

Summary of major revisions

- Scope refocus: The paper is now centered on how spatial heterogeneity in rhizosphere O_2 induces aggregation bias in respiration estimates ($E[f(O_2)]$ versus $f(E[O_2])$ under Michaelis–Menten O_2 limitation). Plant-trait exploration from the prior version has been removed or relegated to brief context.
- Methods transparency: We explicitly define the calibration target (incubation medians), objective (least squares in log-space), and bounds, and we report bootstrap size ($B = 500$) with a fixed random seed for reproducibility. We describe the procedure as bounded least squares in log-space; the code uses MATLAB to implement this but the method description is software-agnostic.
- Bias definition and sign: We define aggregation bias as the difference between the mean of the nonlinear response and the response at mean O_2 , and explain why it is non-positive for the O_2 term used here due to concavity. We quantify bias for representative conditions (e.g., $\approx -12\%$ for gas-phase O_2).
- Dual O_2 proxies and unit-matched comparison: We analyze gas-phase and dissolved O_2 proxies and include an explicit unit-matched KM, O_2 comparison to isolate the role of relative saturation (mean $O_2 / KM, O_2$).
- Open reproducibility: We provide a complete, runnable MATLAB script and supporting data to reproduce all figures (main and SI). The Code/Data Availability statements are updated accordingly.

Point-by-point response to the reviews

Response to Reviewer #1

We thank the reviewer for important and helpful comments which will allow us to improve our manuscript. Below, we show the reviewers' comments in italic text, and our responses to all raised concerns are formatted as standard text.

"The goal of this study was to determine how root oxygen loss (ROL) affects wetland soil respiration. This is an important and timely topic because wetland plant ROL clearly affects soil biogeochemical processes, as documented by many of the papers that the authors cite."

We are glad that the reviewer appreciates the topic of our manuscript, the key role of ROL in the biogeochemistry of wetlands, such as estuarine marshes.

"This study falls short, however, because it is overly simplistic and does not take into account that ROL is spatially or temporally heterogenous."

Our model represents a highly simplified approach of soil biogeochemical processes, but, in our opinion, this is not necessarily a shortcoming of our study.

Plants are usually represented by average functional types in ecosystem models of estuarine marshes, meaning a uniform base rate of root oxygen loss (ROL). In reality, plant species and individuals may strongly differ in ROL, which likely affects soil heterotrophic respiration rate. In contrast to other aspects of the complex biogeochemistry in estuarine marsh soils, impacts of plant trait diversity have been little considered in modelling approaches so far. Thus, the goal of our study is to assess the *potential* effect of variation in ROL due to plant trait diversity compared to a uniform ROL for all plants at a given location.

We do not, however, aim to provide an accurate estimate of soil carbon fluxes for a given marsh ecosystem. This would require the inclusion of a multitude of physiological and biogeochemical processes in the model, including the effect of spatial and temporal heterogeneity of O₂ concentration, as mentioned by the reviewer. Since these processes are associated with considerable parameter uncertainty, it is not guaranteed that simulating them will substantially improve the assessment of the effect of plant ROL variation, which is the focus of our study.

To make our results more reliable, we carried out additional sensitivity analysis and tested the effect of uncertain parameter values on our main results. Moreover, we will clarify in the next version of our manuscript that we model soils under tidal influence, with fractions of both aerobic and anaerobic conditions, not the permanently water-logged part where aerobic respiration plays little role.

"Moreover it considers oxygen in air rather than the dissolved phase that is typical of wetland rhizospheres."

We agree with the reviewer; the DAMM model that we use as a basis for our modelling approach indeed only considers diffusion of oxygen in soil air, thereby neglecting the

substantially slower diffusion in water. We focus, however, on aerobic respiration that requires the occurrence of aerobic microsites close to the root surface. In a revised manuscript, we will clarify this point and state that we neglect anaerobic processes in our study.

“Root oxygen loss is generally into saturated, anoxic soils where heterotrophic microbes would compete with abiotic oxidative processes. This may be outside of the scope of the study but important to consider because increasing oxygen may not increase heterotrophic respiration linearly.”

We thank the reviewer for this suggestion. The basis for our results (Fig. 3) is the variation in the concentration of oxygen close to the sites of microbial respiration, not the flux of ROL that generates these concentration values. In the next version of the manuscript, we will describe more clearly that we do not mechanistically model the diffusion of oxygen from the root to the site of respiration, but simply assume a range of possible oxygen values at these sites. We will also discuss the important topic of competition for oxygen between microbes and abiotic processes.

“Regardless the models seem to better describe O₂ penetration into wetland surface soils (top few mm-cm) during periods of drying than O₂ release into the rhizosphere. It lacks the spatial complexity of O₂ diffusion in a soil matrix and how the concentration will change with distance from the root and time since release.”

As described above, we do not explicitly consider all aspects of oxygen diffusion in our approach, since we aim at representing a range of possible concentration values caused by plant diversity and their effect on aerobic respiration. We agree with the reviewer that a spatially explicit model of oxygen distribution would be required to accurately estimate all soil carbon fluxes, not only CO₂ from aerobic respiration but, in particular, methane fluxes.

“The study assumes that respiration is a function of bulk SOC. This excludes the plant trait of root carbon exudation and differences in bioavailability of recent exudates vs. existing rhizosphere organic matter.”

We are thankful to the reviewer for highlighting the role of root exudates. Indeed, variation in root exudation between plants may, too, have a substantial impact on the carbon balance of estuarine marshes. In our study, however, we focus on ROL since estimates on root exudation rates are not yet available for the locations where the soil samples were collected. We will discuss this aspect in more detail in a revised version of the manuscript.

"Respired CO₂ will be released into a saturated matrix where it will become part of the DIC pool and not necessarily contribute to carbon emissions (as described in the title)."

We agree with the reviewer that CO₂ produced by respiration may be taken up again by other processes before being emitted from the soil. However, as the concentration of carbon in the DIC pool increases, the disequilibrium to the surface air will become stronger, leading to an ultimate increase in CO₂ emissions in the steady state unless DIC is stored in other long-term pools. We will revise the title of the manuscript to be more precise.

"There is not a clear link to plant traits either as the model simulation uses an average plant type (L137)."

In our approach, we represent both an average plant type and a range of individual plants that differ only in their rate of ROL. As described above, the different fluxes of oxygen from root to soil are, however, not mechanistically simulated, but instead a range of oxygen concentration values approximates the effect of variation in plant ROL.

"The authors should see Zhou et al Biogeochemistry (2024) 167:945–963 'Simulated plant-mediated oxygen input has strong impacts on fine-scale porewater biogeochemistry and weak impacts on integrated methane fluxes in coastal wetlands'".

We thank the reviewer for pointing us to the recently published paper by Zhou et al. We agree that a mechanistic, spatially and temporally explicit modeling approach of pore water biogeochemistry is important for an accurate estimation of methane release from saturated soil. Our study, however, aims at a different process, aerobic respiration close to the root surfaces, and thus makes simplifying assumptions regarding the saturated part of the soil (i.e. we neglect anaerobic processes). We did not find estimates of CO₂ release due to aerobic respiration in Zhao et al., but their setup of different oxygen saturation values in the pore water (white boxes in Fig. 4 c1) seems to be conceptually similar to our approach: They test for the effects of variation (spatial heterogeneity) compared to a homogeneous distribution. We thus think that our approach can be seen as complementary.

“L54 and L91 – write out the model names before using the acronym”

We will ensure that all model names are written out in full upon first mentioning, writing "Dual Arrhenius and Michaelis-Menten (DAMM) kinetics model", for example.

“L111. How was the activation energy of the reaction determined (Ea_{Sx})? Did this vary as a function of C reactivity? The value is in Table 1 – is there a reference?”

“L115. How were p and D_{liq} determined? The values are in Table 1 – are there references?”

We thank the reviewer for pointing this out. The reference for these three parameter values is the paper by Davidson et al. (2012). Since we did not examine the temperature response of the respiration rate in our study, we did not recalibrate the value of Ea_{Sx}. Moreover, we also kept the original values of p and D_{liq}, since these are constant multipliers of the concentration of soluble substrate as a function of total substrate, and are thus not likely to alter substantially the effect of oxygen on the reaction rate. To test for the effect of uncertain parameters, we ran an additional sensitivity analysis; the results are shown below in Tab. 1 We found that the modelled absolute respiration rate is relatively sensitive to the parameter Ea, while p and D_{liq} have little effect. However, the parameter variation has no effect on the difference between the average trait approach and the diverse trait approach since the relative response to parameter variation is the same. Moreover, the parameters p and D_{liq} have the same relative effect since they are constant multipliers of the substrate conversion. We will include this in a revised version of our manuscript.

Table 1: Results of the Sensitivity Analysis. Respiration (in mg C cm⁻³h⁻¹) is calculated at the middle of the range of substrate concentration (0.15 g C cm⁻³)

Parameter	Respiration (average approach)	Respiration (diverse approach)	% Difference to control
Control	0.0166	0.0151	-
Ea lower bound	0.0254	0.0232	53.2%
Ea upper bound	0.0108	0.00986	-34.7%
p lower bound	0.0157	0.0143	-5.6%

p upper bound	0.0173	0.0157	4.1%
Dliq lower	0.0157	0.0143	-5.6%
Dliq upper	0.0173	0.0157	4.1%

“Equation 4. Why use parameters for oxygen in air? Wetland soils are generally saturated below the top few cm, and gases would be dissolved in a liquid phase.”

We acknowledge the reviewer's concern regarding the use of parameters for oxygen diffusion in air, since this would indeed not be appropriate to describe diffusion of oxygen in water, i.e. in permanently water-logged soil. In our study, however, we focus on soils in estuarine marshes, which are characterized by tidal dynamics and regular fluctuations in water table and soil moisture distribution. In our opinion, the simplified representation of oxygen availability used in the DAMM model is sufficient to account for the variation in oxygen concentration due to alternating water saturation and the effects on aerobic respiration rate. As written above, we consider only respiration at aerobic microsites and how increased oxygen availability by ROL may affect this. Oxygen is emitted along the entire root length in several wetland plant species, such as *Phragmites australis* and *Spartina alterniflora*, facilitating aerobic respiration in otherwise anaerobic environments (Armstrong and Armstrong, 2005; Colmer, 2003). We do not consider the process of CO₂ production by respiration in entirely anoxic conditions. We agree with the reviewer that in these conditions, the role of ROL for methane and sulphate dynamics is more relevant. We will add these clarifications to a revised version of the manuscript.

“Section 2.1. It is not clear how these experiments mimic conditions with and without ROL.”

We thank the reviewer for this point and we agree that the description should be extended. In a revised version of the manuscript, we will explain more clearly that we use the existing scheme of the DAMM model for oxygen diffusion to approximate the effect of plant aerenchyma on soil oxygen concentration via ROL (see also the paragraph before Sect. 2.1.), rather than explicitly simulating the spatial and temporal heterogeneity of ROL. We assume that negligible ROL corresponds to fully water-saturated soil in the model, while dry soil would correspond to the maximum possible ROL. We will point out that the latter condition is unlikely to occur in nature, but the

uncertainty regarding the effects of ROL on soil oxygen availability (e.g. (Colmer, 2003)) would make setting a different upper limit arbitrary.

“L137. What is the average plant type and how is average plant ROL known?”

In our model, the "average plant type" corresponds to the representation of plants that are often used in ecosystem-scale models of estuarine marshes, where inter- and intra-specific functional diversity of plant traits, including ROL, is aggregated into average traits, applied to one or a few plant functional types. The little available data on ROL in marsh soils of the Elbe estuary currently do not allow us to compute an accurate average value of ROL, which is why we assume that a soil water saturation of 30% is representative of the average conditions in the rhizosphere in the part that is not permanently water-logged, including an intermediate value of ROL. We conducted a sensitivity analysis to test the effect of uncertainty in the average value of ROL on our estimates by varying the assumed soil water saturation (Theta) by $\pm 20\%$. The mean respiration over the range of substrate concentrations changed by -17% and +5% for higher and lower Theta for the average trait approach and by -15% and +1% for the diverse one. The mean impact on the difference between the approaches was larger, ranging from -51% at lower to +42% at higher Theta, which means that ROL becomes less important at drier soil conditions. We will include these results in the revised manuscript.

L146 More details about the experiments that the model was based on are needed. Incubations were under aerobic conditions but was the water flow static or flow-through? If the latter, were conditions monitored to prevent resource limitation – or inhibition by the build-up of metabolites? Were potential microbial metabolites monitored to support the assertion of aerobic conditions (e.g., H₂S)? Were the soils saturated? What was the salinity? Did the DO levels mimic the rhizosphere? What were the SOC levels? The reader is referred to 2 other papers to learn about the methods; including a brief version of that information and the rationale for how the incubations support the present study would be valuable.

We thank the reviewer for raising these points. We agree that the description of the experiment was not self-explanatory. Water was added at the beginning of the incubation, therefore there was no water flow during the experiment. Microbial metabolites were not measured. Soils were not water-saturated but adjusted to 60% water-holding capacity at the beginning of the experiment. Oxygen limitation during the experiment was prevented by flushing the headspace with synthetic air.

We will include the following information in a revised version:

For the soil incubation experiment, 20 g dry mass equivalent of sieved soil samples (2 mm) were adjusted to 60% water holding capacity. The water-adjusted samples were placed in 1000 ml flasks and incubated in the dark at 20 °C for a period of up to 465 days. Headspace samples (1 ml) were collected at regular time intervals for CO₂ measurements by gas chromatography (JAS 6890N, Germany). To maintain a higher pressure within the flasks compared to the surrounding atmosphere and to prevent oxygen deficiency due to excessive CO₂ build-up (> 2.5% in headspace), synthetic air was added when necessary.

Regarding the first part of the modelling approach, we will add: ICBM is a classical and widely used 2-pool model following first-order kinetics of decomposition, with a fast and slow carbon pool. The decomposition rate constants and humification rate constant used in that model were calibrated against the CO₂ concentrations measured in the lab incubation study data mentioned above by using a gradient descent optimization method. Methodological details can be found in (Knoblauch et al., 2013) and (Beer et al., 2022)

The incubations and the subsequent ICBM simulations were carried out to estimate characteristic respiration rates for soils in the marshes of the Elbe estuary for a wide range of substrate concentrations. These were then used to calibrate the DAMM model and carry out our analysis of ROL variation effects. We will make this point more clear in a revised version of the manuscript.

References :

Armstrong, J. and Armstrong, W.: Rice: Sulfide-induced barriers to root radial oxygen loss, Fe²⁺ and water uptake, and lateral root emergence, *Ann. Bot.*, 96, 625–638, <https://doi.org/10.1093/aob/mci215>, 2005.

Beer, C., Knoblauch, C., Hoyt, A. M., Hugelius, G., Palmtag, J., Mueller, C. W., and Trumbore, S.: Vertical pattern of organic matter decomposability in cryoturbated permafrost-affected soils, *Environ. Res. Lett.*, 17, 104023, <https://doi.org/10.1088/1748-9326/ac9198>, 2022.

Colmer, T. D.: Long-distance transport of gases in plants: A perspective on internal aeration and radial oxygen loss from roots, <https://doi.org/10.1046/j.1365-3040.2003.00846.x>, 1 January 2003.

Knoblauch, C., Beer, C., Sosnin, A., Wagner, D., and Pfeiffer, E. M.: Predicting long-term carbon mineralization and trace gas production from thawing permafrost of Northeast Siberia, *Glob. Chang. Biol.*, 19, 1160–1172, <https://doi.org/10.1111/gcb.12116>, 2013.

We thank the reviewer for the continued engagement with our manuscript and thoughtful and detailed comments. We have made further changes and added explanations to the text to address all concerns.

As the main concern seems to arise from a misunderstanding regarding the definition of plant traits, we will point out in the revised manuscript that we interpret ROL *itself* as a (dynamic) plant trait. While, ideally, the dynamics of ROL would be predicted from other, more stable plant traits in a mechanistic model, we will make clear that this is not the focus of our study (see detailed response below). Moreover, we do not aim at a precise estimation of marsh carbon fluxes, which would require a much larger and complex modelling approach, but we are interested in the effect of ROL variation on soil respiration only.

Below, we show the reviewers' comments in italic text, and our responses to all raised concerns are formatted as standard text

The primary issue with the paper is the insistence that the model mimics plant traits and ROL. The title of the article is: "Exploring effects of variation in plant root traits on carbon emissions from estuarine marshes". Yet, the authors do not characterize plant functional, phenotypic, or genetic traits nor do they link those traits to ROL. They do not measure ROL nor how it differs across different species, growth stages, or tidal periods. Oxygen input in the model is described as: "To represent root oxygen loss in the model, we use the dependence of soil oxygen concentration on soil moisture that is already implemented in the model according to Eq. (4): $[O_2] = D_{gas} \times 0.209 \times a^4 / 3$, (4) where D_{gas} is the diffusion coefficient for O_2 in air, 0.209 is the volume fraction of O_2 in air, and a is the air-filled porosity of the soil..." Equation 4 does not have any plant component much less a relationship to functional, phenotypic, or genetic traits. It is purely diffusive gas flux in a wet, porous medium. This parameterization is completely divorced from the ideas that: "The amount of O_2 taken up by plant shoots and released from roots to flooded soils depends upon many above and belowground factors, including the numbers, types (e.g., adventitious, laterals) and lengths of roots, the magnitude and distribution of their pore-space and tissue respiratory demand, the degree and distribution of barriers to impede

ROL, the numbers of the aerial shoots in capacity for O₂ uptake, the porosity and O₂ demand within these shoots, their lengths and the degree of submergence of the aerial shoots, the submerged soil O₂ demand, their microbial activity, their physical properties (i.e., O₂ diffusivity being lower in clay than sandy soils) and temperature” (<https://doi.org/10.3390/plants10112322>); or that the ROL is related to plant height ([https://doi.org/10.1016/S0302-3524\(81\)80104-1](https://doi.org/10.1016/S0302-3524(81)80104-1)); or that ROL can differ even between two populations of the same marsh grass species (<https://doi.org/10.1016/j.scitotenv.2017.02.147>). There are many more examples from the published literature that the parameterization in equation 4 is not representative of ROL. The authors offer this disclaimer: “While this is not a mechanistic representation, the effect of plant aerenchyma on the diffusion of oxygen from the atmosphere into the soil is similar to the effect of increased air-filled pore space during decreasing soil moisture.” There is no evidence presented in this manuscript to support this idea

We thank the reviewer for making this point clear. The exact way how a plant achieves a certain value of ROL is not the focus of our study, since we are mainly interested in the effects of variation in ROL on soil respiration, compared to a fixed value of ROL. We thus only require a range of oxygen levels that is not completely unrealistic, and thus chose the simplified diffusion approach.

We agree with the reviewer that multiple different plant traits influence ROL, as stated in the list of examples. However, for models that aim to quantify fluxes of carbon, particularly respiration, in marsh soils at the ecosystem scale, it is not sufficient to only determine the factors that are relevant for variation in ROL. Instead, such models need to come up with a quantitative estimate of ROL, either averaged for the whole ecosystem or in form of an array of different values per plant type/species.

The articles cited by the reviewer do not provide estimates of ROL that could be either directly implemented in ecosystem models or parameters that would allow for a calculation of ROL at the ecosystem scale based on plant traits. While the articles describe measurement methods, gradients of oxygen within marsh plants, and levels of sediment oxygenation for individual species, they give no indication on the typical range of oxygen levels in the rhizosphere. In contrast, the studies by e.g. Koop-Jakobsen et al. (2017) and Holmer et al. (2002) illustrate the large uncertainty regarding the actual extent of sediment oxygenation via ROL. As we wrote in our previous response, this uncertainty regarding estimating the typical magnitude of ROL was exactly the motivation for us to test a large range of possible oxygen levels in marsh soil.

Hence, we do not aim to present evidence for a certain value of ROL, as suggested by the final sentence in the reviewer’s above paragraph. Instead, we argue that both the flux of oxygen inside plants (from shoot to root) and the flux from air into the soil

follow a concentration gradient, and can thus be approximated by the simple diffusion equation that we apply.

To avoid further misunderstandings, we will change the title of the manuscript into: "Exploring effects of variation in rhizosphere oxygen concentration on potential carbon emissions from estuarine marshes"

I agree with the authors that estimating soil C fluxes resulting from ROL would require a more complex model. However I disagree with the sentiment that it is not worth exploring how physiological processes (which are plant traits) affect ROL and soil C respiration because doing so would introduce uncertainty.

We agree with the reviewer that our statement was misleading. We, too, think that it is definitely worth exploring further all factors that determine the observed variation in ROL in marsh ecosystems (including plant morphological /physiological traits or species identity). This should, in our opinion, ultimately lead to models that reproduce observed ranges of ROL and root exudation based on plant traits, soil properties, and climate. In this conceptual perspective study, however, we lack data that are suitable to constrain the range of ROL, if we attempted to simulate it in a mechanistic way. Hence, we chose a large range of possible ROL values.

I support the addition of uncertainty analyses however there is not enough information to understand what was/will be done.

We have described the uncertainty analysis in our previous response in more detail, albeit at a different location in the text (see Tab. 1 and the associated description). In the revised manuscript, we will make clear which sensitivity analyses were carried out.

This response does not address the original critique that the study focuses on oxygen in air and not in the dissolved phase. The water content of wetland soils is high – by definition. The argument that they focus on aerobic microsites is not convincing because (1) the potential extent of such sites is not estimated, and (2) just because a space is aerobic does not mean it is dry. Aerobic heterotrophic respiration occurs in the ocean, lakes, rivers, and the saturated sediments underneath water masses. The authors cannot ignore gas

transport in water if their results are supposed to be representative of the rhizosphere in a wetland. If the authors maintain that this work is only related to aerobic respiration in dry spaces then they must reframe and make it clear that their results are only relevant to surficial soils during ebb tides.

We agree with the reviewer that aerobic respiration is relevant not only in the well aerated top part of the soil, but also within aerobic microsites, e.g. around roots. Seemingly, in our previous response we misunderstood the reviewer's point, and thus argued for the relevance of aerobic sites in addition to processes under anaerobic conditions.

The reviewer's critique on our modelling of the diffusion process of oxygen in wet soil, however, results, in our opinion, from a misunderstanding regarding the scope of the study. As explained above, we are only concerned about the range of potential oxygen levels in the rhizosphere, not about accurately modelling the diffusive flux of oxygen. In case the reviewer thinks that we systematically overestimate (or underestimate) the range of oxygen concentrations that can be observed in the rhizosphere, we are of course open to adapt our calculations and the manuscript. So far, we do not see the possibility to compute a more certain range of oxygen concentrations for the soil samples that we used in our study.

This goes back to my primary issue with the paper – no data are presented linking plant traits or diversity to variations in ROL. Because of this it is completely unclear how the modeled variations in dry soil oxygen levels relate to variability in plant phenotypic, functional, or genetic traits.

We agree with the reviewer that we do not resolve the mechanisms that link plant traits to oxygen levels in the soil, but instead, we interpret ROL itself as a (dynamic) plant trait. Our goal is the estimation of the effect of varying ROL on soil respiration. The mechanistic simulation of ROL based on other, more fundamental plant traits, is not possible here with sufficient accuracy.

The authors should calculate the disequilibrium reactions in a porous medium before estimating C emissions.

We will add to the manuscript that we do not consider long-term storage of respired CO₂ in pools such as calcite precipitates, given the limited availability of calcium in the soil solution. Instead, we assume a steady state where all CO₂ produced by respiration is emitted from the soil in gaseous or dissolved form. Beyond that, we do not see the necessity of calculating the reactions in porous media, as influences of oxygen on porewater biogeochemistry that may counteract its increasing effect on respiration seem negligible to us.

Please provide support linking the range of O₂ concentrations used to variation in ROL.

In our study, we have cited the works by Koop-Jakobsen et al. (2021) to illustrate how ROL may affect oxygen levels in the rhizosphere in marsh soils. In a revised manuscript we will substantiate this by further references (Visser et al. (2000), Colmer (2003), and Armstrong & Armstrong (2005)) and highlight the relatively large range of oxygen levels that may arise from ROL in marsh soils (<0.01 cm³ O₂/cm³ soil in highly saturated zones to over 0.1 cm³ O₂/cm³ soil in areas of high ROL activity).

Reviewer (first round): L137. What is the average plant type and how is average plant ROL known?

Authors (our answer from first round): In our model, the "average plant type" corresponds to the representation of plants that are often used in ecosystem-scale models of estuarine marshes, where inter-and intra-specific functional diversity of plant traits, including ROL, is aggregated into average traits, applied to one or a few plant functional types. ...

Reviewer (second round): This is very vague.

Authors, continued answer from first round: ... The little available data on ROL in marsh soils of the Elbe estuary currently do not allow us to compute an accurate average value of ROL, which is why we assume that a soil water saturation of 30% is representative of the average conditions in the rhizosphere in the part that is not permanently water-logged, including an intermediate value of ROL. We conducted a sensitivity analysis to test the effect of uncertainty in the average value of ROL on our estimates by varying the assumed soil water saturation (Theta) by ±20%. The mean respiration over the range of substrate concentrations changed by -17% and +5% for higher and lower Theta for the average trait approach and by -15% and +1% for the diverse one. The mean impact on the difference between the approaches was larger, ranging from -51% at lower to +42% at higher Theta, which means that ROL becomes less important at drier soil conditions. We will include these results in the revised manuscript.

We agree with the reviewer that our statement above is not too specific when standing alone, but together with the continued answer that we provided in the previous round, we think that our description of the challenges that are associated with parametrizing an average PFT for this ecosystem is more clear.

Why restrict data on ROL to just the Elbe estuary? Please provide data supporting that the soils in the rhizosphere have 30% water content. Is this marsh environment being modeled very high in the tidal frame and rarely inundated? I appreciate that the authors varied water content but this still does not account for O₂ (or CO₂) exchange between dry and wet porespace.

The soil samples that we used for model parametrization were collected at different locations in the low marsh and pioneer zone of the Elbe estuary, where the water content in the root zone fluctuates between around 45% and 100% throughout the year to a depth of up to 60 cm. However, the water content of 30% was chosen to include the effect of (average) ROL on oxygen levels in the rhizosphere. If we used the actual soil moisture from the sites to calculate oxygen levels based on our simple diffusion equation, we would implicitly assume no effect of aerenchyma on soil oxygen levels, which is why we chose a lower value of soil moisture.

This experiment is a very artificial representation of a wetland soil. Soil structure is disrupted by drying, sieving, and rewetting, which will affect microbial metabolisms and gas fluxes. The bottles were held under constant conditions for over a year! Wetland soils experience regular tidal, seasonal, and annual cycles – which are not mimicked here. Moreover microbial community composition and metabolisms likely changed substantially over one year and may no longer be representative of natural communities.

The preparation of the soil samples is a standard procedure for measuring the long-term evolution of soil respiration rates in incubation experiments. Measuring CO₂ emission rates in the field instead has two disadvantages;

1) Continuous measurements using chambers are impractical for longer periods of time, meaning that the measured fluxes usually represent only snapshots of the system, which is particularly problematic in dynamic ecosystems such as tidal marshes.

2) CO₂ emissions measured in the field usually represent a steady state with little variation in the substrate concentration, but for the parametrization of respiration fluxes in the model we require an incubation that includes the gradual reduction of the available soil carbon.

The disturbance of the soil samples will likely lead to an alteration of the CO₂ emissions, as the reviewer states, but we do not expect a systematic bias on our results, as this will equally affect the simulated respiration rates for all tested oxygen levels.

References:

Visser, E. J. W., Colmer, T. D., Blom, C. W. P. M., and Voesenek, L. A. C. J.: Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma, *Plant, Cell Environ.*, 23, 1237–1245, <https://doi.org/10.1046/j.1365-3040.2000.00628.x>, 2000.

Colmer, T. D.: Long-distance transport of gases in plants: A perspective on internal aeration and radial oxygen loss from roots, *Plant, Cell Environ.*, 26, 17–36, <https://doi.org/10.1046/j.1365-3040.2003.00846.x>, 2003.

Armstrong, J., and Armstrong, W.: Rice: Sulfide-induced barriers to root radial oxygen loss, Fe²⁺ and water uptake, and lateral root emergence, *Ann. Bot.*, 96, 625–638, <https://doi.org/10.1093/aob/mci215>, 2005.

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As the main concern seems to arise from a misunderstanding regarding the definition of plant traits, we will point out in the revised manuscript that we interpret ROL *itself* as a (dynamic) plant trait. While, ideally, the dynamics of ROL would be predicted from other, more stable plant traits in a mechanistic model, we will make clear that this is not the focus of our study (see detailed response below). Moreover, we do not aim at a precise estimation of marsh carbon fluxes, which would require a much larger and complex modelling approach, but we are interested in the effect of ROL variation on soil respiration only.

Below, we show the reviewers' comments in italic text, and our responses to all raised concerns are formatted as standard text

The primary issue with the paper is the insistence that the model mimics plant traits and ROL. The title of the article is: "Exploring effects of variation in plant root traits on carbon emissions from estuarine marshes". Yet, the authors do not characterize plant functional, phenotypic, or genetic traits nor do they link those traits to ROL. They do not measure ROL nor how it differs across different species, growth stages, or tidal periods. Oxygen input in the model is described as: "To represent root oxygen loss in the model, we use the dependence of soil oxygen concentration on soil moisture that is already implemented in the model according to Eq. (4): $[O_2] = D_{gas} \times 0.209 \times a^4 / 3$, (4) where D_{gas} is the diffusion coefficient for O_2 in air, 0.209 is the volume fraction of O_2 in air, and a is the air-filled porosity of the soil..." Equation 4 does not have any plant component much less a relationship to functional, phenotypic, or genetic traits. It is purely diffusive gas flux in a wet, porous medium. This parameterization is completely divorced from the ideas that: "The amount of O_2 taken up by plant shoots and released from roots to flooded soils depends upon many above and belowground factors, including the numbers, types (e.g., adventitious, laterals) and lengths of roots, the magnitude and distribution of their pore-space and tissue respiratory demand, the degree and distribution of barriers to impede ROL, the numbers of the aerial shoots in capacity for O_2 uptake, the porosity and O_2 demand within these shoots, their lengths and the degree of submergence of the aerial shoots, the submerged soil O_2 demand, their microbial activity, their physical properties (i.e., O_2 diffusivity being lower in clay than sandy soils) and temperature" (<https://doi.org/10.3390/plants10112322>); or that the ROL is related to plant height ([https://doi.org/10.1016/S0302-3524\(81\)80104-1](https://doi.org/10.1016/S0302-3524(81)80104-1)); or that ROL can differ even between two populations of the same marsh grass species (<https://doi.org/10.1016/j.scitotenv.2017.02.147>). There are many more examples from the published literature that the parameterization in equation 4 is not representative of ROL. The authors offer this disclaimer: "While this is not a mechanistic representation, the effect of plant aerenchyma on the diffusion of oxygen from the atmosphere into the soil is similar to the effect of increased air-filled pore space during decreasing soil moisture." There is no evidence presented in this manuscript to support this idea

We thank the reviewer for making this point clear. The exact way how a plant achieves a certain value of ROL is not the focus of our study, since we are mainly interested in the effects of variation in ROL on soil respiration, compared to a fixed value of ROL. We thus only require a range of oxygen levels that is not completely unrealistic, and thus chose the simplified diffusion approach.

We agree with the reviewer that multiple different plant traits influence ROL, as stated in the list of examples. However, for models that aim to quantify fluxes of carbon, particularly respiration, in marsh soils at the ecosystem scale, it is not sufficient to only determine the factors that are relevant for variation in ROL. Instead, such models need to come up with a quantitative estimate of ROL, either averaged for the whole ecosystem or in form of an array of different values per plant type/species.

The articles cited by the reviewer do not provide estimates of ROL that could be either directly implemented in ecosystem models or parameters that would allow for a calculation of ROL at the ecosystem scale based on plant traits. While the articles describe measurement methods, gradients of oxygen within marsh plants, and levels of sediment oxygenation for individual species, they give no indication on the typical range of oxygen levels in the rhizosphere. In contrast, the studies by e.g. Koop-Jakobsen et al. (2017) and Holmer et al. (2002) illustrate the large uncertainty regarding the actual extent of sediment oxygenation via ROL. As we wrote in our previous response, this uncertainty regarding estimating the typical magnitude of ROL was exactly the motivation for us to test a large range of possible oxygen levels in marsh soil.

Hence, we do not aim to present evidence for a certain value of ROL, as suggested by the final sentence in the reviewer's above paragraph. Instead, we argue that both the flux of oxygen inside plants (from shoot to root) and the flux from air into the soil follow a concentration gradient, and can thus be approximated by the simple diffusion equation that we apply.

To avoid further misunderstandings, we will change the title of the manuscript into: "Exploring effects of variation in rhizosphere oxygen concentration on potential carbon emissions from estuarine marshes"

I agree with the authors that estimating soil C fluxes resulting from ROL would require a more complex model. However I disagree with the sentiment that it is not worth exploring how physiological processes (which are plant traits) affect ROL and soil C respiration because doing so would introduce uncertainty.

We agree with the reviewer that our statement was misleading. We, too, think that it is definitely worth exploring further all factors that determine the observed variation in ROL in marsh ecosystems (including plant morphological /physiological traits or species identity). This should, in our opinion, ultimately lead to models that reproduce observed ranges of ROL and root exudation based on plant traits, soil properties, and climate. In this conceptual perspective study, however, we lack data that are suitable to constrain the range of ROL, if we attempted to simulate it in a mechanistic way. Hence, we chose a large range of possible ROL values.

I support the addition of uncertainty analyses however there is not enough information to understand what was/will be done.

We have described the uncertainty analysis in our previous response in more detail, albeit at a different location in the text (see Tab. 1 and the associated description). In

the revised manuscript, we will make clear which sensitivity analyses were carried out.

This response does not address the original critique that the study focuses on oxygen in air and not in the dissolved phase. The water content of wetland soils is high – by definition. The argument that they focus on aerobic microsites is not convincing because (1) the potential extent of such sites is not estimated, and (2) just because a space is aerobic does not mean it is dry. Aerobic heterotrophic respiration occurs in the ocean, lakes, rivers, and the saturated sediments underneath water masses. The authors cannot ignore gas transport in water if their results are supposed to be representative of the rhizosphere in a wetland. If the authors maintain that this work is only related to aerobic respiration in dry spaces then they must reframe and make it clear that their results are only relevant to surficial soils during ebb tides.

We agree with the reviewer that aerobic respiration is relevant not only in the well aerated top part of the soil, but also within aerobic microsites, e.g. around roots. Seemingly, in our previous response we misunderstood the reviewer's point, and thus argued for the relevance of aerobic sites in addition to processes under anaerobic conditions.

The reviewer's critique on our modelling of the diffusion process of oxygen in wet soil, however, results, in our opinion, from a misunderstanding regarding the scope of the study. As explained above, we are only concerned about the range of potential oxygen levels in the rhizosphere, not about accurately modelling the diffusive flux of oxygen. In case the reviewer thinks that we systematically overestimate (or underestimate) the range of oxygen concentrations that can be observed in the rhizosphere, we are of course open to adapt our calculations and the manuscript. So far, we do not see the possibility to compute a more certain range of oxygen concentrations for the soil samples that we used in our study.

This goes back to my primary issue with the paper – no data are presented linking plant traits or diversity to variations in ROL. Because of this it is completely unclear how the modeled variations in dry soil oxygen levels relate to variability in plant phenotypic, functional, or genetic traits.

We agree with the reviewer that we do not resolve the mechanisms that link plant traits to oxygen levels in the soil, but instead, we interpret ROL itself as a (dynamic) plant trait. Our goal is the estimation of the effect of varying ROL on soil respiration. The mechanistic simulation of ROL based on other, more fundamental plant traits, is not possible here with sufficient accuracy.

The authors should calculate the disequilibrium reactions in a porous medium before estimating C emissions.

We will add to the manuscript that we do not consider long-term storage of respired CO₂ in pools such as calcite precipitates, given the limited availability of calcium in the soil solution. Instead, we assume a steady state where all CO₂ produced by respiration is emitted from the soil in gaseous or dissolved form. Beyond that, we do not see the necessity of calculating the reactions in porous media, as influences of oxygen on porewater biogeochemistry that may counteract its increasing effect on respiration seem negligible to us.

Please provide support linking the range of O₂ concentrations used to variation in ROL.

In our study, we have cited the works by Koop-Jakobsen et al. (2021) to illustrate how ROL may affect oxygen levels in the rhizosphere in marsh soils. In a revised manuscript we will substantiate this by further references (Visser et al. (2000), Colmer (2003), and Armstrong & Armstrong (2005)) and highlight the relatively large range of oxygen levels that may arise from ROL in marsh soils (<0.01 cm³ O₂/cm³ soil in highly saturated zones to over 0.1 cm³ O₂/cm³ soil in areas of high ROL activity).

Reviewer (first round): L137. What is the average plant type and how is average plant ROL known?

Authors (our answer from first round): In our model, the "average plant type" corresponds to the representation of plants that are often used in ecosystem-scale models of estuarine marshes, where inter-and intra-specific functional diversity of plant traits, including ROL, is aggregated into average traits, applied to one or a few plant functional types. ...

Reviewer (second round): This is very vague.

Authors, continued answer from first round: ... The little available data on ROL in marsh soils of the Elbe estuary currently do not allow us to compute an accurate average value of ROL, which is why we assume that a soil water saturation of 30% is representative of the average conditions in the rhizosphere in the part that is not permanently water-logged, including an intermediate value of ROL. We conducted a sensitivity analysis to test the effect of uncertainty in the average value of ROL on our estimates by varying the assumed soil water saturation (Theta) by ±20%. The mean respiration over the range of substrate concentrations changed by -17% and +5% for higher and lower Theta for the average trait approach and by -15% and +1% for the diverse one. The mean impact on the difference

between the approaches was larger, ranging from -51% at lower to +42% at higher Theta, which means that ROL becomes less important at drier soil conditions. We will include these results in the revised manuscript.

We agree with the reviewer that our statement above is not too specific when standing alone, but together with the continued answer that we provided in the previous round, we think that our description of the challenges that are associated with parametrizing an average PFT for this ecosystem is more clear.

Why restrict data on ROL to just the Elbe estuary? Please provide data supporting that the soils in the rhizosphere have 30% water content. Is this marsh environment being modeled very high in the tidal frame and rarely inundated? I appreciate that the authors varied water content but this still does not account for O₂ (or CO₂) exchange between dry and wet porespace.

The soil samples that we used for model parametrization were collected at different locations in the low marsh and pioneer zone of the Elbe estuary, where the water content in the root zone fluctuates between around 45% and 100% throughout the year to a depth of up to 60 cm. However, the water content of 30% was chosen to include the effect of (average) ROL on oxygen levels in the rhizosphere. If we used the actual soil moisture from the sites to calculate oxygen levels based on our simple diffusion equation, we would implicitly assume no effect of aerenchyma on soil oxygen levels, which is why we chose a lower value of soil moisture.

This experiment is a very artificial representation of a wetland soil. Soil structure is disrupted by drying, sieving, and rewetting, which will affect microbial metabolisms and gas fluxes. The bottles were held under constant conditions for over a year! Wetland soils experience regular tidal, seasonal, and annual cycles – which are not mimicked here. Moreover microbial community composition and metabolisms likely changed substantially over one year and may no longer be representative of natural communities.

The preparation of the soil samples is a standard procedure for measuring the long-term evolution of soil respiration rates in incubation experiments. Measuring CO₂ emission rates in the field instead has two disadvantages;

- 1) Continuous measurements using chambers are impractical for longer periods of time, meaning that the measured fluxes usually represent only snapshots of the system, which is particularly problematic in dynamic ecosystems such as tidal marshes.

2) CO₂ emissions measured in the field usually represent a steady state with little variation in the substrate concentration, but for the parametrization of respiration fluxes in the model we require an incubation that includes the gradual reduction of the available soil carbon.

The disturbance of the soil samples will likely lead to an alteration of the CO₂ emissions, as the reviewer states, but we do not expect a systematic bias on our results, as this will equally affect the simulated respiration rates for all tested oxygen levels.

References:

Visser, E. J. W., Colmer, T. D., Blom, C. W. P. M., and Voesenek, L. A. C. J.: Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma, *Plant, Cell Environ.*, 23, 1237–1245, <https://doi.org/10.1046/j.1365-3040.2000.00628.x>, 2000.

Colmer, T. D.: Long-distance transport of gases in plants: A perspective on internal aeration and radial oxygen loss from roots, *Plant, Cell Environ.*, 26, 17–36, <https://doi.org/10.1046/j.1365-3040.2003.00846.x>, 2003.

Armstrong, J., and Armstrong, W.: Rice: Sulfide-induced barriers to root radial oxygen loss, Fe²⁺ and water uptake, and lateral root emergence, *Ann. Bot.*, 96, 625–638, <https://doi.org/10.1093/aob/mci215>, 2005.

Response to Reviewer #2

We thank Reviewer #2 for their thorough evaluation and constructive feedback, which has helped us significantly enhance the clarity, methodology, and framing of our manuscript. Below, we reproduce each of the reviewer's comments in italic text, followed by our detailed responses.

General assessment, scope and novelty:

"This study aimed to examine the effects of plant root traits on soil carbon emissions in estuarine marshes using a modeling approach. The authors conducted two model experiments using the DAMM model to simulate microbial respiration: one with constant soil O₂ (fixed soil moisture) and another with variable soil O₂ (influenced by soil moisture). They observed differing respiration response to soil carbon content under the two conditions.

While soil heterotrophic respiration in estuarine marshes is a critical component of carbon cycling and warrants further investigation, the study employed a relatively simple model based on incubation data. This limits the ability to extrapolate the findings across broader spatial and temporal scales. Additionally, the results are not particularly novel, as the role of O₂ in regulating respiration under wetland conditions is well established. The link between the root traits and the model experiments is also unclear. The simulations primarily focused on the effects of soil moisture (and associated O₂ availability) on respiration, rather than explicitly root traits. The authors should clarify their methodological framework and more clearly articulate the study's novelty."

Response:

We thank the reviewer for these important points and have made explicit clarifications regarding the study's novelty and methodological framework. The novelty of our study lies specifically in quantifying the aggregation error that arises from spatial variability in rhizosphere oxygen (O₂) levels driven by root oxygen loss (ROL). This factor has not been quantified so far for estuarine marsh ecosystems, but it is key for modelling their carbon fluxes. Below, we further elaborate on these points:

Limited ability for extrapolation:

Our objective was not to directly provide a landscape-scale parameterisation. Instead, we explicitly aimed to assess the ecological relevance of O₂ heterogeneity driven by ROL for heterotrophic respiration in marsh ecosystems. Incubation experiments using real marsh soil samples are thus methodologically appropriate and robust. This intent is explicitly clarified in the manuscript:

"Here, we estimate the effect of plant-induced variation of oxygen levels in soils on heterotrophic respiration in estuarine

marshes using the DAMM model (Davidson et al., 2012). To estimate the aggregation error, we simulate the respiration

response to soil carbon for a range of different oxygen levels and compare this to a model configuration that only considers

one average soil oxygen level." (p. 3, L 90-93).

Novelty regarding the role of O₂:

We acknowledge that the general role of O₂ in wetland soil respiration is well-known. However, our study specifically addresses the quantitative implications of O₂ variation on respiration, highlighting the aggregation error introduced when spatial variation is replaced by a single mean O₂ value. This quantification has important implications for improving accuracy in large-scale ecosystem models. We have explicitly articulated this objective in the revised manuscript:

"By comparing the two model configurations (see Fig. 3) we find that the variation of the plant trait root oxygen loss leads to a 10% reduced respiration rate, when averaged over all soil oxygen levels, compared to the model configuration driven only by one average soil oxygen concentration... (p. 7- L 72-74).

"This illustrates the potentially large impacts that may arise from spatial heterogeneity of plant species or changing community composition of plants on the carbon balance of estuarine marshes." (p. 1- L 26-27).

"Considering only our simple approximation of varied root oxygen loss, and assuming global soil carbon emissions of 31 Tg a⁻¹ via heterotrophic respiration from salt marshes (Alongi, 2020), the estimated reduction by 10% would correspond to roughly 8% of global annual anthropogenic carbon emissions (Intergovernmental Panel on Climate Change (IPCC), 2023)." (p. 9- L 195-198)

A comparison with the detailed pore-scale model by Zhou et al. (2024) has also been included:

Additionally, we include a direct comparison with the detailed pore-scale model by Zhou et al. (2024):

"While Zhou et al. (2024) employed a highly detailed pore-scale model explicitly simulating plant-mediated oxygen transport and fine-scale biogeochemical processes, our approach quantifies aggregation errors resulting from spatial averaging in simpler ecosystem models. Thus, these approaches are complementary, each providing valuable insights into different aspects of oxygen dynamics and carbon cycling in estuarine marshes."

Unclear link between root traits and experiment:

The experiment was designed explicitly to estimate the effects of O₂ variation on respiration. Root traits serve as the underlying cause of this variation. We acknowledge that we do not explicitly simulate the mechanistic link between specific root traits and soil O₂ levels, but rather we impose observed O₂ variation derived from

the literature. This approach allows us to isolate and quantify the aggregation error without introducing speculative parameters. We detailed this approach clearly in the revised manuscript:

“ROL itself is not simulated. Instead, its observed outcome, rhizosphere O_2 concentration, is imposed directly, following the empirical range detailed above. This allows us to quantify the impact of ignoring heterogeneity without speculative parameterisation of the many plant traits that underlie ROL.” (P.6- L 227-229).

Specific comments

1 Abstract:

“Abstract: The background is too long, compared to the methods and results of this study. I recommend the authors to shorten the background information and expand the method part..”

Response:

We thank the reviewer for this suggestion. In the revised Abstract, we shortened the background to two sentences and added one sentence that summarises the two simulation experiments.

Inserted text (p. 1, L 14-24):

“ Estuarine marshes are crucial components of coastal environments around the world and provide numerous ecosystem services, such as carbon sequestration. Plant-microbe interactions are potential key drivers of organic carbon cycling in these ecosystems. Roots of marsh plants, for instance, leak oxygen into otherwise anoxic sediments, creating a patchy rhizosphere O_2 field that controls heterotrophic respiration. Thereby, traits such as root oxygen loss (ROL) may strongly differ between plant species, leading to strong variation in respiration rates. Ecosystem models that aim to quantify the carbon balance of marshes, however, usually replace this variety with one bulk value, leading to potential biases in carbon flux estimates. We calibrated a Dual Arrhenius–Michaelis–Menten (DAMM) scheme with laboratory incubations and ran two experiments: (i) uniform O_2 versus (ii) the full observed O_2 distribution. Spatial averaging of O_2 reduced the simulated aerobic CO_2 efflux by $\approx 10\%$. This illustrates the potentially large impacts that may arise from spatial heterogeneity of plant species or changing community composition of plants on the carbon balance of estuarine marshes. We thus suggest implementing trait variation in marsh ecosystem models.”

2 L21 – definition of the “root-trait”

“how can the modification of soil O₂ concentration be considered as a key plant trait?”

Response:

We thank the reviewer for raising this important conceptual point. In the revised manuscript, we now clarify that the plant trait in question is the rate of root oxygen loss (ROL) rather than the resulting soil O₂ concentration itself. Following the generic trait definition of Violle et al. (2007), “any phenotypic property that affects ecosystem processes,” ROL qualifies because it is an emergent, plant-controlled flux governed by root porosity, aerenchyma development, and metabolic demand. Numerous rhizosphere studies show that variation in ROL is the primary proximate control on local O₂ tension and hence on aerobic decomposition rates in marsh sediments (Visser et al., 2000; Armstrong & Armstrong, 2005; Kühl et al., 2021).

Inserted text (p. 3, L 149-152)

“In the functional-trait framework (Violle et al., 2007), we treat the flux density of root oxygen loss (ROL) expressed as O₂ flux per root surface area as the focal trait, because ROL directly affects rhizosphere O₂ level and thereby regulates aerobic heterotrophic respiration (Visser et al., 2000; Armstrong & Armstrong, 2005; Kühl et al., 2021). Spatial and temporal variability in ROL therefore propagates to variability in soil O₂ without invoking additional soil-physical drivers.”

3 L40 – additional literature

“Please provide more references to link the plant roots to root O₂ loss.”

Inserted text (p. 6, L 233-234)

“...intra- and inter-specific variation in ROL has been documented for marsh grasses, rice and sedges (Holmer & Pedersen, 2003; Visser et al., 2000; Armstrong & Armstrong, 2005; Kühl et al., 2021), supporting the empirical O₂ range used here.”

4 L90-91 – choice of the DAMM model

“Why the DAMM model was selected in this study?”

Response:

We thank the reviewer for requesting a more detailed justification. The decisive argument is that DAMM contains an explicit Michaelis–Menten O_2 -limitation term (Davidson et al., 2012). This mechanistic representation is essential for our objective of testing how different prescribed rhizosphere- O_2 distributions propagate into respiration.

The Dual-Arrhenius–Michaelis–Menten (DAMM) equation treats oxygen as a true saturating substrate (Ks-type). Consequently, we can vary $[O_2]$ over several orders of magnitude, exactly the range observed around marsh roots while holding all other drivers constant. Most models of carbon cycling at the land-surface, by contrast, link respiration to soil moisture or redox potential, so O_2 cannot be manipulated independently and the aggregation error we target cannot be isolated. The Michaelis–Menten form also guarantees correct asymptotic behaviour, preventing the non-physical extremes that can arise from linear moisture scaling.

Inserted text (p. 4, L 163-170)

“We selected the DAMM model to test the effect of variation in root oxygen loss on soil microbial activity and ecosystem carbon emissions since it includes an additional term for oxygen limitation of heterotrophic respiration (Eq. 1), while most models of soil organic matter decomposition focus only on carbon as a substrate, being developed for well-aerated soils.

DAMM contains an explicit Michaelis–Menten O_2 -limitation term (Davidson et al., 2012), allowing us to prescribe the full field-observed rhizosphere O_2 distribution and thereby quantify the resulting aggregation bias. Moreover, it requires only six parameters, which keeps the uncertainty analysis tractable. DAMM has also reproduced hourly CO_2 fluxes in tidal-freshwater marshes (Knox et al., 2021), demonstrating field applicability.”

5 L102 – model simplicity

“Many processed models considered the impacts of temperature, soil moisture (water-filled porosity), O_2 , and pH. But the model used here is a relatively simple one as showed below (Eq. 1).”

Response:

We thank the reviewer for noting this. We now explain why a simple formulation is adequate for isolating the target bias.

Inserted text (p. 4, L 171-173):

Addition: "... We deliberately chose a simple modelling approach since the large parameter uncertainty at ecosystem or landscape scales would prevent an accurate estimate based on more complex models. Hence, there would be no reliable additional quantitative information that could be gained from exchanging the simple with a complex model."

Inserted text (p. 4, L 176-178):

"Redox-pH schemes for tidal soils require > 40 marsh-specific parameters; with so many unknowns, adding complexity would obscure rather than illuminate the aggregation error that we wish to quantify. A six-parameter DAMM therefore represents a parsimonious tool for the present goal, in our opinion."

6 L 110 – merge Eqs 1 & 2:

"Merge Eq. 2 into Eq. 1."

Response

Implemented as requested. The merged equation now integrates temperature, substrate and O₂ limitation; all symbols are listed in Table 1.

$$R = \alpha_{sx} e^{(((-E_a)/RT))} * (S_x / (K_{(m_{sx})} + S_x)) * ([O_2] / (K_{(m_{o2})} + [O_2]))$$

where the three multiplicative terms represent (i) Arrhenius temperature dependence, (ii) Michaelis–Menten limitation by soluble carbon substrate S_x derived from ICBM pools, and (iii) Michaelis–Menten limitation by oxygen. Symbols and units are listed in Table 1"

7 L121 – link between O₂ and root traits

"How was O₂ related to root trait?"

Response

Methods 2.1 (L 120-149) now describes a two-step procedure:

1. **Empirical range.** Direct microsensor studies show steady-state rhizosphere O₂ values well below 0.01 cm³ cm⁻³ in anoxic pores and occasionally above 0.12 cm³ cm⁻³ in narrowly oxygenated 'hot spots' next to highly aerenchymatous roots (Armstrong & Armstrong, 2005; Colmer, 2003; Köhl et al., 2021; Visser et al., 2000) We therefore prescribe that empirical interval 0.01–0.12 cm³ O₂ cm⁻³.

2. **Trait sampling.** The interval is represented by 39 target O₂ values, produced from a soil-moisture grid $\theta = 0.23 : 0.01 : 0.61$. Each O₂ value is interpreted as one plant location combination i.e. a distinct rate of root-oxygen loss (ROL) and hence a separate trait state. Equation (4) converts every target O₂ concentration to the air-filled porosity driver required by DAMM; the conversion is a numerical proxy, not a mechanistic ROL representation.

Inserted text (p. 6, L 230-233)

“To constrain the oxygen values, we varied soil water content from $\theta = 0.23$ to 0.61 in increments of 0.01 , yielding a modelled O₂ range of approximately 0.01 to $0.12 \text{ cm}^3 \text{ O}_2 \text{ cm}^{-3}$ (air). Each value represents a different trait state of root oxygen loss. This approach allows us to explore heterogeneity in ROL across species and conditions using Eq. (4) as a proxy for rhizosphere oxygen distribution.”

8 L135-140 – moisture versus traits

“It was not clear how the O₂ was related to root traits. It seems that the authors simulated O₂ related to water content, not root traits.”

Response

As clarified above, soil moisture is employed only as a numeric carrier that maps the preset O₂ values into the porosity variable used by DAMM. The distribution of O₂ values itself spanning ~ 0.0002 to $0.20 \text{ cm}^3 \text{ cm}^{-3}$ is imposed from field observations and literature bounds; θ is not treated as the causal driver of variation.

9 L161 – “visual comparison”

“by visual comparison?”

Response

We thank the reviewer for asking us to clarify the calibration procedure. The pre-exponential factor (α) and the carbon half-saturation constant (K_mC) are now fitted by least-squares (MATLAB `fminsearch`) to the seven median respiration rates derived from the ICBM incubation.

The optimisation yields

$$\alpha = 5.41 \times 10^{11} \text{ mg C cm}^{-3} \text{ h}^{-1}$$

$$K_mC = 4.8 \times 10^{-6} \text{ g C cm}^{-3}$$

with RMSE = $2.21 \times 10^{-3} \text{ mg C cm}^{-3} \text{ h}^{-1}$ (Fig. 1).

Inserted text (p. 7, L 282-290)

“Specifically, we estimated the pre-exponential factor α and the carbon half-saturation constant K_{msx} by minimizing RMSE between observed and predicted respiration. The best-fit parameters were:

$$\alpha_{sx} = 5.41 \times 10^{11} \text{ mg C cm}^{-3} \text{ h}^{-1}$$

$$K_{msx} = 4.8 \times 10^{-6} \text{ g C cm}^{-3}$$

$$RMSE = 2.21 \times 10^{-3} \text{ mg C cm}^{-3} \text{ h}^{-1}$$

Parameter uncertainty was estimated via bootstrap resampling (500 replicates), and Supplementary Table 1 lists each parameter along with its estimate, 95% confidence interval (where applicable), units, and provenance. Fitted values include α and K_{msx} , while others are adopted from Davidson et al. (2012).”

10 L161-162 – parameter provenance

“how were these model parameters determined?”

Response

We agree that full provenance and uncertainty ranges should be provided. Supplementary Table S1 now lists each parameter together with its estimate and 95 % bootstrap confidence interval (500 resamples).

α_{sx}	5.41×10^{11}	$4.7\text{--}6.2 \times 10^{11}$	$\text{mg C cm}^{-3} \text{ h}^{-1}$	fitted
K_{msx}	4.8×10^{-6}	$2\text{--}8 \times 10^{-6}$	g C cm^{-3}	fitted
K_{mO_2}	0.121	–	$\text{cm}^3 \text{ O}_2 \text{ cm}^{-3} \text{ air}$	Davidson et al. 2012
E_a	72.3	–	kJ mol^{-1}	Davidson et al. 2012
p-factor	4.14×10^{-4}	–	–	Davidson et al. 2012
D_{liq}	3.17	–	–	Davidson et al. 2012

11 L171-173 – simulation of ROL

“I’m not sure how the plant root oxygen loss was simulated here.”

Response

We thank the reviewer for asking us to clarify this point. ROL is not modelled as a physical flux. Instead we prescribe a set of rhizosphere O_2 concentrations that are generated with the diffusion term already built into DAMM (Eq. 4). By letting soil volumetric water content (θ) vary from air-dry ($\theta \approx 0$) to full saturation we obtain 70 discrete O_2 levels ranging from 2×10^{-4} to $2 \times 10^{-1} \text{ cm}^3 O_2 \text{ cm}^{-3}$. This span represents in-situ microsensor measurements for *Spartina*, *Elymus* and *Phragmites* roots (Visser et al., 2000; Colmer, 2003; Armstrong & Armstrong, 2005; Köhl et al., 2021) and therefore serves as a realistic proxy for the outcome of differing ROL rates. Prescribing O_2 in this way allows us to quantify the aggregation bias without introducing poorly constrained anatomical parameters.

Inserted text (p. 6, L 234-236)

“ROL itself is not simulated. Instead, its observed outcome, rhizosphere O_2 concentration, is imposed directly, following the empirical range detailed above. This allows us to quantify the impact of ignoring heterogeneity without speculative parameterisation of the many plant traits that underlie ROL.

Intra- and inter-specific variation in ROL has been documented for marsh grasses, rice and sedges (Holmer & Pedersen, 2003; Visser et al., 2000; Armstrong & Armstrong, 2005; Köhl et al., 2021), supporting the empirical O_2 range used here.”

12 L172-180 & Fig. 3 – novelty of results

“The results of this study seem to be simple. While the conclusions were clear, the results were not particularly novel. It is understandable that the response of respiration to soil carbon content is influenced by soil O_2 concentration.”

Response

We thank the reviewer for this perspective. Although the qualitative effect of O_2 on respiration is well established, the magnitude of the bias introduced when heterogeneous rhizosphere O_2 fields are replaced by a single bulk value had not been quantified for salt-marsh soils. Our study provides this missing number and demonstrates its budgetary relevance.

Inserted text (p. 11, L 373-379)

“Across the full prescribed O_2 distribution, replacing heterogeneity with a single mean concentration underestimates aerobic CO_2 efflux by $10 \pm 0.6 \%$. Even when the O_2 range is restricted to the inter-quartile span the bias remains 6 % (Fig. S2). Scaling the

10 % correction to the European salt-marsh sink ($30 \pm 5 \text{ Tg C yr}^{-1}$; (McLeod et al., 2011)) adds $\approx 3 \text{ Tg C yr}^{-1}$, a flux comparable to the current global net sequestration attributed to seagrass meadows. Hence, the aggregation error is quantitatively significant and should be addressed in regional and global marsh carbon budgets."

We trust these comprehensive revisions and clarifications fully address the reviewer's valuable feedback, substantially strengthening the manuscript's methodological transparency and highlighting its novel ecological contributions. We sincerely thank the reviewer for their constructive suggestions, significantly enhancing our work's potential scientific impact.

References cited in this response

Alongi, D. M.: Carbon balance in salt marsh and mangrove ecosystems: A global synthesis, *J. Mar. Sci. Eng.*, 8, 1–21, <https://doi.org/10.3390/jmse8100767>, 2020.

Armstrong, J., & Armstrong, W. (2005). Rice: Sulfide-induced barriers to root radial oxygen loss, Fe^{2+} and water uptake, and lateral root emergence. *Annals of Botany*, 96(4), 625–638. <https://doi.org/10.1093/aob/mci215>

Colmer, T. D. (2003). Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant, Cell & Environment*, 26(1), 17–36. <https://doi.org/10.1046/J.1365-3040.2003.00846.X>

Davidson, E. A., Samanta, S., Caramori, S. S., & Savage, K. (2012). The Dual Arrhenius and Michaelis-Menten kinetics model for decomposition of soil organic matter at hourly to seasonal time scales. *Global Change Biology*, 18(1), 371–384. <https://doi.org/10.1111/j.1365-2486.2011.02546.x>

Intergovernmental Panel on Climate Change (IPCC): Global Carbon and Other Biogeochemical Cycles and Feedbacks, in: Climate Change 2021 – The Physical Science Basis, Piers Forster, 673–816, <https://doi.org/10.1017/9781009157896.007>, 2023.

Kühl, M., Scholz, V., Sorrell, B. K., Koop-Jakobsen, K., Meier, R. J., & Mueller, P. (2021). Plant-Mediated Rhizosphere Oxygenation in the Native Invasive Salt Marsh Grass *Elymus athericus*. *Frontiers in Plant Science*, 12, 669751. <https://doi.org/10.3389/FPLS.2021.669751>

Luisetti, T., Turner, R. K., Andrews, J. E., Ferrini, S., Murray, B. C., & Smith, C. J. (2020). Quantifying and valuing carbon flows and stocks in temperate European salt marshes. *Science of the Total Environment*, 740, 140092. <https://doi.org/10.1016/j.scitotenv.2020.140092>

McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., & Silliman, B. R. (2011). A blueprint for blue carbon: Toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10), 552–560. <https://doi.org/10.1890/110004>

Rastetter, E. B., King, A. W., Cosby, B. J., Hornberger, G. M., O'Neill, R. V., & Hobbie, J. E. (1992). Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. *Ecological Applications*, 2(1), 55–70. <https://doi.org/10.2307/1941889>

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/J.0030-1299.2007.15559.X>;WGROU:STRING:PUBLICATION

Visser, E. J. W., Colmer, T. D., Blom, C. W. P. M., & Voesenek, L. A. C. J. (2000). Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. *Plant, Cell and Environment*, 23(11), 1237–1245. <https://doi.org/10.1046/j.1365-3040.2000.00628.x>

Zhou, Y., O'Meara, T., Cardon, Z. G., Wang, J., Sulman, B. N., Giblin, A. E., & Forbrich, I. (2024). Simulated plant-mediated oxygen input has strong impacts on fine-scale porewater biogeochemistry and weak impacts on integrated methane fluxes in coastal wetlands. *Biogeochemistry*, 167(7), 945–963. <https://doi.org/10.1007/S10533-024-01145-Z>/METRICS