Underestimation of Anaerobic Decomposition Rates in *Sphagnum* Litterbag Experiments by the Holocene Peatland Model Depends on Initial Leaching Losses

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Abstract. The Holocene Peatland Model (HPM) is a widely applied model to understand and predict long-term peat accumulation. Here, we test whether the HPM can predict decomposition of available *Sphagnum* litterbag data along a gradient from oxic to anoxic conditionsand estimate parameter values from the litterbag data.

Large uncertainties in available litterbag data allow predictions of the HPM to fit decomposition rates estimated from litterbags
5 by adjusting initial leaching losses and decomposition rates estimated from the litterbag data within the range of their uncertainties. Specifically, with standard parameter values, the HPM assumes larger initial leaching losses and smaller decomposition rates than estimated from the litterbag data alone. Therefore, improved tests of the HPM rely on future litterbag experiments that allow a more accurate estimation of initial leaching losses and decomposition rates.

When estimating HPM parameters from the litterbag data and assuming smaller initial leaching losses, our analysis indicates
10 that the HPM with standard parameter values underestimates anaerobic decomposition rates for several species and assumes a too steep decrease of decomposition rates from oxic to anoxic conditions. This may be caused by not considering effects of water table fluctuations on aerobic and anaerobic decomposition rates.

Whether the discrepancies are reproducible and the estimated parameter values may be an easy fix to account for effects of water table fluctuations in long-term predictions needs further investigation. Based on previous sensitivity analyses of the HPM,
15 the updated parameter estimates can cause differences in predicted 5000 year C accumulation up to 100 kg m^{-2}.

1 Introduction

Decomposition is one of the major controls of how much carbon (C) peatlands can store. Compared to other ecosystems, northern peatlands usually have small decomposition rates because of cold temperatures, high water table levels, acidic pH value, and litter that does not decompose fast even under more conditions facilitating microbial decomposition (van Breemen,
20 1995; Rydin et al., 2013). These slow decomposition rates caused northern peatlands to accumulate at least 400 Gt C (Yu, 2012; Nichols and Peteet, 2019) during the Holocene and changes in the controls of decomposition rates may cause them to loose considerable amounts of C to the atmosphere under climate and land use changes (Frolking et al., 2011; Loisel et al.,

2017). Peatland models are used to better understand past C accumulation and to predict future changes in peat C stocks, but because of the long time scales which have to be considered, they are difficult to test.

25   How to test long-term peatland models is an open problem. Past studies have compared site-adapted simulations of peat height, age, C and N stocks, macrofossil composition, and water table level predicted by peatland models against peat core data (e.g., Frolking et al. (2010), Tuittila et al. (2013), Treat et al. (2021), Zhao et al. (2022)), and have shown that existing peatland models can reproduce observed patterns to some extent.

These tests suffer from two problems. First, they test entire peatland models against observed data and thus can identify the
30   parameter values or model equations that cause observed discrepancies less reliably. Second, there often are large uncertainties on both sides of the test; peatland models have large uncertainties in parameter values and model structure and these may produce a range of predictions as illustrated by uncertainty analyses (e.g. Quillet et al. (2013a), Quillet et al. (2013b)) and model intercomparisons (e.g. Zhao et al. (2022)). Observed data also has uncertainty from measurements, peat dating, or simply missing data, for example for past precipitation. Large uncertainties can make tests inconclusive, no matter how much
35   data we use. An alternative which avoids some of these problems is to test only some part of a model while taking into account relevant uncertainty sources.

Such a test could address the decomposition module of a peatland model. For example, in the Holocene Peatland Model (HPM) (Frolking et al., 2010), we only need to know litter species, peat water content, peat porosity, water table depth, and only five parameters to predict decomposition rates. The predictions can be compared to decomposition rates estimated
40   from litterbag data and therefore future litterbag studies can directly test whether discrepancies are replicable and identify the factors causing the discrepancies. Admittedly, such a test is restricted to short time ranges and not representative for long-term decomposition rates, but future tests with different scope will benefit from the reduced parameter uncertainties and can consider where the model fails already on short time scales.

A test of decomposition modules is relevant because of the importance of decomposition for long-term C accumulation in
45   peatlands. Previous sensitivity analyses of the HPM and applications to peat cores suggest that the anoxia scale length (c_2), the parameter controlling how anaerobic decomposition rates are limited by electron acceptor depletion and accumulation of decomposition products, can result in a doubling of accumulated C, depending on climate conditions (Quillet et al., 2013b; Kurnianto et al., 2015). A test of only the HPM decomposition module can provide better estimates for c_2 and may therefore help to reduce uncertainties in predicted C accumulation rates.

50   Currently, litterbag experiments are not as extensively used for testing peatland models as they could and only a fraction of the information available from litterbag experiments is used to develop models. The HPM uses litterbag data to define average decomposition rates of moss plant functional types, but parameters for environmental controls of decomposition are assumptions which appear to be informed at most qualitatively by litterbag experiments, and it is not tested whether the HPM successfully fits available litterbag data (Frolking et al., 2010). This is also the case for other dynamic peatland models, e.g.
55   Frolking et al. (2001), Bauer (2004), Heijmans et al. (2008), Heinemeyer et al. (2010), Morris et al. (2012), Chaudhary et al. (2018), Bona et al. (2020).

One reason why such tests have been difficult is that suitable litterbag raw data to test peatland models are scarce. Bona et al. (2018) developed a Peatland Productivity and Decomposition Parameter Database, but it contains only data from studies older than 2010 and no error estimates for remaining masses in litterbag data. Since decomposition rates have been estimated with
60   different litterbag decomposition models in previous studies, their values are not directly comparable and therefore raw data are necessary to obtain estimates directly comparable to predictions from a certain peatland model (Yu et al., 2001; Teickner et al., 2024b). Recently, we used available *Sphagnum* litterbag data to estimate decomposition rates which can be directly compared to decomposition rates predicted by the HPM (Teickner et al., 2024b).

Even though tests of only a part of a model are less uncertain than tests of whole models, there still is a risk that they
65   are dominated by uncertainties. Remaining masses in litterbag experiments are often very variable, even under controlled environmental conditions (e.g. Bengtsson et al. (2018)), and for many litterbag experiments, a range of decomposition rates may produce similar predictions for remaining masses if a litterbag decomposition model compatible with the HPM is used (Teickner et al., 2024b). Finally, also only five model parameters, as in the case of the HPM decomposition module, can make predictions uncertain. These uncertainties have to be taken into account to check whether litterbag data are compatible with the
70   peatland model. A possible way to do this is to combine the HPM decomposition module, the litterbag decomposition model from our previous study, and available litterbag experiments into one model and use Bayesian data analysis (Gelman et al., 2014) to estimate uncertainties of data and parameters.

If such a test suggests that decomposition rates predicted by the HPM do not fit estimates from litterbag experiments even if main uncertainty sources are considered, we have identified a discrepancy worth considering in more detail. We can then
75   identify how the estimated parameter values differ from the standard values and analyze whether previous sensitivity analyses of the HPM suggest that these discrepancies may have larger effects on the predicted C accumulation.

Our aim is to test the HPM decmposition module against decomposition rates estimated from available *Sphagnum* litterbag experiments. Specifically, we want to:

1. Test whether the HPM can predict litterbag decomposition rates for different *Sphagnum* species along the gradient from
80   oxic to anoxic conditions.

2. Test whether HPM parameters estimated from litterbag data are compatible with the values originally proposed in the HPM (standard parameter values) (Tab. 1).

We test the following hypotheses:

1. The HPM can successfully predict decomposition rates estimated from litterbag data under oxic and anoxic conditions.

85   2. HPM parameter values ($k_{i,0}$, W_{opt}, c_1, f_{min}, c_2) estimated from litterbag experiments are compatible with the standard values.

To address these aims, we developed a model that combines the HPM decomposition module and our previous *Sphagnum* litterbag decomposition model, which estimates decomposition rates in available litterbag experiments while considering

initial leaching losses (Teickner et al., 2024b). Estimated decomposition rates of this model can be directly compared to de-
composition rates predicted by the HPM because the formula to compute remaining masses from decomposition rates is the
same.

We only test the decomposition module of the HPM, but our results are valuable also for other peatland models that pa-
rameterize their decomposition modules from litterbag experiments because they also require a correct representation of how
decomposition rates are controlled by the water table level. Our test identified discrepancies between the HPM and litterbag
data that could give novel insights into processes controlling anaerobic decomposition rates in future litterbag experiments.

Table 1. Standard values of parameters of the decomposition module in the Holocene Peatland Model (Frolking et al., 2010).

HPM parameter	Standard value	Description
W_{opt} (L_{water} L_{pores}^{-1})	0.450	Optimum degree of saturation for aerobic decomposition.
c_1 (-)	2.310	Curvature of the relation of the aerobic decomposition rate to the degree of saturation (larger values imply a steeper decrease of decomposition rates for degrees of saturation diverging from W_{opt}).
f_{min} (yr^{-1})	0.001	Minimum anaerobic decomposition rate.
c_2 (m)	0.300	Anoxia scale length. Represents limitation of anaerobic decomposition rates with increasing distance below the annual average water table depth due to end product accumulation and limitation of available electron acceptors. Larger values mean that anaerobic decomposition rates decrease less strongly with depth below the average annual water table level.
$k_{0,hollow}$ (yr^{-1})	0.130	Maximum possible decomposition rate for hollow $Sphagnum$ species.
$k_{0,lawn}$ (yr^{-1})	0.080	Maximum possible decomposition rate for lawn $Sphagnum$ species.
$k_{0,hummock}$ (yr^{-1})	0.060	Maximum possible decomposition rate for hummock $Sphagnum$ species.

2 Methods

2.1 *Sphagnum* litterbag data

To test the HPM against litterbag data, we use the Peatland Decomposition Database (Teickner and Knorr, 2024b). In this
study, we use data from Bartsch and Moore (1985), Vitt (1990), Johnson and Damman (1991), Szumigalski and Bayley (1996),
Prevost et al. (1997), Scheffer et al. (2001), Thormann et al. (2001), Asada and Warner (2005), Trinder et al. (2008), Breeuwer
et al. (2008), Straková et al. (2010), Hagemann and Moroni (2015), Golovatskaya and Nikonova (2017), and Mäkilä et al.
(2018) to estimate litterbag decomposition rates and predicted k_0 were tested against k_0 estimated from Johnson and Damman
(1991), Szumigalski and Bayley (1996), Prevost et al. (1997), Straková et al. (2010), Golovatskaya and Nikonova (2017),

105   and Mäkilä et al. (2018) because only these studies reported water table depths required to make predictions with the HPM. Samples originally classified as *Sphagnum magellanicum* are here classified as *Sphagnum magellanicum aggr.* (Hassel et al., 2018).

2.2 Prediction of litterbag decomposition rates with the Holocene Peatland Model

To predict decomposition rates, the HPM decomposition module needs as inputs the litter type in terms of the HPM plant
110   functional types, the fraction of mass already lost due to previous decomposition, the depth of the litter below the peat surface, the water table depth, and the peat degree of saturation (Frolking et al., 2010).

Predicting decomposition rates for the available litterbag data is not straightforward because the HPM does not consider specific features of litterbag experiments, because it does not specify how to assign species to plant functional types, and because required variables such as the degree of saturation are not reported in the litterbag studies and therefore need to be
115   estimated. In addition, we need to link decomposition rates estimated from litterbag data to the decomposition rates predicted by the HPM and this requires to link remaining masses in litterbag experiments to decomposition rates.

The only variables that can be directly linked are the depth of the litter below the peat surface, water table depths (both reported in litterbag experiments). All other variables need additional assumptions that we describe in the following subsections.

2.2.1 Remaining masses and decomposition rates

120   In a previous study, we estimated k_0 for the litterbag data using the decomposition equation of the HPM (equation (7) in Frolking et al. (2010)) and in addition considering initial leaching losses to avoid bias of k_0 estimates (Teickner et al., 2024b):

$$m(t) = \begin{cases} m_0 & \text{if } t = 0 \\ \frac{m_0 - l_0}{(1+(\alpha-1)k_0 t)^{\frac{1}{\alpha-1}}} & \text{if } t > 0 \end{cases} \tag{1}$$

Where $m(t)$ is the remaining mass at time t, m_0 is the mass at time $t = 0$ (the initial mass), l_0 is the initial mass loss due to leaching and respiration of soluble compounds, k_0 is the decomposition rate of litter with no prior decomposition, α
125   controls how the decomposition rate decreases as the fraction of remaining mass decreases and is assumed to describe how decomposition rates decrease with decreasing litter quality over time (Frolking et al., 2001).

2.2.2 Assignment of *Sphagnum* species to PFT

The HPM defines maximum possible decomposition rates ($k_{i,0}$) for three *Sphagnum* PFT (hollow, lawn, and hummock species), but not how to assign species to them. We assigned individual *Sphagnum* species to the three PFT by comparing their niche
130   water table depths with the optimal water table depth for net primary production defined in the HPM. Specifically, we defined fixed average annual water table depth intervals for the PFT: hollow (<5 cm), lawn (≥ 5 cm and < 15 cm), hummock (≥ 15 cm). Then, we used niche water table depths and standard deviations from Johnson et al. (2015) to assign *Sphagnum* species to

these three microhabitats. Using only average values and the microhabitat water table depth thresholds resulted in unintuitive assignments, such as assigning *S. fallax* to hummocks. To avoid such obvious misclassifications, we defined rules to assign

135 species to HPM microhabitats based on the probability a species would occur in the three niche water table depth intervals. To compute the probabilities, we assumed a normal distribution (Johnson et al., 2015):

1. Species with a probability of occurrence $\geq 15\%$ in the intervals of all three PFT were classified as lawn species.

2. In all other cases, species were assigned to the PFT for which their probability of occurrence was largest.

Litterbag data from Prevost et al. (1997) are incubations of peat samples where the species is unknown. Based on descriptions

140 in the paper, it is likely that the peat was formed by hummock species. In addition, decomposition rate estimates for these samples are small. For these reasons, we assigned these samples to the hummock PFT of the HPM.

When estimating parameters of the HPM from the litterbag data (see section 2.3.1), we also estimated the maximum possible decomposition rate ($k_{i,0}$). *Sphagnum* species differ in their decomposition rate and the PFT of the HPM are a simplification which may cause misfits of the HPM to litterbag data. We therefore estimated $k_{i,0}$ for individual *Sphagnum* species in models

145 HPMe-LE-peat and HPMe-LE-peat-l0.

2.2.3 Degree of saturation

We estimated the degree of saturation with the modified Granberg model (ModGberg model) (Granberg et al., 1999; Kettridge and Baird, 2007) from total porosity, the water table depth, and the positions of the litterbags during the incubation. The total porosity was not reported in any study and therefore we assumed an average value of 80% with a standard deviation of 10%,

150 roughly based on values reported for low-density *Sphagnum* peat (Liu and Lennartz, 2019).

2.2.4 Fraction of mass lost during previous decomposition

The HPM assumes that decomposition rates decrease the more of the initial mass has already been decomposed (Frolking et al., 2001, 2010). All litterbag data we use here, except samples from Prevost et al. (1997), are from *Sphagnum* samples collected from the surface of peatlands and therefore can be expected to have not experienced mass loss due to decomposition at the start

155 of the experiments. Prevost et al. (1997) incubated *Sphagnum* peat collected from different depths below the surface and these samples probably have already experienced some decomposition, however it is difficult to estimate how much. To avoid this problem, we estimated $k_{i,0}$ separately for samples from different depths in Prevost et al. (1997), implicitly assuming that these are two different PFT with different maximum possible decomposition rate.

2.3 Testing the HPM against litterbag data

160 ### 2.3.1 Model versions

To test different aspects of the HPM and the additional assumptions we introduce, we computed several models which differ in whether HPM parameters were fixed to their standard values or estimated from data, whether peat properties (porosity, water

content, minimum water content at the surface) are estimated from data or not, whether the litterbag decomposition model and the HPM decomposition module were estimated in two separate Bayesian models or one combined model, and whether the HPM decomposition module was extended to also predict l_0 or not (Tab. 2).

The first model (HPMf) does not estimate any parameters of the HPM (except for α) and does not estimate peat properties from the litterbag data and therefore corresponds to the HPM decomposition module with standard parameter values. Values of k_0 are predicted independently from the litterbag decomposition model.

Each subsequent model combines the HPM decomposition module and the litterbag decomposition model into one Bayesian model. Each of these models estimates an additional set of parameters from the litterbag data relative to the previous model (Tab. 2). First, only the peat properties (HPMf-LE-peat) are estimated, and second all HPM parameters ($k_{i,0}$, c_1, W_{opt}, f_{min}, c_2) (HPMe-LE-peat). Finally, HPMe-LE-peat-l0 extends HPMe-LE-peat by adding formulas to model how l_0 depends on the degree of saturation, similar to how the HPM predicts k_0.

It is important to note that combining the litterbag decomposition model and the HPM decomposition module into one Bayesian model does not only estimate HPM parameters from the litterbag data, but it also adjusts the decomposition rates estimated from litterbag data to the HPM: The HPM serves as prior in the combined model and Bayesian probability theory estimates what parameter values are compatible with the data *and* the combined model. This is exactly what we want because there is uncertainty both in the remaining masses reported in litterbag experiments and in HPM parameters. If HPM parameter estimates from the combined model are not compatible with standard values used in the original model (Tab. 1) even if we adjust them to the HPM within the range allowed by the uncertainties, this is a discrepancy worth testing in future experiments.

HPMf-LE-peat tested whether the HPM can be made compatible with available litterbag data when the HPM decomposition module and the decomposition model for litterbag data are combined and when uncertain peat properties are estimated from data.

HPMe-LE-peat estimates what HPM parameter values are compatible with available litterbag data and therefore allows to test whether the standard parameter values are extreme relative to these estimates. Values of $k_{i,0}$ were estimated for each species separately, as described in section 2.2.2.

HPMe-LE-peat-l0 was computed because decomposition rates estimated from available litterbag experiments are sensitive to initial leaching losses (Yu et al., 2001; Lind et al., 2022; Teickner et al., 2024b). It is therefore interesting to see whether litterbag decomposition rates are adjusted differently in HPMe-LE-peat-l0 — when initial leaching losses are constrained — compared to HPMe-LE-peat — when initial leaching losses can be estimated more independently for each replicate. Based on previous experiments with tea bags it is reasonable to assume that there is some relation between initial leaching losses and the degree of saturation (Lind et al., 2022).

To check whether outliers in the litterbag data could influence our results, we computed one additional model, HPMe-LE-peat-l0-outlier, with the same structure as HPMe-LE-peat-l0, but estimated without littebag experiments identified as outliers. Litterbag experiments were defined as outliers if the reported average remaining mass of any litterbag (batch) during the experiment had a posterior probability $> 99\%$ to be different from the remaining mass predicted by the litterbag decomposition model alone. This procedure identified experiments as outliers where remaining masses increased over time, where litterbags

collected at intermediate time points had unexpectedly low remaining masses, or where initial leaching losses were retarded to later time points, presumably because of freezing after the start of the experiment (Teickner et al., 2024b). In total, 5 litterbag

200 experiments were identified as outliers. Results for HPMe-LE-peat-l0-outlier are shown in supporting information S10 and HPM parameter estimates agree with the other models where HPM parameters were estimated.

Strictly, we do not test the decomposition module in the HPM, but the combination of the decomposition model in the HPM and the modified Granberg model, assuming that uncertainties in water table depths are negligible and that we accounted sufficiently for uncertainties in total porosity. This ambiguity has to be accepted when combining heterogeneous litterbag data

205 where some variables have to be estimated. Litterbag experiments where the degree of saturation is measured would be needed to avoid this ambiguity.

Table 2. Overview of HPM modifications computed in this study. Complete formulas for the models are shown in supporting information S1.

Model	Description
HPMf	Decomposition model from the Holocene Peatland model with default parameter values (Frolking et al., 2010). The model is run with peat water contents estimated with the modified Granberg model, using water table depths and litterbag depths reported from the litterbag studies, and assuming a fixed peat porosity, and minimum peat water content at the surface. Litterbag decomposition rate estimates are from the litterbag decomposition model in Teickner et al. (2024b).
HPMf-LE-peat	The same as HPMf, but combined with the litterbag decomposition model into one Bayesian model. Water table depths, peat porosity, and minimum peat water content at the surface were estimated from data.
HPMe-LE-peat	The same as HPMf-LE-peat, but now also parameters from the HPM decomposition model ($k_{i,0}$, W_{opt}, f_{min}, c_1, c_2) are estimated from the litterbag data.
HPMe-LE-peat-l0	The same as HPMe-LE-peat, but now also an average initial leaching loss for each species and, across all species, a factor by which this average leaching loss increases or decreases as the peat degree of saturation increases are estimated.
HPMe-LE-peat-l0-outlier	The same as HPMe-LE-peat-l0, but computed without litterbag experiments that were identified as outliers and for which the HPM decomposition module predicts decomposition rates (see the text for details).

2.3.2 Tests of model fits to litterbag decomposition rates and comparison between estimated and standard HPM parameter values

For each model, we computed the difference of the decomposition rate predicted by the HPM and estimated from the litterbag
data for each litterbag replicate and from this the average. We then computed the posterior probability that this average differ-
ence is different from zero. A small probability indicates a misfit of the model to available litterbag data. We also tested the
same difference for specific species because graphical checks indicated that the decomposition rate prediction skill of the HPM
depends on species.

For HPMe-LE-peat and HPMe-LE-peat-l0, we computed the posterior probability that that the HPM parameter values esti-
mated from litterbag data ($k_{i,0}$, c_1, W_{opt}, c_2, f_{min}) differ from the standard parameter values (Tab. 1).

2.3.3 Predictive accuracy of the modified Holocene Peatland Model in comparison to the original model

To test whether HPMe-LE-peat-l0 has not only a better fit to available litterbag data, but also a better predictive accuracy
for novel data than the model with standard parameter values (HPMf), we compared how well both can predict the one-pool
decomposition rates from litterbag experiments.

HPM parameters of HPMf are not estimated from data and therefore we could compute the root mean square error of predic-
tion (RMSE$_{test}$) directly with k_0 predicted by HPMf and estimated with the litterbag decomposition model. HPM parameters
of HPMe-LE-peat-l0 are estimated from the litterbag data and we therefore used cross-validation (CV) to estimate RMSE$_{test}$.

Since decomposition rates form the same species and study usually are not independent, we defined blocks which were used
as CV-folds. Each fold consists of the data from one study, except those values that were measured for *Sphagnum* species for
which only this study had data (we want to estimate the predictive accuracy not for new species). Data for species with data
from one study only were always used for model training and not part of the testing folds. This procedure resulted in 5 folds.
HPMf and HPMe-LE-peat-l0 were tested against the same data.

In the text, RMSE$_{train}$ is the RMSE computed with the data a model was estimated with (for HPMf, the data the litterbag
decomposition model was estimated with), and RMSE$_{test}$ is the RMSE computed with independent test data.

2.4 Bayesian data analysis

All models listed in Tab. 2 were computed with Bayesian statistics to account for relevant uncertainty sources and include
relevant prior knowledge (for example that *Sphagnum* decomposition rates are unlikely to be larger than 0.5 yr^{-1}). Bayesian
computations were performed using Markov Chain Monte Carlo (MCMC) sampling with Stan (2.32.2) (Stan Development
Team, 2021a) and rstan (2.32.5) (Stan Development Team, 2021b) using the NUTS sampler (Hoffman and Gelman, 2014),
with four chains, 4000 total iterations per chain, and 2000 warmup iterations per chain. None of the models had divergent
transitions, the minimum bulk effective sample size was larger than 400, and the largest improved $\hat{R}$ was 1.01, indicating that
all chains converged (Vehtari et al., 2021). All models used the same priors for the same parameters and prior choices are listed
and justified in supporting Tab. S1.

We used power-scaling of the prior and likelihood distributions as implemented in the priorsense package (0.0.0.9000)
240 (Kallioinen et al., 2024) to analyze the relative sensitivity of the posterior distribution to small perturbations of the prior
and likelihood in HPMe-LE-peat-l0 for HPM parameters and peat properties. This is a computationally nonexpensive way
to check whether the data provide information about a parameter and where prior and data may provide conflicting informa-
tion (Kallioinen et al., 2024). Results of this analysis and further information on the data analysis are shown in supporting
information S3.

3   Results

3.1   Fit and predictive accuracy of the different versions of the Holocene Peatland Model to available litterbag data

The HPM decomposition module with standard parameter values (HPMf) fitted decomposition rates estimated from litterbag
data to variable degrees (Tab. 3). All other models had an improved overall fit (smaller $RMSE_{train}$) to the data (Tab. 3, Fig. 1).
Despite better fitting the data, HPMe-LE-peat-l0 did not predict k_0 better in the cross-validation than HPMf, as indicated by a
250 large $RMSE_{test}$ (Tab. 3).

Errors of HPMf differed between species (Fig. 2). They were particularly small for *S. fuscum* ($RMSE_{train}$ = 0.02 $yr^{-1}\pm$
0.004, data from 5 studies) as well as *Sphagnum* spec. samples from Prevost et al. (1997) ($RMSE_{train}$ = 0.02 $yr^{-1}\pm$ 0). All rates
were underestimated for *S. angustifolium* ($RMSE_{train}$ = 0.23 $yr^{-1}\pm$ 0.09, data from 3 studies).

Table 3. Training and testing RMSE for decomposition rates as predicted by different versions of the Holocene Peatland Model (see Tab.
2 for a description of the models) and number of misfits. $RMSE_{train}(k_0)$ is the root mean square error of model predictions for litterbag
replicates used during model computation. $RMSE_{test}(k_0)$ is the RMSE for litterbag replicates used in blocked cross-validation. Where no
$RMSE_{test}(k_0)$ is given, it was not computed for these models. Values are averages and lower and upper bounds of central 95% uncertainty
intervals (yr^{-1}). Misfits counts the number of litterbag experiments for which k_0 predicted by the HPM modification differed from k_0 as
estimated from the litterbag decomposition model with a posterior probability of at least 99%. In total, k_0 was predicted with the HPM
modifications for 53 litterbag experiments ($RMSE_{train}(k_0)$) or 29 ($RMSE_{test}(k_0)$).

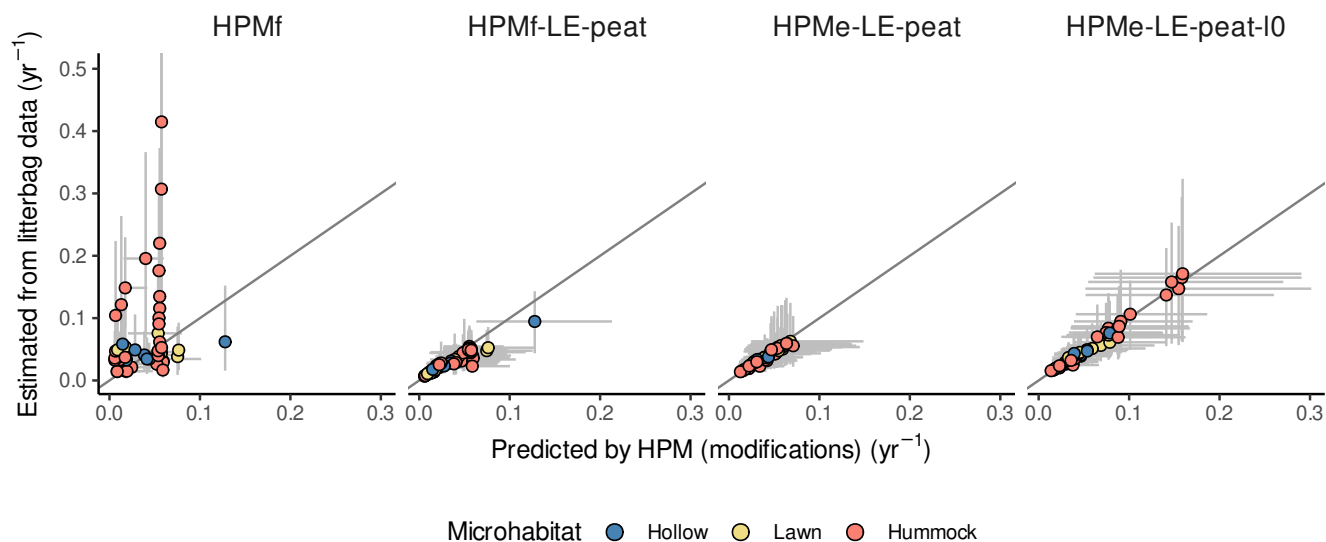| Model	$RMSE_{train}(k_0)$	$RMSE_{test}(k_0)$	Misfits
HPMf	0.105 (0.051, 0.191)	0.136 (0.06, 0.252)	13
HPMf-LE-peat	0.02 (0.013, 0.029)		0
HPMe-LE-peat	0.014 (0.008, 0.021)		0
HPMe-LE-peat-l0	0.022 (0.012, 0.039)	0.088 (0.038, 0.179)	0
HPMe-LE-peat-l0-outlier	0.021 (0.013, 0.032)		0

Figure 1. Comparison of k_0 estimated by the litterbag decomposition model versus k_0 predicted by different modifications of the HPM decomposition module (Tab. 2). Points are colored according to the microhabitat classification of *Sphagnum species* (see the Methods section for details). Error bars exceeding $0.5 \, \mathrm{yr}^{-1}$ are clipped.

3.2 Differences in model behavior of the Holocene Peatland Model and its modifications

The HPM with standard parameter values can fit litterbag data due to large uncertainties in available litterbag data.

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HPMf-LE-peat suggests that it is possible to fit remaining masses in litterbag experiments without changing the standard HPM parameter values, simply by adjusting k_0 and l_0 estimates from the litterbag decomposition model such that they fit the HPM predictions. Fig. 1 shows that HPMf-LE-peat can reproduce these adjusted k_0 estimates. Fig. 2 shows that this better fit is mainly achieved by adjusting k_0 estimates from the litterbag decomposition model (mainly decreased) to the HPM

260 and not because of differences in peat properties estimated from the litterbag data. In combination with the improved fit of HPMf-LE-peat, this indicates that uncertainties in the litterbag data are large enough to make the HPM compatible with the litterbag decomposition rates by varying the magnitude of decomposition rates and initial leaching losses, even though the standard HPM parameters are not necessarily (most) compatible with the data. This indicates that a better test of the HPM decomposition module requires more accurate estimates of initial leaching losses.

Estimates for k_0, l_0, and $k_{i,0}$ differ between modifications of the HPM.

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The two modifications of the HPM where HPM parameters were estimated from litterbag data (HPMe-LE-peat, HPMe-LE-peat-l0) also differed in the magnitude of l_0 and k_0 estimates, as well as the maximum possible initial decomposition rate for each species ($k_{0,i}$). However, they had very similar estimates for the other HPM parameters (c_1, W_{opt}, f_{min}, c_2).

HPMe-LE-peat estimated larger initial leaching losses and smaller decomposition rates than the litterbag decomposition model from Teickner et al. (2024b) alone, similar to HPMf-LE-peat (Fig. 3). This is particularly the case for *S. angustifolium*, for which the separate litterbag decomposition model estimated much larger average decomposition rates and smaller initial leaching losses than the litterbag decomposition model in HPMe-LE-peat (Fig. 2). In contrast to this, initial leaching losses and smaller decomposition rates estimated by HPMe-LE-peat-l0 were more similar to estimates of the separate litterbag decomposition model from Teickner et al. (2024b) (Fig. 3). This indicates again that a better test of the HPM is possible when l_0 can be estimated more accurately.

In line with this, the maximum possible decomposition rates for the species differ between the HPM modifications. HPMe-LE-peat-l0 estimates a larger average maximum possible decomposition rate, particularly for *S. angustifolium*, than the other models (Fig. 2 and supporting Fig. S9).

Estimates for c_1, W_{opt}, f_{min}, c_2 are similar between modifications of the HPM.

In contrast to estimates for k_0, l_0, and $k_{i,0}$, the other HPM parameters had similar estimates for HPMe-LE-peat and HPMe-LE-peat-l0 and as a consequence relative differences of decomposition rates along the water table depth gradient are very similar between all models (Fig. 2). Estimates for f_{min} did not differ much to the prior value and the power-scaling sensitivity analysis indicates a weak influence of the data (supporting information S3) and therefore that available litterbag data provide only little information about minimum decomposition rates under anoxic conditions.

Litterbag data do not indicate a clear relation of l_0 to the degree of saturation in HPMe-LE-peat-l0.

HPMe-LE-peat-l0 suggests that both positive and negative relations of l_0 are compatible with available litterbag data (95% confidence intervals for the slope (logit scale): (-0.28, 0.15), supporting Fig. S13). In contrast to HPMf-LE-peat and HPMe-LE-peat, it estimates on average smaller initial leaching losses, more similar to estimates of the litterbag decomposition model not combined with the HPM (Teickner et al., 2024b) (Fig. 3).
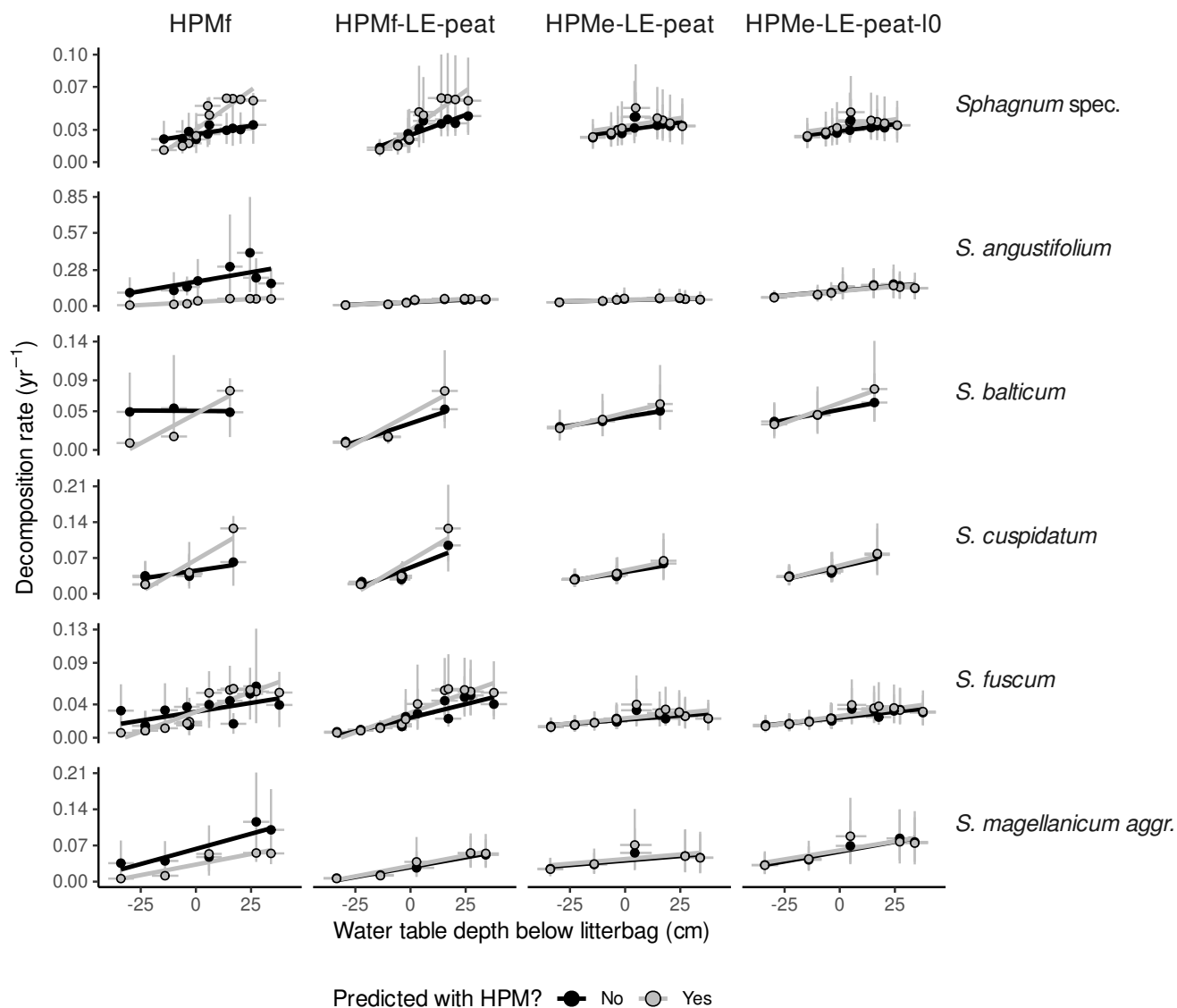
12

Figure 2. k_0 estimated from the litterbag data (Predicted with HPM = No) and predicted by different versions of the HPM decomposition module (Predicted with HPM = Yes) (HPMf, HPMf-LE-peat, HPMe-LE-peat, or HPMe-LE-peat-l0) versus reported (HPMf) or estimated (HPMf-LE-peat, HPMe-LE-peat, or HPMe-LE-peat-l0) average water table depths below the litterbags. Points represent average estimates and error bars 95% posterior intervals. Lines are predictions of linear models fitted to the average estimates. *Sphagnum* spec. are samples that have been identified only to the genus level. Only data for species with at least three replicates are shown.
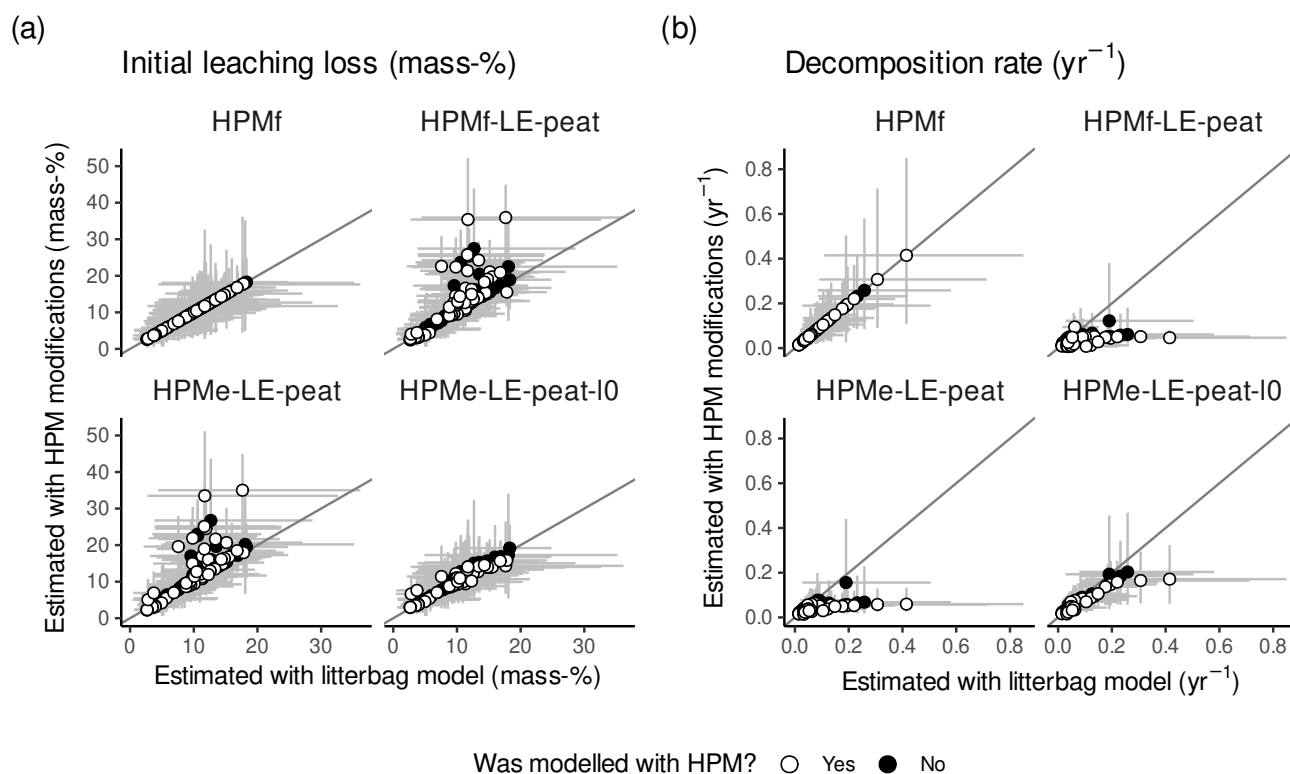
Figure 3. Plot of l_0 (a) or k_0 (b) as predicted by litterbag decomposition models combined with different modifications of the HPM (see Tab. 2) versus estimates of the litterbag decomposition model from Teickner et al. (2024b) for the same data. Litterbag experiments for which the HPM decomposition module could make predictions (water table depths reported in the studies) and to which the HPM parameters were fitted are shown as white points. Estimates for experiments from Hagemann and Moroni (2015) are not shown because these always had large estimates for k_0, were not directly tested against the HPM, and would make it difficult to represent the pattern for samples for which the HPM predicted k_0.

3.3 Comparison between standard HPM parameter values defined in Frolking et al. (2010) and estimated from litterbag data

Figure 4 shows marginal posterior densities of the maximum possible decomposition rate for each species and the four other HPM parameters for HPMe-LE-peat, with standard parameter values as defined in Frolking et al. (2010) indicated by vertical lines. For both HPMe-LE-peat and HPMe-LE-peat-l0, the range of parameter estimates contains the standard values, but there are large posterior probabilities that c_2 ($P_{\text{HPMe-LE-peat}}(c_2 > 0.3 \text{ m}) = 1$ and $P_{\text{HPMe-LE-peat-l0}}(c_2 > 0.3 \text{ m}) = 1$) and W_{opt} ($P_{\text{HPMe-LE-peat}}(W_{opt} > 0.45 \text{ L}_{\text{water}} \text{ L}_{\text{pores}}^{-1}) = 1$ and $P_{\text{HPMe-LE-peat-l0}}(W_{opt} > 0.45 \text{ L}_{\text{water}} \text{ L}_{\text{pores}}^{-1}) = 0.98$) have larger values than

the standard parameter values, indicating a discrepancy between the HPM and available litterbag data (Fig. 4 and supporting Fig. S11).

Both models also estimate a large posterior probability ($> 95\%$) that *S. russowii* and *S. rubellum* have a larger, and that *S.*
300   *cuspidatum* has a smaller maximum possible decomposition rate ($k_{0,i}$) than the standard values for the respective PFT (Fig. 4 and supporting Fig. S11). However, because of the larger variability of $k_{0,i}$ in the cross-validation (compare with the previous subsection), this discrepancy is probably more uncertain when new data would become available.
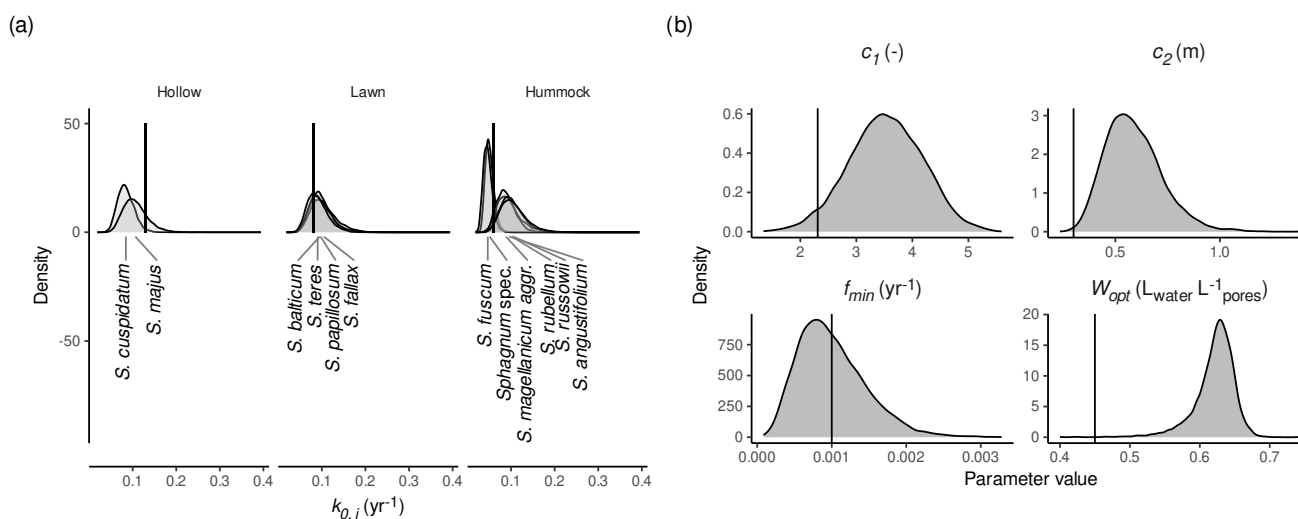
Figure 4. Marginal posterior distributions of HPM decomposition model parameters as estimated by HPMe-LE-peat. (a) $k_{0,i}$ (maximum possible decomposition rate for species i) estimated for each species. Species were assigned to HPM microhabitats as described in section 2.2.2. (b) other HPM parameters. Vertical black lines are the standard parameter values from Frolking et al. (2010). *Sphagnum* spec. are samples that have been identified only to the genus level.

4   Discussion

Our aims were to test whether the HPM can predict litterbag decomposition rates for different *Sphagnum* species along the
305   gradient from oxic to anoxic conditions, and to test whether HPM parameters estimated from litterbag data are compatible with the HPM standard values.

Our analysis suggests that the HPM decomposition module with standard parameter values can fit available litterbag data, but only because the uncertainties in litterbag data are large enough to support a range of parameter values. The price to be paid for this is to assume larger initial leaching losses and smaller decomposition rates than estimated with the litterbag
310   decomposition model alone (Teickner et al., 2024b) (Fig. 3). Comparable or better fits could be achieved by estimating HPM parameters from litterbag data (HPMe-LE-peat and HPMe-LE-peat-l0) and similar decomposition rate and initial leaching losses as estimated from litterbag data alone were predicted by a model that assumes smaller initial leaching losses (HPMe-

LE-peat-l0). Decomposition rates can be estimated more accurately from litterbag experiments when initial leaching losses are estimated more accurately (Teickner et al., 2024b). Therefore, an important result of our study is that stronger tests of the HPM

315 decomposition module and other peatland models require litterbag experiments that allow to estimate initial leaching losses more accurately than is possible with available experiments.

Despite these uncertainties, our analysis of the HPM suggests that better fits to available litterbag data are possible only if several HPM parameter values are adjusted, namely the maximum possible decomposition rates for HPM PFT or *Sphagnum* species ($k_{0,i}$), the optimum degree of saturation for decomposition (W_{opt}), and the anoxia scale length (c_2).

320 In the following sections, we discuss these discrepancies. In particular, we show that they imply a less steep gradient of decomposition rates from oxic to anoxic conditions than assumed by the standard HPM. We discuss how reliable this pattern is, considering that the data are from heterogeneous studies, what processes may cause the less steep gradient, and how important the suggested differences in parameter values are for the predicted C accumulation.

4.1 HPM parameters for which estimates differ from their standard values

325 Three HPM parameters had estimates contrasting to their standard values:

1. There is a large posterior probability that c_2 is larger than the standard value of 0.3 m. c_2 is the anoxia scale length of decomposition and is assumed to represent limitation of anaerobic decomposition below the water table depth as consequences of the accumulation of decomposition end products and depletion of electron acceptors (Frolking et al., 2010). A larger value implies larger anaerobic decomposition rates at the same depth below the water table.

330 2. There is a large posterior probability that W_{opt} is larger than the standard value of 0.45 $\mathrm{L_{water}\,L_{pores}^{-1}}$. W_{opt} is the degree of saturation at which the decomposition rate is largest. Larger values mean that the largest decomposition rates are reached at larger degrees of saturation.

3. For some species, there is a large posterior probability that $k_{0,i}$ is smaller (*S. cuspidatum*) or larger (*S. russowii* and *S. rubellum*) than the standard value for the HPM microhabitat class we assigned them to. In addition, $k_{0,i}$ was not

335 consistent between HPMe-LE-peat and HPMe-LE-peat-l0 and also differed between models estimated when removing portions of the data during the cross-validation (supporting Fig. S12). $k_{0,i}$ defines how decomposition rates differ between *Sphagnum* species and is therefore an important control of C accumulation if there are vegetation changes.

Of these parameters, c_2, and $k_{0,i}$ are of particular relevance for C accumulation in the HPM, as indicated by previous sensitivity analyses (Quillet et al., 2013a, b). Explaining the discrepancies and finding ways to test them more accurately than

340 possible with available litterbag data should therefore improve our understanding of peat C accumulation.

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4.2 Estimated c_2 and W_{opt} suggest larger anaerobic decomposition rates relative to aerobic decomposition rates than the standard HPM

The discrepancies in c_2 and W_{opt} together imply smaller aerobic and larger anaerobic decomposition rates and therefore a less steep decrease of decomposition rates from oxic to anoxic conditions (Fig. 2). These relative rates are scaled by $k_{0,i}$ to

345 absolute decomposition rates. With $k_{0,i}$ estimated from litterbag experiments, the discrepancies in c_2 and W_{opt} also indicate larger anaerobic decomposition rates than assumed by the HPM for several species (Fig. 5). Therefore, the discrepancies to the HPM indicate a less steep decrease of decomposition rates from oxic to anoxic conditions and, at least for some species, larger absolute anaerobic decomposition rates.

To illustrate that the estimated c_2 and W_{opt} imply smaller aerobic and larger anaerobic decomposition rates, we simulated

350 decomposition of *S. fuscum* incubated at different depths in a peatland with water table depth of 40 cm below the surface, a porosity of 0.7 $L_{pores} L_{sample}^{-1}$, and a minimum water content at the surface of 0.05 $g_{water} g_{sample}^{-1}$. We predicted average k_0 of *S. fuscum* with HPMe-LE-peat-l0 ($k_{0,modified}$(HPMe-LE-peat-l0)) and with HPMe-LE-peat-l0 setting either c_1, W_{opt}, f_{min}, or c_2 to the standard value ($k_{0,standard}$(HPMe-LE-peat-l0)) and computed their differences. This gives the difference in decomposition rates of HPMe-LE-peat-l0 if we would set individual HPM parameters to their standard values. We plotted this difference versus

355 the depth of the water table below the litter (litter at the surface has a value of +40 cm, litter at the water table level of 0 cm, and litter below the water table level has negative values), as shown in Fig. 6.

With the standard W_{opt} value, HPMe-LE-peat-l0 predicts larger decomposition rates above and smaller decomposition rates below the water table than when using the parameter values estimated from litterbag data. Similarly, setting c_2 to its standard value also results in smaller decomposition rates below the water table level. The other parameters do not have a qualitative

360 influence (Fig. 6). Thus, the discrepancies in W_{opt} and c_2 are the main drivers of the less steep decrease of decomposition rates from oxic to anoxic conditions in HPMe-LE-peat-l0 compared to the standard HPM.
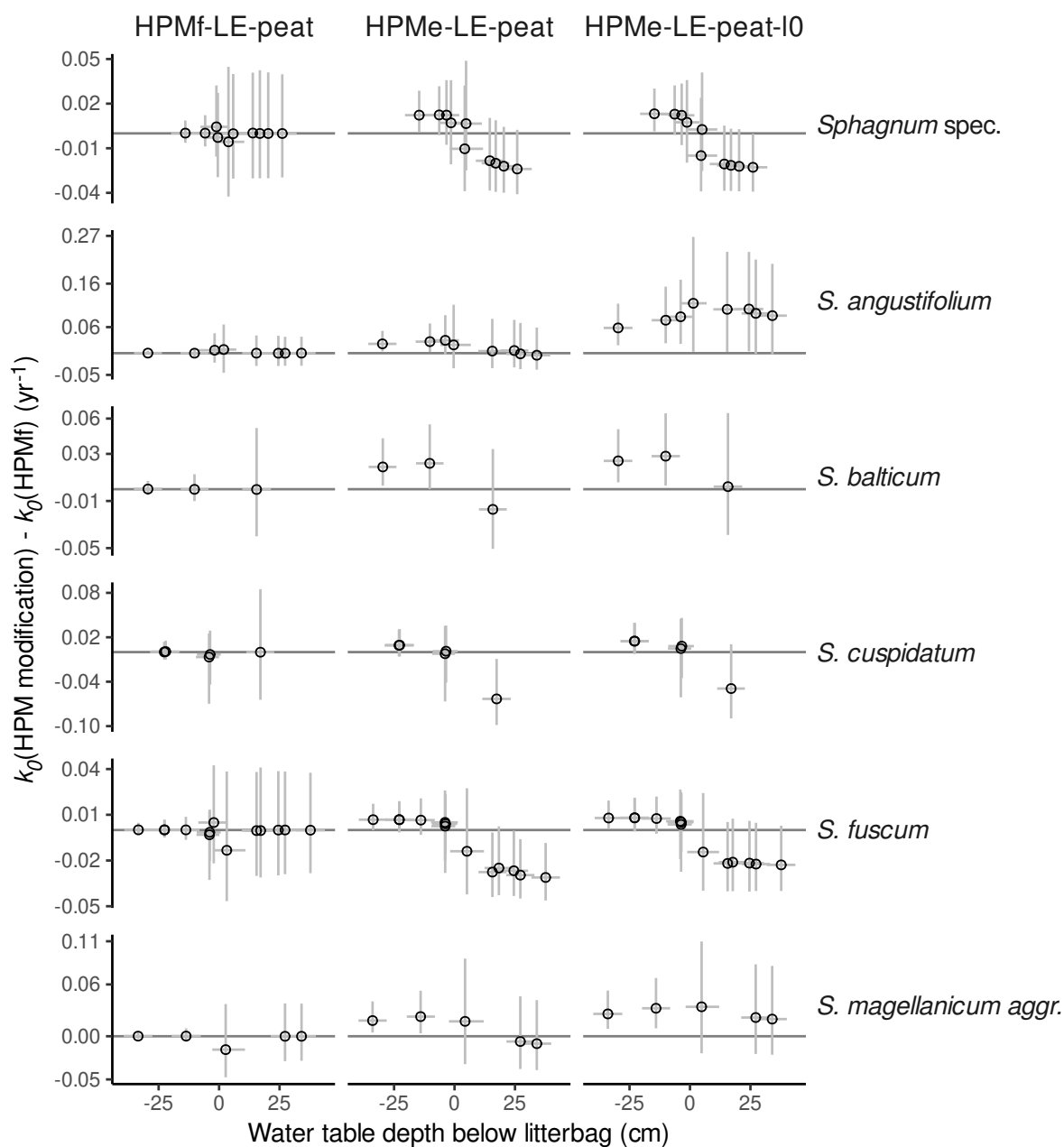
Figure 5. k_0 predicted by HPM modifications (either HPMf-LE-peat, HPMe-LE-peat, or HPMe-LE-peat-l0) minus k_0 predicted by the HPM with standard parameter values (HPMf) versus estimated average water table depths below the litterbags. Points represent average estimates and error bars 95% posterior intervals. *Sphagnum* spec. are samples which that been identified only to the genus level. Only data for species with at least three replicates are shown.
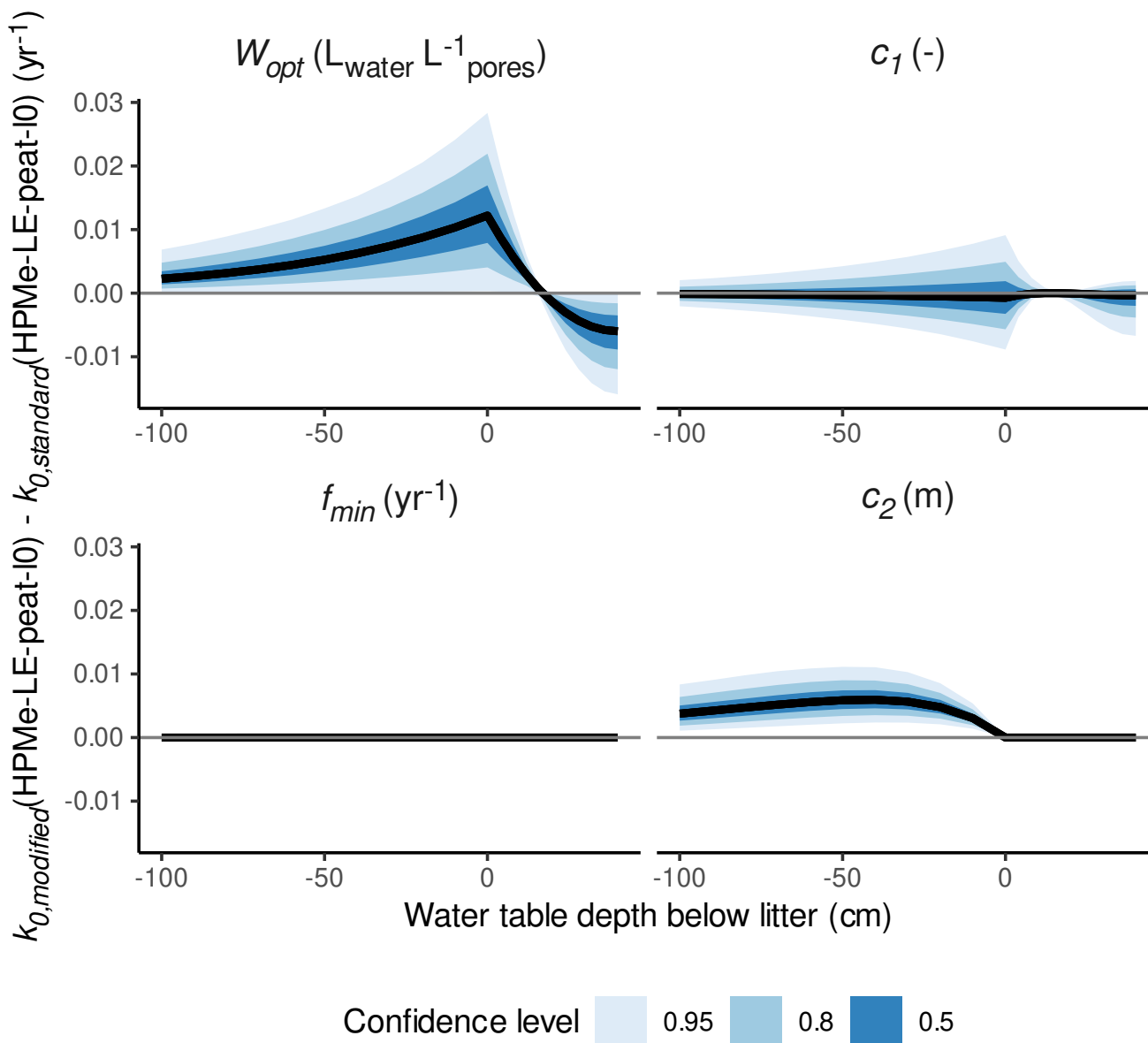
Figure 6. Difference between decomposition rates for *S. fuscum* predicted with parameter values estmated by HPMe-LE-peat-l0 ($k_{0,\mathrm{modified}}$(HPMe-LE-peat-l0)), and when setting the HPM parameter in the panel title to its standard value ($k_{0,\mathrm{standard}}$(HPMe-LE-peat-l0)). Panels show results when different parameters are set to their standard values. Positive $k_{0,\mathrm{modified}}$(HPMe-LE-peat-l0) $- k_{0,\mathrm{standard}}$(HPMe-LE-peat-l0) means that decomposition rates are larger when using the estimated parameter value compared to using the standard parameter value.

4.3 Reliability of the identified discrepancies

Before analyzing potential causes of the discrepancies found for c_2 and W_{opt} we first ask if combining different litterbag experiments is reliable evidence for the less steep gradient in decomposition rates from oxic to anoxic conditions.

365   If we take a look at the misfits of the standard HPM (HPMf) shown in Fig. 2, many, but not all underestimations of aerobic decomposition rates could have been caused by other factors: For example for *S. balticum* the difference may have been caused by differences in the two litterbag experiments from which we collected the data because the replicate with positive water table depth is from Straková et al. (2010), whereas the two others are from Mäkilä et al. (2018).

The less pronounced gradient in measured decomposition rates above the water table depth is, however, also visible for *S.*
370   *fuscum* replicates within the same study (Johnson and Damman, 1991; Golovatskaya and Nikonova, 2017; Mäkilä et al., 2018) and in addition similar across these (independent) studies (supporting information S8), indicating that this pattern cannot be explained in all cases by differences between studies. In addition, during the cross-validation, we removed data from individual studies from the model and the remaining subsets still resulted in similar estimates for c_2 and W_{opt} (supporting Fig. S12). Finally, numerous previous studies suggest that water table depth is an important control of decomposition rates (e.g., Blodau
375   et al. (2004)) and one may therefore expect that also between different studies decomposition rate differences should be controlled to a large degree by differences in water table depths. Thus, even with the heterogeneous litterbag data which is currently available, a less steep gradient of decomposition rates from oxic to anoxic conditions appears to be replicable between studies and species. Controlled litterbag experiments should test this.

The W_{opt} suggested by HPMe-LE-peat-l0 is also near the average optimum of heterotrophic respiration estimated across
380   a range of mineral soils (Moyano et al., 2013). The estimate is also in line with a study where the largest decomposition rates of the same litter type were observed at or just above the average water table level in hummocks (Belyea, 1996), and with maximum CO_2 production rates around 13 cm above the water table level in a mesocosm study (Blodau et al., 2004). According to the ModGberg model the degree of saturation at this depth is near the W_{opt} suggested by HPMe-LE-peat and HPMe-LE-peat-l0. For example, for our simulation analysis used to produce Fig. 6, the average W_{opt} estimated by model
385   HPMe-LE-peat-l0 (0.57 L_{water} L_{pores}^{-1}) is reached around 16 cm above the water table level, as shown in Fig. 7. At shallower depths, the degree of saturation decreases below W_{opt} which would decrease decomposition rates as observed in Belyea (1996). In contrast, according to the the ModGberg model, a degree of saturation corresponding to the standard W_{opt} value (0.45 L_{water} L_{pores}^{-1}) is reached at shallower depths and in the same simulation with this standard W_{opt} value, no pronounced sub-surface peak in decomposition rates is observed (supporting Fig. S16). In hollows, the optimum degree of saturation suggested by HPMe-
390   LE-peat-l0 is reached near the surface for either W_{opt} value (supporting Fig. S16). Thus, a larger W_{opt} would be compatible with results from several previous studies.

Larger and smaller c_2 than the standard value have been estimated for several permafrost peatland cores with a modified version of the HPM with monthly time step (Treat et al., 2021, 2022). Smaller values have been estimated for tropical peatlands (Kurnianto et al., 2015). To our knowledge, no litterbag experiment directly estimated c_2. A difficulty is that available litterbag

395   experiments cover only a comparatively small depth below the water table level (at most around 30 cm, Fig. 2) and therefore
gradients in anaerobic decomposition rates across larger depths below the water table currently cannot be estimated.
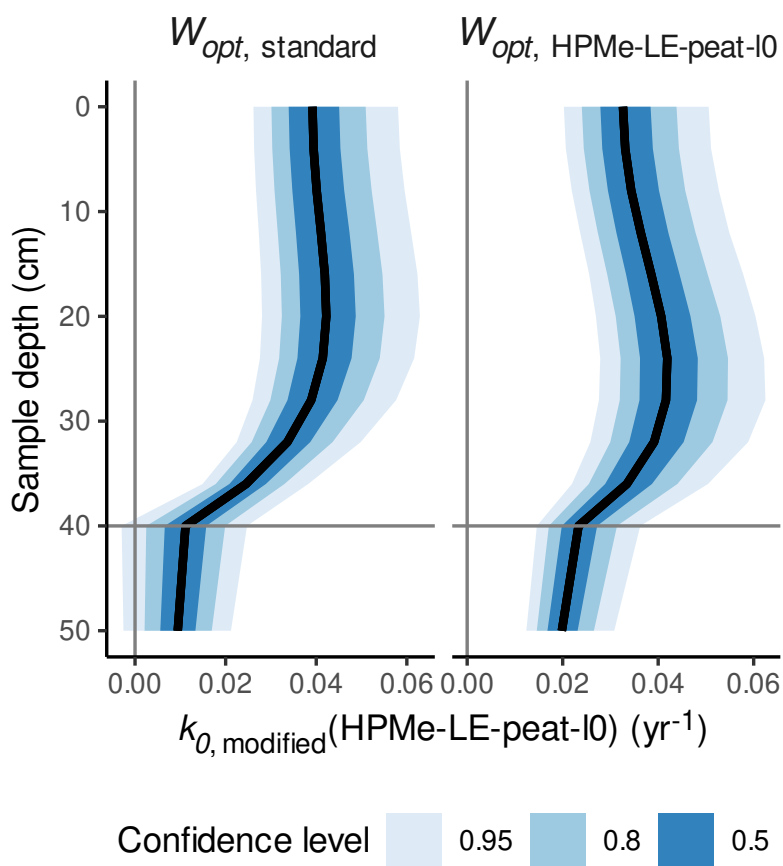

Figure 7. Decomposition rates predicted with HPMe-LE-peat-l0 ($k_{0,\text{modified}}$(HPMe-LE-peat-l0)) for *S. fuscum* (hummocks), using either the
standard value for W_{opt} or the W_{opt} value estimated by HPMe-LE-peat-l0 versus depth of the litter below the peat surface. The horizontal
line is the average water table depth.

4.4   Water table fluctuations may explain the discrepancies in c_2 and W_{opt} and larger anaerobic and smaller aerobic decomposition rates.

The HPM predicts decomposition rates based on average annual water table depths (Frolking et al., 2010). Our evaluation of
400   the HPM also assumed an average water table depth during the litterbag experiments and the HPM translated this into a clear
pronounced transition between anaerobic and aerobic decomposition rates (Fig. 2). In reality, water table depths fluctuate and
this causes transient and nonlinear changes in decomposition rates due to variations in the availability of oxygen and other
electron acceptors, flushing of end products of anaerobic decomposition, and possibly other factors (Siegel et al., 1995; Blodau

and Moore, 2003; Blodau et al., 2004; Beer and Blodau, 2007; Knorr and Blodau, 2009; Walpen et al., 2018; Campeau et al.,
405   2021; Kim et al., 2021; Treat et al., 2022; Obradović et al., 2023). A possible explanation why the gradient in decomposition
rate from oxic to anoxic decomposition is less steep, on average across litterbag experiments, than suggested by the standard
HPM could therefore be that an averaging effect of fluctuating water table levels on both aerobic and anaerobic decomposition
rates is neglected by the HPM.

An additional factor may be that litterbags are buried over a depth range, but we assumed a single fixed depth. If the buried
410   litterbags cover some depth range, this would spatially average decomposition rates, with similar effects as the temporal average
caused by water table fluctuations.

According to our results, c_2 would have to be re-interpreted as transition parameter that accounts both for limitation of
anaerobic decomposition under anoxic conditions and for the effects of periodically oxic conditions. Similarly, W_{opt} would
have to be re-interpreted as the optimum average degree of saturation for decomposition under water table level variations and
415   its value would be necessarily different from the optimum degree of saturation for depolymerization under static degree of
saturation.

Adjusting the HPM parameters as implied by our modified models may be an easy way to account for the effect of sub-
annual variation in water table levels on decomposition rates, if the discrepancies are caused by fluctuating water tables and if
the model is representative for different effects variations in water table level may have on decomposition rates (e.g. short-term
420   fluctuations compared to seasonal water table variations compared to prolonged droughts). What we have not considered due
to limited data is that c_2 can be expected to depend on long-term changes in groundwater flow (e.g., Siegel et al. (1995)) or
site-specific differences in hydrology and other factors (e.g., Treat et al. (2021), Treat et al. (2022)). Therefore, c_2 may differ
between litterbag studies and our data only indicate that c_2 is larger on average, whereas more research is necessary to estimate
and understand site-specific controls of c_2 and how a change in hydrology controls c_2. Similarly, W_{opt} may differ between
425   sites and over time. It would be interesting to know whether litterbag experiments can quantify these controls and whether c_2
estimated from litterbag experiments is generally larger in peatlands with larger water table fluctuations.

4.5   Implications of the discrepancies in W_{opt} and c_2 for long-term C accumulation

A larger c_2 implies larger anaerobic decomposition and may thus indicate that the HPM underestimates anaerobic decomposi-
tion rates. Previous sensitivity analyses identified c_2 as influential for C accumulation in the HPM (Quillet et al., 2013a, b).
430   If c_2 is varied within the range from the standard value (0.3 m) to the average posterior estimate from HPMe-LE-peat-l0
(0.64 m), this would cause differences in predicted C accumulation of a maximum of ca. 20% in the sensitivity experiment of
Quillet et al. (2013a) (depending on precipitation, Fig. 1 c in Quillet et al. (2013a)). If values are changed across the complete
posterior range compatible with litterbag data and if other HPM parameters would also be varied, the effect would be even
larger (Fig. 2 c in Quillet et al. (2013a)).

435   Due to parameter interactions and feedbacks, an increase in anaerobic decomposition rates can result in smaller or larger
C accumulation of the HPM, depending on environmental conditions (Quillet et al., 2013a). Small anaerobic decomposition
may cause too rapid C accumulation resulting in a low water table level, a thick aerobic zone, and thus smaller overall C

accumulation after a longer time. Larger anaerobic decomposition may result in higher water table levels and this can increase C accumulation in the long-term. Too large anaerobic decomposition decreases C accumulation (Quillet et al., 2013a).

440 A larger W_{opt} implies that the largest aerobic decomposition rates are reached under more saturated conditions. W_{opt} has not been identified as influential in a sensitivity analysis of the HPM (Quillet et al., 2013a), but as shown above, it contributes to the less steep decrease of decomposition rates from oxic to anoxic conditions. Importantly, since the HPM does not have a seasonally resolved water table depth, the two sensitivity analyses did not consider how seasonal variations of the water table depth may control long-term C accumulation, and consequently the re-interpreted W_{opt} may be more important to long-term

445 C accumulation than previously assumed. In addition, HPMe-LE-peat-l0 suggests an average W_{opt} value of 0.57 L_{water} $_{pores}^{-1}$, which is outside the range of values tested in Quillet et al. (2013a) (0.3 to 0.5 L_{water} $_{pores}^{-1}$). This implies that the sensitivity of long-term C accumulation to W_{opt} has been evaluated over a too small range.

A further aspect that needs to be considered is that HPMe-LE-peat and HPMe-LE-peat-l0 estimate parameter distributions based on available data, whereas existing studies defined fixed parameter values or ranges of parameter values based on expert

450 knowledge. Based on Quillet et al. (2013a), the uncertainties would cause non-negligible differences in predicted long-term C accumulation. For example, values within the uncertainty range of c_2 estimated by HPMe-LE-peat-l0 ((0.4, 0.97), 95% confidence interval), would imply differences up to 100 kg m^{-2} of accumulated C over 5000 years in some simulations (Fig. 1 (c) in Quillet et al. (2013a), with a maximum total accumulation of ca. 430 kg$_C$ m^{-2}). Simulations of remaining masses for different *Sphagnum* species under different conditions also indicate large uncertainties in predicted remaining masses

455 (supporting info S11). This implies that more work is required to estimate parameters accurately enough to detect even relative large differences among peatland models and between model predictions and peat cores.

Summarized, based on existing sensitivity analyses of the HPM the parameter discrepancies suggested by HPMe-LE-peat and HPMe-LE-peat-l0 can translate into non-negligible differences in long-term C accumulation rates. They also imply gaps in previous sensitivity analyses of the HPM, namely that W_{opt} has been analyzed over a too restricted value range and may

460 play a more important role if water table fluctuations are taken into account.

4.6 Large errors in $k_{0,i}$ estimates for individual species cause large errors in decomposition rates predicted by the HPM

We found some discrepancies between the maximum potential decomposition rates ($k_{0,i}$) HPMe-LE-peat-l0 estimated for some species and the standard HPM values after assigning species to the three HPM microhabitat PFT (hollow, lawn, hummock

465 *Sphagnum* mosses), however as noted above, these discrepancies were neither consistent between the two modifications of the HPM (HPMe-LE-peat and HPMe-LE-peat-l0) (supporting information S6), nor when HPMe-LE-peat-l0 was fitted to different subsets of the data during cross-validation (supporting Fig. S12).

Altogether, this indicates that the $k_{0,i}$ for many of the *Sphagnum* species are difficult to estimate from available litterbag data and more research should address this task. For example, HPMe-LE-peat-l0 could be extended, with suitable data, by

470 modelling how $k_{0,i}$ is controlled by factors such as temperature or within-species differences in litter chemistry.

We expect that better estimating $k_{0,i}$ is an important step to improve the predictive accuracy of the HPM because the cross-validation of HPMe-LE-peat-l0 indicated a larger RMSE$_{\text{test}}$ than RMSE$_{\text{train}}$, with only small variability in estimates of c_1, W_{opt}, f_{min}, and c_2, but much more variability in estimates of $k_{0,i}$. This indicates that a large part of the difference between RMSE$_{\text{test}}$ and RMSE$_{\text{train}}$ of HPMe-LE-peat-l0 may be explained by missing information about $k_{0,i}$.

475 Moreover, as noted above, $k_{0,i}$ scales the relative differences in anaerobic versus aerobic decomposition rates to absolute decomposition rates. For example, as shown in Fig. 5, HPMe-LE-peat-l0 indicates that the standard HPM underestimates aerobic and anaerobic decomposition rates for *S. angustifolium* and *S. magellanicum aggr.* litterbag data, whereas for *S. fuscum* only anaerobic decomposition rates are underestimated.

Values of $k_{0,i}$ can be estimated more accurately if decomposition rates in the litterbag experiments can be estimated more
480 accurately and there is again a direct link to initial leaching losses. Our analysis of differences in behavior of HPMf, HPMf-LE-peat, HPMe-LE-peat, and HPMe-LE-peat-l0 suggests that HPMf-LE-peat and HPMe-LE-peat produced smaller decomposition rate estimates and larger initial leaching loss estimates to make the litterbag data compatible with the (smaller predictions of the) HPM, whereas HPMe-LE-peat-l0 did not (Fig. 3) and consequently had larger estimates for $k_{0,i}$ than the other two models (Fig. 2). Thus, more accurate estimation of initial leaching losses — which vary a lot for the same species between different
485 studies (Teickner et al., 2024b) — should make decomposition rate estimates more accurate, and this should improve accuracy of $k_{0,i}$ in the HPM, according to our analyses.

5 Conclusions

Estimating HPM parameters from *Sphagnum* litterbag experiments suggests larger anaerobic decomposition rates and a less steep gradient of decomposition rates from oxic to anoxic conditions than implied by the HPM with standard parameter values.
490 With these modifications, the HPM fits available litterbag data within the range of uncertainties. However, due to large uncertainties in available litterbag data, particularly about how much of the mass is lost due to initial leaching and how much due to decomposition, the HPM with standard values can achieve comparable fits if mass loss in litterbag experiments is explained by larger initial leaching and slower subsequent decomposition. Therefore, stronger tests of the HPM require more accurate estimates for initial leaching losses and decomposition rates.

495 The larger anaerobic decomposition rates and less steep gradient of decomposition rates from oxic to anoxic conditions compared to the HPM with standard parameter values are a consequence of larger estimates for the anoxia scale length (c_2) and the optimium degree of saturation for decomposition (W_{opt}). This discrepancy may be caused by neglecting an increase of decomposition rates below the annual average water table depth due to water table fluctuations, differences in groundwater flow, or spatial averaging in litterbag experiments. Our estimates may be an easy way to account for such effects in the HPM if
500 effects of these fluctuations on decomposition rates can be averaged over time as implied by the suggested parameter estimates.

Less limitation of anaerobic decomposition rates than suggested by the HPM would imply differences in predicted C accumulation rates of up to 100 kg$_C$ m^{-2} over 5000 years (with a maximum total C accumulation of ca. 430 kg$_C$ m^{-2}), according to previous sensitivity analyses. Future litterbag experiments should improve the accuracy of initial leaching loss and decom-

position rate estimates and then test whether the identified parameter discrepancies are reproducible and whether they can be

505 described by known, but not yet fully quantified, controls of decomposition rates in dependency of water table fluctuations.

Code and data availability. Data and code to reproduce this manuscript are available from Teickner et al. (2024a). The data used in this study are derived from Teickner and Knorr (2024b). An R package to make predictions for litterbag experiments with model HPMe-LE-peat-l0 is available from Teickner and Knorr (2024a).

Competing interests. The authors declare no competing interests.

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