Dissertationes Forestales 303

Environmental controls of boreal forest soil CO_2 and CH_4 emissions and soil organic carbon accumulation

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Academic dissertation

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A Time for Everything (Solomon, c.450–180 BCE*)

3 There is a time for everything,
    and a season for every activity under the heavens.

**Solomon, c.450–180 BCE, Ecclesiastes 3, Holy Bible, New International Version, 2011, Biblica Inc.*

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ABSTRACT

Process-based soil carbon models can simulate small short-term changes in soil organic carbon (SOC) by reconstructing the response of soil CO_2 and CH_4 emissions to simultaneously changing environmental factors. However, the models still lack a unifying theory on the effects of soil temperature, moisture, and nutrient status on the boreal landscape. Thus, even a small systematic error in modelled instantaneous soil CO_2 emissions and CH_4 emissions may increase bias in the predicted long-term SOC stock.

We studied the environmental factors that control CO_2 and CH_4 emissions in Finland in sites along a continuum of ecosystems (forest-mire ecotone) with increasing moisture and SOC (I and II); soil CO_2 emissions and SOC in four forest sites in Finland (III); and SOC sequestration at the national scale using 2020 forest sites from the Swedish national forest soil inventory (IV). The environmental controls of CO_2 and CH_4 emissions, and SOC were evaluated using non-linear regression and correlation analysis with empirical data and by soil C models (Yasso07, Q and CENTURY).In the forest-mire ecotone, the instantaneous variation in soil CO_2 emissions was mainly explained by soil temperature (rather than soil moisture), but the SOC stocks were correlated with long-term moisture. During extreme weather events, such as prolonged summer drought, soil CO_2 emissions from the upland mineral soil sites and CH_4 emissions from the mire sites were significantly reduced. The transition from upland forest to mire did not act as a hot spot for CO_2 and CH_4 emissions. The CO_2 emissions were comparable between forest/mire types but the CH_4 emissions changed from small sinks in forests to relatively large emissions in mires. However, the CH_4 emissions in mires did not offset their CO_2 sinks. In the Swedish data, upland forest SOC stocks clearly increased with higher moisture and nutrient status. The soil carbon models reconstructed SOC stocks well for mesotrophic soils but failed for soils of higher fertility and wetter soils with a peaty humus type. A comparison of measured and modelled SOC stocks and the seasonal CO_2 emissions from the soil showed that the accuracy of the estimates varied greatly depending on the mathematical design of the model's environmental modifiers of decomposition, and their calibration.

Inaccuracies in the modeling results indicated that soil moisture and nutrients are mathematically underrepresented (as drivers of long-term boreal forest soil C sequestration) in process-based models, resulting in a mismatch for both SOC stocks and seasonal CO_2 emissions. Redesigning these controls in the models to more explicitly account for microbial and enzyme dynamics as catalysts of decomposition would improve the reliability of soil carbon models to predict the effects of climate change on soil C.

Keywords: carbon dioxide, methane, hydrology, ecotone, climate change, peatland, process modeling, soil carbon models, temperature (T), water (W)

ACKNOWLEDGEMENTS

I am grateful to Dr. John Derome who was the first to hire me in Finland for a traineeship in Rovaniemi funded by Centrum for International Mobility of students (CIMO). On my return to Slovakia, Prof. Jaroslav Škvarenina, supervisor of my Slovak Ph.D. encouraged me to apply for another CIMO traineeship in Finland. This time in Joensuu for a CO_2, CH_4, and N_2O study in peatland buffers with Docent Jukka Alm.

Thanks to this experience I was accepted for a PhD program in Helsinki supervised by Prof. Jukka Laine, Prof. Eero Nikinmaa, and Docent Kari Minkkinen and funded by Nordic Centre for Studies of Ecosystem Carbon Exchange and its Interactions with the Climate System. I thank Jukka L. and Kari for the overarching theme of my Finnish Ph.D. “underlying processes behind CO_2 and CH_4 exchange” and for selecting the sites forming unique forest-mire ecotone. Prof. Hannu Ilvesniemi provided a soil moisture probe, Eero provided a data logger and weather sensors, and Kari a portable infrared CO_2 analyzer. Many thanks go to Dr. Terhi Riutta for helping with important details regarding greenhouse gas measurements in the field, gas chromatography in the lab, and for lending me her car multiple times to get between Lakkasuo and Hyytiälä station. Hyytiälä staff was friendly and helpful. I am grateful for their support during three seasons of field and laboratory work, and to Dr. Michal Gažovič and Dr. Tommy Chan and everyone who helped me to collect data.

When studying in Helsinki at the Department of Forest Sciences and Physics, the physicists inspired me to use Matlab. After Prof. Jukka Laine moved to Parkano, I appreciate Prof. Eero Nikinmaa for taking over as my main supervisor. Initially, our communication stumbled, as I had little knowledge about plant physiological process modeling, but thanks to that a new collaboration started with Prof. Jukka Pumpanen, Prof. Timo Vesala, Dr. Pasi Kolari, Docent Ilkka Korpela, Prof. Harri Vasander, and Prof. Mike Starr. I thank Ilkka and Harri for organizing airborne survey and lidar flights above the Vatiharju – Lakkasuo ecotone. Mike helped with planning measurements of soil water nutrients and with the scientific language of the first “CO_2 ecotone” thesis paper. I was happy about the revision but understood the limits of my writing ability. Furthermore, I’ve got stuck with the analysis of the “CO_2 moisture” paper. The moisture signal in CO_2 data was surprisingly weak. In a search for the reason, Prof. Pertti Hari thankfully sparked my interest in statistical methods. Inevitably my three and half years funding ended. Thanks to three months grant from the Finnish Society of Forest Science, and three months’ salary from Timo for analysis of CH_4 and N_2O data, and a three months position on CarboEurope project with Dr. Marcus Lindner in European Forest Institute, I was paid a little longer. Without funding eventually, I returned to Slovakia for over a year.

However bad it seems, I am thankful for reconnection with family; mainly mother, father, brother, uncle, grandmother, cousins, friends, nature, and myself. I considered abandoning science and changing professions. Science prevailed by Prof. Ladislav Tužinský insisting on the completion of my Slovak Ph.D. With data from Docent Peter Fleischer and with a regression modeling I finalized and defended monograph on “O_3 in a mountainous forest”. Also “CO_2 moisture” manuscript seemed to advance. Eero was impressed with the amount of work done and offered me a new chance to complete it. I returned to Finland and since then revised it three times, without success. However, thanks to published article on “European forest C modeling” with Marcus and a handful of Earth system modelers science held on to me.

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To cut a long story short, I want to thank all mentioned here and also many other friends and colleagues who supported me and whom I could not list here for the lack of space, and last but not least God for forming me by saving grace.

LIST OF ORIGINAL ARTICLES

The doctoral thesis is based on the following publications, which are referred to in the text by their roman numerals.

I. **Ťupek B.**, Minkkinen K., Starr M., Kolari P., Chan T., Vesala T., Alm J., Laine J., Nikinmaa E. (2008). Forest floor versus ecosystem CO_2 exchange along boreal ecotone between upland forest and lowland mire. Tellus B 60(2): 153–166. https://doi.org/10.1111/j.1600-0889.2007.00328.x

II. **Ťupek B.**, Minkkinen K., Pumpanen J., Vesala T., Nikinmaa E. (2015). CH_4 and N_2O dynamics in the boreal forest–mire ecotone. Biogeosciences 12(2): 281–297. https://doi.org/10.5194/bg-12-281-2015

III. **Ťupek B.**, Launiainen S., Peltoniemi M., Sievänen R., Perttunen J., Kulmala L., Penttilä T., Lindroos A.J., Hashimoto S., Lehtonen A. (2019). Evaluating CENTURY and Yasso soil carbon models for CO2 emissions and organic carbon stocks of boreal forest soil with Bayesian multi-model inference. European Journal of Soil Science 70(4): 847–858. https://doi.org/10.1111/ejss.12805

IV. **Ťupek B**., Ortiz C. A., Hashimoto S., Stendahl J., Dahlgren J., Karltun E., Lehtonen A. (2016). Underestimation of boreal soil carbon stocks by mathematical soil carbon models linked to soil nutrient status. Biogeosciences 13(15): 4439–4459. https://doi.org/10.5194/bg-13-4439-2016

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Other selected closely related peer-review articles not included in the thesis summary:

Schneider J., **Ťupek B.,** Lukasheva M. et al. (2018). Methane Emissions from Paludified Boreal Soils in European Russia as Measured and Modelled. Ecosystems 21: 827–838. https://doi.org/10.1007/s10021-017-0188-y

Hashimoto S., Nanko K., **Ťupek B**., Lehtonen A. (2017). Data-mining analysis of factors affecting the global distribution of soil carbon in observational databases and Earth system models. Geoscientific Model Development 10(3): 1321–1337. https://doi.org/10.5194/gmd-10-1321-2017

Ťupek B., Zanchi G., Verkerk P. J., Churkina G., Viovy N., Hughes J. K., Lindner M. (2010). A comparison of alternative modelling approaches to evaluate the European forest carbon fluxes. Forest Ecology and Management 260(3): 241–251. https://doi.org/10.1016/j.foreco.2010.01.045

AUTHOR'S CONTRIBUTION

I & II The first author (author) contributed to the planning and establishment of the study, and by collecting data. TC contributed by data collection. JL, KM, TV, MS, and EN contributed to the planning and coordination of the studies. The author analyzed the data, interpreted the results, and wrote the papers. MS revised paper **I**. All authors contributed to papers by helpful comments.

III The author, AL, MP, and TP contributed to the planning and establishment of the study and carried out and supervised measurement campaigns. The author analyzed the data, run the CENTURY model, run Yasso model simulations on a monthly time step with help of RS, JP, and AL, interpreted the results with AL, SL, MP, LK, and RS, and wrote the paper. All authors contributed to the study with helpful comments.

IV The author contributed to the study by analyzing, and interpreting the data, and wrote the paper. The author had run Yasso and CENTURY model simulations. CAO run Q model. SH helped with running CENTURY. AL, the author, and SH coordinated the analysis. JS, JD, EK provided inventory data. All authors contributed to the paper with helpful comments.

TABLE OF CONTENTS

REVIEW OF THE ARTICLES

I. We studied the relations between the ecosystem component CO_2 fluxes and meteorological and environmental factors on nine sites along the forest-mire ecotone. The non-linear regression models were used to upscale instantaneous forest floor (FF) fluxes to the annual level with continuous records of temperature and light. The CO_2 fluxes of forest stand were based on an inventory-based forest growth model. The contribution of forest floor component fluxes to ecosystem fluxes significantly varied between sites. FF photosynthesis contributed from 4–90% to gross ecosystem photosynthetic production. FF respiration contributed from 70–98% to gross ecosystem respiration. The upscaled annual CO_2 fluxes correlated with site-specific factors. Tree stand biomass played a major role in controlling FF photosynthesis through intercepted light (correlation coefficient $r = -0.96$) and FF respiration through the stand foliar biomass ($r = 0.77$). The long-term moisture was not significantly correlated with soil respiration; however, it was significantly correlated with the thickness of an organic horizon.

II. We studied variable CH_4 and N_2O fluxes measured during wet, intermediate, and dry years in nine sites along the forest-mire ecotone. The statistical differences were evaluated by two-way analysis of variance. The relations between forest floor CH_4 and N_2O fluxes and soil temperature, moisture, and pH were evaluated by non-linear regression models and their residual sensitivity analysis. Small mineral soil forest FF CH_4 sink linearly increased from zero to over -100 ug $m^{-2}h^{-1}$ with increasing temperature and decreasing moisture. FF CH_4 exchange of forest-mire transitions was neutral and weakly correlated only to moisture. In contrast with small negative fluxes of mineral and organo-mineral soils, the histic soils in mires were large CH_4 sources. There, the modeled optimum net CH4 emissions reached 1200 ug $m^{-2}h^{-1}$ under conditions of -18 cm of water level depth and 14 ºC of topsoil temperature. All sites showed similar close to 0 ug $m^{-2}h^{-1}$ net N_2O FF exchange over intermediately moist and dry year. The net N_2O FF emission slightly increased to 50 ug $m^{-2}h^{-1}$ in late spring and early autumn, presumably due to a small increase of typically low N mineralization potential. For the landscape-level modeling, forest-mire transitions can be thus regarded as CH_4 and N_2O neutral and not as hot spots.

III. We evaluated soil CO_2 emissions and soil organic carbon (SOC) stocks of Yasso and CENTURY models against measurements on four forest sites in Finland. We aimed to evaluate seasonal dependencies of CO_2 fluxes and SOC stocks on environmental variables and compare the model outputs to empirical data. The results indicated that models with a default setting estimated well SOC stocks but underestimated CO_2 fluxes. Bayesian CO_2 data assimilation improved the level of the CO_2 estimates. Although the seasonal discrepancies prevailed. This highlighted the need for re-designing the modifiers to better account for seasonality or missing processes e.g. microbial growth. The calibrated CENTURY model using the environmental function with precipitation showed a better fit to the CO_2 data against the model with soil moisture. Also, the Yasso model outperformed the CENTURY. The better performing models had fewer parameters in the environmental functions and used precipitation instead of soil moisture. Thus, considering the CENTURY’s effect of soil properties on decomposition and carbon sequestration could be an asset only if moisture function is simplified and soil moisture data is of high quality.

IV. In this study, we compared Swedish forest soil carbon inventory data with SOC sequestration estimated by process-based models of increasing complexity (Q, Yasso07, and CENTURY). The modes were primarily driven by plant litter input. The decomposition of litter on these models depends on temperature (Q), precipitation/moisture (Yasso07/CENTURY), and soil physicochemical properties such as clay content or topsoil N (CENTURY). Models accurately estimated SOC typically for mesotrophic soils but underestimated for fertile soils. CENTURY accounting for soil properties outperformed Yasso07 and Q models in clay soils but not in fertile soil with high topsoil N. We concluded that for accurate SOC stock modeling soil nutrient status should be re-evaluated in soil carbon models to account for the long-term C sequestration processes associated with microbial C transformation and C interactions with soil minerals.

1 INTRODUCTION

1.1 Boreal forest feedback to climate warming

Increasing atmospheric concentrations of greenhouse gas (GHG) e.g. carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) in the atmosphere with their higher radiative forcing and higher heat capacity than clean air cause climate warming (Santer et al. 2013, IPCC 2018, IPCC 2019a). CO_2 is the most abundant but least effective GHG. The radiative efficiency and global warming potential (GWP) of CH_4 is 21 times higher than for CO_2, and the GWP of N_2O is 310 times higher than for CO_2 (IPCC 2018).

Without mitigation globally increasing air temperature will also increase the frequency and severity of devastating extreme events such as droughts and fires (Turetsky et al. 2015, Holmberg et al. 2019, Walker et al. 2019). The northern latitude climate warming outpacing warming in other regions (Bintanja et al. 2011, Post et al. 2019). Climate warming is human-induced and natural contribution is minimal (Hegerl et al. 2011). The boreal forests taking up CO_2 from the atmosphere act as net C sinks (Goodale et al. 2002) with the photosynthesis counterbalancing the respiration and accumulating C mainly into the soil. It is not clear whether positive feedback of increased photosynthesis due to prolonging the vegetative season (Churkina et al. 2005) could counterbalance negative feedback of increased respiration due to warming the non-vegetative season (Piao et al. 2008, Vesala et al. 2010). However, the boreal forest soil C pool 400 Pg (10^{15} g) (Scharlemann et al., 2014) is temperature and moisture sensitive and under global warming, the soils could turn from a C sequestration to a loss (Crowther et al. 2016) thus triggering significant warming feedback.

In the boreal landscape, most GHG studies have focused on dominant forest and mire ecosystems whose C pools and fluxes significantly differ with water drainage (Weishampel et al., 2009). However, we also need to clarify greenhouse gas exchange in transitional zones which have been considered as potential biogeochemical hotspots in the landscape (McClain et al. 2003) due to their high water and nutrients dynamics (Howie and Meerveld 2011).

Locally CO_2 fluxes are controlled by moisture, whereas at regional and global scale temperature drives C sinks (Gong et al. 2013, Jung et al. 2017). Multiscale measurements such as chamber and eddy covariance techniques (Kolari et al. 2009, Aurela et al. 2007) are needed for the parametrization, evaluation, and further development of the models. Ecosystem and soil carbon models such as e.g. CENTURY (Parton et al. 1988), Biome-BGC (Thornton 1998), Yasso07 (Tuomi et al., 2011) among others are needed for reconstructing natural processes and their extrapolation in time and space and for evaluating feedback of climate change. As a result, Earth system models include drivers of scale-dependent processes. However, in modeling local and global feedback of climate warming on boreal forest C sink we still search for unifying functional representation of soil carbon change responses to drivers such as temperature and moisture (Todd Brown at al. 2013, Sierra et al. 2015) while accounting for soil nutrient status (Orwin et al. 2011, Fernández-Martínez et al. 2014, Hashimoto et al. 2017).

1.2 Forest-atmosphere C exchange

1.2.1 Forest and mire CO_2 and CH_4 fluxes

Soil heterotrophic respiration is the major ecosystem source of CO_2 emissions in a well-drained forest, while in mires soil CO_2 and net CH_4 emissions are equally important (Frolking et al. 2011, Oertel et al. 2016). Although net ecosystem CO_2 exchange (NEE) (a difference between fluxes of gross photosynthetic production (GPP) and total respiration (R), Figure 1) can be similar between forests and peatlands, the major C fluxes and pools are different. In a well-drained forest, net primary production (NPP, GPP minus growth and maintenance respiration (Ra)) results in relatively larger tree growth and C storage in the living biomass compared to the NPP of peatlands where tree growth is reduced in water-saturated soils due to limited oxygen and nutrient availability. As the living biomass regenerates, its litterfall (e.g. leaves, branches, and roots) is a source of organic matter for the soil decomposition processes (Rh), transformation, and accumulation of the soil organic matter by soil macro- and micro-biota (Cotrufo et al, 2013). The microbial activity and Rh vary spatially and seasonally with soil temperature and moisture, the amount and nutrient status of the organic substrate (Bond-Lamberty et al. 2004, Davison et al. 2012, Sierra 2012a,b, Pumpanen et al. 2015, Manzoni et al. 2017).

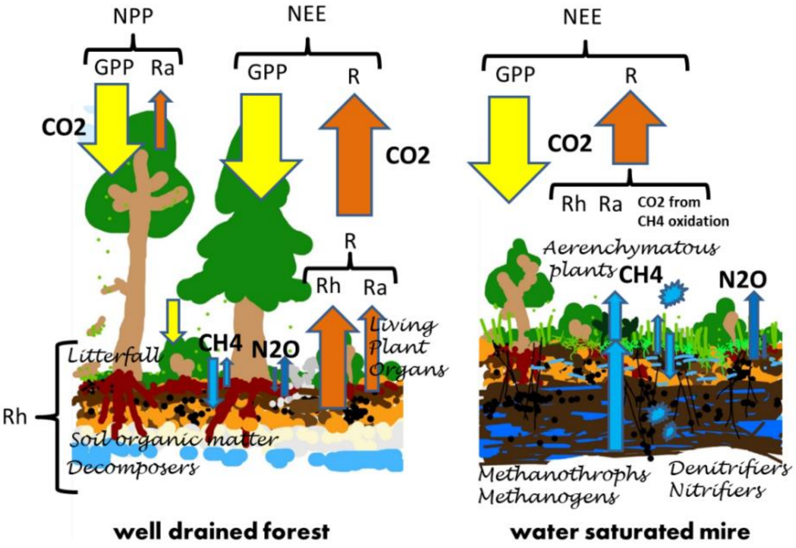


Figure 1. Schematic illustration indicating the main processes of component CO_2, CH_4, and N_2O gas exchange between the atmosphere and the forest or the mire ecosystem. In an atmospheric view, the forest – atmosphere CO_2 interactions are described from the perspective of the concentration change of the atmosphere. Component ecosystem fluxes that remove C from the atmosphere are shown by downward arrow (sinks, GPP, and CH_4 oxidation), and fluxes adding C to the atmosphere are shown by upward arrow (sources, R, Rh, and Ra, CH_4 emission).

Methane production and net emissions also vary spatially and temporally depending on the moisture, temperature, mosses, arenchymatous plants, and peatland nutrient status (Bubier et al. 1995, Riutta et al. 2007, Larmola et al. 2010, Yrjäla et al. 2011, Turetsky et al. 2014). Well-drained mineral soil forests and also boreal forestry –drained peatlands act as small net CH_4 sink (Moosavi et al. 1997, Ojanen et al. 2010, Marushchak et al. 2016) whereas mires are CH_4 sources (Riutta et al. 2007, Frolking et al. 2011, Gong et al. 2013, Marushchak et al. 2016, Raivonen et al, 2017). The CH_4 sink in mineral soils is primarily a result of oxidation whereas in mires the CH_4 is produced by methanogenic bacteria in anoxic conditions. In the presence of fresh organic input of deep roots in summer, methanogens dissimilate acetate (acetate pathway) while in winter CH_4 is produced by reduction of bicarbonate (hydrogen pathway) (Hines et al. 2008). Produced methane is then transported to the atmosphere by diffusion, ebullition, or by arenchymatous plants, or it is oxidized to CO_2 by methanotrophs while passing through the aerobic soil layer (Larmola et al. 2010, Raivonen et al, 2017).

1.2.2 Modeling soil C dynamics

Soil carbon dynamics can be modeled while incorporated into ecosystem models e.g. as in CENTURY (Parton et al., 1988), Forest-BGC (Running and Gower 1991), and TECO (Weng and Luo 2008). If the plant litter input is provided then soil carbon dynamics can be modeled by soil carbon models e.g. Yasso07 (Tuomi et al., 2009), ROMUL (Chertov et al., 2001), and RothC (Coleman & Jenkinson, 1996). Conventionally soil organic carbon (SOC) change in time is in mathematical terms expressed by first-order decay of C in soil pools (accounting for C input, decay rates, transfers and feedbacks between pools, and output) which is either inhibited or accelerated by environmental conditions.

For example, the Yasso07 (Tuomi et al., 2009; Tuomi et al., 2011) and CENTURY (Parton et al. 1988, Metherell et al. 1993, Del Grosso et al. 2001) models of the soil organic matter decomposition can be summarized by a set of differential equations as described by (Sierra et al., 2012) for the general dynamic model (Eq. 1)

$$\frac{dc(t)}{dt} = i(t) + \xi(t)A(t)c(t) \qquad \text{Eq. 1}$$

Where $\boldsymbol{c}(t)$ is a vector of n C pools at time t, the model structure $\mathbf{A}(t)$ is described by $n \times n$ matrix with decomposition rates for each pool in a diagonal and coefficients of transfers and feedbacks below and above the diagonal defining cross-pool C flows. The environmental modifier $\xi(t)$ is a scalar describing the environmental effect on decomposition rates and $\boldsymbol{i}(t)$ is a vector of carbon inputs to each pool.

The second-order decay models, apart from the principles of first-order models (mass balance, pools specific substrate dependence of decay, heterogeneity and transfers of organic matter between pools, and environmental effects), also account for nonlinear organic matter interactions (Manzoni & Porporato 2009, Sierra et al. 2015, Moyano et al. 2018). For example, the decay rate is proportional to microbial biomass whereas the production of substrate for decay is controlled by Michaelis–Menten reaction kinetics.

Although the models can have similar generic form, the individual model equations differ in the partitioning of the litter into the carbon pools, the number of pools and C flows, the environmental effect of air temperature, water stress and other variables e.g. bulk density (BD), sand and clay content of the soil. Accounting for some predictors explicitly e.g. measured BD may decrease the need for process based SOC modeling. As measured SOC stock is derived from the C concentration in the soil profile and bulk density (BD) (Poeplau et al. 2017) thus both variables can be measured together. However, considering relatively easily available information on land fertility and land cover could spatially improve process based SOC predictions (Hashimoto et al. 2017).

1.2.3 Effects of T, W, and substrate on CO_2 and CH_4 emissions

The form of the empirically derived functions between CO_2 and CH_4 emissions and factors such as temperature and water largely depend on the collected data (e.g. Alm et al. 1999, Riutta et al. 2007, Ojanen et al. 2010). As a result, CO_2 empirical functions of temperature and moisture in biogeochemical models show high variation Sierra et al. (2012, 2015). Most temperature functions used in the models agree with Arhenius' type of increase of decomposition with increased temperature, however, some functions reduce decomposition at high temperatures. In Bayesian optimization of the Yasso07 model, Tuomi et al. (2008) also found that the Gaussian type temperature response fitted best to the respiration data. This could result from the confounded response of low soil moisture content under high-temperature constraining soil respiration. In the field conditions, soil water limits respiration either by limiting the solute transport or gas transport to microbes (Figure 2). The bell-shaped response of respiration thus results in two combined substrate responses of Oxygen and available solute on respiration if each follows Michaelis-Menten (MM) kinetics (Davidson et al. 2012).

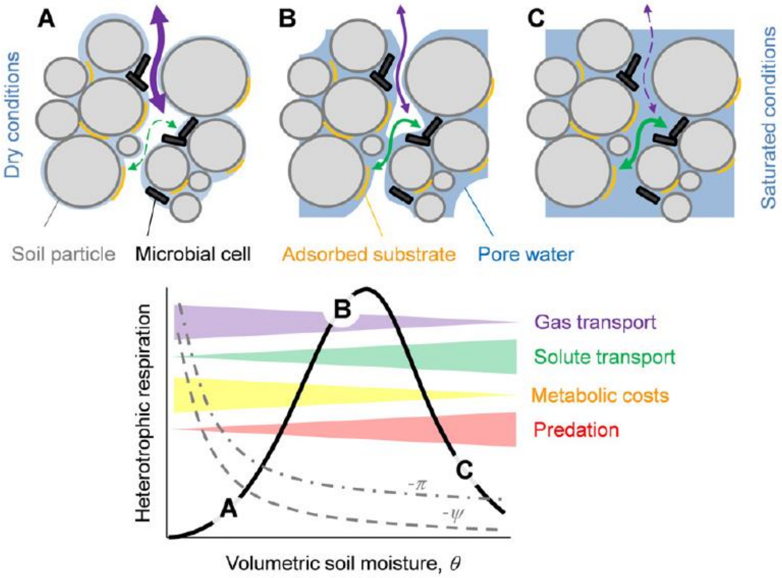


Figure 2. Soil moisture effects on microbial activity during dry conditions limiting solute transport (A), during optimal conditions for solute and gas transport (B), and during water-saturated conditions limiting the gas transport (C) (as presented by Moyano et al. 2013). The gray lines show the correlation between decreasing soil water potential ψ and microbial cell osmotic potential π.

In the soil incubation experiment, Sierra et al. (2017) found that under unconstrained substrate and moisture conditions, the temperature does not limit enzyme denaturation and follows Arrhenius temperature kinetics. In the same incubation experiment, Sierra et al. (2017) clarified that respiration, under unconstrained substrate and oxygen, saturates with increasing water content following MM kinetics. The MM saturation kinetics of respiration also applies to increasing Oxygen under an unconstrained substrate. The Michaelis-Menten type kinetics are characteristic for microbial enzyme models for soil CO_2 (Sierra et al. 2012, Davidson et al 2012, Moyano et al. 2013, Sierra et al. 2015, Manzoni et al. 2016, Abrahamoff et al. 2017, Moyano et al 2018) and CH_4 (Davidson et al 2014, Raivonen et al. 2017, Sihi et al. 2020). In microbial models, Arrhenius temperature kinetics are combined with water limitation through diffusivity of oxygen, and enzymatic transport in the soil pore space.

1.3 Aims of the study

The aims of this study were (1) to clarify in situ effects of environmental factors, namely temperature and water, on the boreal forest soil CO_2 and CH_4 emissions and SOC stocks (**I - III**), and (2) evaluate the impact of environmental factors on the mismatch between the measured soil CO_2 emissions and SOC stocks and the estimates of Yasso07 and CENTURY soil carbon models (**III - IV**). We evaluated these models due to them being listed among other models as potential tools for national greenhouse gas reporting to The United Nations Framework Convention on Climate Change (IPCC, 2019b) and their wide use (Yasso07 by several European countries, CENTURY by USA and Japan) (UNFCCC, 2019).

2 MATERIALS AND METHODS

2.1 Study sites

*2.1.1 Forest-mire ecotone (**I- II**)*

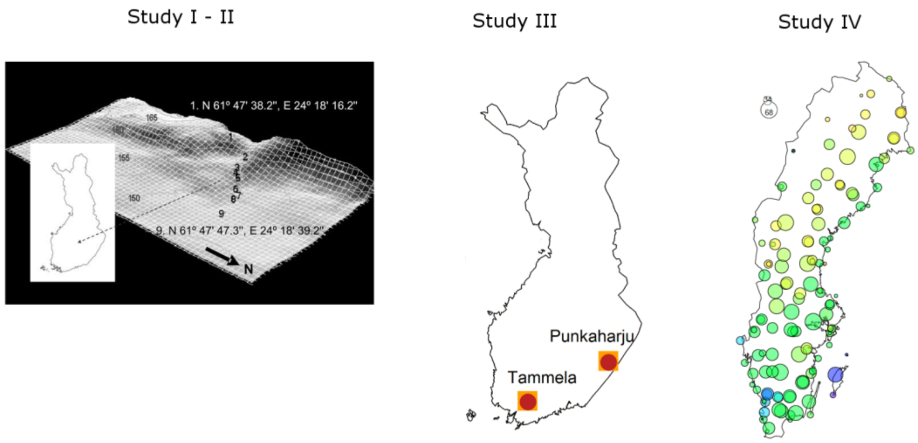
Nine forest/mire site types of Vatiharju-Lakkasuo ecotone form a gradient of soil moisture, nutrient conditions, and species distribution situated on the well-drained hill down the slope and wet depression in southern Finland (61° 47', 24° 19') (Figure 3). The ecotone extends from upland forests on mineral soil, through forest and mire transitions on gleyic soil, down to sparsely forested mires on histosoil. The soils form a catena of increased fertility from the xeric and saturated ends towards the midslope, and increased water saturation down the slope towards peatland. The site types were classified based on vegetation composition and production by the Finnish forest and mire classification systems (Cajander 1949; Laine et al. 2004). Sites range from four upland Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) dominated forests (1) xeric, (2) subxeric, (3) mesic and (4) herb-rich forest types (CT - *Calluna*, VT - *Vitis Idea*, 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 depression (8 - 9) with sparsely forested wet mire type (VSR1 and VSR2 - *Tall Sedge Pine Fen*). The forest/mire sites are situated along a 450 m transect on a 3.3 % slope facing NE with a relative relief of 15 meters (Figure 3). More detailed stand, soil, and climate characteristics were reported in **I – II**.

*2.1.2 ICP - Level II forest sites (**III**)*

The four European intensive forest monitoring (ICP – Level II) forest sites included two Scots pine and two Norway spruce dominated forest sites situated in southern Finland (Figure 3). These four sites were part of a larger network of sites across Europe intensively monitored for litter-fall measurements, nutrient cycles, growth, defoliation, ground vegetation, biotic and abiotic damage, background air quality, and meteorological characteristics. We have chosen these sites because of available measurements of the soil and biomass carbon stocks, biomass growth, litter input to the soil, as well as meteorological variables needed for the evaluation of soil carbon models. We measured soil CO_2 emissions, heterotrophic respiration (Rh), to monitor seasonal SOC changes. The forest floor on each site was trenched on three locations (1 x 1 m) to exclude tree roots respiration from total CO_2 efflux. The ingrowth of tree roots was prevented. More detailed stand, soil, and climate characteristics were reported in **III**.

*2.1.3 Swedish forest soil inventory (**IV**)*

In study **IV**, we evaluated SOC stock estimates of soil carbon models using exceptionally large soil carbon data set collected by Swedish forest soil inventory (SFSI) (Stendahl et al. 2010). The 2020 SFSI sample plots corresponded to a subsample of larger Swedish forest inventory (SFI). The sites were aggregated by the closest distance to weather stations of the Swedish Meteorological and Hydrological Institute (SMHI) network (Figure 3). More detailed forest stand, soil, and climate characteristics were reported in **IV**. The samples in SFSI data contained in addition to soil C and N stocks numerous physicochemical characteristics.



Study I - II

Study III

Study IV

Figure 3. Geographical locations of the forest – mire ecotone sites (**I-II**) and ICPII forest sites (**III**) in Finland and aggregated number of sites of National Forest Inventory to the nearest weather station in Sweden (**IV**).

The high variability of physicochemical conditions in a large data set was ideal for model evaluations and identifying conditions where the models perform well or fail. Similar Finnish data is four times smaller and was used in another study by Lehtonen et al. (2016) for evaluating structural differences in Yasso07 and ROMUL soil carbon models.

2.2 Field data

*2.2.1 CO_2, CH_4, and weather (**I- III**)*

During 2004, 2005, and 2006 we simultaneously measured meteorological conditions and forest floor total CO_2 emissions ($gCO_2\ m^{-2}\ h^{-1}$) and forest floor net CH_4 fluxes ($\mu g\ m^{-2}\ h^{-1}$) on 9 sites with 3 plot replicates on each (**I - II**). The measurement campaigns were conducted 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 CO_2 emissions were measured by chamber technique with a portable infrared analyzer (EGM4, SRC-1 PP systems Inc.). The emissions were calculated from the CO_2 concentration increase in the non-transparent chamber measured every 4.8 s during 80 s intervals.

The net forest floor CH_4 fluxes were measured by static chamber technique and air sampling from the chamber into 5 syringes sampled every 5 min (**II**). The samples were subsequently analyzed in a laboratory with a gas chromatograph (Hewlett-Packard, USA) model number HP-5890A fitted with a flame ionization detector (FID). The net CH_4 fluxes were calculated from the concentration change in the non-transparent chamber.

Monitored meteorological conditions included soil temperatures at 5 cm depth ($T_{5,}$ °C) measured with a thermometer, the depth of the water level (WT, cm) measured with contact meter, and the volumetric soil moisture at depths of 10cm ($SWC_{10,}$ %, $m^3\ m^{-3}$) measured with a portable ML2 ThetaProbe (Delta-T Devices Ltd) (**I-III**).

In **III** the four ICPII stands we measured forest soil CO_2 emissions ($g\ CO_2\ m^{-2}\ h^{-1}$) on 12 trenched plots on each site (3 trenched 1 x 1 m squares per site, each sub-divided to 4 segments). Except for the trenching of the plots for measurements of CO_2 emissions the measurement setup in **III** was the same method as in **I-II**.

*2.2.2 Swedish Forest soil inventory (**IV**)*

Swedish forest soil inventory (SFSI) dataset which originated from a stratified national grid survey of vegetation and physicochemical properties of soils was identical to the one used in Stendahl et al. (2010).

2.3 Modeling instantaneous CO_2 and CH_4 fluxes (I-III)

*2.3.1 Empirical CO_2 models (**I, III**)*

We used models (i) to evaluate responses of environmental factors to respiration and (ii) to extrapolate R to monthly and annual levels. Nonlinear least squared regression analysis (NLS) was used at each site to fit empirical models of total forest floor respiration (R_{ff}, $g\ CO_2\ m^{-2}\ hour^{-1}$) to soil temperature at 5 cm depth (T_5, °C) (**I**) and (**III**) heterotrophic forest soil respiration (R_h, g CO_2 m^{-2} $hour^{-1}$) to T_5 and volumetric soil water content at 10 cm depth (SWC_{10}, %). In study **I**, the R_{ff} NLS model used Loyd and Taylor (1994) exponential response to T_5 (Eq. 2):

$$R_{ffij} = R_{ffref}e^{\left(b\left(\frac{1}{56.02}-\frac{1}{T_5+46.02}\right)\right)} + \varepsilon_{ij} \qquad \text{Eq. 2}$$

where i^{th} forest site and j^{th} observation, R_{ff} is forest floor respiration (g CO_2 m^{-2} h^{-1}), T_5 (°C) is predictor, R_{ffref}, and b are parameters, and ε_{ij} is the error for observation *j* in i^{th} forest type.

The R_h NLS model for heterotrophic soil respiration in **III** was a combined exponential Q_{10} based response to T_5 modified by a bell-shaped response to SWC_{10} accounting for the optimum soil water content (Davidson et al. 2012) (Eq. 3).

$$R_{hij} = R_{href}d^{(\mathrm{SWC_{opt}}-\mathrm{SWC_{10}})^2}Q_{10}^{\left(\frac{T_5-10}{10}\right)} + \varepsilon_{ij} \qquad \text{Eq. 3}$$

Where i^{th} forest site and j^{th} observation R_h is soil respiration (g CO_2 m^{-2} h^{-1}), T_5 and SWC_{10} are predictors, and R_{href}, Q_{10}, SWC_{opt}, and *d* are parameters, and ε_{ij} is the error for observation *j* in i^{th} forest type.

2.3.2 Empirical CH_4 models (**II**)

The net CH_4 uptakes (µg m^{-2} h^{-1}) in mineral soil forest and small net CH_4 uptakes or emissions in the forest-mire transitions were fitted to T_5 and SWC_{10} by linear mixed-effects regression models with a random effect for forest types (Pinheiro et al. 2013).

The CH_4 fluxes for upland forests and transitions with SWC_{10} and T_5 as predictors were modeled as in following equations (Eq. 4 and Eq. 5):

$$yu_{ij} = \beta_{CT}\,SWC_{10} + \beta_{VT}\,SWC_{10} + \beta_{MT}\,SWC_{10} + \beta_{OMT}\,SWC_{10} + \beta_{CT}\,T_5 + \beta_{VT}\,T_5 + \beta_{MT}\,T_5 + \beta_{OMT}\,T_5 + b_{CT} + b_{VT} + b_{MT} + b_{OMT} + \varepsilon_{ij}, \qquad \text{Eq. 4}$$

$$yt_{ij} = \beta_{OMT}SWC_{10} + \beta_{KgK}SWC_{10} + \beta_{KR}SWC_{10} + \beta_{OMT}T_5 + \beta_{KgK}T_5 + \beta_{KR}T_5 + b_{OMT+} + b_{KgK} + b_{KR} + \varepsilon_{ij}, \qquad \text{Eq. 5}$$

where for i^{th} forest type and j^{th} observation of upland forests or transitions, $yu_{ij,}$ and yt_{ij} is the CH_4 flux (µg m^{-2} h^{-1}), and β_{CT} through β_{KR} are the fixed effect coefficients. The predictors SWC_{10} and T_5 were fixed effect variables, b_{CT} … b_{KR} are intercepts for the random effect for i^{th} forest type, and ε_{ij} is the error for observation j in i^{th} forest type.

The response function used for net CH_4 emissions accounted for a possible optimum in WT and T_5 (Turetsky et al. 2014). Thus the net CH_4 emissions (µg m^{-2} h^{-1}) of mires were fitted by using the NLS model with a combined response to T_5 and water table depth (WT) (Eq. 6):

$$y_{ij} = a_0e^{\left(-0.5\left(\frac{WT-WTopt}{WTtol}\right)^2\right)}e^{\left(-0.5\left(\frac{T5-Topt}{Ttol}\right)^2\right)} + \varepsilon_{ij} \qquad \text{Eq. 6}$$

where for i^{th} mire and the j^{th} observation yij is the CH_4 flux (µg m^{-2} h^{-1}), WT and T_5 are predictors, a_0, WT_{opt}, T_{opt}, WT_{tol}, and T_{tol} are fitted parameters, and ε_{ij} is the error for observation j in ith forest/mire type. The predictors and the errors were assumed to be multivariate normally distributed.

2.4 Boreal forest soil C and CO_2 modeling (III - IV)

The performance of two widely used biogeochemical models Yasso07 (Tuomi et al., 2009; Tuomi et al., 2011), and CENTURY (Parton et al. 1988, Metherell et al. 1993, Del Grosso et al. 2001) was evaluated against measurements of SOC stock and monthly extrapolated soil CO_2 emissions on four sites over two years (**III**) and SOC stocks of Swedish forest soil inventory sites (**IV**). The modeled SOC represented the equilibrium state between the litter input and decomposition for each site. The modeled CO_2 was calculated as the difference between monthly SOC change and the litter input (**III**). Modeled SOC strongly depends on the estimated litter input. In **III** and **IV**, the litter input was the same for both models and it was based on the method used in Liski et al. (2006).

Both soil C models use similar theoretical principles to divide litter input into the pools by chemistry e.g. percentage of cellulose and lignin (Tuomi et al., 2011, Adair et al. 2008) (Figure 4). Although the models structurally differ in mathematical representations of the principles of mass balance, pools specific substrate dependence of decay, heterogeneity, and transfers of organic matter between pools, and environmental effects described in more detail in following sections 2.4.1 and 2.4.2.

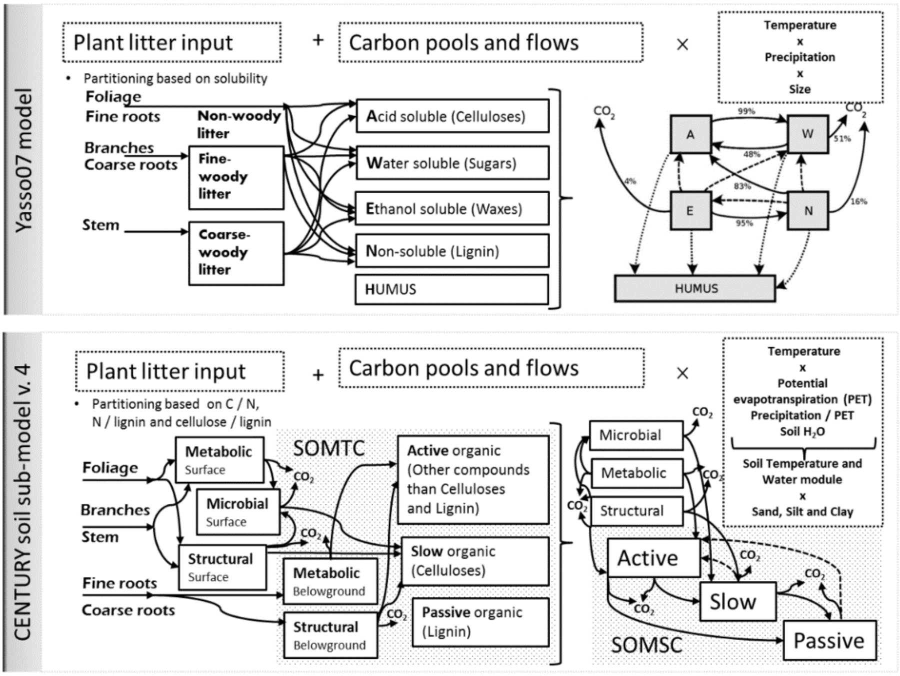


Figure 4. Comparison of the general form of C polls and flows and environmental modifiers between Yasso07 and CENTURY soil C models (based on Tuomi *et al.,* 2011; Parton et al. 1988) (**III**).

*2.4.1 Yasso07 soil C model (**III-IV**)*

In Yasso07 model (Tuomi et al., 2011) the C input is divided based on the solubility of organic material into five pools $c_A \ldots c_N$ from which three are fast (acid (c_{A}), water (c_{W}), ethanol (c_{E})), one is slow (non-soluble (c_{N})) and one is stable (humus (c_{H})). The structural matrix **A** (5 × 5) consists of mass flow parameters $\alpha_{\mathrm{A}} \ldots \alpha_{\mathrm{H}}$ and decomposition coefficients $k_{\mathrm{A}} \ldots k_{\mathrm{H}}$ as matrix diagonal. The model can be expressed mathematically as a set of differential equations as in Eq. 7:

$$\frac{\mathrm{d}\boldsymbol{c}(t)}{\mathrm{d}t} = \begin{pmatrix} i_{\mathrm{A}} \\ i_{\mathrm{W}} \\ i_{\mathrm{E}} \\ i_{\mathrm{N}} \\ i_{\mathrm{H}} \end{pmatrix} + \xi(t) \begin{pmatrix} -k_{\mathrm{A}} s_{\mathrm{L}} & \alpha_{\mathrm{A,W}} k_{\mathrm{W}} & \alpha_{\mathrm{A,E}} k_{\mathrm{E}} & \alpha_{\mathrm{A,N}} k_{\mathrm{N}} & 0 \\ \alpha_{\mathrm{W,A}} k_{\mathrm{A}} & -k_{\mathrm{W}} s_{\mathrm{L}} & \alpha_{\mathrm{W,E}} k_{\mathrm{E}} & \alpha_{\mathrm{W,N}} k_{\mathrm{N}} & 0 \\ \alpha_{\mathrm{E,A}} k_{\mathrm{A}} & \alpha_{\mathrm{E,W}} k_{\mathrm{W}} & -k_{\mathrm{E}} s_{\mathrm{L}} & \alpha_{\mathrm{E,N}} k_{\mathrm{N}} & 0 \\ \alpha_{\mathrm{N,A}} k_{\mathrm{A}} & \alpha_{\mathrm{N,W}} k_{\mathrm{W}} & \alpha_{\mathrm{N,E}} k_{\mathrm{E}} & -k_{\mathrm{N}} s_{\mathrm{L}} & 0 \\ \alpha_{\mathrm{H}} k_{\mathrm{A}} & \alpha_{\mathrm{H}} k_{\mathrm{W}} & \alpha_{\mathrm{H}} k_{\mathrm{E}} & \alpha_{\mathrm{H}} k_{\mathrm{N}} & -k_{\mathrm{H}} \end{pmatrix} \begin{pmatrix} c_{\mathrm{A}} \\ c_{\mathrm{W}} \\ c_{\mathrm{E}} \\ c_{\mathrm{N}} \\ c_{\mathrm{H}} \end{pmatrix} \qquad \text{Eq. 7}$$

where, and $\boldsymbol{i}$ defines a vector of initial carbon pools $i_{\mathrm{A}} \ldots i_{\mathrm{H}}$, $\xi(t)$ is the scalar of the environmental rate modifier, $\alpha_{o,p}$ defines mass transfer coefficients from pool p to pool o and $k_{\mathrm{A} \ldots} k_{\mathrm{H}}$ maximum decomposition rate coefficients affected by the litter size function S_L delaying decomposition for large woody type litter (e.g. snags) (Eq. 8).

$$s_{\mathrm{L}} = f(d_{\mathrm{L}}) = (1 + \delta_1 + \delta_2)^r \qquad \text{Eq. 8}$$

Where δ_1, δ_2, and r are parameters, and $\mathrm{d_L}$ (cm) is the diameter of the fine-woody and coarse-woody litter (e.g. 2 and 20), whereas $\mathrm{d_L}$ of non-woody litter is zero and not effecting decay rates. Empirical tests of this function showed that for typically managed forest litter (not including snags) the model can be run for all pools together reaching almost identical equilibrium with or without $\mathrm{S_L}$ modifier.

Although the model was calibrated for running on annual time steps (**IV**), it can also run on monthly time steps (**III**) if the litter input is provided on a monthly level. Then $\xi(t_m)$ (**III**) is formulated as a function of monthly air temperature (T_{m}) and 1/12 of annual precipitation (P_{a}/12) (Eq. 9).

$$\xi(t_{\mathrm{m}}) = k_i e^{\left(\beta_1 T_{\mathrm{m}} + \beta_2 T_{\mathrm{m}}{}^2\right)} \left(1 - e^{\gamma \frac{P_{\mathrm{a}}}{12}}\right) \qquad \text{Eq. 9}$$

Where k_i is the maximum decomposition rate of the ith carbon pool, β_1, β_2, and γ are parameters of the environmental function. For running the model on the annual time step as in Tuomi et al. (2011) $\xi(t_a)$ function uses annual temperature ($\mathrm{T_a}$) modified by approximation of temperature seasonality and annual precipitation ($\mathrm{P_a}$) (**IV**).

*2.4.2 CENTURY soil C model (**III-IV**)*

In the CENTURY model (Metherell et al. 1993) the C input is divided between eight carbon pools $c_1 \ldots c_8$ (surface and soil structural, surface and soil metabolic, surface microbial, active, slow, and passive) (Figure 4). The structural matrix **A** (8 × 8) consists of mass flow parameters $\alpha_1 \ldots \alpha_8$ and decomposition coefficients $k_1 \ldots k_8$ as matrix diagonal. The model can be expressed mathematically as a set of differential equations as in Eq. 10:

$$\frac{\mathrm{d}\boldsymbol{c}(t)}{\mathrm{d}t} = \boldsymbol{i}\begin{pmatrix} F_\mathrm{m} \\ F_\mathrm{s} \\ 0 \\ F_\mathrm{m} \\ F_\mathrm{s} \\ 0 \\ 0 \\ 0 \end{pmatrix} + \xi(t)\begin{pmatrix} -k_1 e^{-3L_\mathrm{s}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & -k_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ \alpha_{3,1}k_1 e^{-3L_\mathrm{s}} & \alpha_{3,2}k_2 & -k_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & -k_4 e^{-3L_\mathrm{s}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & -k_5 & 0 & 0 & 0 \\ 0 & 0 & 0 & \alpha_{6,4}k_4 e^{-3L_\mathrm{s}} & \alpha_{6,5}k_5 & -k_6 f\left(T_\mathrm{SiC}\right) & \alpha_{6,7}k_7 & \alpha_{6,8}k_8 \\ \alpha_{7,1}k_1 e^{-3L_\mathrm{s}} & 0 & \alpha_{7,3}k_3 & \alpha_{7,4}k_4 e^{-3L_\mathrm{s}} & 0 & \alpha_{7,6}k_6 f\left(T_\mathrm{SiC}\right) & -k_7 & 0 \\ 0 & 0 & 0 & 0 & 0 & \alpha_{8,6}k_6 f\left(T_\mathrm{C}\right) & \alpha_{8,7}k_7 f\left(T_\mathrm{C}\right) & -k_8 \end{pmatrix}\begin{pmatrix} c_1 \\ c_2 \\ c_3 \\ c_4 \\ c_5 \\ c_6 \\ c_7 \\ c_8 \end{pmatrix}$$

Eq.

10

Where $\boldsymbol{i}$ is the vector of plant C input partitioned between the above- and below-ground structural and metabolic pools with F_m and F_s fractions. The L_s is the lignin (structural) fraction. Maximum decomposition rates in the active, slow, and passive pool are also affected by functions of soil silt and clay contents $f(T_\mathrm{SiC})$ or function of clay content $f(T_\mathrm{C})$.

The environmental rate modifier $\xi(t)$ is a function of monthly temperature $f(T)$ and water $f(W)$ as in Adair et al. (2008) (Eq. 11) (**III-IV**) and Kelly et al. (2000) and (Eq. 12) (**III**).

$$\xi = \frac{1}{1+w_1 e^{w_2 W}}\, t_1\, e^{\frac{t_2}{t_3}\left(1-\left(\frac{T_{max}-T}{T_{max}-T_{opt}}\right)^{t_3}\right)\left(\frac{T_{max}-T}{T_{max}-T_{opt}}\right)^{t_2}} \qquad \text{Eq. 11}$$

Where w_1, w_2, t_1, t_2, t_3, T_{max}, and T_{opt} are parameters, W is the ratio between precipitation and potential evapotranspiration, and T is mean monthly air temperature (°C).

$$\xi = \left(\frac{\frac{W}{1-\frac{bulkd}{partd}}-w_2}{w_1-w_2}\right)^{w_4\left(\frac{w_2-w_1}{w_1-w_3}\right)}\left(\frac{\frac{W}{1-\frac{bulkd}{partd}}-w_3}{w_1-w_3}\right)^{w_4}\left(t_1+t_2 e^{t_3 T}\right) \qquad \text{Eq. 12}$$

Where w_1, w_2, w_3, w_4, t_1, t_2, and t_3 are parameters, bulkd is bulk density, partd is particle density, W is volumetric soil water content (%), and T is mean monthly air temperature (°C).

3 RESULTS AND DISCUSSION

3.1 Controls of forest floor C fluxes in empirical models

*3.1.1 CO_2 emissions (**I**)*

The NLS analysis used to fit empirical models of total forest floor respiration (R_{ff}, g CO_2 m^{-2} $hour^{-1}$) to soil temperature at 5 cm depth (T_5, °C) showed a relatively high percentage of explained variance of measured data (R^2 in the range between 0.72 in VSR2 and 0.88 in VT) (Table 1) (**I**). The highly explained variance by temperature indicated that during the typical climatic conditions for the region the effect of soil moisture variation on forest floor respiration was lower than that of temperature regardless of the high spatial variation of long-term moisture. This agreed with Webster et al. (2008) whose empirical model of measured soil respiration in a forest – mire transect in Canada related majority of the variance to temperature (48%) and only 9% to moisture.

The parameter of the basal respiration in **I** was comparable to the values of other studies in similar conditions (Riutta et al. 2007, Kolari et al. 2009, Pumpanen et al. 2015) but it was not a clear indicator of the spatial differences between forests and mires. Although the base respiration was higher for upland forest and transition compared to mires which could indicate either larger contribution of heterotrophic respiration from deeper soil layers but also a potentially larger contribution of autotrophic respiration of tree roots. Separation of the forest floor autotrophic and heterotrophic respiration components would be crucial for understanding the expected response of soil carbon to the warming climate (Bond-Lamberty et al. 2004, Wieder et al. 2013, Pumpanen et al. 2015). However, the activation energy of sites with the largest SOC such as swamp (KR) and mires (VSR) was significantly higher than in other forest sites with less SOC (CT…KgK). The higher activation energy of respiration in KR and VSR indicated that their SOC was lower quality, required larger enzyme pool to decompose, and it was thermally more stable than in CT…KgK (Allison et al. 2010, Sierra et al. 2012a).

Weak soil moisture effect on R_{ff} was seen also from the lack of significant correlation in Pearson correlation analysis. On the other hand, the strong ($r = 0.92$) correlation between the depth of the organic horizon and the annual mean soil moisture was highly significant (p-value = 0.01) (**I**). In conditions of warming climates, with more frequent droughts and water table drawn down, different changes to C stocks could be expected between peatlands and forested peatlands (Minkkinen et al. 1999, Lohila et al. 2011), nevertheless, the peatland's potential role as C sinks in the boreal landscape would be more pronounced (Leifeld and Menichetti 2018).

Table 1. Statistics (s) and parameters (p) of the non-linear regressions (Eq. 1) between the forest floor respiration (g CO_2 m^{-2} h^{-1}) and soil temperature at 5 cm depth (T5, °C) fitted for each forest/mire type including upland forests on mineral soils (CT, VT, MT, OMT), forest-mire transitions (OMT+, KgK, KR) and mire (VSR1, VSR2).

		Forest/mire types								
p	s	CT	VT	MT	OMT	OMT+	KgK	KR	VSR1	VSR2
	R^2	0.74	0.88	0.82	0.80	0.77	0.80	0.72	0.74	0.72
R_{ffref}	Mean	0.38	0.27	0.30	0.50	0.34	0.33	0.39	0.21	0.26
	SD	0.07	0.02	0.02	0.07	0.04	0.07	0.08	0.04	0.05
b, K	Mean	350	412	401	344	379	394	507	525	518
	SD	58	54	30	12	37	36	67	63	107

*3.1.2 CH_4 exchange (**II**)*

The mineral soils (in upland forests CT...OMT) and organo-mineral soils (in the forest – mire transitions) (OMT+…KR) showed small but significantly different net mean CH_4 oxidation between -26 and -58 (µg m^{-2} h^{-1}) (Table 2, parameters bi and "group bi") and occasionally small CH_4 emissions (<100 µg m^{-2} h^{-1}). The range of the mean CH_4 oxidation (Table 2) was relatively small in comparison with the order of magnitude larger differences in mean CH_4 emissions of organic soils in mires (VSR1, VSR2) (Table 3, parameter a0). The increasing SWC_{10} for both upland and transitional forests significantly correlated with reducing CH_4 oxidation up to around zero CH_4 exchange at maximum water content in transitions. The positive significant correlation between CH_4 oxidation and T_5 was observed only for uplands (Figure 5). In transitions, T_5 was not a significant ($p = 0.629$) predictor of CH_4 exchange (Table 2). Similar correlations for well-drained sites were found by Ullah et al. (2011) who extrapolated their CH_4 emissions with exponential relationship to the combined response of moisture and temperature.

In this study (**II**) we found that the CH_4 fluxes in undisturbed forest-mire transitions were near-zero, despite high SWC_{10} (SWC10 > 70 %) and close to surface annual average water level (WT -24 cm). Near-zero CH_4 fluxes agree with Ojanen et al. (2010) who for drained forested peatlands in Finland reported an exponential increase in CH_4 emissions with annual WT level increase from around -30 cm depth to the surface. Although the CH_4 exchange for their sites between -30 cm and -10 cm varied largely, between zero and 4 g CH_4 m^{-2} $year^{-1}$. The difference in WT depth of forest-mire transitions and lack of CH_4 emissions could be also attributed to the uncertainty of differences in nutrient status and differences in species composition (Turetsky et al. 2014).

Table 2. CH_4 flux (µg m^{-2} h^{-1}) model statistics (parameters, their standard errors and root mean square error) for the upland forest types (CT, VT … OMT (Eq. 4), and for the forest-mire transitions (OMT+, KgK, and KR (Eq. 5) fitted with volumetric soil moisture at 10 cm (%) and soil temperature at a depth of 5 cm (°C).

Eq. 4	bi	group bi	group bi SE	βi1	βi1 SE	βi2	βi2 SE	N	RMSE
CT	-39.3	-43.6	9.1	0.7^{a}	0.3	-1.2	0.2	137	35.2
VT	-26.2							143	25.1
MT	-51.0							139	25.2
OMT	-58.0							144	32.1
Eq. 5									
OMT+	-49.9	-50.2	7.5	0.6	0.1	-0.1^{b}	0.2	139	22.3
KgK	-48.2							146	17.9
KR	-52.6							149	31.5

$p < 0.001$ for all parameters, except ^{a} $p = 0.011$, ^{b} $p = 0.629$

βi1 - soil moisture at 10 cm, βi2 - soil temperature at 5 cm

Table 3. CH_4 flux (µg m^{-2} h^{-1}) model statistics (parameters, their standard errors and root mean square error) for the mires (VSR1, VSR2 (Eq. 6) fitted with water table depth from the surface (cm) and soil temperature at a depth of 5 cm (°C).

Eq. 3	a0	a0 SE	T_{opt}	T_{opt} SE	T_{tol}	T_{tol} SE	WT_{opt}	WT_{opt} SE	WT_{tol}	WT_{tol} SE	N	RMSE
mires	1207	127	13.9	1.4	6.4	1.3	18	1.9	16.6	2.1	324	656
VSR1	1570	155	13	0.8	5.8	0.8	18.6	1.6	15.5	1.7	162	424
VSR2	801.3	191	16.6^{a}	6.8	8.7^{b}	4.5	17.3^{c}	5.3	20.7^{d}	9.7	162	558

p values < 0.001, except ^{a} p = 0.016, ^{b} p = 0.053, ^{c} p = 0.002, ^{d} p = 0.035

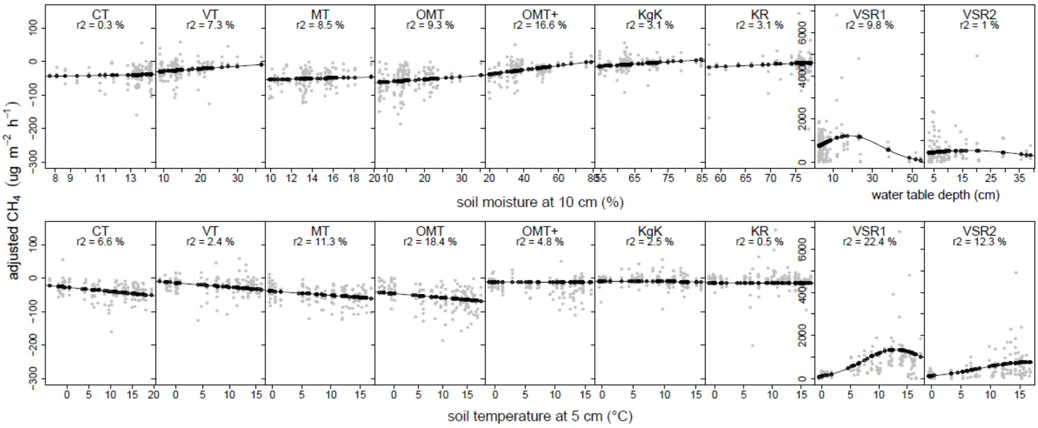


Figure 5. Residual figures of CH_4 fluxes (µg m^{-2} h^{-1}) of the NLS models and volumetric soil moisture at 10 cm (%) (CT…KR), water table depth (VSR1, VSR2), and soil temperature at a depth of 5 cm for nine forest/mire types. The CH_4 flux response for each factor is showed by modeled value for allowing only one factor at a time to vary while the other was at its mean. Black points show the model function and gray points show the corresponding residual for unexplained model variation. The r2 value is the percentage of explained variance. The sites are arranged from forests (left) to mires (right).

In comparison to few existing studies finding small CH4 emissions for forest –mire transects in Canada and Europe (Moosavi and Crill 1997, Ullah et al. 2011, Schneider et al. 2018), similarly in this study, the CH4 exchange of forest – mire transitions was near zero during wetter periods and a small sink during drier periods. In landscape biogeochemistry, forest-mire transitions have the potential to become small sources of CH4 if their water level increases closer to the surface, but their CH4 emissions are expected to be smaller than in mires.

The net CH4 emissions in mires showed asymmetric Gaussian response form to WT depth and T5. If the temperature was at its optimal 13.9 °C then CH4 emission peaked at

1207 μg m−2 h−1 at 18 cm WT depth (Table 3), decreased to 670 μg m−2 h−1 as WT rose to the surface and 115 μg m−2 h−1 with WT drawn down to its minimum (54 cm). The effect of T5 on CH4 emissions in mires also showed asymmetric Gaussian form with significant optimum for both mires fitted together (Table 3). However, in VSR2 the fitted function showed insignificant temperature optimum (Table 3, Figure 5).

Although gaussian functional WT response accounts for a wider range of conditions, depending on the measured data linear, exponential, and sigmoidal functions can sufficiently explain the observed variation (Kettunen et al. 2000, Alm et al. 2007, Ojanen et al. 2010, Ullah et al. 2011, Marushchak et al. 2016). The explained variances of the fitted Gaussian models in this study (II) were relatively low due to large temporal variation in water level variations and moisture (Figure 5) and due to processes unaccounted by empirical functions with T and WT. For example, besides T and WT in tall - sedge fens vegetation distribution is a major control of CH4 emissions by photosynthetic production of aerenchymal vegetation and supply of acetate for CH4 production and its direct transport to the atmosphere (Shurpali and Verma 1998, Hines 2007, Rinne et al. 2018). The dynamics of CH4 production, consumption and transport mechanisms and their driving environmental variables such as vegetation development, photosynthesis, variation in water level, peat oxygenation, and temperature could be expressed more explicitly by process-based models e.g. HPM (Frolking at al. 2010, 2014), HIMMELI (Raivonen et al. 2017), or ORCHIDEE-PEAT (Qiu et al. 2019). Although the HPM and ORCHIDEE-PEAT models simulate primarily peat development than CH4 exchange, information on available soil C is key for simulating decomposition in Michaelis-Menten type gas exchange models (Davidson et al. 2014) such as HIMMELI. In HIMMELI, the anaerobic respiration (a product of vascular plants NPP and anaerobic peat decomposition) is a required input for O2 limited CH4 production while both aerobic respiration and CH4 oxidation follow substrate (O2 and CH4) dependent MM kinetics (Raivonen et al. 2017).

The models with moisture dependency expressed by dual substrate MM functions are mechanistically more reasonable but not fundamentally different from Gaussian moisture function fitted empirically. The performance between the two may be similar; however, if substrate C accessible to enzymes is dynamic then MM model performance improves (Davidson et al. 2014).

3.2 Controls of soil C stock change in process models

*3.2.1 T, W effects on soil heterotrophic respiration (**III**)*

The empirical environmental modifiers of decomposition in Yasso07 and CENTURY soil C models (Eq. 9, 11, and 12) show exponential or Gaussian dependence on air temperature, and sigmoidal or Gaussian dependence on water (precipitation or volumetric soil water content) (Figure 6) (**III**). Calibrating these functions with monthly R_h measurements (Figure 6) strongly improved the fit between the measured and modeled CO_2 values (Figure 7) demonstrating the need for their improvement towards more mechanistic representation.

For example, the environmental function of the Yasso07 model (Eq. 9) largely changed after calibration by reducing the inversion point of the Gaussian temperature modifier. The Yasso07 model's precipitation curve has not visibly changed after calibration. Although these environmental modifiers are not necessarily the best for all applications, the estimated CO_2 emissions of the Yasso07 model after calibration showed the best match with the measurements in this study (Figure 7). For modeling, fine-scale spatial differences of SOC distributions and predicting response of SOC to warming, climate use of soil temperature instead of air temperature would be in the boreal region more feasible due to the lag between air and soil warming (Todd-Brown et al. 2013, Halim and Thomas 2018, Soong et al. 2020). The Gaussian air temperature function showed the best fit with calibrated data (Tuomi et al. 2008). This may not be the best if measurements of soil temperature would be used instead. Sierra et al. (2017) clarified that under the range of soil temperature in the boreal forests, the temperature response of decomposition is exponential due to no enzymatic constraints. However, the aerobic decomposition rate at a given temperature is limited due to dual substrate limitations (lack of O_2 is limiting microbial physiology under high moisture and physical constraints are limiting C solute transport to microbes during low moisture conditions) (Moyano et al. 2013, Manzoni et al. 2016). The study sites in **III** were well-drained mineral soil forests with a small number of measurements over the soil moisture optimum for which the model slightly overestimated CO_2 emissions. For higher soil moisture levels such as in forest – mire transitions, defining the modifier based on MM kinetics or Gaussian response would be more crucial as it would account for the reduction of respiration.

In Eq. 11 (CENTURY.A), the temperature response with default parameters showed steep increase just over 20 °C with an optimum over 30 °C but after the calibration the response was linear (Figure 6). The moisture effect of the same function remained similar after the calibration (Figure 6). As expected, the CENTURY.A model residuals after calibration showed a small mismatch with measurements (Figure 7).

Exponential relation with temperature and Gaussian relation with soil moisture in Eq. 12 (CENTURY.K) were like the NLS empirical Q_{10} temperature function and Gaussian moisture function of Eq. 3. The NLS functions were used for the extrapolation of hourly measurements to a monthly level. However, the CENTURY.K results remained similar after calibration and residuals have improved less compared to CENTURY.A (Figure 7) which could be an indication of the poor-quality soil water content measurements used. This points to the need for high-quality soil water data if those are to be used in the models.

Modeled soil respiration divergence with measurements after the calibration, the overestimation in spring, and underestimation in autumn highlights a need for reformulating the environmental modifiers. The modeled early increase of spring respiration could indicate the unaccounted lag between air and soil warming (Todd-Brown et al. 2013) whereas an early decline in autumn respiration could indicate unaccounted microbial pathway (Averill *et al*., 2014; Wieder *et al*., 2013, Luo *et al*., 2016).

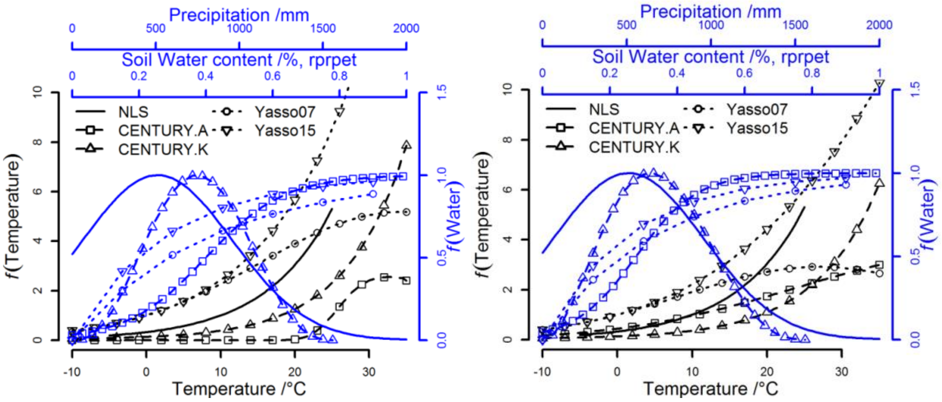


Figure 6. (Left) Default temperature and water functions of the Yasso and CENTURY models in comparison to the nonlinear model fit to the respiration measurements (Eq. 3). (Right) Calibrated functions with the respiration measurements (**III** Supplement).

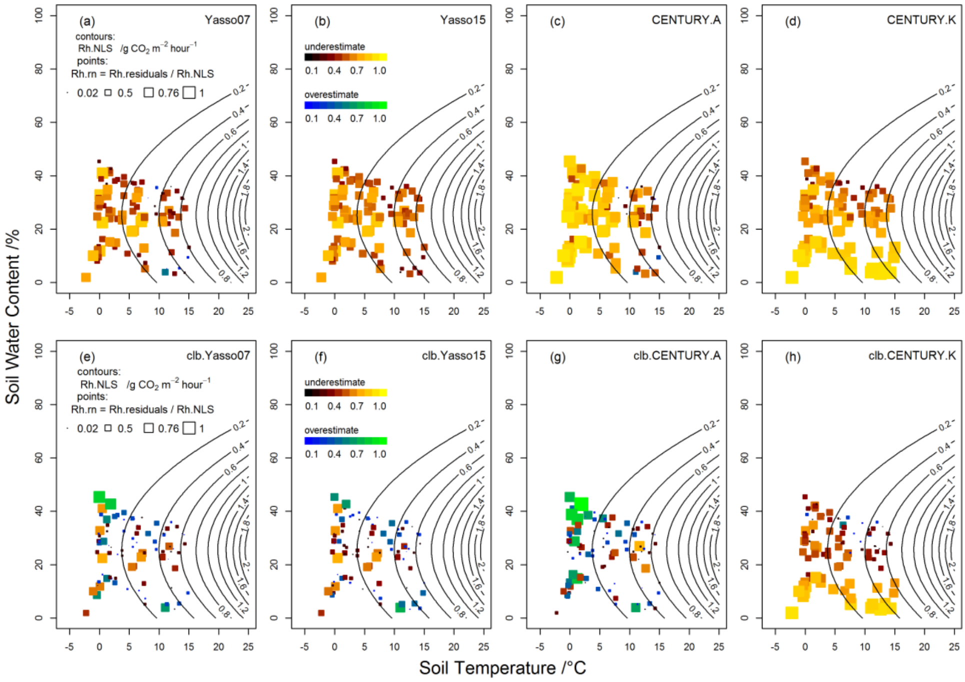


Figure 7 Point distributions of normalized model residuals (Rh.rn) of soil respiration (Rh, g CO_2 m^{-2} $hour^{-1}$) plotted in space of soil temperature and moisture. Contour lines, based on Rh measurements, show interpolated Rh.NLS values with Eq. 3. The Rh residuals were normalized (Rh.rn) with Rh.NLS values. The panels show model outputs with default parameters (a)…(d) and those with calibrated empirical models (e)…(h).

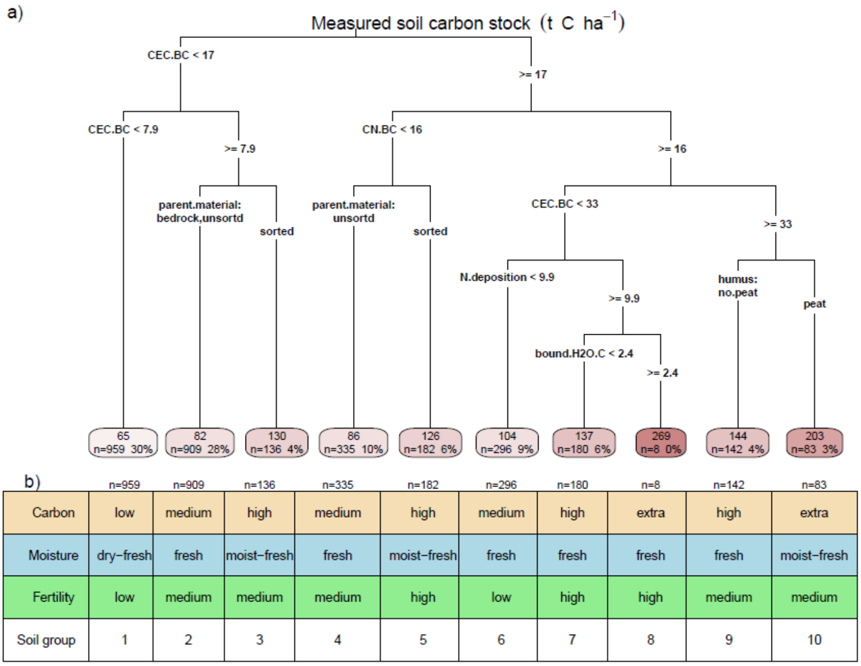
*3.2.2 Effect of soil W and nutrient status on SOC (**IV**)*

The well-drained mineral soils of Swedish forest soil inventory (SFSI) data were separated based on physicochemical soil properties into 10 groups by using the regression tree model (Figure 8). The main predictor for SOC levels was the cation exchange capacity of the BC horizon (CEC, $\mathrm{mmol_c\,kg^{-1}}$) (**IV**) linked to the soil nutrient status. This supported conclusion on the importance of nutrient status on SOC accumulation based on ecosystem carbon use efficiency derived from forest CO_2 balance (Fernández-Martínez et al. 2014). The CEC levels had divided 2/3 of all SFSI SOCs to lower SOC stock groups (between 65 and 130 t C $\mathrm{ha^{-1}}$) and 1/3 to larger groups (between 86 and 269 t C $\mathrm{ha^{-1}}$) (Figure 8). Besides CEC, the sorted soil parent material (linked with higher clay content), the N deposition over 10 kg N $\mathrm{ha^{-1}\ y^{-1}}$ and peat humus type were also influential controls for larger SOCs linked to site fertility (Figure 8).

The modeled Yasso07 and CENTURY SOCs matched the 2/3 of the lower level SOCs of sites with low and medium nutrient status, and underestimated 1/3 of SOCs of sites with higher fertility (Figure 9) (**IV**). The performance of both models was similar. Though, CENTURY, due to considering C association with soil minerals, outperformed Yasso07 for soils with higher clay content (group 5 in Figure 9). In the comparison of SOC from 11 ESM against observational databases, Todd-Brown et al. (2013) attributed modeled divergence from observations to uncertainty in input data, incorrect environmental response functions, and missing formulation of essential processes in seemingly uniform first-order decay models. Although the C/N ratio was identified as a key factor related to SOC accumulation in northern observational databases, the nutrient status is underrepresented in Earth system models (ESM) (Hashimoto et al. 2017).

Yasso07 and CENTURY models have also relatively similar structure (Figure 4) and use similar environmental functions (Figure 6). Although, the individual equations and parameters differ (see Eq. 7 and Eq. 9 for model structure, and Eq. 9 and Eq. 10 for environmental modifier). Yasso07 did not require soil properties and the variation in soil fertility was reflected in data through a difference in the quantity of litter input and chemistry between plant species and its components.

In contrast, CENTURY in addition to variation in litter input accounted for SOC association with soil clay content and for SOC increase with soil N content. However, the effect of the CENTURY’s topsoil N function on SOC stock, when tested in **IV**, was negligible compared to the effect of litter input. Thus, in **IV** we had run only C sub-model of CENTURY. The CENTURY model also accounted for an optional reduction of decomposition using the approach of Reich et al. (2000) which was originally meant to be applied for poorly drained soils; thus, the approach could have been insufficient for simulating larger SOCs in relatively well-drained groups in **IV**.



	n=959	n=909	n=136	n=335	n=182	n=296	n=180	n=8	n=142	n=83
Carbon	low	medium	high	medium	high	medium	high	extra	high	extra
Moisture	dry−fresh	fresh	moist−fresh	fresh	moist−fresh	fresh	fresh	fresh	fresh	moist−fresh
Fertility	low	medium	medium	medium	high	low	high	high	medium	medium
Soil group	1	2	3	4	5	6	7	8	9	10

Figure 8. a) The regression tree for the SFDI SOC (t ha^{-1}) separated into 10 groups based on soil physicochemical properties and site environmental characteristics; the cation exchange capacity of BC horizon (CEC.BC, mmol$_c$ kg^{-1}), the C/N ratio (CN.BC), the nitrogen deposition (N.deposition, kg N ha^{-1} y^{-1}), the highly bound soil water of C horizon (bound.H2O.C, %), and soil class variables as type of sorted or unsorted soil parent material and humus type. The mean SOC and number and percentage of samples are shown for each group. b) The 10 physicochemical soil groups of the regression tree model are interpreted by increasing levels of carbon, soil moisture, and fertility from left to right.

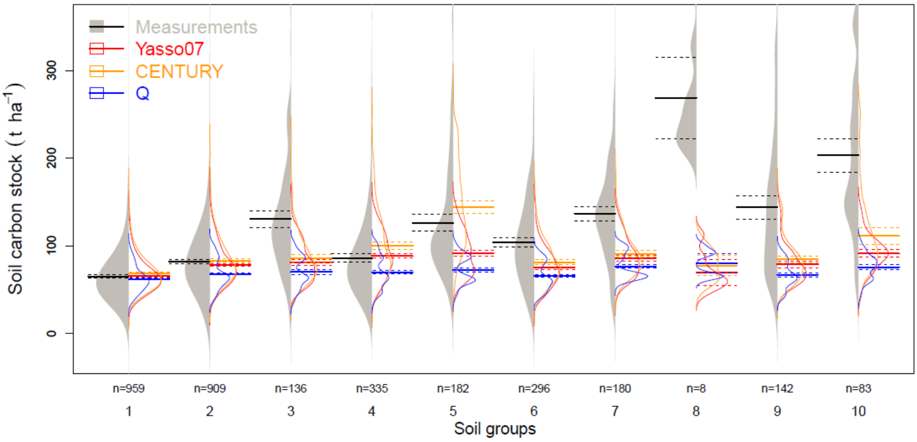


Figure 9. Measured (area) and modeled distributions (lines) of Yasso07, CENTURY, and Q models for 10 physicochemical groups of the soil carbon (t ha^{-1}). The thin lines are the density distributions. The thick lines are the group means and dashed lines are their confidence intervals. The n is number of samples. For a description of group levels of SOC stocks, moisture, and fertility see Figure 8.

In **IV**, we tested models against measured data with their default parameters. The default parameterization, as seen on the calibration of its environmental functions in **III**, contributed to data mismatch. The soil carbon models were parameterized globally for Yasso07 or regionally for CENTURY (coniferous forest) and do not require further calibrations. Nevertheless, the models could be calibrated for specific regions and datasets e.g. Nordic countries (Rantakari et al. 2012) where SOC responses to mean annual temperature, precipitation, and soil C/N ratio differ from the global trend (Hashimoto et al. 2017). However, in **IV** the Yasso07 model comparison against SFSI SOCs data showed larger underestimation with Nordic parameters from Rantakari et al. (2012) than with global parameters from Tuomi et al. (2011). Therefore, the SOCs underestimation for SFSI sites with higher moisture and fertility could also indicate the misconception in sensitivities to moisture (insufficient reduction of decomposition in wetter sites) and nutrient status (negligible increase with increasing soil N content).

Thus, the models could benefit from reformulating sensitivity to soil moisture and nutrient status. Moisture function could explicitly formulate MM substrate diffusion fluxes (O_2 and C substrate accessible to an enzyme) (Davidson et al. 2012) during soil drying. If the C substrate is modeled dynamically (e.g. with pool-specific MM kinetics), models could account for both drying and wet up events (Oikawa et al. 2014, Davidson et al. 2014, Sihi et al. 2018). In a study by Goll et al. (2017), Yasso environmental modifier affecting the decomposition rate of C_A, C_W, C_E, and C_N pools was found to be downregulated by N depending on the soil supply and demand by microbes and plants. Resulting SOC accumulation was smaller for soils with limited N. The structure of the N sub-model in CENTURY is the same as for C (Metherell et al. 1993, Del Grosso et al. 2001) and like that of Goll et al. (2017). Coupled CENTURY C-N sub-models were run e.g. in modeling SOC sequestration of European arable soils (Lugato et al. 2014). Mechanisms of increased SOC accumulation with higher soil nutrient status related with reduced C uptake and increasing microbial carbon use efficiency with available N (Manzoni et al. 2016) were integrated already in microbial enzyme MM models (Allison et al. 2010, Wieder et al. 2014, Abramoff et al. 2017) and combined microbial MM and first-order decay model (Moyano et al. 2018).

In **III** and **IV**, the forest soils were relatively well-drained, as Yasso07 and CENTURY models are meant for application on mineral soils. Improved representations of model functions would be especially important for extending the application of modeling studies from mineral soils to organic soils. Although mineral soils are most common, the less represented organic soils could be more crucial for climate change related dynamics of boreal zone soil carbon storage (Turetsky et al. 2015, Leifeld and Menichetti 2018). As indicated by studies in the gradient of soil moisture and nutrient status (**I** and **II**), the forest – mire transitions on organo-mineral forest soil and peatlands, with the largest soil C storage, have the largest potential for acting as soil C sink in the landscape or the vulnerability to become C sources.

4 CONCLUSIONS

In **I-IV**, the main controls of boreal forest soil organic carbon (SOC) accumulation and CO_2 and CH_4 emissions were demonstrated and discussed in the order of importance; soil temperature and water (**I-III**), and nutrient status (**IV**). The main emphasis was to evaluate the empirical representation of the controls in the data, and their mathematical formulation in the semi-empirical process-based models (Yasso07 and CENTURY) concerning current knowledge of the processes and the model development.

Spatially, soil temperature (and not the soil moisture) explained the most instantaneous variation of soil CO_2 emissions, although the long-term moisture strongly correlated with SOC socks (**I**). However, during extreme weather events such as prolonged summer drought, mainly soil CO_2 emissions in mineral soil forests and CH_4 emissions in mires were significantly reduced (**II**). Similar temperature and moisture sensitivities of forest-mire transitions to upland forests indicated that transitions do not act as hot spots of CO_2 and CH_4 emissions in the boreal landscape (**I -II**). Both parametrization and formulation between the representation of temperature and moisture functions in Yasso07 and CENTURY affected the fit between the measured and modeled seasonal soil CO_2 emissions (**III**). Similarly, at the country level, the forest SOC stocks in Sweden increased with higher moisture and nutrient status (**IV**). Yasso07 and CENTURY reconstructed SOCs well for mesotrophic soils but failed for soils with higher fertility and wetter soils (**IV**).

The main conclusion is that the empirically based representation of soil temperature, water, and productivity controls in Yasso07 and CENTURY models affected the mismatch between measured and modeled seasonal CO_2 emissions and long-term SOC sequestration. These models are currently applicable on mineral soils, however, due to a large C storage in organo-mineral and organic soils in boreal landscape, we also need models for forest-mire transitions and peatlands. Thus, further model development could be more explicit about a supply of the C-N to microbes, microbial C-N uptake related to nutrient status and enzyme kinetics. Including microbial and enzyme kinetics in the models would account for climate – plant – soil – microbial C-N interactions more mechanistically. As a result, more mechanistic and spatially applicable models would improve the estimates of boreal forest soil C feedback to changing climates.

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