is readily available for microbial attack? What is the nature of the competition for necromass fate between sorption to mineral surfaces vs. microbial attack? It seems like the model assumes that necromass is always available for microbial attack which doesn’t parallel empirical mechanisms where microbes are living and dying in intimate contact with soil minerals so that they are preferentially stabilized on mineral surfaces.

We thank the reviewer for this comment. The model does separate between necromass that is freely accessible to microbial decay and necromass that is adsorbed to the soil mineral surface. The latter one is not available for enzymatic depolymerization, but for biochemical mineralization (P-only). Sorption and desorption are represented by Langmuir equilibrium. Therefore, only a fraction of the necromass is readily available for microbial attack. Uncertainty in the fraction emerges from the sorption capacity of the soil, which is challenging to parameterise with readily available data. We did mention this already in section 2.3. In the revised manuscript this is mentioned in line 205:

“Organo-mineral associated DOM and necromass pool are protected from depolymerisation, but are exchanged with the ‘free’ DOM/ necromass pool via first-order sorption kinetics (Fig. 2, process 5). “

and clarify this with table 1

We also further discuss this in line 573:

“Additionally, necromass is partially protected from decomposition by association with soil mineral surfaces. Our model accounts for this process but we are lacking measurements for site-specific sorption capacity and affinity. Less mineral protection would translate in stronger microbial necromass cycling, as the simulated depolymerization flux depends on availability of decomposable material. Further, the model simulates increased desorption of mineral-associated necromass under eCO_2. This is partly caused by additional root exudation competing with necromass for sorption sites, but also by model assumptions about the amount of available mineral soil sorption sites with increasing organic matter and litter. This model assumption increased microbial-available N-rich material and may have enhanced the CO_2 effect on necromass decomposition in the model."

All models have issues and the comments above are not meant to say that the model is wrong. Instead, there just needs to be a thoughtful discussion of how the model assumptions/issues impact the main conclusions.

We thank the reviewer for this thoughtful and encouraging comment. We will use those comments to prepare a revised version with more clarifications of critical points and an improved thoughtful discussion.

- **What about mycorrhizal fungi? Assuming that all the surplus C goes into root exudation ignores the fact that the eucalyptus is ectomycorrhizal and more than likely has high levels of colonization and biomass that could account for the missing vegetation pool as well. You should include this in your discussion of your results.**
    - We agree that the topic of mycorrhiza needs to be further elaborated in the discussion. An explicit parametrization of mycorrhiza fungi requires additional parameters even though we would not be able to capture all benefits of mycorrhiza colonization (Thurner et al., 2023). We here only assumed a general flux from plants to (all) microbes in soils. Clearly this interpretation has its limits.

      We revised our manuscript and touch on the role of mycorrhiza in our estimation of root exudation (line 483):

      "Our estimate therefore also includes other belowground allocations, e.g., mycorrhiza and losses through mucilage, and root exudation in deeper soil layers, which likely explains the differences between our results and global estimations (Brunn et al., 2025; Johansson et al., 2009; Jones et al., 2004)."

      And further discuss this in suggestions for further advancements in modeling and experimental work in line 636:

      "Additional uncertainty comes from the role of mycorrhizal associations under eCO_2 (Terrer et al., 2016). We assume that mycorrhizal activity and C allocation to mycorrhizal community are covered by a general microbial pool and root exudation flux. We thereby neglect variations in plant nutrient acquisition strategies (Reay et al., 2025; Talbot et al., 2008; Wen et al., 2022) but reduce the amount of additional parameters. Field experiments need to further quantify C allocation to mycorrhiza, to estimate total plant belowground allocation. However, implementation of mycorrhiza in TBMs remains a subject of ongoing debate regarding necessary mechanisms and model simplifications."

Line by line:

We will implement below suggestions as far as the comments have not been resolved by a restructuring of the respective sentence/paragraph. We provide comments where further explanation is needed.

line 24: Need period

- Revised

line 33: “not measured vegetation flux” is awkward and unclear.

- Agreed. We revised this into (line 29):
- “In this experiment, eCO_2 increased gross primary productivity (GPP) and soil respiration, but more than half of additional GPP under eCO_2 could not be assigned to measured biomass production or autotrophic respiration, and was likely allocated belowground.”

line 57: change affect to determine or control

- removed sentence, now reads (line 54):

  “Under elevated CO_2 (eCO_2), plants may allocate additional C derived from increased photosynthesis to root exudation and mycorrhizae to compensate for nutrient limitations, by increasing microbial decomposition and mineralization of organic matter (Drake et al., 2011; Phillips et al., 2011; Reay et al., 2025). “

line 64-65: last clause in this sentence hangs. Could just switch comma for and

- whole paragraph revised, sentence removed

line 65: insert may between mechanism and regulate

- revised sentence (line 112):

  “[...] to investigate three competing mechanisms that may regulate soil C sequestration response in microbial necromass [...]”

line 70: maybe call this waste respiration like in Schimel and Weintraub 2003

- Revised (line 119):

  “[...] excess C will be respired as waste respiration, [...]“

line 75: maybe include something about sorptive capacity

- For the narrative of the paper and in alignment with research questions we removed mineral protection of necromass from the here studied mechanism. Nonetheless is this process extremely important for understanding long-term C sequestration in soils. Our model accounts for this process (see comment above). We mention the process in the introduction (line 108):

  “Microbes fulfill a central role in soil C sequestration, by decomposing and respiring organic material, controlling nutrient release and contributing to organic matter formation and long-term C sequestration, via production of necromass and its formation of organo-mineral associations (Kästner et al., 2021; Liang et al., 2017, 2019; Sokol et al., 2019). “

- And mention it again (with sorption capacity) in the discussion (line 572-579):

“Additionally, necromass is partially protected from decomposition by association with soil mineral surfaces. Our model accounts for this process but we are lacking measurements for site-specific sorption capacity and affinity. Less mineral protection would translate in stronger microbial necromass cycling, as the simulated depolymerization flux depends on availability of decomposable material. Further, the model simulates increased desorption of mineral-associated necromass under eCO_2. This is partly caused by additional root exudation competing with necromass for sorption sites, but also by model assumptions about the amount of available mineral soil sorption sites with increasing organic matter and litter. This model assumption increased microbial-available N-rich material and may have enhanced the CO_2 effect on necromass decomposition in the model."

line 88: I would make it obvious that this sentence pertains to all 4 mechanisms

- We deleted this sentence from the introduction

line 96: remove where

- Revised (line 64/65):
  "...while in ORNL FACE progressive N limitation decreased the response of BP under eCO_2 after 10 years …"

line 98: it may be interesting to discuss Terrer 2021 Nature here

- To keep the narrative of the introduction close to FACE experiments, we decided to not further discuss Terrer (2021) here. However, we added it as reference as it describes the same mechanism suspected for DUKE FACE (line 68) :

  "… by promoting enhanced decomposition of soil organic matter (SOM) via increased root exudation, thereby increasing N mineralization but offsetting accumulation of C in soil pools (Drake et al., 2011; Terrer et al., 2021)"

line 108: change for to in

- We removed this sentence to shorten the introduction

line 116: remove P between widespread and globally and add a comma after globally

- Revised (line 79):

  "Despite the fact that P limitation is widespread globally (Du et al., 2020), previous forest "

line 126: change did only invoke to only invoked

- To strengthen the focus of the introduction, we removed this sentence

line 128: remove that between synthesis and done and remove :

- Revised whole sentence into (line 91) :

  "Similar to model-data synthesis for N limited forest, model-data synthesis for EucFACE identified nutrient limitation and C allocation as key mechanisms for understanding BP and soil activity response to eCO_2. Medlyn et al. (2016) found that in models with integrated P cycle, under eCO_2 plant uptake remained unchanged, preventing a strong response in BP to eCO_2, whereas in other models eCO_2 increased BP up to 20 %."

line 133: What do you mean by trade mechanisms?

- We refer to root exudation and mycorrhiza representation, and its role in plant nutrient acquisition. The rewrote this sentence (line 94) into:

> “Jiang et al. (2024a) compared 8 TBMs, to the experimental results of EucFACE, and further pointed to the lack of adequate representation of plant C allocation. ”

line 136: I would be specific here and speak to root exudation

- To streamline the introduction we deleted this sentence and altered the previous sentence in (line 96-98):

> “This disagrees with C budget results from (Jiang et al., 2020) and indicates a missing representation of root exudation and plant-microbe interactions in these models, therefore neglecting possible implication for soil C storage under eCO_2.”

line 141: decompose really isn’t the best word here

- We removed this sentence and rather use “disentangle “ in line (111):

> “Observational data alone may not be sufficient to disentangle contributions of individual processes. Therefore, we use our model to investigate three competing mechanisms that may regulate soil C sequestration response in microbial necromass to altered microbial growth and nutrient acquisition as a result of increased root exudation (Fig. 1) “

line 144-153: maintain active voice first person here and be consistent#

- We revised the research objectives (see above)

Figure 1: What are the pools that start with as like asDOM and asRES?

- We thank the reviewer for this observation. AsDOM and asRES refer to DOM and RES (microbial necromass) sorbed to the soil mineral surface. We will clarify this in the revised manuscript.
- we updated the figure (now fig. 2) and caption and modified table 1

Table 2: How did you validate these parameters? The description in section 2.6 is very brief.

- See our answer to major comments above. Model parameters cannot be validated.

line 303: Does this downward trend impact your interpretation?

- We thank the reviewer for this observation. The downward trend does not result in major bursts in nutrient input. Therefore it is unlikely that it reflects on interpretation results. We now added in the line 306:

“The trend did not cause major pulses in nutrient input and therefore unlikely reflects in CO_2 effects on nutrient-dependent root exudation and microbial C cycling..”

Table B1: There are clear errors in NPP and soil C.

- In the revised manuscript we will mention the error in NPP in the evaluation of model performance under ambient conditions and further pick up on this in the discussion. We note that soil C is highly variable between rings and underlies uncertainties in observations. Our overestimation of the mean estimate by 13 % is well within the observational range. We now mention the underestimation in the result section (line 350) :

> “Simulated GPP had a 9 % bias, but was still within standard deviation of the observation-based estimate. However, the model underestimated BP by 25 %.“

and further pick up on this in the discussion (line 492) :

> “Uncertainties in exudation rates at EucFACE remain considerable. We parameterized our model using ambient GPP and plant pool observations and calculated root exudation flux based on fine root N concentration. The deviation from simulated BP and fine root C: N to observations leads to parameter uncertainty. “

Table B2: These wider stoichiometric constraints would have a direct impact on the exudation flux. You should discuss this as well.

- A wider fine-root C:N ratio would have resulted in a 16 % lower baseline root exudation flux, because the baseline is tied to the fine root N concentration. However the actual exudation flux is also determined by labile pool dynamics. Additionally the root exudation was calibrated via ambient GPP and biomass pools. Nonetheless the deviation from simulated fine root C:N to observed fine root C:N leads to parameter uncertainty. We now mention this in line (492):

> “Uncertainties in exudation rates at EucFACE remain considerable. We parameterized our model using ambient GPP and plant pool observations and calculated root exudation flux based on fine root N concentration. The deviation from simulated BP and fine root C: N to observations leads to parameter uncertainty. “

Table B3: You have more carbon coming into the system and more going to belowground production that is then exacerbated by the root exudation flux. How does this impact what you see in your results and what you state in your conclusions? Roots are a nutrient rich pool which would enhance microbial limitation.

- We thank the reviewer for this comment. Even though under eCO_2 biomass production increased by 33 %, annual litterfall did only increase by 11 %. Annual fine root litterfall increased by 11 % and annual coarse root litterfall increased by 13 %. This additional input contributed to increased heterotrophic respiration (original manuscript figure 4), but did not result in a strong nutrient input. Litter input contributed to additional microbial growth under eCO_2. However the contribution of litter to microbial growth under eCO_2 in N and P (elevated $CO_{2;}$ N: 5%, P: 1%) was substantially lower than for microbial recycling (elevated CO_2; N: 32%, P: 39%), depolymerised necromass (elevated $CO_{2;}$ N: 36%, P: 14%) and biochemical mineralization (original manuscript figure 5). We remain with the conclusion that in our model changes in root exudation and the imposed microbial nutrient demands are a key driver for increased cycling of organic matter and heterotrophic respiration at this site. However we cannot exclude that in our simulations litter input influenced microbial limitations and its consequences on necromass cycling. We now discuss this in line 500-504:

> “The model also simulated a 33 % increase in overstorey BP under eCO_2, which was not observed in EucFACE. In the simulation, C accumulated primarily in woody biomass and labile plant pool (Fig. B10), but this had only a minor influence on soil processes because plant litter contributed little to microbial growth in C, N and P in the treatment period (Fig. 7). Instead, root exudation dominated the additional C input and the supply to microbial growth under eCO_2. Observational studies suggest that plant P limitation suppressed plant growth under eCO_2

> (Jiang et al., 2020), suggesting that the model likely underestimates P constraints or overestimates plant adaptability to P limitation.“

Line 350: These numbers are fairly high compared to the Chari paper which you cite later and may want to cite here. Your flux may be high because you assume all roots exude, you have more roots, more GPP, and don’t account for mycorrhizae. You should acknowledge how this impact your conclusions.

- Agreed. We revised the discussion, see comment on line 535

Figure 3: You show soil C sequestration in this figure that is not observed at the site that is due to I think mostly the deep roots sending out carbon and the greater root production.

- Agreed. Especially as the sequestration happens in deeper soil layers. We now discuss this in soil C sequestration section of the discussion (see comment above)

line 410: what assumption?

- We assume that microbial carbon use efficiency is constrained between 0.3 and 0.5, which impacts the amount of possible respiration of overflow respiration. We revised the sentences as (line 402):

> “In our model, CUE for microbial growth is dependent on the stoichiometric imbalance between the source material and microbial biomass, and constrained within a range of 30% to 50%. Further 15 % of additional heterotrophic respiration under eCO_2 were caused by decomposition of necromass, i.e., priming. “

Line 416: are these deep roots really doing this or is this a model artifact?

- This refers to simulated results. We revised this and now discuss how this model behaviour influences simulated C sequestration (see section about deep root soil above)

Line 435: I think this is clearly wrong and you mean a high C:N ratio. In the same vein, it seems like the exudate C:N is a big driver of your microbial limitation. Basically you are pumping a bunch of C into the soil and it drives nutrient limitation. What if you varied the C:N ratio like JE Drake 2013 Biogeosciences.

- Correct, we meant high C:N ratio. Yes, our model assumes very high root exudation C:N ratios. We briefly discussed the consequences of high C:N ratio in the original manuscript at section 4.3 and 4.4. We will discuss this in more detail in the revised manuscript.
- A low C:N ratio, like in Drake 2013, would mostly relate to loss of plant N. Root exudation would be, under considerations of use-efficiencies, closer to microbial C:N ratio. As a consequence increased root exudation under eCO_2 would result in less N demand, potentially reducing priming, and resulting in positive net mineralization effect (Thurner et al., 2023). A majority of this N would be stored in SOM or lost. Microbes would depend more on root exudation nutrient input, slowing down the cycling of microbial necromass and possibly increasing the decomposition of litter.

- There is the possibility that high N exudation is part of a mechanism in which plants allocate C and N to soil microorganisms (including mycorrhiza) to obtain higher P mineralisation and uptake. Testing this in the current model would require extending the microbial enzyme allocation algorithm to account for this N dependency. Such an extension is interesting, but challenging to parameterise and we consider this beyond the scope of the existing study.
- We now discuss this in (line 547- 557)

> “Finally, simulated microbial nutrient demand is substantially controlled by root exudation stoichiometry. In our model root exudation C to N ratio was 176 (no P exudation), whereas microbial C to N ratio was 4.3 (N: P = 4.1). Simulated C:N ratio is higher than root exudation measurements (Li et al., 2021; Su et al., 2022; Zhang et al., 2016) but ensures that modelled root exudation does not cause an extensive N loss in plants. As a consequence, increased root exudation enhanced microbial nutrient demand, and plant-microbial competition for N and P (Thurner et al., 2023). Under a root exudation stoichiometry closer to microbial stoichiometry, increased root exudation may further promote microbial growth. Microbial N supply may be less dependent on decomposition of microbial necromass, resulting in stronger decomposition of litter for C acquisition. Instead, a substantial amount of N would be stored in SOM, unavailable for plants. Root exudation C:N ratio remains a key variable in plant- microbe nutrient dynamics, but further research regarding the fate of exudate N is needed to improve model assumptions in plant C-for-N trade mechanisms (Drake et al., 2013; Rumeau et al., 2025).”

Line 450: Why is this fixed and how does it impact the necromass results?

- It is fixed, based on the assumption of microbial homeostasis in terms of stoichiometry, given a fixed composition of cytoplasma and cell walls/membrane. This is a clear limitation of the model, however, data availability limits the ability to adequately constrain a model formulation in which the stoichiometry and the carbon-use efficiency vary dynamically A higher recycling value (flux toward DOM) would accelerate the nutrient cycling by microbes and reduce necromass C : N : P ratio. As a result necromass would be less attractive for microbial attack.. We revised this sentence now as (line 430):

> “Recycling of microbial biomass on turnover is controlled by a constant; therefore, we expect little change regarding this flux. ”

and discuss in line 540

> “NH_4 availability and recycling of microbial nutrients on microbial turnover strongly contributed to microbial N acquisition under eCO_2, but remain poorly constrained and require further field observations.”

Line 520: Is this true? You have a lot of things that aren’t quite right. I would soften this language and again talk about the big conclusion but also the things that aren’t quite right in the model. I think there is a compelling case that this is important to explain the EUCFACE results but what is presented here is a first pass and it generates important hypotheses and questions. It doesn’t really solve the case of the missing carbon for good.

- We deleted this sentence and altered the discussion.
- We now write (line 466):

> “We found that – in our model – increased root exudation represents a possible explanation for not measured GPP allocation fluxes under eCO_2 and improved simulated allocation of additional GPP (Fig. 4, Fig. B8, Fig. B9). “

- and write in (line 472-476)

> “Nevertheless, our results provide a first mechanistic insight on the role of root exudation and microbial dynamics in the CO_2 response observed in EucFACE. We evaluate simulated root exudation flux and microbial-mediated C sequestration dynamics, formulated in the research objectives (Fig. 1), against previous studies. We further discuss model limitations in relation to discrepancies between simulations and observations. and derive implications for future research in modeling and observational approaches. “

Line 535: I disagree with this statement as you don’t account for mycorrhizae which could take up a big chunk of this carbon and the deep root issue.

- Agreed. We revised this paragraph and now hint towards methodological differences which could explain the difference (line 482)

“ Our estimate therefore also includes other belowground allocations, e.g., mycorrhiza and losses through mucilage, and root exudation in deeper soil layers, which likely explains the differences between our results and global estimations (Brunn et al., 2025; Johansson et al., 2009; Jones et al., 2004). “

Line 568: This contradicts what I think is wrong in 435 and also raises an important question. What if the C:N was different?

- We revised this. Also see comment on Line 435

Line 608: Why did it enhance necromass desorption?

- In our simulation increased microbial biomass and DOM, but also increased litter input, decreased soil sorption capacity, by altering the volumetric content of mineral soil in soil layers. We added this to the discussion (line 578):

> “Additionally, necromass is partially protected from decomposition by association with soil mineral surfaces. Our model accounts for this process but we are lacking measurements for site-specific sorption capacity and affinity. Less mineral protection would translate in stronger microbial necromass cycling, as the simulated depolymerization flux depends on availability of decomposable material. Further, the model simulates increased desorption of mineral-associated necromass under eCO_2. This is partly caused by additional root exudation competing with necromass for sorption sites, but also by model assumptions about the amount of available mineral soil sorption sites with increasing organic matter and litter. This model assumption increased microbial-available N-rich material and may have enhanced the CO_2 effect on necromass decomposition in the model.”

Line 696: Your results and model efforts do not support a grand global statement like this. As stated above, there are issues with this model exercise and as such you are raising cool hypotheses and potential mechanisms but there is not nearly enough evidence for statements like this.

- Agreed. We revised the conclusion.