Modeling boreal forest's mineral soil and peat C dynamics with Yasso07 model coupled with Ricker moisture modifier

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Highlights

- The revision of functional water control in soil C and Earth systems models with large data across scales is needed to improve their spatial and temporal projections.
- Substituting the Yasso07 soil C model's original saturation type dependency of decomposition on precipitation with a one parameter hump-shaped Ricker moisture function improved modelled SOC stocks in a catena of mineral and organic/peat soils in boreal forest.
- The Ricker moisture function which was set to peak at rate 1 and calibrated against SOC and CO_2 data using Bayesian MCMC approach showed a maximum rate of decomposition in well-drained soils along the forest – mire soil moisture gradient.
- Using forest-mire SOC and CO_2 data together with the moisture data only from the topsoil humus layer in model optimization was crucial to accurately model the spatial SOC increase from mineral soil forests to peatlands.
- The functional dependencies based only on soil CO_2 emissions failed to estimate accurate SOC stocks (of forested peatlands) but showed good performance statistics for CO_2 estimates.

Abstract

As soil microbial respiration is the major component of land CO_2 emissions, differences in the functional dependence of respiration on soil moisture among the Earth system models (ESM) contributes significantly to the uncertainties in their projections.

Using soil organic C (SOC) stocks and CO_2 data from a boreal forest – mire ecotone in Finland and Bayesian data assimilation, we revised the original precipitation-based monotonic saturation dependencyenvironmental function of the Yasso07 soil carbon model by using non-monotonic Ricker function based on soil volumetric water content. We fit the revisedis functional dependency of moisture to the observed microbial respiration response to moisture and SOC stocks and compared its performance against the original Yasso07 model and the version used in the JSBACH land surface model with a reduction constant for decomposition rates in wetlands.

The Yasso07 soil C model coupled with the calibrated unimodal Ricker moisture function with an optimum in dry well-drained soils accurately reconstructed observed SOC stocks and soil CO_2 emissions and clearly outperformed previous model versions on paludified organo-mineral soils in forested peatlands and water-saturated organic soils in mires. The best estimate of the posterior moisture response of decomposition used both measurements of SOC stocks and CO_2 data from the full range of moisture conditions (from dry/xeric to wet/water-saturated soils). We observed unbiased residuals of SOC and CO_2 data modelled with the moisture optimum in well-drained soils, suggesting that this modified function accounts more precisely for the long-term SOC change dependency according to ecosystem properties as well as the contribution of short-term CO_2 responses including extreme events.

The optimum moisture for decomposition in boreal forests was found in ~~dry~~ well-drained soils instead of the mid-range between dry and water-saturated conditions as is commonly assumed among soil C and ESM models. Although the unimodal moisture modifier with an optimum in well-drained soils implicitly incorporates robust biogeochemical mechanisms of SOC accumulation and CO_2 emissions, it needs further evaluation with large scale data to determine if its use in land surface models will decrease the uncertainty of projections.

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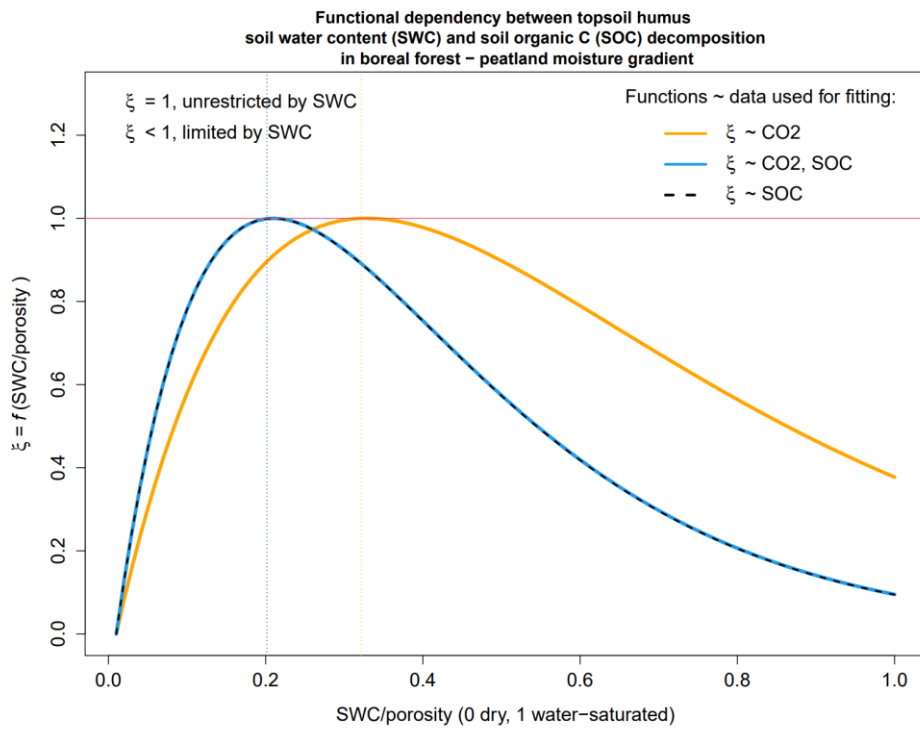
Graphical abstract

1   Introduction

Soil moisture and soil C stocks in boreal forests are higher in forested peatlands on frequently paludified organo-mineral soils and peatlands on water-saturated organic soils than in well-drained forests on mineral soils (Weishampel et al., 2009; Ťupek et al., 2008; Bhatti et al., 2006; Hartshorn et al., 2003). Almost a quarter of the total terrestrial C (440 Pg C) stored in boreal moist and dry soils has accumulated since the last glaciation (Scharlemann et al., 2014) and is expected to create large C losses under warming climates (Hararuk et al., 2015). Moist organic soils are crucial for modelling dynamics of the global C cycle as they store five times more carbon than dry mineral soils (Leifeld and Menichetti 2018; Turetsky et al., 2015; Scharlemann et al., 2014). However, soil organic carbon (SOC) stocks modelled by Earth System models (ESM) show large uncertainty due to structural model differences (Hashimoto et al., 2017; Hararuk et al., 2014, 2015; Todd-Brown et al., 2013), and differences in environmental drivers and their functional dependencies used by soil C models (Thum et al., 2020; Ťupek et al., 2019; Falloon et al., 2011).

Despite soil moisture being a dominant driver of variation in C dynamics (Humphrey et al., 2022), ESMs lack consensus on the response of decomposition to soil moisture and temperature (Yan et al., 2018; Sierra et al., 2015; Falloon et al., 2011). The functional forms of the temperature and moisture modifiers of default decomposition rates among models disagree in their representation of extreme cold/dry and hot/wet conditions (Sierra et al., 2015). For example, the moisture decomposition dependency in the Yasso07 soil C model (Tuomi et al., 2011, 2009) is based on annual precipitation, has a ~~functional~~ form ~~reaching~~ of monotonic saturation~~.,~~ and is uninformed about soil characteristics. By a monotonic saturation function, we mean a function which is entirely nondecreasing, initially increasing rapidly and later slowly approaching maximum. The use of the saturation function is limited to well drained soils as under wet or poorly drained forest soils such model results to underestimation of the C stocks (Dalsgaard et al., 2016, Ťupek et al., 2016). The soil module of the CENTURY model (Adair et al., 2008; Parton et al., 1996; Metherall et al., 1993) uses precipitation and basic soil data (bulk density, clay, and silt contents) to calculate soil moisture, which similarly to Yasso07 assumes saturation of decomposition rates. Other functional dependencies of moisture such as DAYCENT, Demeter, Standcarb, Candy, Gompertz, Mayers, Moyano, and Skopp assume ~~all kinds~~ various ~~of~~ functional forms~~.~~ E~~(~~e.g., non-monotonic Gaussian increase with optimum and reduction of decomposition (DAYCENT, Standcarb, Moyano), linear increase until optimum and linear reduction (Skoop), ~~continuous~~ monotonic linear and non-linear increase (Demeter and Myers, respectively) or ~~with~~ monotonic saturation functions (CENTURY, Candy))~~, linear increase until optimum and linear reduction)~~ (Kelly et al., 2000; Foley, 2011; Harmon and Domingo, 2001; Bauer et al., 2008; Janssens et al., 2003; Mayers et al., 1982; Moyano et al., 2013; and Skopp et al., 1990 as cited by Sierra et al., 2015). The wide variation in commonly used moisture functions may result from the variety of data from different soil types and climates used to constrain these moisture indices.

If environmental response functions were calibrated for mineral soils only, then these functions may not adequately represent responses in the moisture range characteristic of organic soils. For example, default response functions of soil C models cannot represent anoxic inhibition of decomposition rates in paludified peatland forest soils. However, the inhibition of decomposition

can be accounted for even in monotonic functions, e.g., by a reduction parameter such as "anerb" in CENTURY (Metherall et al., 1993). Due to variable water level and its determination of soil oxic/anoxic conditions and SOC accumulation in peatlands,

95 peat SOC stocks are typically modelled with models specifically developed for peatlands (Bona et al., 2020; Kleinen et al., 2012; St-Hilaire et al., 2010; Frolking et al., 2010, 2001; Clymo 1992). However, for global applications on peatlands, the general soil models in ESMs can be modified for peat soil by adjusting parameters such as the hydraulic conductivity, as seen in models like JULES (Chadburn et al., 2022) and ORCHIDEE (Qiu et al., 2018), or by reducing decomposition rates for wetlands as in LPJ (Wania et al., 2010) and JSBACH (Goll et al., 2015). The land surface model JSBACH coupled with the

100 Yasso soil C model adopts heuristic 65% reduction of decomposition for wetlands (Kleinen et al., 2021; Goll et al., 2015). Using CENTURY model at the site-level, Raich et al. (2000) opted for improvement in modelled SOC of wetlands by modifying the environmental function with the anoxic inhibition for sites with insufficient drainage. This approach improved CENTURY compared to default Yasso07 in poorly drained forested peatlands in Sweden, though the SOC stocks of both models were still underestimated (on average by 10 and 13 kg C m^{-2}, respectively) (Ťupek et al., 2016). Similar magnitude of

105 SOC underestimation of Yasso07 model with default dependency on precipitation was also observed for poorly drained forest soils (e.g., gleysols and organic soils) in Norway (Dalsgaard et al., 2016).

We hypothesised that the SOC stocks and CO_2 emissions of mineral and organic (peat) soils can be modelled accurately by revising the original precipitation-based environmental modifier of a parsimonious model like Yasso07 with a function accounting for the reduction of decomposition based on the long-term near surface moisture. Near surface moisture is strongly

110 correlated with the ground water level depth in peatlands (Dimitrov et al., 2022) and the moisture values between mineral soil forests and peatlands are comparable on the same scale, which makes soil volumetric water content (SWC) a suitable variable for representing landscape moisture variation. Boreal forest SWC can either be measured in-situ or derived in high resolution using hydrological models (e.g., Leppä et al., 2020; Launiainen et al., 2019) and at larger scale by remote sensing and machine learning (Han et al., 2023). We aimed to develop the original Yasso07 model with ~~global~~ parameters as in Tuomi et al. (2011)

115 by adding a revised unimodal moisture-based environmental function. We then optimized this function using Bayesian data assimilation of measurements from a boreal forest-mire hillslope catena of mineral, organo-mineral, and organic soils, and tested whether we could correctly reconstruct observed SOC stocks and CO_2 emissions.

2   Methods

2.1   Study sites

120 Nine forest/mire site types in this study were situated along the hillslope from Vatiharju esker to Lakkasuo mire in southern Finland (61° 47', 24° 19') (Fig. 1) and formed a forest-mire ecotone, a gradient in soil moisture and nutrient status, vegetation composition, biomass production, and SOC stocks (Dimitrov et al., 2014). The sites were situated along a 450 m transect on a 3.3 % slope facing NE with a relative relief of 15 meters. The site typology described below was based on the vegetation

composition reflecting site wetness, fertility, and location on the slope according to Finnish forest and mire classification
125 systems (Cajander 1949; Laine et al., 2004).

On the crest of the esker was a well-drained xeric Scots pine forest (CT – Calluna type) which changed down the slope to subxeric mixed Scots pine - Norway spruce forest (VT – Vitis-idaea type), and in mid-slope to mesic and herbrich Norway spruce dominated forest (MT – Myrtillus type, OMT - Oxalis-myrtillus type) together referred to as mineral soils upland forests. On the toe of the slope were forest-mire transitions on gleyic organo-mineral soils or mixed spruce pine birch forests
130 (OMT+ - Oxalis-myrtillus Paludified type, KgK – Myrtillus Spruce Forest Paludified type, and KR – Spruce Pine Swamp type). On the level were water-saturated sparsely forested mires on histosols (VSR1 and VSR2 - Tall Sedge Pine Fen types).

The understory or forest floor vegetation along the ecotone changed from being dominated by *Calluna* and *Vaccinium Vitis-idaea* dwarf-shrubs and typical forest mosses on the uppermost sites (CT, VT), to *Vaccinium myrtillus* dwarf-shrubs with herbs in the mid-slope (MT, OMT), *Vaccinium myrtillus* dwarf-shrubs with herbs and *Sphagnum* in the transitions (OMT+, KgK,
135 KR), and *Vaccinium oxycocus* and *Betula nana* dwarf-shrubs with *Menyanthes triofoliata, Carex* and *Sphagnum* species on the level (VSR1, VSR2) (Fig. 1). More detailed tree stand, soil and climate characteristics for these sites were reported by Ťupek et al. (2008, 2015).

2.2 Auxiliary measurements

Soil temperature, water content, and CO_2 emissions (gCO_2 m^{-2} h^{-1}) were measured simultaneously during years 2004, 2005,
140 and 2006. The measurement campaigns were conducted weekly, and we measured each plot once and all plots in one or two days between 7 am and 6 pm weekly during the vegetative season of 2004 (July-November), 2005 (May-November), 2006 (May-September), and monthly during the non-vegetative season (December-April). The summer seasons of the years 2004, 2005, and 2006 showed exceptionally different monthly weather patterns. Data from Finnish meteorological station, located 3 km north-east from the ecotone in Juupajoki, showed that the summer season in 2004 was rainy and colder in comparison to
145 long-term typically mild weather, in 2005 weather was typical, and in summer 2006 the weather was sunny and warm. The exceptional drought in 2006 caused by the lack of rain and increased temperatures in June and later July – early August (Gao et al., 2017) caused visible drying of the moss layer along all the sites of the ecotone. The 2006 summer drought ended with showers in mid-August and with more frequent rain in autumn the soil moisture recovered to a normal level.

2.2.1 Soil temperature and moisture conditions

150 The soil temperature was measured at depths of 5 cm (T_5, °C) with a portable thermometer, and the soil volumetric water content at depth of 10 cm (SWC_{10}, %, m^3 m^{-3}) in all sites with a portable ThetaProbe (Delta-T Devices Ltd) calibrated for each site type. The SWC calibration accounted for the bulk density/porosity of forest type specific soils (Ťupek et al., 2008, 2015). Because the forest-mire variation of soil organic layer bulk density was relatively small 0.34+/-0.07 g cm^{-3} (porosity 74+/-5%) (Ťupek et al., 2015) the values SWC of top 10 cm were in the same order of magnitude between the forest/mire site types.
155 For missing field campaigns during months with the snow cover (Nov 2004, Feb – Apr 2005, Dec 2005 – Apr 2006) we

interpolated the measured monthly mean T_5 and SWC_{10} time series with a spline function. The SWC_{10} values among the forest and mire site types ranged between 0 and 1 (or 0 and 100 %) (Figure Fig. 3), whereas in comparison to water level depth the values range from 8 cm in tall-sedge mire to 881 cm in pine forest on the top of the esker (Tupek et al. 2008).

2.2.2 Soil CO$_2$ emissions

160 Measurements of forest soil heterotrophic respiration (R_h, gCO_2 m^{-2} h^{-1}, positive sign) were taken using opaque cylindrical chambers (30 cm diameter, 21.2 L) placed on metallic collars (30 cm in diameter) which were installed permanently into 30 cm soil depth. The collars locations (3 for each site type, 12 for mineral soil forests, 9 for transitions, and 6 for mires, together 27) were selected to represent the spatial variation of each site type and the spatial variation along the forest-mire ecotone (e.g., dominant forest floor vegetation, microtopography, soil drainage, and nutrient status).

165 The aboveground forest floor vegetation inside each collar was clipped at the time of collars installation and any plant regrowth of e.g., mosses was clipped approximately half an hour before the flux measurements. At the time of the collar installation the roots of the understory vegetation and trees were cut with a saw along the collars' perimeter. The metallic collars installed to 30 cm soil depth prevented the regrowth of the roots. Due to the vast majority of tree and understory roots in boreal forest occurring in the humus layer, the 30 cm depth was considered sufficient to cut the roots thus remove the signal of the root 170 autotrophic respiration from the net CO_2 emissions. In transitions and mires the depth of peat could be more than 30 cm (in range from 0.15 m in OMT+ to 1.2 m in VSR2 (Ťupek et al., 2008)) but the prevailing high ground water levels (in range from 33 cm in OMT+ to 7 cm in VSR1 (Ťupek et al., 2008)) limit the root growth into the upper/sub-surface layer.

The soil CO_2 emissions were measured every 4.8 s during 80 s intervals with a portable infrared CO_2 analyser (EGM4, SRC-1 PP systems Inc.). We calculated CO_2 flux rates from the development of CO_2 concentration over time inside the chamber.

2.2.3 Soil organic carbon stocks

175 The soil data from the 2006 sampling up to 30 cm depth (Ťupek et al., 2015) were combined with additional soil sampling cores of up to 100 cm depth in October 2015 (3 per site) (Fig. S1). The bulk density, C and N concentrations for new samples were determined as in Ťupek et al. (2015).

The SOC content (g cm^{-3}) of separate soil layers were interpolated for the whole profile with the fitted spline functions and 180 summed up for each depth and each forest/mire site (Fig. S1). The SOC content was similar in the upper-most humus layers of all forest/mire types (below 0.3 g cm^{-3} in a layer 0-10 cm), but in the sub-surface level (10-30 cm) clearly doubled from uplands to transitions and mires (from below 0.2 to above 0.4 g cm^{-3}) (Fig. S1). In the soil layers below 30 cm the SOC content showed differences in degrees of magnitude (around 0, 0.01, and 0.1 g cm^{-3} for forests, transitions, and mires, respectively) (Fig. S1). The SOC stock (kg C m^{-2}) was a result of SOC content multiplied by a bulk density.

185

2.2.4 Biomass of tree stand and understory vegetation

Breast height diameter and height of all Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and Silver birch (*Betula pendula*) trees on each forest site type were measured in 2006. The biomass components for each species (leaves, branches, stems, coarse-roots) were estimated with biomass conversion functions (Repola et al., 2008, 2009) and fine-roots with functions by Lehtonen et al. (2015). Forest floor plants from three 0.07 m^2 sample plots located nearby soil respiration measuring collars were harvested for each forest/mire site type in June-July 2004 (Ťupek et al., 2008). Plants were separated to herbs, mosses, and shrubs, dried and weighed for each category and each sample plot. The stand density and the tree biomass increased from xeric (CT) and mesic upland forest sites (VT and MT) towards the herb-rich forest site (OMT) and transitions (OMT+, KgK, and KR), and decreased to very sparse canopy in peatlands/mires (VSR sites) (Fig. 1b). The understory aboveground biomass correlated negatively with the density of the canopy cover thus positively with the light intercepted onto the forest floor (Ťupek et al., 2008).

2.3 Data analysis

2.3.1 Yasso07 SOC and CO_2 modelling

Equilibrium SOC stocks of up to 1 m depth, SOC changes and soil CO_2 emissions (Rh) for the forest/mire types were modelled using the Yasso07 soil carbon model (Tuomi et al., 2009, 2011) with specific litter input and weather data in accordance with the method of Finnish greenhouse gas inventory (Statistics Finland, 2023). The ‑temperature and precipitation data for the weather input was from the nearest Finnish meteorological institute (FMI) weather station located 3 km away from our study sites. We first ran the Yasso07 model using the original formulation of the environmental function with precipitation and air temperature data, and then we ran the Yasso07 model fitted with the environmental modifier function based on SWC_{10} and T_5 of the forest/mire site types using the Bayesian data assimilation technique.

2.3.1.1 Yasso07 soil C model

The Yasso07 is a semi-empirical process-based soil carbon model where soil C is divided based on the organic matter solubility into five pools (C_A, C_W, C_E, C_N, and C_H) from which three are fast (acid- (A), water- (W), and ethanol- (E) soluble), one is slow (non-soluble (N)) and one is almost stable (humus (H)) (Tuomi et al., 2011). The rates of C decomposition in each pool and C transfers between the pools are affected by climate. The model can be expressed mathematically as a set of differential equations where decomposition of the entire structural matrix of C pools C_A…C_H defined by default mass flow parameters $\alpha_{A,W}$…α_H and decomposition coefficients k_A…k_H (A_{YS}) is scaled by the time step dependent scalar of the environmental rate modifier $\xi(t)$ Eq. (1).

$$\frac{dc(t)}{dt} = \begin{pmatrix} i_A \\ i_W \\ i_E \\ i_N \\ i_H \end{pmatrix}(t) + \xi(t) \begin{pmatrix} -k_A & \alpha_{A,W}k_W & \alpha_{A,E}k_E & \alpha_{A,N}k_N & 0 \\ \alpha_{W,A}k_A & -k_W & \alpha_{W,E}k_E & \alpha_{W,N}k_N & 0 \\ \alpha_{E,A}k_A & \alpha_{E,W}k_W & -k_E & \alpha_{E,N}k_N & 0 \\ \alpha_{N,A}k_A & \alpha_{N,W}k_W & \alpha_{N,E}k_E & -k_N & 0 \\ \alpha_H k_A & \alpha_H k_W & \alpha_H k_E & \alpha_H k_N & -k_H \end{pmatrix} \begin{pmatrix} c_A \\ c_W \\ c_E \\ c_N \\ c_H \end{pmatrix}(t) \qquad (1)$$

215 Where t is time, i defines a vector of initial carbon pools i_A… i_H, and subscripts in α indicate mass transfer pools (e.g., $α_{A,W}$ defines mass transfer from pool W to pool A). The total soil respiration or CO_2 efflux (Rh) is a product of a column vector by a row vector C(t), where the elements of the column vector are the fractions that were not transferred among the pools (Sierra et al. 2012).

The model was originally calibrated for running on annual time steps (Tuomi et al., 2009), but it can run on monthly steps with
220 monthly decomposition rates (1/12 of annual k_A…k_H), and monthly litter and climate data (Ťupek et al., 2019). Then $ξ(t_m)$ is defined by a combined function of monthly air temperature (T_m) and 1/12 of annual precipitation (P_a/12) (Eq. (2)).

$$ξ_T(t_m) = e^{(β_1 T_m + β_2 T_m^2)} \left(1 - e^{γ \frac{P_a}{12}}\right)$$ (2)

Where $β_1$, $β_2$, and γ are parameters of the environmental function and t_m is the monthly time step. To test our hypothesis of running the model for a catena of soils with gradually increasing moisture content (from xeric to mesic, paludified, and
225 saturated), we re-defined the $ξ(t_m)$ function for the use with soil temperature based on a Q_{10} exponential function to T_5 (used by Davidson et al. (2012) as an alternative to Arrhenius kinetics), and moisture data using adjusted hump shaped Ricker function (Bolker, 2008) for response to SWC_{10} which limits decomposition rate outside the optimum soil water content ($ξ_{AR}$, Eq. (3)).

$$ξ_{AR}(t_m) = Q_{10}^{\left(\frac{T_5-10}{10}\right)} aSWC_{10} e^{(-ae^{-1}SWC_{10})}$$ (3)

230 Where the Q_{10} parameter represents the increase of the temperature function over 10 °C difference in T_5, and the *a* controls both ascending and descending slopes of the moisture function when the peak is set to 1. In the Ricker function with a and b parameters and an independent variable vector x (axe^{-bx}), the height of the peak can be inferred as $(a/b)e^{-1}$, and the x value of the peaks location as 1/b (Bolker, 2008). Thus, in our formulation by setting the peak in the Ricker function to 1 we could substitute b parameter by ae^{-1} and the SWC_{10} optimum (the SWC_{10} when decomposition is at optimum) was inferred as $1/ae^{-1}$.

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The Yasso07 model versions in this study run accordingly:

1. the Yasso07.$ξ_{TW}$ version is the Yasso07 coupled with original $ξ_T$ (Eq. (2)) and with the original global parameter set (Tuomi et al., 2011) but with two k-rates parameter sets, (i) the original k_A…k_H rates for application on mineral soils applied for mineral and organo-mineral soil forests (CT, VT, MT, OMT, OMT+, KgK, KR) and (ii) with an inhibitor
240   reducing k-rates by 35% ($0.65k_A$…$0.65k_H$) for application on wetlands (Goll et al., 2015, Kleinen et al., 2021) applied for mire sites (VSR1 and VSR2);
2. the Yasso07.$ξ_W$ wetland version is the same as the Yasso07.$ξ_{TW}$ but with a fine-tuned k-rates inhibitor to fit the SOC of mire sites (VSR1 and VSR2);

3. the Yasso07.ξ_{AR} version for soil moisture gradient from mineral to peat soils (e.g., as in boreal forest - mire ecotone) is the Yasso07 model coupled with ξ_{AR} (Eq. (3)) with the original global parameter set of the structural matrix and optimized parameters of ξ_{AR}.

The initial equilibrium SOC stock (C_o) for each forest/mire type for the pre-trenching period was simulated analytically (Xia et al., 2012) (Eq. (4)).

$$C_o = -\xi A_{YS}^{-1}\bar{u} \tag{4}$$

Where ξ is the environmental modifier, A_{YS} is a structural matrix formulation of Yasso07 model's differential equations, and $\bar{u}$ is the litter input (mean annual litter of foliage, branches, stem, stump, roots, and understory).

The Yasso07 model source code, used here, was built in R software (R Core Team 2023) on the platform of the SoilR package (Sierra et al., 2012) according to the mathematical description and parameters of Tuomi et al. (2011). The model outputs are monthly SOC stocks and soil CO_2 emissions. The model was run with data inputs of above- and below-ground litterfall (accounting for its chemical composition) and climate data (described in more detail below). Monthly model outputs of heterotrophic soil respiration were compared to mean monthly Rh measurements.

2.3.1.2   Climate and litter C input data for Yasso07 model

The Yasso07.ξ_{TW} was run with monthly air temperature and precipitation from the nearby Juupajoki weather station of the Finnish meteorological institute. The Yasso07.ξ_D was run using site type specific continuous monthly T_5 and SWC_{10} time series.

The litter C input of the forest/mire types (Fig. S2 and Fig. S3) used by Yasso07 was estimated as in Lehtonen et al. (2016) based on turnover rates of tree stand biomass components (including fine- and coarse-roots, stump, branches, and foliage) and understory vegetation. The litter C input was separated into Yasso07 A, W, E, N pools according to the component and species (or species groups) specific A, W, E, N ratios taken from the literature (Berg et al., 1991a, 1991b, 1993; Gholz et al., 2000; Trofymow et al., 1998; Vávřová et al., 2009; Straková et al., 2010) (Table S2). The annual litter was distributed to monthly resolution by accounting for seasonal trends of foliage, fine-roots, and understory (Ťupek et al., 2019; Zhiyanski 2014) or evenly. The litter input before trenching was assumed to represent the long-term average of the equilibrium state forest (Fig. S2a, Fig. S3). During trenching the severed fine- and coarse-roots made up the major component of the total litter (Fig. S2b) and resulted in a clear peak in the monthly litterfall time series (Fig. S3). After trenching the monthly litter levels decreased as the sum of components excluded the roots (Fig. S2c, Fig. S3).

2.3.1.3   Bayesian SOC and CO_2 data assimilation

The Bayesian MCMC data assimilation has proven useful in improving soil organic carbon estimates (e.g., Xu et al., 2006; Hararuk et al., 2014). The Bayesian posterior uncertainty provides updated information on parameter values based on pre-existing information on the parameters and the data through the likelihood function (Speich et al., 2021). The d, Q_{10}, and

275 SWC_{opt} parameters of the ξ_D (Eq. (4)) coupled with Yasso07 model were optimized on the level of the forest-mire ecotone using Bayesian data assimilation technique (Luo et al., 2011; Hartig et al., 2012; Speich et al., 2021) with observed SOC stocks and monthly Rh data of forest/mire types with prior information on best parameter values obtained from a purely empirical NLS model (Table 1) and the defined parameter range in Table S1. During the optimization, the Yasso07.ξ_D model was first run only with observed SOC stocks and second with both SOC stocks and Rh data combined obtaining a probability distribution

280 of model parameters of ξ_D (the posterior uncertainty p(θ|y) conditional on the observations (y) and prior knowledge on the parameter values p(θ)). The sum of the probability density for the target parameter set (θ) between the model predictions and observations was maximized for the best agreement using the likelihood defined by a modified Laplace probability density function p(y|θ) (the probability of observing the data y with the model parameters set θ) where we allowed the width of the distribution to be affected by the observed SOC and Rh values (Eq. (5)).

285 $$p(y \mid \theta) = \prod_{j=1}^{2} \prod_{i=1}^{N_j} \frac{1}{2(a_j + b_j x_{j,i})} \; e^{\frac{-\left|(x_{j,i} - \mu_{j,i})\right|}{a_j + b_j x_{j,i}}} \tag{5}$$

where $\mu_{j,i}$ is the observed j^{th} variable (e.g., SOC, CO_2, or SOC and CO_2) of ith observations, x_i is the modelled prediction, N is the total number of observations, and a, b are parameters affecting the width of the distribution. In the combined SOC and CO_2 likelihood, the likelihood function p(y | θ) was then the multiplication of the distributions of SOC and CO_2 at all observation times. We evaluated the variation in the estimated parameters by separating data for fitting the models and testing with 9-fold

290 cross validation technique.

The model parameters of ξ_{AR} and p(y|θ) were sampled from an assumed uniform distribution within their prior ranges (Table S1). Posterior probability distributions of parameters (Table 2) were derived by using the differential evolution (DEzs) Markov Chain Monte Carlo (MCMC) sampler ~~(ter Braak and Vrugt, 2008) with~~ used by the runMCMC function from the BayesianTools package in R (Hartig et al., 2012) and by computing three chains in parallel. The convergence of MCMC runs

295 was evaluated using Gelman–Rubin multivariate potential scale reduction factor (psrf) (Brooks and Gelman, 1998). The MCMC simulation was considered converged if psrf was below 1.03 for all parameters (1.01, 1.01 and 1.016 for p(θ|SOC)–, p(θ| CO_2) and p(θ|SOC–CO_2), respectively). Trace plots of MCMC runs for target parameters showed effective sampling and unimodal parameter density with clearly defined peaks. The differences in parameter uncertainties (difference between 97.5% and 2.5% quantiles of the 95% confidence interval) were not significant (p = 0.99) when evaluated with a Welch Two Sample

300 t-test between two posterior distributions p(θ|SOC), and p(θ|SOC–CO_2) (Table 1).

2.3.1.4   Performance evaluation of Yasso07.ξ_{TW} and Yasso07.ξ_{AR}

The performance of Yasso07 model versions (i) Yasso07.ξ_{TW} and (ii) Yasso07.ξ_{AR} with ξ_{AR} parameter set θ from two posterior distributions, p(θ|SOC) , p(θ| CO_2) and p(θ|SOC–CO_2), was evaluated with the modelled SOC and CO_2 outputs against the observed data in the forest mire-ecotone with the coefficient of determination (R^2), the mean absolute error (MAE), mean bias

305 error (MBE), the root-mean-square error (RMSE), the Akaike information criterion (AIC) for considering the number of model

parameters in the error calculation as in Abramoff et al. (2022), and the fitted linear trends of normalized SOC and CO_2 model residuals with observations against T_5 and SWC_{10} data.

3   RESULTS

3.1   Distributions of SOC stocks and Rh in relation to SWC

310   The SOC stock measurements (to a depth of 1 m) in forest-mire ecotone were distributed in range between 20 in well-drained soils of upland forests and 125 kg C m^{-2} in poorly drained soils in peatlands/mires (Fig. 2). The SOC stock values strongly correlated with the long-term moisture levels. The median Rh values ranged between 0.4 and 0.6 gCO_2 m^{-2} h^{-1} for upland forests, 0.4 and 0.5 gCO_2 m^{-2} h^{-1} for forest-mire transitions, and 0.3 and 0.4 gCO_2 m^{-2} h^{-1} for mires (Fig. 2). The forest/mire site type differences in median Rh values expressed per m^2 were small and poorly correlated with the mean soil moisture levels.

3.2   Distribution of Rh in climate space of soil T and SWC

315   The site-specific time series of hourly R_h measured in the forest/mire ecotone during years 2004, 2005, and 2006 followed a typical seasonal pattern of temperature and was distributed in range between 0.08 and 1.6 gCO_2 m^{-2} h^{-1} depending on the corresponding soil temperature and moisture conditions (Fig. 3). The Rh values were generally larger during wet years than during a typical year, and lowest during dry years (Fig. 3).

320   The T_5 and SWC_{10} values showed a typical seasonal variation (in range between around 0 and 20°C, driest in summer and wettest in late autumn/spring) (Fig. 2b and 3c). The T_5 showed similar magnitude among the forest/mire sites, whereas the SWC_{10} increased from driest (upland forest) to intermediate (forest-mire transition), and from upland to lowland for the wettest (mire) sites located on the slope (Fig. 3). The volumetric SWC_{10} (%) were comparable in the same order of magnitude between the forest/mire site types because the forest-mire variation of the soil organic layer bulk density was relatively small 0.34+/-
325   0.07 g cm^{-3} (porosity 74+/-5%). The forest-mire ecotone soil moisture at 10 cm depth ranged from 5% to 91%. The minimum, maximum and mean SWC at 10 cm depth between forests, transitions, and mires clearly differed showing the gradient of increasing moisture from forests to mires (Fig. 2a, Fig. 3). Due to highly variable weather (wet, typical, and dry year) all ecosystems experienced periods of extremely low and high SWC_{10} values. The SWC_{10} of upland forest ranged between 5 and 25%, between 17 and 70% in transitions and mires between 49 and 91% (Fig. 3). The variation of soil temperature at 5 cm
330   depth along the ecotone was similar among the forest/mire types and ranged between -3 and 22 °C (Fig. 3). The R_h values during dry 2006 year were in comparison to previous years clearly reduced mostly in upland forest and forest-mire transitions (Fig. 3). The spatial soil moisture gradient of forest/mire types was not clearly reflected in distribution of Rh values when expressed in gCO_2 m^{-2} h^{-1} (Fig. 2) (unless expressed as a C fraction of SOC). The short-term SWC variation impacted the typical seasonal levels of Rh values mainly during the extreme events (rainy summer period in wet years, or drought summer
335   period in dry years) (Fig. 3).

3.3 ξ_{AR} optimized with Yasso07.ξ_{AR}

The optimization of ξ_{AR} (Eq. (3)) coupled with Yasso07 showed that in the catena of mineral and organic soils of the boreal forest-mire the optimum moisture content for decomposition and CO_2 emissions was in well drained mineral soil forests (SWC_{opt} medians between 14 and 27%, Table 1, Fig. 4). The MCMC fit with CO_2 data produced larger SWC_{opt} and larger tail in the Ricker function (compared to SOC or $SOCCO_2$ fit). The decomposition rate outside the moisture optimum reduced decomposition similarly for the two data sources (SOC and SOC–CO_2) used for calibration. However, the temperature and moisture functions were different when only CO_2 was used for calibration.

The two SOC and $SOCCO_2$ based Q_{10} functions showed a similar increase with T_s until 10 °C (Fig. 4a). The combined non-linear temperature and moisture response in whole climate data range showed larger nonlinear the variation of the change in ξ for mineral soil forests than forest mire transitions and peatlands (Fig. 5). The ξ_{AR} in the Fig. 5 panels a and b for SOC and $SOCCO_2$ based ξ_{AR} are similar showing that both SOC and $SOCCO_2$ parameterization is almost the same whereas the ξ_{AR} in the Fig.5c ξ_{AR} is different. ~~Similar patterns were observed for ξ_{AR} in the climate space of T_s and SWC_{10} (Fig. 5a and b).~~ The ~~stronger~~ CO2 based temperature sensitivity of ~~$\xi_{AR, p (\theta | CO2)}$~~ with median $\xi_{AR}Q_{10}$ ~~Q_{10}~~ value 4.5 resulted in a more pronounced increase in decomposition rates especially in climate space with high water saturation (Fig. 4 and Fig. 5c). The SOC and SOC–CO_2 based $\xi_{AR}Q_{10}$ values for the forest – mire ecotone (medians 2.3 or 2.5, Table 1) were lower.

3.4   Performance of Yasso07.ξ_{TW}, Yasso07.ξ_W and Yasso07.ξ_{AR}

The model performance evaluation showed that the soil water and temperature modifier ξ_{AR} coupled with Yasso07 model (Yasso07.ξ_{AR}) outperformed the original Yasso07 environmental function even after 65 % reduction of decomposition rates for wetlands was applied (Yasso07.ξ_{TW}) (Table 2, Fig. 5). Although, the Yasso07.ξ_{TW} model version accurately predicted SOC stocks of mineral soil forests (CT…OMT), it heavily underestimated the SOC stocks of organo-mineral forested peatlands and mires (OMT+…VSR2), thus it showed the most biased model performance metrics (highest RMSE, MBE, MAE, AIC and lowest R^2_{adj}) among the model versions compared (Table 2). Reduction of decomposition rates of 65% for mires in Yasso07.ξ_{TW} was not sufficient to simulate their SOC stocks as simulated SOC of mires were only about 10 % of measured values (Figs 5a, 5b, and 5c). The SOC simulations for VSR mires with Yasso07.ξ_W would have required as much as a 96% reduction of the decomposition rates. The optimized Yasso07.ξ_{AR} model version accurately simulated SOC stocks throughout the forest – mire ecotone.

The version Yasso07.$\xi_{AR, p (\theta | SOC)}$ outperformed Yasso07.$\xi_{AR, p (\theta | SOC-CO2)}$ when evaluated against SOC data and both models were similar when evaluated against CO_2 data (Table 3, Fig. 5). The Yasso07.$\xi_{AR, p (\theta | CO2)}$ outperformed the functions based on SOC or $SOCCO_2$ against measured CO_2 data but failed when evaluated against measured SOCs. The Ricker function improved the representation of decomposition for drier soils and the representation of optimal SWC for decomposition.

The SWC optimum was derived from the fitted ascending slope parameter and its values were between 14 and 27 % (depending on the data used for fitting; 14% for SOC and CO_2 and 27% for CO_2). The MCMC fit with CO2 data produced larger SWCopt

and larger tail in the Ricker function (compared to SOC or SOC-CO_2 fit). However, the CO_2 only fit also underestimated SOC stocks of forested peatlands (Fig. 5a). The normalized SOC residuals of the two Yasso07.ξ_{AR} models based on SOC or SOC and CO_2 did not show any large T_5 or SWC_{10} trends (Figs 5a, 5b, and 5c). Although, measured Rh fluxes during the cold season may be slightly overestimated.

The soil CO_2 emissions simulated with the original Yasso07.ξ_{TW} agreed unexpectedly well with observed Rh values (Table 2, Figs. 6d, 6e and 6f) outperforming the Yasso07.$\xi_{AR, p(\theta \mid SOC)}$ version (Table 2, Fig 6e). On the other hand, the Rh simulated with Yasso07.$\xi_{AR, p(\theta \mid SOC)}$ performed similarly as Yasso07.ξ_{TW} in terms of RMSE (same RMSE 0.16 g CO_2 m^{-2} hour^{-1} for both models). The performance statistics for Yasso07.ξ_{AR} based on SOC and SOCCO$_2$ were better compared with Yasso07.ξ_{TW} for SOC and about the same for Rh (Table 2). The performance statistics for Yasso07.ξ_{AR} based on CO_2 were best among the models for CO_2 but fail in similar fashion for SOCs as Yasso07.$\xi_{TW.}$ The normalized modelled residuals showed that both Yasso07 model versions (Yasso07.ξ_{TW} and Yasso07.$\xi_{AR, p(\theta \mid SOC)}$) showed small Rh biases in extreme, very cold and in very warm temperatures (Fig. 6e). The normalized CO_2 residuals of the Yasso07.$\xi_{AR, p(\theta \mid CO2)}$ showed no bias among the functions (0 MBE, Table 2). The normalized CO_2 residuals evaluated against with SWC_{10} did not show any bias for any of the models (Fig. 6f).

4   Discussion

The Yasso07 model (Tuomi et al., 2011) coupled with a revised and optimized empirical Q_{10} soil temperature and Ricker moisture function ξ_{AR} (Eq. (3), Fig. 4), successfully reconstructed observed variation of SOC stocks and soil heterotrophic CO_2 emissions with increasing soil wetness in mineral, organo-mineral, and peat soils in boreal forest (Fig. 6). ~~The Bayesian MCMC data assimilation has proven useful also in other studies (e.g., Xu et al., 2006; Hararuk et al., 2014).~~ The original Yasso07 monotonic precipitation function is effective due to easily available data on upper boundary condition, but also flawed in case of shallow water table when the lower boundary is equally important in defining the water content on the soil. Therefore, the usage of soil water content as a variable is structurally superior, and can be proved by inductive reasoning, e.g., from the test model runs. Separating the effect of structure against calibration would require more test runs with data from larger number of study sites.

Our application of Yasso07 models on the hillslope accounted for the continuity in moisture conditions which was reflected in the modelled gradient of mineral and peat soils carbon stocks. The Yasso07 model initially developed for mineral soils was improved for application in peatlands by accounting for the soil temperature and volumetric moisture, as these are better predictors of heterotrophic respiration than air temperature and precipitation (Jian et al., 2022). Although, the empirical Ricker function ξ_{AR} used here was heuristic, its form implicitly accounted for prevailing intrinsic micro-scale processes on the hillslope controlling Rh and SOC accumulation e.g., plant and microbial communities, long-term and short-term limitation of oxygen and substrate with moisture (Davidson et al., 2012, Moyano et al. 2012, Ghezzehei et al. 2019).

The ξ_{AR} being able to simulate gradually increasing SOC stocks from mineral to organic soils makes it a preferable rate
400 modifier for the Yasso07 model, instead of simply adjusting decomposition with a reduction constant for wetlands (e.g., Goll
et al., 2015; Kleinen et al., 2021), which underestimated the SOC stocks of peatlands (Yasso07.ξ_{TW} in Fig. 5). In this study,
the constant 96% reduction (0.04*k-rates) was proposed for the existing Yasso07.ξ_{TW} for more accurate SOC modelling in
mires, a value comparable to rates of anaerobic decomposition (Schuur et al., 2015). ~~Currently, 80% reduction of rates is used~~
~~for water-saturation in an updated moisture modifier in the JULES model (Chadburn et al., 2022). Although~~ The 96% reduction
405 is comparable to JULES which accounts for oxygen inhibition with gradual ~~reduces~~ reduction of decomposition ~~linearly~~ from
the maximum rate 1 at the moisture optimum (30% - 75% SWC) to a reduced rate 0.2 in water-saturated peat soils (Chadburn
et al., 2022).~~.~~

4.1 The moisture response

The use of gradually changing near surface soil moisture avoids biases in land surface modelling related to ignoring high SOC
410 stocks of organo-mineral soils of forested peatlands (Dalsgaard et al., 2016, Ťupek et al., 2016), e.g., forest-mire transitions
(Fig. 1, and Fig. 2). The modelling decomposition rates accurately with diffusion-based moisture functions accounting for
microbial processes requires correct representation of the drivers of heterotrophic respiration (Yan et al., 2018; Moyano et al.,
2012, 2013; Manzoni et al., 2012; Ghezzehei et al., 2019). However, uncertainty in functional moisture - soil respiration
dependencies are high (Sierra et al., 2015; Falloon et al., 2011) and dependencies vary with the soil properties, e.g., SWC
415 optimum increases for soils with higher organic C content (from 30% to 75% SWC, Moyano et al., 2012, 2013). The ξ_{AR}
function's SWC_{opt} found in dry and well-drained conditions and reduction of default decomposition rates (k) with increasing
soil wetness contrasted with responses from the short-term laboratory incubation soil respiration studies (weeks, months)
showing increase in decomposition from dry conditions until reduction in very wet (Sierra et al., 2017; Moyano et al., 2012,
2013; Kelly et al., 2000; Skopp et al., 1990; Yan et al., 2018). The ξ_{AR} optimized with SOC and CO_2 data showed that the
420 optimum/maximum decomposition rate in the forest-mire ecotone was in dry well-drained conditions around 14% of mean
long-term near surface SWC (around 20 % WFPS, corresponding to sub-xeric and mesic forest site types) (SWC_{opt} parameters
inferred from a parameter in Table 1, Fig. 4b) whereas the moisture optimum of studies based only on respiration from
laboratory soil incubations was around 40% - 60% (Fairbairn et al., 2023; Moyano et al., 2013; Kelly et al., 2000; Skopp et
al., 1990; Yan et al., 2018).

425 The moisture optimum ~~found in~~ derived from the field sites soil respiration datasets ~~of sites~~ from a larger moisture range was
found in 50% water-filled pore space (WFPS) and corresponding to around 31% SWC assuming mean porosity of 62%,
Hashimoto et al., 2011). Our SWC_{opt} between 14 and 27% SWC (Table 1) was comparable to the optimum derived from the
field sites data which was ~~somewhat~~ lower ~~than in other~~ compared to laboratory ~~studies~~ incubations. The SWC_{opt} discrepancy
of the ξ_{AR} function highlights the difference between (1) the responses from the field-based or long-term soil respiration
430 measurements reflecting moisture responses of older, stabilized and slowly decomposing SOC, and (2) the short-term
incubation-based soil respiration studies which predominantly capture decomposition of newly available, labile and rapidly

decomposing, SOC pool (González-Domínguez et al., 2022; Huang and Hall, 2017). Over longer periods of incubation high Q_{10} can be observed (Zhou et al., 2019). The enhanced C mineralization can occur during periods of elevated moisture under Fe reduction when microbes can access previously protected labile C (Huang and Hall, 2017). The incubations are short term
435 (from few days to few months) and are useful to identify short term processes. Moreover, they are performed on disturbed soils (sometimes even sieved) and therefore the soil structure is not representative of the field.

The ecosystem scale application of moisture reduction functions obtained in the laboratory can be hindered by several factors. There are number of feedback mechanisms which modify the response obtained on a limited size soil sample. Among them is a change in microbial community composition, the texture-and- structure-dependent effect of pore-scale connectedness of soil
440 solutions and competition between plants and microorganism for resources under different environmental stress conditions. Under changing climate these feedback mechanisms may lead to the system behaviour unpredictable from extrapolation. Therefore, the validation of the models at the site level with series of various in-situ stress levels is necessary for reliable future predictions.

In its impact on decomposition of the ξ_{AR} functions (calibrated with SOC, SOCCO$_2$, and CO$_2$ data) incorporated into Yasso07
445 soil C model were comparable (e.g., all found the moisture optimum in ~~dry~~ well-drained soils of forest-mire ecotone). Although, the soil temperature and moisture functions showed a relatively small differences in Q_{10} between the model fits, the "a" parameter of the moisture functions of CO$_2$ based fit was larger than from SOC and SOCCO$_2$ fit ~~Although, the soil temperature and moisture function showed a relatively small differences in Q₁₀, the a parameter of CO₂ based fit was larger than from SOC and SCOCO2 fit~~ (Table 1). In terms of the Yasso07 model constants, if temperature and moisture conditions
450 are favourable for organic matter stabilization then the ξ_{AR} is reduced (Fig. 4, and 5) which reduces decomposition rates of fast and slow C pools, reduces their CO$_2$ emissions, and increases C storage. The forest-mire sites' heterotrophic respiration per unit of area did not show a clear difference between well-drained and water-saturated soils whereas the C mineralization per unit SOC was clearly reduced in soils with mean long term field soil moisture (Fig. 2). Reduction in decomposition rates in the environmental gradient from low to higher field moisture, indicates possible a difference in the soil C stabilization
455 mechanisms under low- and high-water content (Das et al., 2019). Ghezzehei et al. (2019) suggested that empirical moisture sensitivity curves should be calibrated individually for each soil. However, our study shows that the common modifier function, based on the SWC of the topsoil humus layer which has comparable properties across the soil types, could provide insights into a more generalizable moisture sensitivity function. The mechanistic diffusion-based moisture functions (e.g., by Ghezzehei et al., 2019, Yan et al., 2018) could be in follow up studies compared against deterministic moisture functions to
460 evaluate their applicability and interpretation.

The ξ_{AR} function and its reduction with increasing wetness from dry soils was based on a large range of forest/mire soil C stocks (between 11 and 134 kg C m^{-2}) reflecting a spatial long-term moisture gradient between forests and mires (Fig. 2) and its short-term moisture and CO$_2$ dynamics over years with contrasting climate (Fig. 3). The soil respiration data from three years covered exceptionally contrasting wet and dry summers and likely captured a full range dependency on the soil moisture

465 induced by short-term weather variation in a spatial/long-term forest-mire gradient in soil moisture, soil C pools, vegetation litter input dynamics (Fig. S2 and S3), and microbial composition. The short-term deviations in respiration indicative of wetting/drying cycles (Barnard et al., 2020; Patel et al., 2021) could be seen by the respiration increases in wet summers or during and after a period of drought (Figure 3). Thus, the $\xi_{AR,p(\theta|SOC-CO2)}$ curve calibrated with highly variable SOC and CO_2 data from a forest-mire ecotone represented a mean robust moisture-decomposition dependency smoothing short-term weather

470 dependent fluctuations with the spatial variation of organic matter decomposition across ecological gradients. This function could meet the land surface modelling criteria for spatial accuracy on small scales but also cost efficiency for running or forecasting the C dynamics at large scales (Luo and Schuur, 2020).

~~The ξ_{AR} function's SWC_{opt} found in dry conditions and reduction of default decomposition rates (k) with increasing soil wetness contrasted with responses from the short-term laboratory incubation soil respiration studies (weeks, months) showing~~

475 ~~increase in decomposition from dry conditions until reduction in very wet (Sierra et al., 2017; Moyano et al., 2012, 2013; Kelly et al., 2000; Skopp et al., 1990; Yan et al., 2018). The ξ_{AR} optimized with SOC and CO_2 data showed that the optimum/maximum decomposition rate in the forest-mire ecotone was in dry conditions around 14% of mean long-term near surface SWC (around 20 % WFPS, corresponding to sub-xeric and mesic forest site types) (SWC_{opt} parameters inferred from a parameter in Table 1, Fig. 4b) whereas the moisture optimum of studies based only on soil respiration was around 40% –~~

480 ~~60% (Fairbairn et al., 2023; Moyano et al., 2013; Kelly et al., 2000; Skopp et al., 1990; Yan et al., 2018).~~

~~I~~The including SOC data or combination of SOC and CO_2 data in model fitting resulted to lower SWC_{opt}, and the model fitting based only on CO_2 showed larger SWC_{opt} and larger tail (descending slope) of the Ricker moisture function. Thus, in comparison to other studies, which dependencies were limited to relatively short-term responses of only soil heterotrophic CO_2 respiration from mainly mineral soils in laboratory conditions, the differences in SWC_{opt} observed in our studies could ~~be~~

485 ~~expected~~be expected from difference in data source used in model calibration. Unlike the data from controlled laboratory condition, we used data from field measurements (mineral soil and peat SOC stocks, litter input, soil CO_2 respiration, T_5 and SWC_{10} measured under extreme weather variability during three years. In optimizing model performance with a multi-variable data set, Keenan et al. (2013) found that a combination of data with fast and slow turnover (e.g., soil respiration and soil carbon stocks) leads to the largest improvement in model performance. The Yasso07.ξ_{AR} based only on slow (SOC) was as good as

490 constraining with SOC and CO_2, as both approaches accurately observed soil CO_2 emissions and SOC stocks along the site types of the forest-mire ecotone with no clear bias in residuals (Fig. 6). Thus, in a catena of mineral and peat soils of forest-mire ecotone, and in the combined measured SOC and CO_2 data assimilation in ξ_D (9 and 2369, respectively), the relatively small number of SOC stocks (9 forest/mire types) largely determined the SWC response form reflecting both a spatial moisture gradient and its temporal variation. Whether the deterministic modifier rate was estimated correctly or not also for the drained

495 peatlands should be tested in follow up studies, as our data did not include drained peatlands. The Ricker functional dependency has performed well for the drier region but the performance in soils with high water status still could be improved. This could

be deduced from better statistical performance of CO_2 only fit with CO_2 data (compared to SOC or SOCCO$_2$ fit) which produced larger tail of the Ricker function. ~~T~~Although, ~~t~~he CO_2 only fit also underestimated SOC stocks of forested peatlands.

500 ~~The SWC$_{opt}$ discrepancy of the ξ$_{AR}$ function highlights the difference between (1) the responses from the field-based or long-term soil respiration measurements reflecting moisture responses of older, stabilized and slowly decomposing SOC, and (2) the short-term incubation-based soil respiration studies which predominantly capture decomposition of newly available, labile and rapidly decomposing, SOC pool (González-Domínguez et al., 2022; Huang and Hall, 2017). Over longer periods of incubation high Q$_{10}$ can be observed (Zhou et al., 2019). The enhanced C mineralization can occur during periods of elevated moisture under Fe reduction when microbes can access previously protected labile C (Huang and Hall, 2017).~~

505 Although, the moisture representation of the ξ_{AR} environmental function was accurate at the forest-mire ecotone level, at the forest site level the contrasting respiration responses to moisture (i.e., either respiration reduction during soil drying or increased CO_2 emissions with rewetting (Barnard et al., 2020; Patel et al., 2021) for dry soils or the opposite for wet soils), were likely not captured sufficiently. Soil C modelling might be further improved using a moisture response that accounts separately for microbial respiration with increased water availability, and for oxygen limitation in soil reaching water saturation

510 (Sierra et al., 2015). However, as the aim of the environmental modifier used in this study was applying the above concepts in a cost-efficient way using an ~~empirical functions~~empirical function with easily interpretable parameters (Q_{10} and a which informs about SWC optimum) (Davidson et al., 2012), the mathematical representation of the moisture function with increased complexity still needs to be evaluated in further studies testing different functional forms with larger regional data availability. Ghezzehei et al. (2019) suggested that empirical moisture sensitivity curves should be calibrated individually for each soil.

515 The mechanistic diffusion-based moisture functions (e.g., by Moyano et al., 2013, Yan et al., 2018, Ghezzehei et al., 2019) could be in follow up studies tested against deterministic moisture functions (e.g., as in Davidson et al. 2012) to evaluate their applicability and interpretation. However, our study shows that the common modifier function, based on the SWC of the topsoil humus layer which has comparable properties across the soil types, could provide insights into a more generalizable moisture sensitivity function.

520 In this study, we constrained the soil carbon model using both SOC (stock) and CO_2 (flow) data. Few studies have constrained the soil carbon model to both SOC and CO_2 data. Our study demonstrates the importance of extensive constraints on the soil carbon model to obtain a reliable model output. The SOC constraint improved the model performance; at the same time, intensive SOC and CO_2 constraint did not result in the improvement of model performance, which implies the need for further model development and testing. One potential improvement in modelling could be the different responses to the environment

525 (e.g., soil moisture) among different pools like the temperature dependency separated between the soil layers and soil C fractions in more recent versions of Yasso model e.g., Yasso15 and Yasso20 (Viskari et al. 2020, 2022). The Yasso07 model adapts one common response function among different pools for simplicity; however, the fresh plant litter moisture limitation of decomposition may be expected to differ from the moisture limitation on older stabilized C in the humus horizon and mineral-associated C. Another factor could be the vertical process. The SOC is vertically distributed in the soil, and soil C

530 fractions differ among soil depths. Accounting for the depth of the soil layer with the largest proportion of net CO_2 emissions (Davidson et al. 2006, 2012) which is expected to vary with fluctuating water level in forested peatlands may further improve the soil respiration estimates for organic soils. On a process level the key to understanding of the difference in moisture reduction function at different soil depth may lay in the nature of the physical and biochemical availability of substrate to enzymes released by microbial decomposers (Sainte-Marie et al, 2021).

535

4.2 The temperature response

The original air temperature-based modifier in Yasso07 was replaced by the Q_{10}Arrhenius type temperature function driven by soil temperature (Davidson et al., 2012). This function was found to best represent the enzyme kinetics under unconstrained substrate and oxygen (Sierra et al., 2017). The optimized temperature function with SOC, and combined SOC and CO_2 data
540 produced slightly more biased Rh estimates than modifier based on CO2 data with Q10 around 4.5 (Table 1, Fig. 6). The Q_{10} values around 4.0 were comparable with the well-, moderately-, and poorly- drained forest soils for similar climates (Chen et al., 2020; Davidson et al., 1998; Karhu et al., 2010; Pumpanen et al., 2008). However, the optimization of the Q_{10}Arrhenius type temperature response only with SOC data and SOC and CO_2 with Q_{10} (2.3) (Table 1), showed lower R^2_{adj} values than for the Gaussian type temperature dependency in the Yasso07.ξ_{TW} (Fig. 5). Thus, due to the comparable predictive power when
545 using soil and air temperature (Jian et al., 2022), the original Gaussian air temperature dependency could be more accurate than Q_{10}Arrhenius response for the optimization with soil temperature (Tuomi et al., 2008).

Discrepancies in modelled respiration during winter (Fig. 6) could be also caused by a scarcity of winter field CO_2 measurements potentially resulting in larger random errors (e.g., due to difficulties of measuring relatively small respiration fluxes during soil freezing/thawing cycles, measurements on soil covered by snow layer, and reduced precision of gas analysers
550 during measurements in lower temperature range). Density of CO_2, temperature and SWC measurements can be seen in Fig.3. The less frequent measurements during the near zero soil temperature might have affected the fit of the temperature function. However, our main emphasis was on the moisture which in near zero temperature conditions plays only a minor role on controlling respiration.

5 Conclusions

555 The Yasso07 soil carbon model was developed and parameterized at global scale for mineral soils; however, it has also been applied for land surface modelling coupled with the JSBACH model with a 65% reduction of default decomposition for wetlands. In this study we emphasized on improving representation of the response of soil organic C stock change and respiration to soil moisture in Yasso07 model for forest - mire ecosystems. At the forest site level, we evaluated the performance of the Yasso07 model with an original climate modifier based on air temperature and precipitation against the
560 model coupled with a revised environmental modifier based on soil temperature and moisture. We found that the Yasso07

model coupled with revised climate dependencies performed similarly for mineral soils but outperformed the original configuration with the JSBACH modification for undrained peatland soils.

The optimization of moisture dependency conducted in this study accounted for both a spatial moisture gradient and its temporal variation. The moisture optimum at dry soils has not changed depending on whether the function was optimized using both slow (SOC) and fast (CO_2) turnover data (combined SOC and CO_2 data) or only slow (SOC) data.

The SOC stocks in peatland forests were an order of magnitude larger in comparison to forests on mineral soil. On a landscape level, these peatland SOC stocks had the largest influence on calibrated the moisture optimum, when they were included along with fluxes in optimization. This could be inferred from the same calibrated moisture optimum when using calibration with only SOC or SOCCO_2 as data source, whereas for only CO_2 based calibration the optimum differs. The function implicitly accounted for relative contribution of C fluxes from short term biogeochemical processes in a long-term SOC accumulation. Thus, for accurate estimates of the boreal forest soil carbon pools with Yasso07 model, the SOC accumulation related to inhibition of decomposition with increasing wetness was more pronounced than the one related to dryness.

This study illustrated the limitation of the default moisture functions used for peatland forest soil C modelling. Also, the unimodalnon-monotonic Ricker function with a proposed moisture optimum in well-drained mineral soils needs further evaluation with regional boreal forest data. The exact representation of the functional form of the soil moisture dependency is characteristic to conditions of our study e.g., the distribution of organic and mineral soil forests in the data. Broader extrapolation of the conclusions e.g., to climate change or forest management on drained peatlands would require more model testing with spatially larger data and lower water levels in forests on organic soils. However, Iif the dry soil moisture optimum of litter decomposition in forests on well drained mineral soils of boreal forest landscape proves to be robust, then in the future warmer and drier climates the boreal forest could be expected to enhance soil C emissions to the atmosphere due to water level drawdown of presently water-saturated peat soils with large C stocks. In contrary However, rewetting of previously drained peatlands could be expected to reduce soil C emissions, turning SOC loss to long-term C sequestration.

6   Data and code availability

The input data (soil CO_2 fluxes, soil temperature and moisture, air temperature and precipitation, tree stand and understory inventory, and soil C stocks) as well as the analysis (R codes) needed to run the Yasso07 model versions and reproduce the results of this study are available on Zenodo, https://doi.org/10.5281/zenodo.8111475.

7   Author contribution

BT designed the hypothesis, collected data (soil respiration, micrometeorology, tree and understory inventory, and soil C), and carried out the analysis (input data preparation, the model reformulation on SoilR platform, the model update, calibration, and evaluation). KM contributed to design of the ecological gradient of study sites, and design of measurements of soil respiration

and micrometeorology. AY contributed to soil sampling and soil C data preparation. AL contributed to codes on biomass and litter estimation. XT contributed to formulation of likelihood for model calibration. BT prepared and revised the manuscript with contributions from all co-authors.

8   Competing interests

We have no conflict of interest to declare.

9   Acknowledgments

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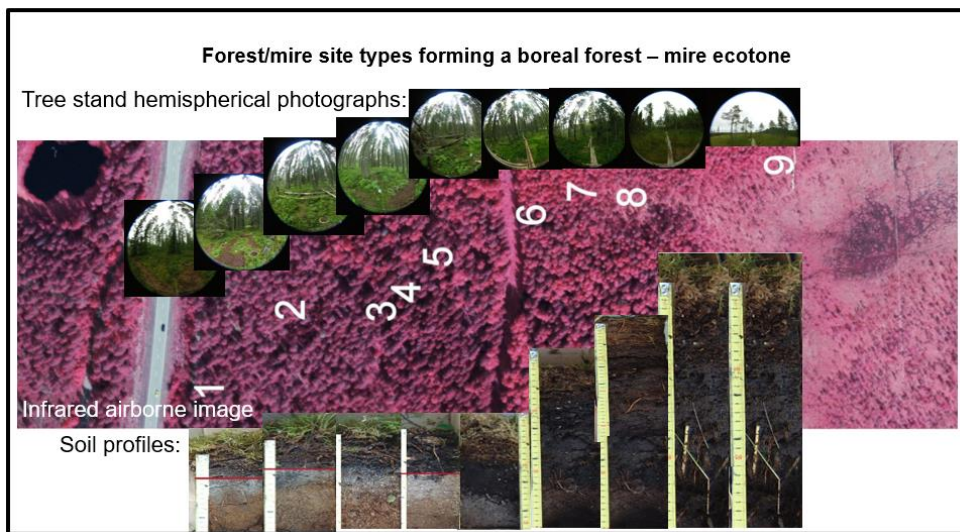


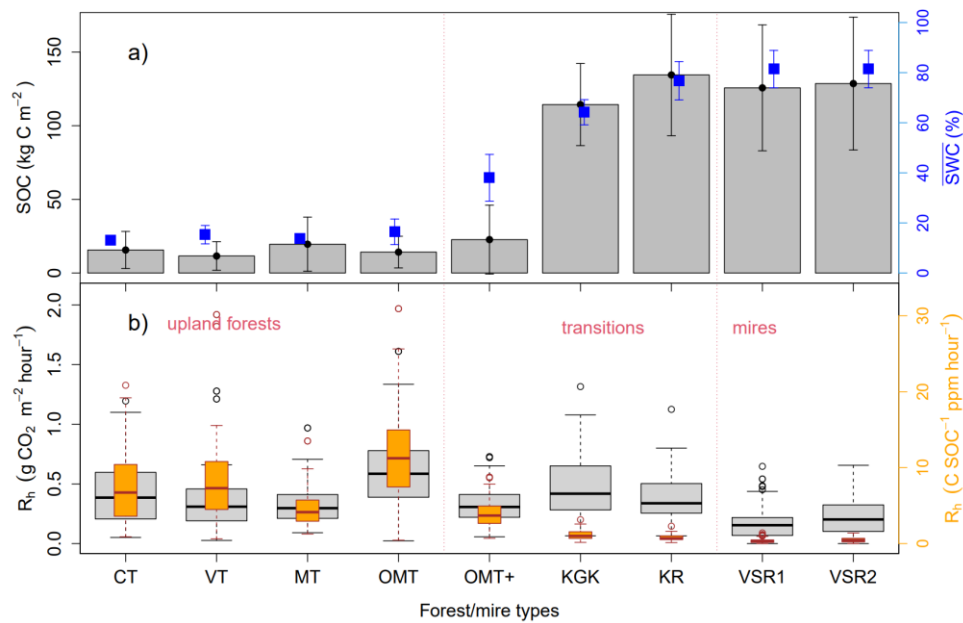
Figure 1. Infrared areal image showing the location of nine studied forest/mire types forming a transect of approximately 450 m on the northern hillslope in Finland (61° 47', 24° 19'). The series of hemispherical images of forest stands on the top of the aerial image show the increasing gradient in the canopy openness from upland forests (left) to mires (right). The series of soil profiles show the increasing gradient of the organic layer depth. The images in the series arranged from left to right mimic the site type location on the slope from the hill to depression. Sites range from upland (1) xeric, (2) sub-xeric, (3) mesic and (4) herb-rich forest types (CT - Calluna, VT - Vitis Idaea, MT - Myrtilus, OMT - Oxalis-Myrtillus), through paludified forest - mire transitions (5 - 7) (OMT+ - Oxalis-Myrtillus Paludified, KgK – Myrtillus Spruce Forest Paludified, KR – Spruce Pine Swamp), to sparsely forested mires/peatlands in depression (8 - 9) (VSR1 and VSR2 - Tall Sedge Pine Fen).

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Figure 2. Forest/mire site type specific observations of soil organic carbon (SOC) stocks (kg C m^{-2}, summed up to 1 m) and the mean volumetric soil water content (SWC) at 10 cm depth (%) (with error bars showing one standard deviation of all measured values) (a) in comparison to their distributions of heterotrophic soil CO_2 emissions/respiration measurements (Rh, gCO_2 m^{-2} h^{-1}) and R_h expressed as the emitted C fraction per site specific SOC stock (C SOC^{-1} ppm h^{-1}) (b). The CT, VT, MT,

870 and OMT types represent upland forests, OMT+, KgK, and KR forest-mire transitions, and VSR1 and VSR2 mires. The boxplot horizontal lines show 25th and 75th interval with median in between, and 5th and 95th confidence interval (whiskers).

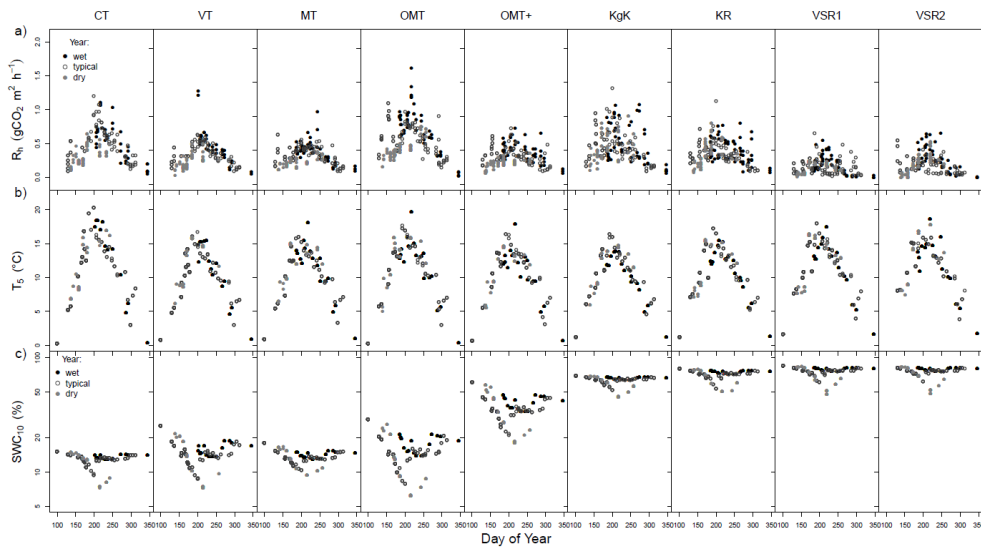



Figure 3. The three years' time series (2004 - wet, 2005 - typical, and 2006 - dry) of instantaneous measurements of a) soil heterotrophic respiration (R_h, gCO_2 m^{-2} h^{-1}, positive sign), b) soil temperature at 5 cm depth (°C), and c) soil moisture at 10 cm depth (%)) of 9 forest/mire sites (4 upland forests (CT,MT, and OMT), 3 forest-mire transitions (OMT+, KgK, and KR) and 2 mires (VSR1 and VSR2). The sites are arranged from left to right according to their position on the slope (see Fig. 1).

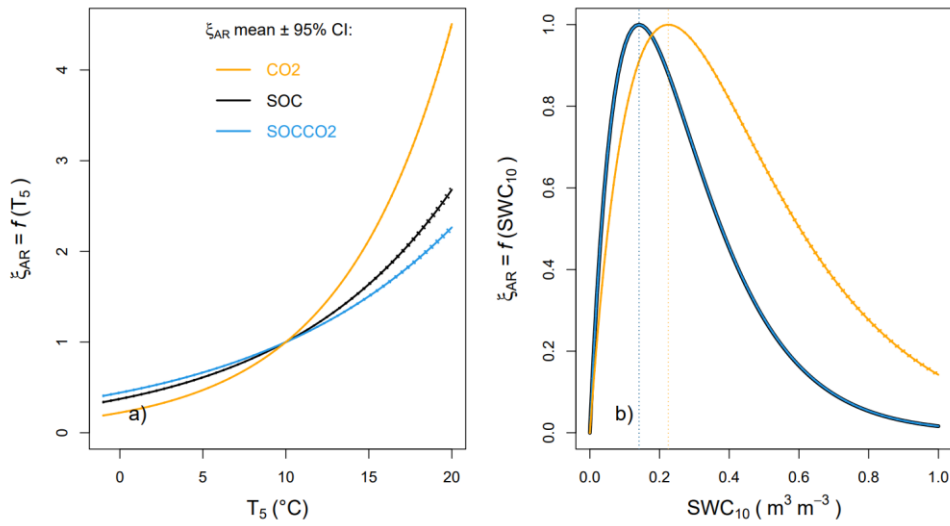



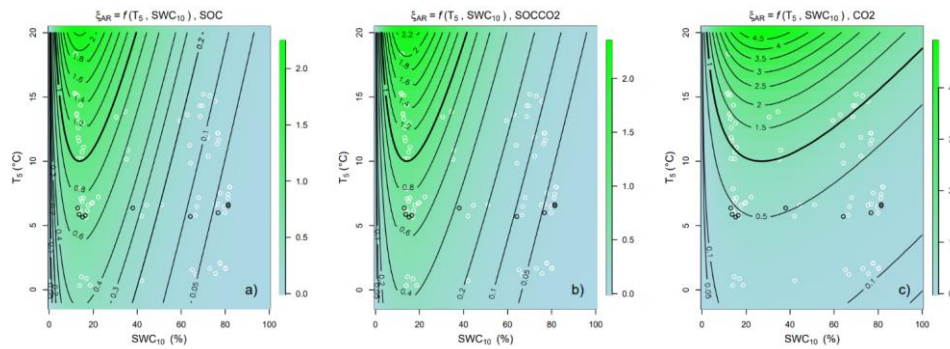
Figure 4. The optimized environmental modifier of default decomposition rates ξ_{AR} (Eq. (3)) (coupled with Yasso07 model)
880 drawn with mean posterior values of parameters and their confident intervals (dashed lines) (Table 1) for separate responses
to (a) soil temperature at 5 cm, $\xi_{AR} = f(T_5)$ when $f(SWC_{10}) = 1$, (b) to soil water content at 10 cm, $\xi_{AR} = f(SWC_{10})$ when $f(T_5)$
$= 1$. The functions were fitted based on only CO_2, SOC and CO_2, or only SOC data.

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Figure 5. The colors and contour lines showing optimized environmental modifier of default decomposition rates ξ_{AR} (Eq. (3)) (coupled with Yasso07 model) drawn with mean posterior values of parameters (Table 1) for combined responses to soil temperature at 5 cm, $\xi_{AR} = f(T_5)$ and to soil water content at 10 cm, $\xi_D = f(SWC_{10})$ based on only SOC (a), SOC and CO_2 (b), or only CO_2 (c) data. In the panels of combined ξ_{AR} white circles show pairs of corresponding monthly means of T_5 and SWC_{10},

890 and the black circles show the annual T_5 and SWC_{10} means for 9 forest/mires site types.
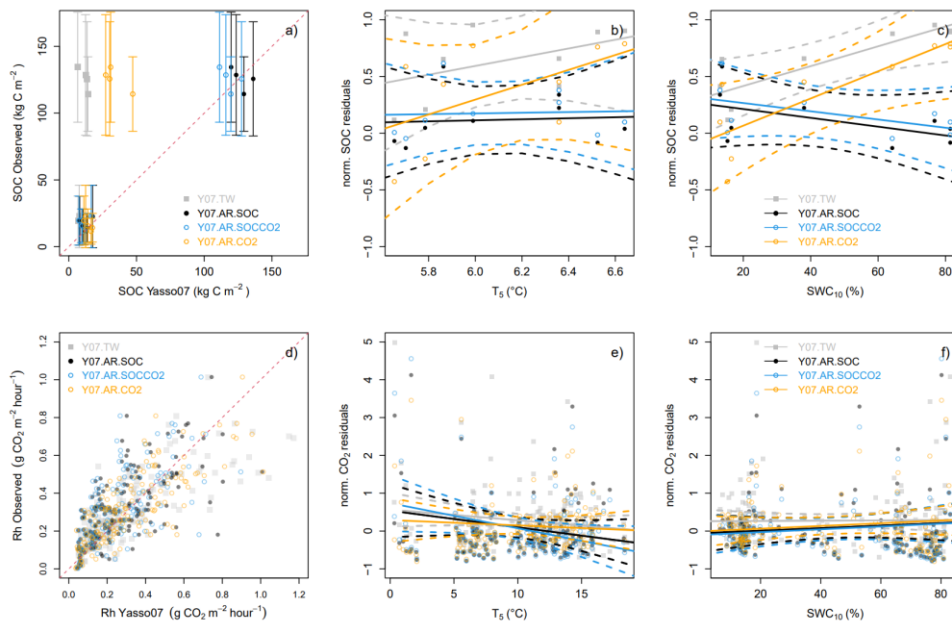
Figure 6. Scatterplots between observed SOC (kg C m^{-2}) and Rh (g CO_2 m^{-2} hour^{-1}) from the forest-mire ecotone against modelled values with the two versions of Yasso07 model (i) Y07.ξ_{TW} – Yasso07 coupled with the default environmental modifier (ξ_T, Eq. (3)) based on air T and precipitation with global parameter set (Tuomi et al., 2011) (applied for CT…KR mineral and organo-mineral soil forest sites) and with the reduction of decomposition rates by 65% for wetlands (Goll et al., 2015, Kleinen et al., 2021) (applied for VSR1, VSR2 mires sites), and (ii) Y07.ξ_{AR} - Yasso07 coupled with environmental modifier (ξ_{AR}, Eq.3) based on based on SOC, SOC-CO2, or CO2 data (a, d) compared with 1:1 line (dashed red line). The model residuals normalized with the observations (norm. SOC and CO_2 residuals = residuals/observations) are plotted against the T$_5$ and SWC$_{10}$ with the trendlines of the linear fits and with their confident intervals (dashed lines) (b, c, e, and f).

Table 1. The posterior distribution of parameters of Yasso07 soil carbon model (parameters same as in Table S1) coupled with environmental function ξ_D (Eq. (3), parameters d, Q_{10}, SWC_{opt}) optimized with observations of SOC stocks (p (θ | SOC)) or SOC stocks and CO_2 emissions (p (θ | SOC-CO2)) from forest/mire ecotone sites using Bayesian data assimilation (Hartig et al., 2012). The PSRF stands for Gelman–Rubin potential scale reduction factor and MAP for a maximum a posteriori probability. $1/ae^{-1}$. The SWC_{10} optimum (the SWC_{10} when the SOC decomposition in the foreal forest -mire ecotone was at optimum) was inferred as $1/ae^{-1}$ and ranged between 14 and 27 % (for $a_{MAP\,SOC}$ and $a_{MAP\,CO2}$, respectively).

Posterior p(θ | data)	ξ_{AR} parameters	PSRF	MAP	2.50 %	50 %	97.50 %
SOC	Q_{10}	1.001	2.239	1.157	2.503	4.72
SOC	a	1.001	19.576	18.172	19.271	20.538
SOC	ae1	1.002	0.099	0.032	0.077	0.099
SOC	be1	1.001	0	0	0	0.002
SOC, CO_2	Q_{10}	1.016	2.342	1.611	2.213	3.103
SOC, CO_2	a	1.015	19.15	18.725	19.261	19.93
SOC, CO_2	ae1	1.017	0.015	0.011	0.029	0.121
SOC, CO_2	be1	1.024	0.01	0.01	0.01	0.012
SOC, CO_2	ae2	1.018	0.5	0.453	0.496	0.5
SOC, CO_2	be2	1.026	0.995	0.337	0.982	0.999
CO_2	Q_{10}	1.004	4.897	3.525	4.57	4.982
CO_2	a	1.001	10.066	10.07	11.741	16.21
CO_2	ae	1.008	0.5	0.48	0.496	0.5
CO_2	be	1.01	0.999	0.923	0.986	0.999

910 Table 2. The SOC and CO_2 performance statistics of Yasso07 (Y07) model versions against the measured data in boreal forest-mire ecotone where N is the number of observations, MAE is the mean absolute error, MBE is the mean bias error, RMSE is the root mean square error, R^2_{adj} is the adjusted coefficient of determination, and AIC is the Akaike Information Criterion. The units of MAE, MBE, and RMSE are in kg C m^{-2} and kg CO_2 m^{-2} $month^{-1}$ for SOC and CO_2, respectively.

Data	Yasso07 model	MBE	MAE	RMSE	R^2_{adj}	AIC
SOC	Y07.ξ_{TW}	-54.97	54.97	76.67	0.05	87.06
SOC	Y07. $\xi_{AR.SOC}$	-1.76	7.59	9.18	0.97	65.95
SOC	Y07. $\xi_{AR.SOCCO2}$	-6.03	7.63	10.25	0.97	66.95
SOC	Y07. $\xi_{AR.CO2}$	-42.17	43.98	62.2	0.63	83.17
CO_2	Y07.ξ_{TW}	0.01	0.11	0.16	0.6	-233.65
CO_2	Y07. $\xi_{AR.SOC}$	-0.04	0.12	0.16	0.44	-237.37
CO_2	Y07. $\xi_{AR.SOCCO2}$	-0.06	0.12	0.16	0.44	-238.31
CO_2	Y07. $\xi_{AR.CO2}$	0	0.1	0.13	0.63	-266.9

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