



# 1 Soil and forest floor carbon balance in drained and undrained 2 hemiboreal peatland forests

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4 Aldis Butlers<sup>1</sup>, Raija Laiho<sup>2</sup>, Kaido Soosaar<sup>3</sup>, Jyrki Jauhiainen<sup>2</sup>, Thomas Schindler<sup>3</sup>, Arta Bārdule<sup>1</sup>,  
5 Muhammad Kamil-Sardar<sup>3</sup>, Andreas Haberl<sup>4</sup>, Valters Samariks<sup>1</sup>, Hanna Vahter<sup>3</sup>, Andis Lazdiņš<sup>1</sup>, Dovilē  
6 Čiuldienē<sup>5</sup>, Kęstutis Armolaitis<sup>5</sup>, Ieva Līcīte<sup>1</sup>

7 <sup>1</sup>Latvian State Forest Research Institute (Silava), Salaspils, 2169, Latvia

8 <sup>2</sup>Natural Resources Institute Finland (Luke), Helsinki, P.O. Box 2, 00791, Finland

9 <sup>3</sup>Department of Geography, University of Tartu, Tartu, 51014, Estonia

10 <sup>4</sup>Michael Succow Foundation partner in the Greifswald Mire Centre, 17489 Greifswald, Germany

11 <sup>5</sup>Department of Silviculture and Ecology, Lithuanian Research Centre for Agriculture and Forestry, Kėdainiai distr., 58344,  
12 Lithuania

13 *Correspondence to:* Aldis Butlers (aldis.butlers@silava.lv)

14 **Abstract.** Drainage of organic soil is associated with increasing soil carbon (C) efflux, which is typically linked to losses in C  
15 stock. In previous studies, soil in drained peatland forests has been reported as both a C sink and source depending on, e.g.,  
16 soil nutrient and moisture regimes. However, most of the earlier research was done in boreal sites, and the impact of soil  
17 moisture regime on soil C stock is likely to vary across different climatic conditions and ecosystems, depending further on  
18 vegetation. In this study, we examined the soil and forest floor (including ground vegetation) C balance in drained and  
19 undrained hemiboreal forests to evaluate drainage impact on C balance. A two-year study was conducted in 26 drained and  
20 undrained forest stands with nutrient-rich organic soil in the Baltic states (Estonia, Latvia, Lithuania). To assess the C balance,  
21 measurements of soil heterotrophic and total respiration were carried out, along with the evaluation of C influx into the soil  
22 through litter, including fine foliar litterfall, herbaceous ground vegetation, and fine roots of trees. The CO<sub>2</sub> emissions did not  
23 significantly differ between the study countries; therefore, one emission factor can be applied to characterize soil emissions in  
24 the Baltic States. It was observed that C influx into the soil through litter can compensate for the C losses caused by  
25 heterotrophic soil respiration, and neither drained nor undrained soils were proven to be losing their C stock. Comparing the  
26 C balances in drained and undrained sites, it was found that drainage of organic soils reduces their C sequestration by  
27 0.43±2.69 t C ha<sup>-1</sup> year<sup>-1</sup>.

## 28 1 Introduction

29 Soil in peatlands, characterized by its high content of partially decomposed plant matter, is a major terrestrial organic carbon  
30 (C) stock, estimated to range from 504 to 3000 Gt C (Scharlemann et al., 2014). Although northern peatlands make up only 2-  
31 4% of the global land area, they contain a substantial amount of soil C, ranging from 126 to 621 Gt C (Yu, 2012), highlighting  
32 the significance of these peatlands in the global C budget. About 28% of the pristine (undrained) peatlands globally are  
33 inherently covered by forest (Zoltai and Martikainen, 1996), and those forested peatlands in the boreal biome can accumulate  
34 C into the soil at similar rates to non-forested peatlands; the higher decomposition rates observed in forested peatlands (Beaulne  
35 et al., 2021) can be compensated by higher litter inputs (Straková et al., 2011). To enhance wood biomass increment, peatland  
36 drainage for forestry purposes has been commonly applied in the past. Drainage facilitates oxygen access to deeper peat layers,  
37 thereby promoting tree root survival and function, but also the mineralization of organic matter and the release of C into the  
38 atmosphere in the form of CO<sub>2</sub>. Therefore, the conservation of organic soil C stocks in managed peatlands has attracted attention  
39 in the context of climate change.



40 The approximately 13 million ha of forestry-drained organic soils in Europe have been estimated to emit 17 million tons of  
41 CO<sub>2</sub> per year (Pilzecker et al., 2022). In the Baltic states (Estonia, Latvia, and Lithuania), the total area of drained organic  
42 forest soils is reported to be 0.8 million ha, with emissions of 1.8 million tons of CO<sub>2</sub> per year (Ministry of the Environment  
43 of Republic of Estonia, 2021; Konstantinavičiūtė et al., 2023; Skrebele et al., 2023). Thus, countries with a relatively small  
44 total land area yet a considerable proportion of organic soil can have a considerable role in organic soil management. This  
45 underscores the importance of acquiring precise estimates for the impact of organic soil drainage on CO<sub>2</sub> emissions in this  
46 region.

47 The Baltic States are located next to each other in the hemiboreal vegetation zone (Ahti et al., 1968) – halfway between the  
48 temperate and boreal zones – and thus, similarities in soil CO<sub>2</sub> emissions may be expected. However, the emission estimation  
49 approach is currently not harmonized as the countries use different emission factors to estimate emissions (Ministry of the  
50 Environment of Republic of Estonia, 2021; Konstantinavičiūtė et al., 2023; Skrebele et al., 2023). A similar issue can also be  
51 observed in a broader geographic scale, leading to problems of comparability of estimated emissions within and between  
52 different climate regions, as emission factors are best suited for application in geographic areas that share similar conditions,  
53 rather than being bound by country borders.

54 Guidelines of Intergovernmental Panel on Climate Change (IPCC) intends to address anthropogenic greenhouse gas emissions  
55 (Eggleston et al., 2006). Therefore, when evaluating human-induced emissions, it should be a good practice to consider the  
56 natural background emissions as well. In the context of organic soil drainage, the corresponding emissions should be expressed  
57 as difference between emissions from undrained and drained soil, rather by expressing direct emissions from drained soils. For  
58 this reason, in inventories the off-site CO<sub>2</sub> emissions are evaluated by comparing leaching of dissolved of organic C in  
59 undrained and drained organic soils. However, while the IPCC guidelines aim to address the impact of drainage on CO<sub>2</sub>  
60 emissions from organic soil, data limitations hinder the elaboration of such default emission factors (EF) for on-site CO<sub>2</sub>  
61 emissions. As a result, for elaboration of default IPCC EF study results on CO<sub>2</sub> emissions from drained soils are compiled.

62 According to National Greenhouse Gas Inventories submissions of 2023, the CO<sub>2</sub> emissions of drained organic forest soil in  
63 the Baltic states, except Latvia, were estimated using the default EF provided by IPCC for the temperate region (Calvo Buendia  
64 et al., 2019). Currently only one default IPCC EF for the whole temperate climate region is available and it does not involve  
65 any data measured in the Baltic states (Hiraishi et al., 2013a). EF is elaborated using results from 8 sites with drained soil  
66 (Hiraishi et al., 2013a) published in 5 articles (Glenn et al., 1993; Minkkinen et al., 2007; Yamulki et al., 2013; Von Arnold et  
67 al., 2005b, a) on studies representing a wide climatic gradient and different CO<sub>2</sub> estimation methods, which further complicates  
68 the comparability of the results that have been aggregated (Jauhiainen et al., 2019, 2023). A recent synthesis study evaluated  
69 whether default IPCC EF can be improved by compiling results from most recent studies. Still, only modest, and insignificant  
70 changes judging by confidence intervals of IPCC EFs could have been introduced for the temperate climate region [16]. This  
71 was because both the number and the geographical representation of studies of drained soil done in the temperate zone is still  
72 scarce and does not enable further stratification of site conditions within the region. Recognizing that additional data on  
73 undrained soils are necessary for assessing the net impact of drainage on CO<sub>2</sub> emissions, the knowledge on drainage related  
74 organic soil CO<sub>2</sub> emissions is poor. In the few studies on drained and undrained soil C balance conducted in the Baltic states,  
75 using both chamber and soil inventory methods, findings have been inconsistent (Vigricas et al., 2024; Butlers et al., 2022;  
76 Lazdiņš et al., 2024; Bārdule et al., 2022). Organic soils have been identified as both C sinks and sources, with no decisive  
77 conclusions reached regarding the factors driving such variation. This indicates the need for continued efforts to conduct local  
78 studies to fill the knowledge gaps on organic soil CO<sub>2</sub> emissions in Cool Temperate Moist climate region (Calvo Buendia et  
79 al., 2019) overlapping with hemiboreal vegetation zone.

80 In this study, we evaluated the nutrient-rich soil and forest floor C balance in drained and undrained hemiboreal peatland  
81 forests with different tree species in Estonia, Latvia, and Lithuania. The aim was to quantify the impact of drainage on CO<sub>2</sub>  
82 emissions by comparing soil and forest floor (including ground vegetation) C influx and efflux in drained and undrained sites.

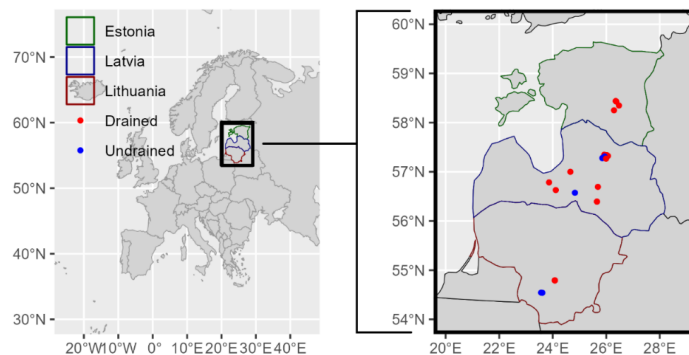


83 For this purpose, research was carried out in 26 forest stands over two years, analyzing forest floor CO<sub>2</sub> emissions and C inputs  
 84 by tree fine roots, ground vegetation, and fine foliar litter. We hypothesized that in the Baltic states, consistent emission factors  
 85 can be used to estimate organic soil CO<sub>2</sub> emissions, whether they are tailored to the dominant tree species or applied as a single  
 86 factor across all forest lands. Results acquired can provide empirical data for future syntheses aiming to elaborate static or  
 87 dynamic emission factors.

## 88 1 Materials and methods

### 89 1.1 Study sites

90 In total, 26 study sites (Figure 1) were established in stands dominated by black alder (*Alnus glutinosa* (L.) Gärtner), birch  
 91 (*Betula pendula* Roth, *Betula pubescens* Ehrh.), Scots pine (*Pinus sylvestris* L.), and Norway spruce (*Picea abies* (L.) Karst.)  
 92 of different ages (Table 1). The study sites included both drained (n=19) and undrained (n=7) soils, with the peat layer thickness  
 93 ranging from 27 cm to over 2 meters. Soil drainage status was determined based on the presence of drainage ditches along the  
 94 forest stand borders. According to forest type classification, all of the sites were characterized as nutrient-rich (Bušs, 1981).  
 95



96  
 97 **Figure 1: Locations of the study sites.** Points indicate the locations of study site clusters.

98 Despite the more numerous drained sites showing greater variation than the undrained sites, overall, the two groups of sites  
 99 had similar stand characteristics (Table 1). The mean stand age of both groups was 74 years, with a range of 26-162 years for  
 100 drained and 44-96 years for undrained sites. Average basal areas in turn were 27 for drained and 30 m<sup>2</sup> ha<sup>-1</sup> for undrained sites,  
 101 respectively. Detailed information on stand characteristics, including mean soil water table level (WTL) and coordinates, is  
 102 provided in Table S 1.

103

104 **Table 1: Summary of tree stand characteristics in the study sites.**

Parameter	Dominant tree species							
	Black alder		Birch		Pine		Spruce	
	Drained	Undrained	Drained	Undrained	Drained	Undrained	Drained	Undrained
Site count	n = 2	n = 2	n = 5	n = 2	n = 5	-	n = 7	n = 3
Age, year	30...80	44...74	24...45	44...61	60...141	-	40...162	81...96
Mean height, m	13...20	16...28	13...18	9...20	12...21	-	10...23	15...20
Mean diameter, cm	12...21	16...28	12...22	8...21	12...22	-	10...25	17...21
Basal area, m <sup>2</sup> ha <sup>-1</sup>	26...36	30...36	15...23	22...23	17...48	-	18...36	25...42

105



106 The annual mean air temperature during the study period varied from 6.4 °C in Estonia to 8.5 °C in Lithuania, while the annual  
107 precipitation in the whole region was 600.9±76.7 mm (Table S2) (Estonian Environment Agency. Climate normals, 2024;  
108 Latvian Environment, Geology and Meteorology Centre. Climate normals, 2024; Lithuanian Hydrometeorological Service.  
109 Climate normals, 2024). The long-term (1990-2020) annual mean air temperatures in Estonia, Latvia and Lithuania were  
110 6.4 °C, 6.8 °C and +7.4 °C, respectively, while the mean annual precipitations were 662 mm, 686 mm and 695 mm,  
111 respectively (Estonian Environment Agency. Climate normals, 2024; Latvian Environment, Geology and Meteorology Centre.  
112 Climate normals, 2024; Lithuanian Hydrometeorological Service. Climate normals, 2024).

113 At each study site, three sampling locations (subplots) were selected, ensuring a minimum separation distance of 15 m along  
114 a transect. Transects were positioned perpendicular to drainage ditches in drained areas and perpendicular to stand borders in  
115 undrained areas. In the drained sites, the first subplot was located five to ten m from the nearest drainage ditch.

116 Empirical data was gathered from January 2021 to December 2022 in Estonia and Latvia, and from July 2021 to June 2023 in  
117 Lithuania. The sites were visited monthly in Latvia and Lithuania, and biweekly in Estonia.

## 118 1.2 Total respiration

119 Forest floor respiration (including ground vegetation) further defined as total respiration ( $R_{tot}$ ) measurements included both  
120 soil heterotrophic respiration and autotrophic respiration of aboveground and belowground parts of ground vegetation. In the  
121 article  $R_{tot}$  is equivalent to forest floor respiration, including respiration of ground vegetation. Gas samples were collected  
122 from manual closed static opaque chambers (PVC, volume 0.0655 m<sup>3</sup>) as described in the literature (Hutchinson and  
123 Livingston, 1993) for subsequent laboratory analysis. Five to six ring-shaped chamber collars (area 0.196 m<sup>2</sup>) were  
124 permanently installed in the soil at a depth of five cm in each study site at least one month prior to the first sampling to avoid  
125 the installation effect on fluxes. The soil surface and vegetation were kept intact throughout the whole flux monitoring period.  
126 Thus, the  $R_{tot}$  measurements include CO<sub>2</sub> emissions caused by the decomposition of litter and autotrophic respiration of  
127 ground vegetation plants included in the collar and the chamber headspace during the gas sampling.

128 The gas samples were collected during a measurement campaign by obtaining four samples from each chamber in pre-  
129 evacuated (0.3 mbar) glass vials (100 cm<sup>3</sup>). During the sample collection, the air within the chamber was not mixed, and  
130 samples were taken from the sampling tube inserted approximately at the center of the chamber. The first sample was taken  
131 immediately after placing the chamber on the collar, following the removal of dead volume from the sampling tube using a  
132 syringe. Subsequent samples were taken at either 10 or 20 (Estonia) minute intervals over 30- or 60-minute monitoring periods,  
133 respectively (Vigricas et al., 2024; Butlers et al., 2022).

134 The gas samples were analyzed using a Shimadzu GC-2015 gas chromatograph (Shimadzu USA manufacturing, Inc., Canby,  
135 OR, USA) equipped with an electron capture detector (ECD). The uncertainty of the method used was estimated to be 20 ppm  
136 of CO<sub>2</sub>. Linear regression was applied to relate the CO<sub>2</sub> concentrations with the time elapsed since chamber closure for each  
137 measurement. Subsequently, the measurement data was screened to identify deviations from the recognized trend, considering  
138 the removal of measurements with identified errors. All measurements were discarded if the regression coefficient of  
139 determination ( $R^2$ ) was less than 0.9 ( $p < 0.01$ ), except for cases where the difference between the highest and lowest measured  
140 CO<sub>2</sub> concentration in the chamber was less than the uncertainty of the method (specifically applicable during non-vegetation  
141 periods).

142 The data that met the quality criteria were used to determine the slope coefficient of the linear regression, which was then used  
143 to calculate the instantaneous  $R_{tot}$  according to the ideal gas law equation (Fuss and Hueppi, 2024):

$$R_{tot} = \frac{M \times P \times V \times slope}{R \times T \times A \times 1000} \quad (1)$$

144 where  $R_{tot}$  is the instantaneous total respiration, mg CO<sub>2</sub>-C m<sup>2</sup> h<sup>-1</sup>; M is the molar mass of CO<sub>2</sub>-C, 12.01 g mol<sup>-1</sup>; R is the  
145 universal gas constant, 8.314 m<sup>3</sup> Pa K<sup>-1</sup> mol<sup>-1</sup>; P is the assumption of air pressure inside the chamber, 101.300 Pa; T is the air



146 temperature in the chamber,  $K$ ;  $V$  is the chamber volume,  $0.0655 \text{ m}^3$ ; slope is the  $\text{CO}_2$  concentration change over time,  $\text{ppm}$   
147  $\text{h}^{-1}$ ; and  $A$  is the collar area,  $0.19625 \text{ m}^2$ .

### 148 **1.3 Soil heterotrophic respiration**

149 Heterotrophic soil respiration ( $R_{\text{het}}$ ) was measured by applying the manual closed dynamic nontransparent chamber method  
150 (Denmead, 2008; Hutchinson and Livingston, 1993). For each measurement location, a  $60 \times 90 \text{ cm}$  ( $W \times L$ ) trenched (Ngao et  
151 al., 2007) plot was prepared at the end of the previous year's growing season to a depth of at least  $40 \text{ cm}$ , using geotextile on  
152 the sides to prevent root ingrowth and by removing alive vegetation and litter layer. In each subplot, measurements were done  
153 in 3 replicates, in total, nine measurement points in each study site. Every measurement lasted three minutes using the EGM-  
154 5 portable  $\text{CO}_2$  gas analyzer (PP Systems, Amesbury, MA, USA) and a fan-equipped chamber (area  $0.07 \text{ m}^2$ , volume  $0.017$   
155  $\text{m}^3$ ) placed in the center of the trenched surface without using a collar. The measurement data was stored at a  $1 \text{ Hz}$  frequency.  
156 Between the measurement campaigns,  $R_{\text{het}}$  measurement points were covered with geotextile, which was covered with an  
157 equivalent quantity of debris and litter as nearby soil, aiming to simulate natural conditions.  
158 Before flux calculations, the first 15 seconds of the measurement data were discarded due to the potential error in the results  
159 due to the placing of the chamber in the soil. To estimate the slope of the linear regression equation representing  $\text{CO}_2$   
160 concentration change in time, the same approach as for  $R_{\text{tot}}$  was used (Figure 1).

### 161 **1.4 Environmental variables**

162 Manual WTL measurements were carried out using nylon-mesh-coated, perforated piezometers ( $5 \text{ cm}$  in diameter) in all  
163 subplots. The lower end of the piezometer tube was installed at a depth of  $140 \text{ cm}$ . Also, manual soil temperature measurements  
164 were carried out in all subplots, while continuous measurements - in the centermost subplot only. Manually, soil temperature  
165 was measured at depths of  $5, 10, 20,$  and  $40 \text{ cm}$  using a Comet data logger (COMET SYSTEM, s.r.o., 756 61 Roznov pod  
166 Radhostem, Czech Republic) equipped with Pt1000 temperature probes, and continuous measurements were carried out at  
167 depths of  $10$  and  $40 \text{ cm}$ . Together with the manual soil temperature measurements, soil moisture was assessed at a depth of  $5$   
168  $\text{cm}$  using a ProCheck meter (Decagon Devices, Pulman, WA / USA) equipped with a moisture sensor GS3. All manual  
169 measurements were carried out at the same time as  $\text{CO}_2$  flux measurements. The continuous soil temperature measurements  
170 with data loggers (Maxim Integrated DS1922L2F, iButtonLink Technology, Whitewater, WI 53190 USA) recorded values  
171 every 30 minutes.  
172 Soil samples were taken up to a depth of  $75 \text{ cm}$  at two locations in each subplot during the establishment of the study sites.  
173 Two separate sample sets were collected – for the determination of bulk density, ash content and chemical parameters (pH,  
174 concentrations of total carbon (TC), nitrogen (TN), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg)). The  
175 samples were collected with a volumetric  $100 \text{ cm}^3$  cylinder (Cools and De Vos, 2010) at  $10 \text{ cm}$  intervals to a depth of  $50 \text{ cm}$ .  
176 Two additional samples were taken from soil depths of  $50\text{-}75$  and  $75\text{-cm}$  with a soil auger. Soil samples collected for  
177 determination of bulk density were oven-dried ( $105 \text{ }^\circ\text{C}$ ) and weighed (LVS ISO 11272:2017), while soil samples for chemical  
178 analyses were prepared by air drying ( $\leq 40 \text{ }^\circ\text{C}$ ), sieving and homogenizing (LVS ISO 11464:2006). Organic carbon (Corg)  
179 content was calculated by multiplying the ash content measurement result derived soil organic matter content by factor  $0.5$ ,  
180 thus assuming that organic matter is  $50\%$  Corg (Pribyl, 2010). Once per month, soil water samples were collected from separate  
181 piezometers ( $7.5 \text{ cm}$  in diameter) explicitly installed for water chemical analysis, not the ones used for WTL measurements.  
182 Water chemical parameters such as water pH, electrical conductivity (EC), and concentrations of dissolved organic carbon  
183 (DOC), total nitrogen (N), nitrate ( $\text{NO}_3^-$ ), ammonium ( $\text{NH}_4^+$ ), and phosphate ( $\text{PO}_4^{3-}$ ) ions were determined.  
184 All soil and water analyses were done in an ISO 17025 certified laboratory using ISO standard methods (Table S 3).



185 **1.5 Biomass and litter measurements**

186 Dry matter biomass of the total annual foliar fine litter (fLF) and coarse woody litter (cLF), ground vegetation of herbaceous  
187 (vascular) plants (GV), moss production (MP), and tree fine-root (FR) production (FRP) were determined, and their C contents  
188 analyzed in all study sites. Biomass of dwarf shrubs, moss and total belowground biomass was measured in some sites only  
189 (Table S 8). fLF and cLF samples were collected once every four weeks, and GV, moss, FRP, dwarf shrubs and total root  
190 biomass samples were collected once during the entire study period.

191 To avoid double accounting of foliar litter biomass, all fine fractions of litter and branches with a diameter of up to 1 cm and  
192 a length of up to 10 cm were considered fLF. Branches with larger dimensions were considered cLF. fLF biomass samples  
193 were collected with conical litter traps (area 0.5 m<sup>2</sup>) set one meter above the ground (Latvia) or with square mesh frames (0.5  
194 x 0.5 m) placed on the ground (Estonia and Lithuania). In each study site, five replicate litter collectors were placed in the  
195 centermost subplot of the transect.

196 GV aboveground (aGV) and belowground (bGV) biomass and MP biomass samples were collected in 2021 in five replicates  
197 per subplot. GV biomass was collected from square sampling points with an area of 0.0625 cm<sup>2</sup>. GV belowground biomass  
198 was collected from the top 20-30 cm of the soil layer. In the process of biomass determination bGV biomass was separated  
199 from tree roots by wet sieving and morphological properties. MP biomass samples were collected by anchoring a square mesh  
200 (0.01 m<sup>2</sup>) on the moss at the end of vegetation season and collecting the moss biomass that grew through the mesh during the  
201 next growing season. Also, GV samples were collected at the end of the growing season.

202 To estimate FRP, a modified ingrowth core method (Laiho et al., 2014) was applied. The method is based on a cylindrical  
203 mesh bag (diameter 2.5 cm, mesh size 2 mm) filled with peat collected from the subplot. Ingrowth cores were installed in each  
204 subplot in five replicates and removed from the soil after two growing seasons. In addition, total root biomass was estimated  
205 by collecting undisturbed sample cores (18 cm<sup>2</sup>) from the 0-40 cm soil layer. The collected samples were transported to the  
206 laboratory, where the biomass of the ingrown FR was determined by morphological properties after wet sieving and separating  
207 GV roots from tree roots.

208 All biomass samples were oven-dried (70 °C), weighed and milled prior to further analysis. Chemical analyses were performed  
209 according to ISO standard methods (Table S 3).

210 **1.6 Estimation of annual soil and forest floor carbon balance**

211 We estimated the annual soil and forest floor (including ground vegetation) C balance of the sites by combining C input and  
212 output: either R<sub>tot</sub> or R<sub>het</sub> were used to represent the output of C, while the C inputs by plant litter were used identically for  
213 both approaches. Consequently, results acquired by using R<sub>het</sub> as C output represent soil C balance, while approach with R<sub>tot</sub>  
214 – the C balance of forest floor. While we directly measured R<sub>het</sub>, we utilized the R<sub>het</sub> value derived from the results of R<sub>tot</sub>.  
215 Such an approach was necessary because our R<sub>het</sub> values were consistently higher than R<sub>tot</sub> in numerous study sites (Figure  
216 S 4). This appears to be an artifact, which explains our decision not to use directly measured R<sub>het</sub> (see Results and Discussion).  
217 It made more sense to use R<sub>tot</sub> because relying on R<sub>het</sub> would overestimate soil C loss. R<sub>het</sub>, which excludes autotrophic  
218 respiration, unlike R<sub>tot</sub>, should not be higher than R<sub>tot</sub>.

219 To estimate annual C output, the results of the instantaneous R<sub>tot</sub> measurements were first interpolated to annual cumulative  
220 R<sub>tot</sub> during the study period. Interpolation was carried out by evaluating the relationship between R<sub>tot</sub> and soil temperature  
221 measured in each study site and constructing site-specific regression equations for the purpose. Hourly R<sub>tot</sub> were then  
222 calculated using the hourly soil temperatures collected by data loggers at each study site. Consecutively, annual R<sub>tot</sub> was  
223 calculated by summing the interpolated hourly emissions in a specific study year.

224 We derived annual R<sub>het</sub> from estimated annual R<sub>tot</sub> empirically using equation (2). The equation characterizes the relationship  
225 between soil surface respiration (R<sub>s</sub>) and R<sub>het</sub>, it was created using results of previous studies (Jian, J. et al., 2021) in boreal  
226 zone (Figure S 5). We assumed R<sub>tot</sub> is equal with R<sub>s</sub>, i.e., aboveground autotrophic respiration has a minor role in R<sub>tot</sub>



227 (Hermans et al., 2022; Munir et al., 2017) and applied the equation to annual  $R_{tot}$  directly. Such assumption was justified by  
 228 observation that there was no relationship found between share of  $R_{het}$  and  $R_s$  ( $p=0.14$ ) in partitioned  $R_{tot}$  data analyzed.

$$R_{het} = -0.7 + 0.78 \times R_s \quad (2)$$

229 To estimate the annual C input, the measured annual litter biomass (Table S 7) was recalculated to C amount using biomass C  
 230 content values evaluated in the study (Table 2). For the estimation of C balance, the annual C input during the study period was  
 231 considered to consist of fLF, aGV and bGV litter and FR litter (estimated based on FRP). Only these sources of C input were  
 232 used because their decomposition resulting  $CO_2$  emissions are directly accounted for in the  $R_{tot}$ . We assumed that FR biomass  
 233 was essentially not changing over the study years, and thus we could assume that FRP equaled litter production. Since the root  
 234 ingrowth cores were removed from the soil after two growing seasons, the FRP estimate was calculated by dividing the FR  
 235 biomass in the cores by two (Bhuiyan et al., 2017). We also assumed that measured GV is equal to annual GV litter.

236  
 237 **Table 2: Mean C and N content (mean±SD) in dry matter of biomass (%).** Abbreviations: aGV and bGV – above- and belowground  
 238 biomass of herbaceous vegetation, FR – tree fine roots, M – moss, fLF – fine litterfall, cLF – coarse woody litterfall.

Element	aGV	bGV	FR	M	fLF	cLF
C	49.34±2.45	50.95±2.02	51.21±5.16	48.38±2.13	52.50±0.25	53.88±0.67
N	2.18±0.64	1.53±0.43	1.47±0.44	1.10±0.75	1.30±0.41	1.04±0.20

239  
 240 The results on cLF, moss, dwarf shrubs at total root biomass (Table S 8) presented in the ‘Annual litter and biomass production’  
 241 section were not factored into the C balance estimation. The values provided there are for informational purposes only (refer  
 242 to the Results and Discussion section for more details). The inclusion of cLF in C inputs would lead to biased C balance  
 243 estimation, as cLF cannot be representatively included in  $R_{tot}$  measurements. The reason for the exclusion of MP was that we  
 244 could not equate moss production directly to litter production, given that moss cover was not measured. Similarly, while we  
 245 measured the total biomass of roots and shrubs, the litter of those C pools was not estimated; hence data on shrubs and total  
 246 root biomass was also not applied in soil C balance estimation and the corresponding results should be regarded as descriptive  
 247 of the sites.

248 To summarize, soil C balance or forest floor C balance was calculated by summing either annual  $R_{het}$  or  $R_{tot}$ , respectively  
 249 with C content of annual fLF, aGV and bGV litter and FR litter. The impact of drainage on C balance was assessed by  
 250 subtracting the estimated C balance in drained sites from undrained sites, utilizing C balance results obtained with both  
 251 approaches.

## 252 1.7 Statistical analysis

253 Statistical analyses were performed using the software R version 4.3.1 (packages ‘MASS’, ‘stats’, ‘nlme’, ‘Hmisc’,  
 254 ‘lmerTest’), using  $p=0.05$  as the limit for statistical significance. The compliance of the data with the normal distribution was  
 255 checked formally with the Shapiro-Wilk normality test and visually by density and quantile-quantile (Q-Q) plots. Data on  
 256 instantaneous and annualized  $R_{tot}$ , WTL measurements and soil properties analysis results grouped by subcategories (drainage  
 257 status, dominant tree species, country) were compared for differences by pairwise Wilcoxon rank sum test with continuity  
 258 correction, and the  $p$ -values were adjusted by Bonferroni correction. Multivariate data relationships were observed through  
 259 Principal Component Analysis (PCA), and  $CO_2$  emission-related relationships were confirmed by fitting raw data to the non-  
 260 linear Arrhenius equation (Lloyd and Taylor, 1994) and transformed data to linear mixed-effects models using the study site  
 261 as a random effect. As data transformation has a considerable impact on the results of statistical analyses, to improve the  
 262 normality of the data, a logarithmic and Box-Cox transformation was evaluated (Box and Cox, 1964; Liaw et al., 2021; Wutzler  
 263 et al., 2020). A method that achieved the best conformity to the normal distribution was used to transform the data. The



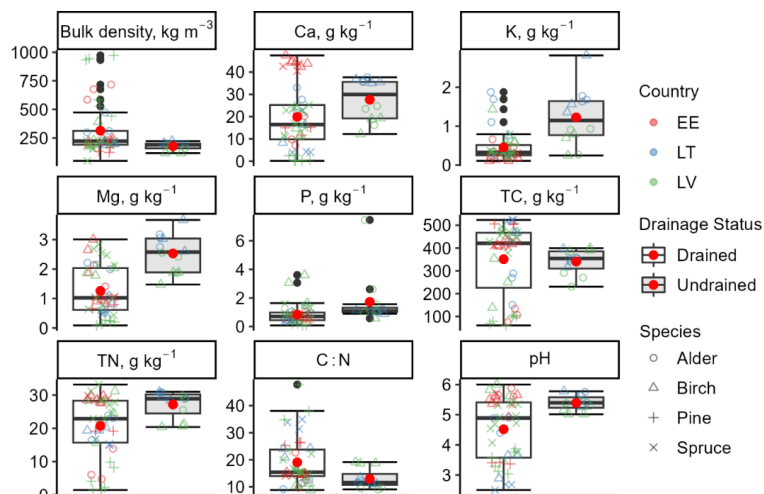
264 performance of elaborated models for flux data interpolation by continuous soil temperature measurements was compared by  
 265 root mean square error of prediction (RMSE). Figures are prepared by using packages ‘ggplot2’, ‘corplot’, ‘ggbiplot’.  
 266 A descriptive evaluation of the hypothesis was evaluated by segregating instantaneous and annualized  $R_{tot}$  data by country  
 267 origin and checking for differences by PCA and by pairwise Wilcoxon rank sum test. Formal testing of the hypothesis was  
 268 performed by evaluating the significance of the country variable impact on the relationship between soil temperature and  $R_{tot}$ .  
 269 The exclusion of litter data from hypothesis testing was justified by litter being a proxy of  $R_{tot}$ .

## 270 2 Results

### 271 2.1 Soil and soil water characteristics

272 The peat layer depth in the study sites with drained soil ranged from 27 to 212 cm (mean  $81 \pm 47$  cm) and in undrained sites  
 273 from 100 to 230 cm (mean  $167 \pm 49$  cm). Soil bulk density (0-30 cm depth) in the drained sites (mean  $314 \pm 215$   $\text{kg m}^{-3}$ ) was  
 274 characterized by both higher variation and higher mean density ( $p=0.003$ ) compared to undrained sites (mean  $168 \pm 32$   $\text{kg m}^{-3}$ ).  
 275 Soil drainage status had no impact on Corg content ( $p=0.11$ , total mean  $416 \pm 130$   $\text{g kg}^{-1}$ ). However, drained soils had a higher  
 276 mean C:N ratio ( $22 \pm 7$ ;  $p=0.01$ ) than the undrained soils ( $17 \pm 3$ ) (Table S 4). A trend could be observed that undrained soils  
 277 had higher nutrient concentrations and higher pH than the drained soils (Figure 2).  
 278

278

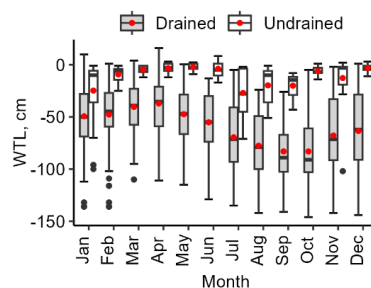


279

280 **Figure 2: Variation of soil chemical and physical properties at soil depth 0-30 cm.** The clear box represents the drained, grey-shaded  
 281 box the undrained sites. The bottom and top edges of the box represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles, summarizing the interquartile  
 282 range (IQR). The whiskers extend to the smallest and largest values within  $1.5 \times$  IQR from the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. Black dots  
 283 mark outliers. A red dot and a solid horizontal line in the box indicate mean and median values, respectively.

284 The range of mean WTL was from  $-23$  to  $-112$  cm (mean  $-60 \pm 25$  cm) in the drained sites and from  $-7$  to  $-17$  cm (mean  
 285  $-13 \pm 4$  cm) in the undrained sites, respectively. In the undrained sites, the WTL was mainly rather elevated (see interquartile  
 286 range in Figure 3) and had comparably smaller variation (mean standard deviation 16 cm) than in the drained sites (mean  
 287 standard deviation 23 cm); however, in all sites except LTC108, WTLs below 30 cm were also observed (Figure 4). In the  
 288 undrained sites, the range of min-max WTL was from  $3 \pm 3$  cm to  $-63 \pm 27$  cm, while the WTL in drained sites had a greater  
 289 absolute variation and ranged from  $-14 \pm 19$  cm to  $-104 \pm 28$  cm.





290

291 **Figure 3: Yearly variation of water table level (WTL) in the study sites.** The edges of the box represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles,  
 292 encapsulating the interquartile range (IQR). The whiskers extend to the smallest and largest values within 1.5 \* IQR from the 25<sup>th</sup> and 75<sup>th</sup>  
 293 percentiles, respectively. Black dots mark outliers. A red dot and a solid horizontal line indicate the average values of the date represented  
 294 – mean and median, respectively.

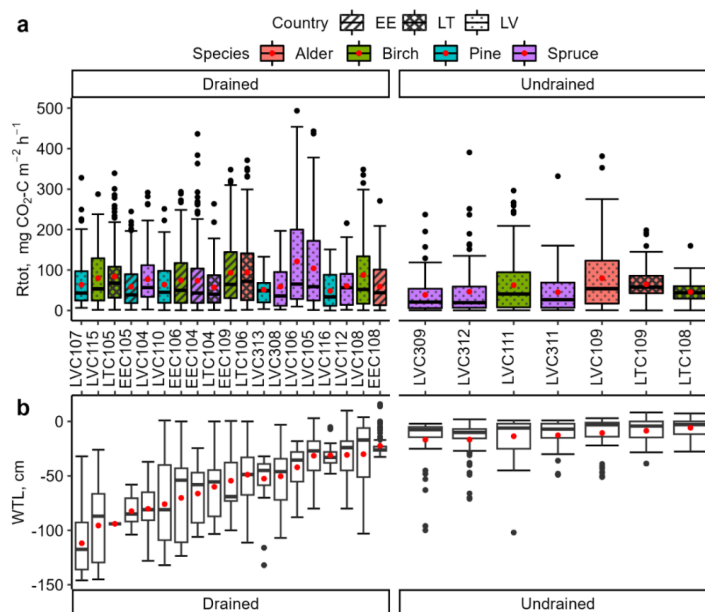
295 The concentrations of all measured chemical parameters in the soil water, except for NH<sub>4</sub><sup>+</sup>, were, on average, higher (p<0.05)  
 296 in the drained sites (

297 Figure S 1). The most remarkable differences in mean concentrations were observed in the DOC, N, and NO<sub>3</sub><sup>-</sup> concentrations,  
 298 which in the water of undrained sites were, on average, 1.5, 3.2, and 10 times higher, respectively (Table S 5).

299 **2.2 Instantaneous total respiration**

300 In the drained sites, the mean instantaneous R<sub>tot</sub> varied from 48 to 125 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup> and from 38 to 80 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup>  
 301 in the undrained sites (Figure 4: 44). The relative variations of the instantaneous R<sub>tot</sub> in drained (CV=90±9%) and undrained  
 302 (CV=106±29%) sites were comparable. Although the study sites represented a broad soil WTL gradient, no significant impact  
 303 of the site mean WTL on the mean instantaneous R<sub>tot</sub> emission was observed (r=0.16, p>0.05). Furthermore, no significant  
 304 correlations were found between instantaneous R<sub>tot</sub> and groundwater parameters.  
 305

305

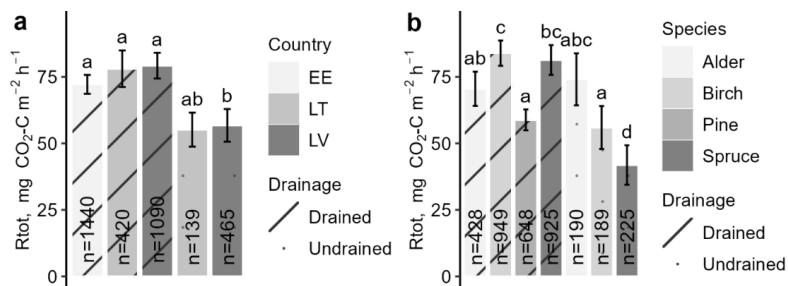


306

307 **Figure 4: 4 Variation of instantaneous total respiration (R<sub>tot</sub>, panel “a”) and water table level (WTL, panel “b”) in the study sites.**  
 308 The clear box represents the drained, grey-shaded box the undrained sites. The bottom and top edges of the box represent the 25<sup>th</sup> and 75<sup>th</sup>  
 309 percentiles, summarizing the interquartile range (IQR). The whiskers extend to the smallest and largest values within 1.5 × IQR from the  
 310 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. Black dots mark outliers. A red dot and a solid horizontal line in the box indicate mean and median  
 311 values, respectively.



312 Mean  $R_{tot}$  in sites with the same drainage status did not differ ( $p > 0.05$ ) between countries (Figure S 2). Stratified by country,  
 313 the instantaneous  $R_{tot}$  in drained sites (mean:  $76 \pm 3$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ) was overall higher ( $p < 0.05$ ) than those from undrained  
 314 soil (mean:  $56 \pm 5$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ). The measured  $R_{tot}$  of undrained soil were smaller in both Latvia (mean  $57 \pm 6$   
 315 mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ) and Lithuania ( $55 \pm 6$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ) compared to  $R_{tot}$  from drained soil in the Baltic states ranging  
 316 from mean  $72 \pm 4$  to  $79 \pm 5$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$  (Figure 5:5, panel “a”).  
 317



318  
 319 **Figure 5:5 Mean instantaneous total respiration ( $R_{tot}$ ) by drainage status and country (a) or dominant tree species (b).** Error bars  
 320 indicate confidence interval. Shared letter indicates that differences are not significant.

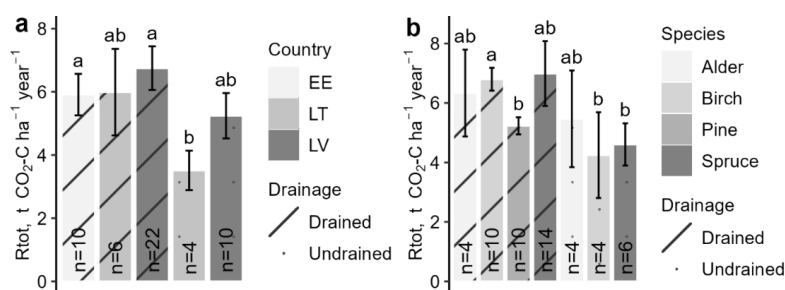
321 There were few apparent differences in the mean  $R_{tot}$  between stands of different tree species (Figure 5:5, panel “b”).  $R_{tot}$   
 322 was lowest at undrained sites dominated by spruce and highest at drained sites dominated by birch. Furthermore,  $R_{tot}$  values  
 323 in drained birch-dominated sites were not significantly different from those in both drained spruce- and undrained alder-  
 324 dominated sites.  $R_{tot}$  was significantly different ( $p < 0.05$ ) between coniferous forest sites with different dominant tree species  
 325 and soil moisture regimes, where  $R_{tot}$  ranged from mean  $42 \pm 7$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$  in undrained spruce forests to  $59 \pm 4$  and  
 326  $81 \pm 6$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$  in drained pine and spruce forests, respectively. In deciduous stands, the moisture regime and  
 327 dominant tree species had less impact on the mean flux;  $R_{tot}$  was higher ( $p < 0.05$ ) in drained birch stands (mean  $84 \pm 5$   
 328 mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ) than those in undrained sites ( $56 \pm 8$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ), while in alder stands the mean  $R_{tot}$  was similar  
 329 regardless of the soil moisture regime (total average  $67 \pm 9$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$ ), (Figure 5:5, panel “b”). In drained coniferous  
 330 and deciduous sites, the mean  $R_{tot}$  was similar, but in undrained sites, emissions in deciduous forests were about 40% higher.  
 331 Evaluating the impact of country, drainage status, dominant tree species, WTL, and WTL category (above or below 30 cm) on  
 332 the relationships in mixed-effects models predicting  $R_{tot}$  by soil temperature, it was observed that all WTL-related model  
 333 factors had a significant impact, but the country and dominant tree species had no role in  $R_{tot}$  prediction. The impact of  
 334 drainage is also indicated by the mean measured  $R_{tot}$ , which was  $87 \pm 3$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$  in drained and  
 335  $57 \pm 3$  mg  $\text{CO}_2\text{-C m}^{-2} \text{h}^{-1}$  in undrained sites if WTL depth of 30 cm threshold was considered as a threshold separating drained  
 336 and undrained soil. However, including WTL-related factors did not improve the fit of models (Table S 9) and prediction  
 337 improvement was negligible. These results confirm that neither country nor dominant tree species significantly impact  
 338 instantaneous  $R_{tot}$ .

### 339 2.3 Annual total respiration

340 The strongest correlation between instantaneous  $R_{tot}$  and soil temperatures measured at different depths was found for soil  
 341 temperature at 10 cm depth, with a mean Pearson correlation coefficient ( $r$ ) of  $0.86 \pm 0.04$  across the study sites. For the other  
 342 soil depths (5, 20, 30, 40 cm),  $r$  ranged from  $0.71 \pm 0.07$  to  $0.79 \pm 0.05$ . Accordingly, soil temperature at 10 cm depth (Figure S  
 343 3) was used in constructing  $R_{tot}$  prediction models and for emission interpolation. Linear models developed using Box-Cox  
 344 transformed data provided the best  $R_{tot}$  prediction power. A lambda value of 0.3411 was used for all data transformations, as  
 345 individual data transformations for each site resulted in comparatively less successful data normalization. With this approach,  
 346 the RMSEP (Root Mean Square Error of Prediction) of instantaneous  $R_{tot}$  predictions for individual sites decreased by an



347 average of  $16 \pm 14\%$ , compared to linear models with logarithmically transformed data or non-linear models with untransformed  
 348 data (Table S 6). Interestingly, while the R10 (forest floor respiration at  $10\text{ C}^\circ$ ) value increased by  $20 \pm 7\%$ , the estimated  
 349 cumulative annual  $R_{tot}$  decreased by  $2 \pm 9\%$ .  
 350 Annualized  $R_{tot}$  indicated similar mutual relationships among the study site dominant tree species and drainage status  
 351 categories as the instantaneous  $R_{tot}$ . Consequently, the estimated annual emissions from drained sites among the Baltic states  
 352 did not differ significantly (overall mean  $6.21 \pm 0.43\text{ t CO}_2\text{-C ha}^{-1}\text{ year}^{-1}$ ) and were generally somewhat higher than  $R_{tot}$  from  
 353 undrained soils in Latvia and Lithuania (Figure 6, panel “a”). Also, in undrained soil category, no significant difference was  
 354 found between the countries (total mean  $4.38 \pm 1.20\text{ t CO}_2\text{-C ha}^{-1}\text{ year}^{-1}$ ).  
 355



356  
 357 **Figure 6: Annualized total respiration ( $R_{tot}$ ) in study sites stratified by drainage status and country (panel “a”) or dominant tree**  
 358 **species (panel “b”).** Error bars indicate confidence interval. Shared letter indicates that differences are not significant.

359 Similarly, when categorizing data according to drainage status and dominant tree species, the differences between categories  
 360 in the annualized  $R_{tot}$  are statistically less significant than in the case of instantaneous  $R_{tot}$  data (Figure 6, panel “b”). For  
 361 instance, the annual  $R_{tot}$ , regardless of the soil drainage status, did not significantly differ in most forests with various dominant  
 362 tree species. Among the drained sites, the lowest mean annual  $R_{tot}$  was estimated for pine forests ( $5.23 \pm 0.29\text{ t CO}_2\text{-C ha}^{-1}\text{ year}^{-1}$ ), while in spruce, birch, and alder forests, the means were similar ( $p > 0.05$ ), amounting  
 363  $6.71 \pm 0.31\text{ t CO}_2\text{-C ha}^{-1}\text{ year}^{-1}$ . Emissions from undrained soils in alder, birch, and spruce forests are lowered, ranging from  
 364  $4.6 \pm 0.71$  in spruce forests to  $5.47 \pm 1.63\text{ t CO}_2\text{-C ha}^{-1}\text{ year}^{-1}$  in alder forests (overall mean  $4.86 \pm 0.71$ ).  
 365

366 The correlation between  $R_{tot}$  and WTL was low, however, the drainage status (drainage dich presence) impact on  $R_{tot}$  is  
 367 indicated by the PCA results, where undrained sites tend to have more similar characteristics, i.e., higher comparability.  
 368 Meantime drained sites show greater diversity when both instantaneous and annualized  $R_{tot}$  data is evaluated. However, clear  
 369 patterns of dominant tree species and country impact on  $R_{tot}$  are not recognized by PCA (Figure S 7 and Figure S 8).

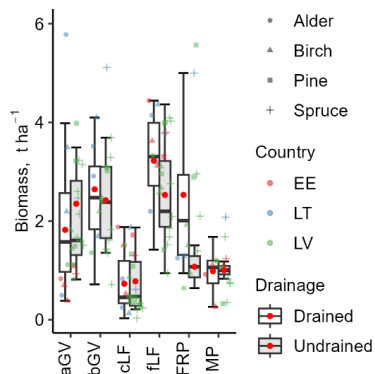
370 When comparing the chemical and physical properties of different soil layers with the estimated annual cumulative  $R_{tot}$ , as  
 371 well as the measured mean instantaneous  $R_{het}$  and  $R_{tot}$ , mean measured  $R_{het}$  consistently shows a higher correlation with all  
 372 evaluated soil parameters. The only exception is Corg, where in all correlation combinations, it was not present ( $r$  around -  
 373 0.1). Excluding Corg, the other soil chemical parameters generally have a low to moderate correlation (mean  $r = 0.4$ ) with  $R_{het}$ .  
 374 The highest correlation is with pH, K, Mg, and P (mean  $r = 0.5 \pm 0.07$ ,  $p < 0.05$ ), and it is consistent across all evaluated soil  
 375 layers, while correlation with BD (mean  $r = -0.2$ ,  $p > 0.05$ ) tends to increase with deeper soil layers reaching the highest  
 376 correlation ( $r = -0.3$ ) in layer 20-30 cm (Figure S 6). In addition, higher C:N ratio is associated with lower  $R_{het}$  emissions  
 377 (mean  $r = -0.4$ ,  $p < 0.05$ ).

### 378 2.4 Annual litter and biomass production

379 The estimated mean biomass of different plant litter categories in both drained and undrained sites were mostly similar,  
 380 typically not differing by more than 20%. Only fLF and FRP tended to be considerably higher in the drained sites, FRP on  
 381 average even more than twice as high. Compared to undrained sites, bGV in drained sites was about 20% higher on average,



382 while aGV was about 20% lower on average (Figure 7). However, regardless of the soil drainage status, the proportion of aGV  
 383 in the total GV biomass was  $54 \pm 18\%$ . The estimated moss biomass dry matter (dm.) averaged  $5.02 \pm 0.87$  t dm. ha<sup>-1</sup>, and MP  
 384 averaged  $0.98 \pm 0.25$  t dm. ha<sup>-1</sup>, or  $22 \pm 10\%$  of the total moss biomass (Table 3). In total, the sum of annual forest floor biomass  
 385 production (excluding small shrubs), cLF and fLF in the drained and undrained study sites was  $9.68 \pm 2.95$  and  $8.68 \pm 2.10$  t dm.  
 386 ha<sup>-1</sup>, respectively.  
 387

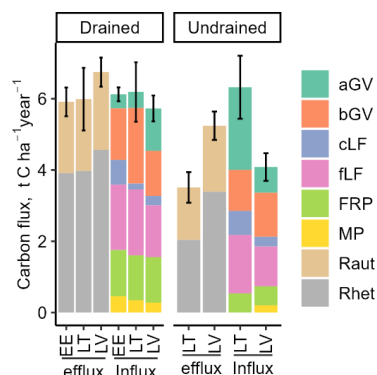


388  
 389 **Figure 7: Variation of biomass measurement results.** Abbreviations: aGV and bGV – above- and belowground biomass of herbaceous  
 390 vegetation, cLF – coarse woody litterfall, fLF – fine litterfall, FRP – tree fine root production, MP – moss production (assuming 100%  
 391 projection). The bottom and top edges of the box represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles, summarizing the interquartile range (IQR). The  
 392 whiskers extend to the smallest and largest values within  $1.5 \times$  IQR from the 25<sup>th</sup> and 75<sup>th</sup> percentiles, respectively. Black dots mark outliers.  
 393 A red dot and a solid horizontal line in the box indicate mean and median values, respectively.

394 **Table 3: Biomass (mean±CI, t dm. ha<sup>-1</sup>) measurement results stratified by drainage status.** Abbreviations: aGV and bGV – above- and  
 395 belowground biomass of herbaceous vegetation; respectively; S – small shrubs; FRP – tree fine root production; M – moss; MP – moss  
 396 production (assuming 100% projection); fLF – fine litterfall; cLF – coarse woody litterfall; RB - total root biomass.

Category	Drained	Undrained
aGV	1.82±0.52	2.35±1.61
bGV	2.89±0.85	2.42±0.84
S	0.84±0.45	4.27±2.5
FRP	2.53±0.77	1.08±0.57
M	5.02±0.87	-
MP	0.98±0.25	1.01±0.23
fLF	3.22±0.44	2.53±1.06
cLF	0.73±0.27	0.78±0.62
RB	39.3±11.1	52.7±18.7

397  
 398 Both bGV ( $r=0.6$ ) and FRP ( $r=0.7$ ) biomass have a significant negative correlation with soil pH but a positive with the C:N  
 399 ratio in soil layer 0-30 cm. Additionally, FRP has a significant negative correlation ( $r=-0.7$ ) with the content of biogenic  
 400 elements (N, Ca, Mg) in the soil. No explanatory factors for aGV and MP biomass have been identified. Moderate correlation  
 401 ( $r=0.5$ ,  $p<0.05$ ) is found between stand age and fLF, while cLF has a weak relationship with stand parameters.  
 402 The study's estimated sum of annual gross ground vegetation biomass production and litter in sites with drained soil ranges  
 403 from 4.58 to 8.29 t C ha<sup>-1</sup> year<sup>-1</sup> (mean  $5.91 \pm 1.10$  t C ha<sup>-1</sup> year<sup>-1</sup>), while in sites with undrained soil, it ranges from 3.41 to  
 404 5.40 t C ha<sup>-1</sup> year<sup>-1</sup> (mean  $4.72 \pm 1.16$  t C ha<sup>-1</sup> year<sup>-1</sup>) (Figure 8).



405

406 **Figure 8: Forest floor, including ground vegetation, carbon balance (sum±combined CI).** Abbreviations: aGV and bGV – above- and  
 407 belowground biomass of herbaceous vegetation; respectively; cLF – coarse woody litterfall; fLF – fine litterfall; FRP – tree fine root  
 408 production; MP – moss production (assuming 100% projection); Raut – soil autotrophic respiration; Rhet – soil heterotrophic respiration.  
 409 The assumption is used that biomass is equivalent to the average results obtained from sites with the same drainage status in other countries  
 410 in cases the corresponding carbon pool was not estimated in some countries, such as bGV and FRP in EE and FRP in certain sites in LT and  
 411 LV. Figure should not be interpreted as soil C balance (see Materials and Methods).

412 **2.5 Annual soil and forest floor carbon balance**

413 Based on assumption (2) the estimated Rhet proportion of R<sub>tot</sub> varied between 54 and 71% (mean 65%). Consequently, the  
 414 estimated annual gross C losses from drained soil in the form of Rhet emissions in the study sites ranged from 2.36 to 7.49  
 415 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup> (mean 4.30±1.20 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>), while for undrained soils, gross C loss range from 1.63 to 4.68  
 416 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup> (mean 3.00±0.99 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>). In drained and undrained sites, C input applied in C balance  
 417 estimation ranged from 3.81 to 7.03 t C ha<sup>-1</sup> year<sup>-1</sup> (mean 5.20±0.91 t C ha<sup>-1</sup> year<sup>-1</sup>) and 2.89 to 5.98 t C ha<sup>-1</sup> year<sup>-1</sup> (mean  
 418 4.19±1.10 t C ha<sup>-1</sup> year<sup>-1</sup>), respectively. When these averages are compared with the estimated Rhet C losses for both drained  
 419 and undrained soils, it is found that the soil C stock did not diminish during the study period, irrespective of drainage status.  
 420 For instance, direct comparison of the mean estimated C influx and efflux in drained and undrained soils shows that during  
 421 the study period soil C stock increased by mean 0.9±1.51 and 1.19±1.48 t C ha<sup>-1</sup> year<sup>-1</sup>, respectively. These results show that  
 422 drainage of soil reduces C sequestration capacity by average 0.29 t C ha<sup>-1</sup> year<sup>-1</sup>. However, a more conservative C balance  
 423 estimation approach, assuming C efflux is equal to measured R<sub>tot</sub>, estimated that annual net C efflux of forest floor in drained  
 424 sites was 1.05±0.98 t C ha<sup>-1</sup> year<sup>-1</sup> on average, whereas in undrained sites a C source amounting mean 0.48±1.61 t C ha<sup>-1</sup> year<sup>-1</sup>  
 425 (Table S 10). This approach reveals that forest floor in drained sites contributed to a higher net C efflux, averaging 0.57 t C  
 426 ha<sup>-1</sup> year<sup>-1</sup>. Consequently, both C balance estimation approaches consistently indicate a negative impact of drainage -  
 427 0.43±2.69 t C ha<sup>-1</sup> year<sup>-1</sup>.

428 **3 Discussion**

429 The study highlights the critical need to assess the accuracy of Rhet measurements before their application in subsequent  
 430 analyses and result compilation. In our case, we observed errors in the measurements because it was possible to compare the  
 431 results with R<sub>tot</sub>. In studies where R<sub>tot</sub> measurement is not the primary objective, control measurements near a trenched area  
 432 could be introduced as a necessary Rhet measurement quality assurance measure. This issue led us to use R<sub>tot</sub> as a proxy to  
 433 characterize soil emissions, which likely introduces additional complications in assessing the impact of influencing factors on  
 434 soil C balance. Therefore, in the subsequent sections, we will explore the relationships identified in connection with individual  
 435 C balance components.



436 **3.1 Soil heterotrophic respiration**

437 The higher correlation of all soil parameters except Corg with Rhet is likely due to higher role of autotrophic respiration  
438 component in Rtot emissions which introduces additional "noise". While no correlation was found between flux and Corg  
439 content of the soil, it is probably because the soil in the study sites does not represent a wide gradient of Corg concentration.  
440 It is observed that higher Corg content is related to lower soil CO<sub>2</sub> emissions, as in peatlands lower soil C content is often  
441 related to higher nutrient availability (Jauhainen et al., 2023). Although uncorrelated Corg and Rhet observations are common.  
442 Probably our study had limited opportunities to identify relationships because all the study sites are classified as nutrient rich.  
443 Negative correlation found between C:N and Rhet allows to assume that if C:N ratio is related to the degree of soil  
444 mineralization, it is more indicative of past elevated emissions rather than currently increased mineralization process. In other  
445 words, increased emissions likely occurred when the soil was recently drained compared to current situation when ecosystem  
446 likely tends towards new equilibrium after the initial disturbance. Despite the scarcity of research on the long-term impact of  
447 drainage on soil CO<sub>2</sub> emissions, some evidence suggests that the role of Rhet in Rtot declines in time since drainage (Munir et  
448 al., 2017), and effects of initial disturbances can be mitigated after 100 years (Hommeltenberg et al., 2014; Vanguelova et al.,  
449 2019). This might explain the absence of significantly increased emissions in the historically drained peatlands that we  
450 investigated. Another related reason emissions from drained soils may not be significantly increased is soil compaction  
451 resulting from the drainage process. This is indicated by the increased BD of drained soil, which is associated with lower soil  
452 Rhet emissions (mean  $r=-0.2$ ). The reason may be reduced soil porosity limiting gas exchange between the soil and the  
453 atmosphere (Ball, 2013; Novara et al., 2012). Reduced porosity also leads to higher water level fluctuations in drained peat  
454 soils (Figure 3 and Figure 4: 4), consequently stimulating redox processes and CO<sub>2</sub> emissions (Wang et al., 2018). In the case  
455 of BD correlation, a different trend is observed compared to other soil parameters: instead of being comparably uniform across  
456 soil layer it tends to increase with deeper soil layers, being highest ( $r=-0.3$ ) in the 20-30 cm layer, which is also the layer that  
457 showed the highest correlation between Rhet and chemical properties. Thus, while this layer may be prone to a high  
458 decomposition rate, flux driving processes seem to be countered by increased soil compaction. Therefore, a long time after  
459 drainage, although the soil CO<sub>2</sub> flux from drained soil is likely higher ( $4.30\pm 1.20$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) they may not differ  
460 significantly from undrained soil (mean  $3.00\pm 0.99$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) as shown by Rtot derived Rhet estimation of this study.

461 **3.2 Soil heterotrophic respiration interpretation issues**

462 Acquired Rhet data was excluded from annual soil C balance estimation as there was sufficient evidence of error in the acquired  
463 results. One of the probable main reasons for the failure of Rhet measurements is indicated by the correlation ( $r$ ) achieved  
464 between soil temperature and Rhet, ranging from a mean of  $0.28\pm 0.12$  to  $0.51\pm 0.12$ . Thus, significantly lower compared to  
465 correlation found with Rtot, indicating measurement error as both root and microbial respiration are temperature dependent  
466 (Davidson and Janssens, 2006). In our case reduced correlation seems introduced generally due to high emission outliers at  
467 elevated soil temperatures, which may lead to considerable Rhet overestimation by flux interpolation models restricted to  
468 predict reduced emissions at increased temperatures when soil moisture regime does not favor microbial activity (Khomik et  
469 al., 2009; Yueqian and Sc, n.d.). The reason for affected Rhet measurement quality may have been the study design's deficiency  
470 in measuring soil temperature. Temperature readings, taken at the center of the subplot, may not have accurately reflected  
471 potential temperature differences between areas with intact vegetation and trenched sections. The environmental parameter  
472 measurements did not consider that soil temperature and moisture conditions in trenched areas might differ. The error of  
473 measured Rhet is evident in the observed relationship between Rhet or Rtot and temperature, indicating higher Rhet emissions  
474 at the same temperatures (Figure S 4).

475 Trenching altered soil conditions (Ojanen et al., 2012) can be a reason for biased Rhet measurements (Pumpanen et al., 2010)  
476 as soil respiration is influenced not only by soil temperature but also by water availability (Davidson and Janssens, 2006). Not  
477 accounting of moisture regime in interpolation of flux measurement results can lead to overestimation as Rhet prediction



478 models have to be available to predict lower emissions at even increased temperatures if soil moisture is limiting microbial  
479 activity (Jovani-Sancho et al., 2018; Liaw et al., 2021). No availability of temperature and soil moisture continuous and manual  
480 measurements directly in trenched spots did not allow to empirically address these issues.

481 Also, direct comparison of measured  $R_{tot}$  and  $R_{het}$ , ignoring temperature relationships, indicates that comparability has been  
482 disturbed as  $R_{het}$  exceeded  $R_{tot}$  measurement results. Impact of analytical instruments used was excluded as bias of  
483 measurement results was not observed during initial comparison of two used instrumental methods (gas chromatograph and  
484 portable analyzer) performed in controlled conditions. However, it must be noted that during this comparison the same chamber  
485 was used. Therefore, probably reasons for  $R_{het}$  measurement errors may be not only soil conditions altered by trenching, but  
486 also: disturbance of natural conditions may have been further stimulated by covering trenched area by geotextile between  
487 measurements; differences in flux measurement technical aspects - chamber sizes, measurement time, application of fan for  
488 mixing air inside the chamber headspace.

489 Even if the trenching process did not alter soil temperature and moisture levels, a significant source of error could stem from  
490 the decomposition of severed roots. Soil trenching was conducted before winter, and by spring, when measurements began,  
491 the cut roots decomposition accelerated and that reflected in  $R_{het}$  measurements. To assess the potential impact of the cut  
492 roots, we collected total belowground biomass samples from the top 40 cm of soil using a soil probe and found that the total  
493 root biomass in drained and undrained was, on average,  $39.3 \pm 11.1$  and  $52.7 \pm 18.7$  t ha<sup>-1</sup>, respectively. Considering that around  
494 50% of roots can decompose over two years (Straková et al., 2012; Moore et al., 1999), the study period's underground biomass  
495 decomposition could have led to a significant artificial increase in measured  $R_{het}$  of drained ( $11.67$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) and  
496 undrained ( $14.37$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) soils. Specifically, the decomposition of roots may have raised the  $R_{het}$  value by 4.90  
497 and 6.59 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>, respectively. Although this estimation is rough, it quite well illustrates the potential  
498 overestimation by root decomposition, especially since the measured  $R_{het}$  in the study exceeded the  $R_{tot}$  by an average of  
499  $5.8 \pm 3.1$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>. Therefore, the primary source of error in  $R_{het}$  measurements was likely the decomposition of  
500 roots.

### 501 3.3 Total respiration

502 The gradient of the mean air temperature from Estonia to Lithuania varied from 6.4 to 8.5 °C. However, no significant  
503 differences in  $R_{tot}$  measurements were observed across the countries. Similarly, no clear impact of dominant tree species on  
504  $R_{tot}$  was found. Mean instantaneous  $R_{tot}$  measurements results indicate a greater relationship with the dominant tree species  
505 is the study sites, compared to the results of annual cumulative  $R_{tot}$  estimated. However, in both cases, the influence of species  
506 on  $R_{tot}$  is weak. Which was also confirmed by PCA and mixed-effects modeling. This points to difficulties of evaluating the  
507 role of dominant tree species on emissions. However, there is some evidence found that emissions in undrained sites tend to  
508 be higher in deciduous stands, particularly alder stands, according to results of measured instantaneous emissions. The  
509 enhanced soil CO<sub>2</sub> efflux observed in the presence of alder can be attributed to the symbiotic nitrogen fixation process  
510 associated with these trees (Warlo et al., 2019), which increases nitrogen availability in the soil. Nitrogen availability, in turn,  
511 can stimulate decomposition processes, leading to a higher rate of CO<sub>2</sub> release. Although statistically unconfirmed, a tendency  
512 can be noticed that in drained sites  $R_{tot}$  emissions tend to be higher in birch stands, but lower in pine forests. Also, previous  
513 studies indicated that deciduous stands are responsible for higher CO<sub>2</sub> emissions (Jauhainen et al., 2023).

514 While both drainage status and WTL threshold above or below 30 cm can be used as a predictor of  $R_{tot}$ , meaningful correlation  
515 between WTL and  $R_{tot}$  was not found. Furthermore, although the absolute variation of the WTL was higher in drained sites,  
516 the relative variation in both WTL level and  $R_{tot}$  was indifferent to the drainage status. The observation suggests that raised  
517 WTL conditions in undrained sites, while decreases  $R_{tot}$  emissions, does not guarantee higher resilience to moisture regime  
518 disturbances, i.e., more stable emissions. Main reason is just as the presence of drainage ditches cannot consistently lower  
519 WTL both spatially and temporally, in undrained sites too, WTL frequently falls below 30 cm (Butlers et al., 2023) ensuring



520 aerobic conditions in soil layers containing labile organic matter. Furthermore, this typically happens in summer (Butlers et  
521 al., 2023) when increased temperatures further promote organic matter mineralization of undrained soil. Role of WTL  
522 dynamics is reflected also in results in PCA, showing increased diversity of drained sites likely due to higher absolute variation  
523 in WTL depth. This may be the reason complicates quantification of relationships between flux and the affecting factors,  
524 especially in drained sites.

525 To aim towards accurate  $R_{tot}$  annualization using periodic flux measurements, data interpolation by modeling approaches is  
526 necessary. Both advantages and shortcomings of different data transformation methods and modeling approaches are reported  
527 by previous studies (Yueqian and Sc, n.d.; Wutzler et al., 2020; Liaw et al., 2021; Moulin et al., 2014; Box and Cox, 1964;  
528 Khomik et al., 2009). Although the bias in predicted annual  $R_{tot}$  varied among study sites, the overall impact of different flux  
529 modeling approaches on annual  $R_{tot}$  estimations was minimal. Specifically, the mean bias of results obtained through the  
530 implementation of the Box-Cox transformation was  $-2\pm 9\%$ , indicating a rather consistent accuracy compared to other methods  
531 used.

### 532 **3.4 Carbon balance estimation**

#### 533 **3.4.1 Carbon efflux**

534 Since direct  $R_{het}$  measurements were excluded from the soil C balance calculation, the C efflux ( $R_{het}$ ) was derived from  $R_{tot}$   
535 measurement results empirically using the  $R_{het}/R_s$  factors of previous studies.  $R_{het}$  and  $R_s$  values from database (Jian, J. et  
536 al., 2021) on forests soil flux in the boreal zone were used, as existing experience suggests that organic soil emissions in  
537 hemiboreal forests are more likely to align with boreal rather than temperate conditions (Krasnova et al., 2019; Heikkinen et  
538 al., 2023; Bārdule et al., 2022; Butlers et al., 2022; Dubra et al., 2023; Lazdiņš et al., 2024). Choice of using only boreal data  
539 tends towards use of higher share of  $R_{het}$ , compared if temperate data were used, as illustrated in Figure S 4. This approach  
540 aimed to avoiding the underestimation of soil C losses. The share acquired using boreal data is  $0.65\pm 0.04$ , while using  
541 temperate data -  $0.60\pm 0.15$ , or around 10% difference. According to this approach we estimated mean  $R_{het}$  of drained soil as  
542 mean  $4.30\pm 1.20$  t  $\text{CO}_2\text{-C ha}^{-1} \text{ year}^{-1}$ , which is slightly higher than mean  $R_{het}$  of  $3.71\pm 0.53$  t  $\text{CO}_2\text{-C ha}^{-1} \text{ year}^{-1}$  found in  
543 previous studies of forest organic soil (Jian, J. et al., 2021). However, conclusions or observations of studies in the boreal zone  
544 may not be directly applicable to the hemiboreal zone. One reason for this is the larger removals by net ecosystem exchange  
545 observed in the hemiboreal zone than northern forests, which also creates greater potential for C influx by litter to offset  $R_{het}$   
546 C loss (Krasnova et al., 2019), which should be linked also to  $R_{het}$  rates.

547 The role of ground vegetation autotrophic respiration in  $R_{tot}$  increases with its biomass (Munir et al., 2017). Consequently,  
548 the applied approach of empirical  $R_{het}$  calculation may have overestimated  $R_{het}$ . This aspect is considerable in our assessment  
549 of soil C balance. However, when estimating the impact of drainage on the soil C balance, any bias introduced was likely  
550 negligible, because the mean ground vegetation biomass did not significantly differ between drained and undrained sites  
551 ( $\Delta=0.53$  t dm.  $\text{ha}^{-1}$ ). Consequently, any bias introduced in the calculation of  $R_{het}$  is offset when making relative comparisons  
552 of the soil C balance between drained and undrained sites to determine the impact of drainage.

#### 554 **3.4.2 Carbon influx**

555 When interpreting the study results, it is essential to consider the C fluxes included in the C balance calculations. In estimation  
556 of C influx, we considered data only for fLF, aGV, bGV, and FRP, excluding cLF, MP and dwarf shrubs. This approach was  
557 chosen because it is rational to directly compare these measurements with  $R_{tot}$ , as the mineralization produced  $\text{CO}_2$  emissions  
558 of these litter is directly included in  $R_{tot}$ . However, including litter such as cLF, MP, and shrubs in the calculation would  
559 overestimate C input into the soil, because cLF due to its dimensions and scarce coverage could not be objectively included in  
560 chamber measurements. Furthermore, while fLF is relatively uniform in forest area, the coverage of mosses and dwarf shrubs  
561 is not always so, therefore it is necessary to know their area of projection to be included in C balance estimation. One of the





562 solutions for incorporating cLF influx is to use assumptions on litter mineralization rate. One example of how the issue can be  
563 tackled is the use of modeling approaches such as Yasso (Alm et al., 2023). Information on small shrubs and moss biomass  
564 can be added in modelling as well by considering their annual production and turnover rate. For these reasons litter biomass  
565 (mean  $4.70 \pm 1.43 \text{ t C ha}^{-1} \text{ year}^{-1}$ ) used in calculation of soil C balance likely overestimates soil C loss, as inclusion of cLF and  
566 MP can increase soil C input by up to mean  $0.9 \text{ t C ha}^{-1} \text{ year}^{-1}$ , according to the study data.

567

### 568 3.4.3 Carbon balance

569 By applying different data aggregation approaches (e.g., by country or dominant tree species), varying results for soil C balance  
570 estimation were achieved. For instance, by categorizing the data according to drainage status and dominant tree species and  
571 adopting the approach of using  $R_{\text{tot}}$  as the C output value, we determined that forest floor, including ground vegetation, in  
572 both drained and undrained sites were sources of  $\text{CO}_2$  emissions. Specifically, in drained deciduous species sites, average  
573 estimated net soil C efflux is  $1.84 \pm 0.93 \text{ t C ha}^{-1} \text{ year}^{-1}$ , forest floor in coniferous stands show an estimated soil C sequestration  
574 of  $0.39 \pm 0.57 \text{ t C ha}^{-1} \text{ year}^{-1}$ . Meanwhile, forest floor in undrained deciduous stands experienced a mean C loss efflux  $0.16 \pm 0.64$   
575  $\text{t C ha}^{-1} \text{ year}^{-1}$ , while in spruce stands showed a loss  $0.9 \pm 1.46 \text{ t C ha}^{-1} \text{ year}^{-1}$ . Thus, confirming previous observations that  
576 drained deciduous forests can be associated with higher soil  $\text{CO}_2$  emissions (Jauhiainen et al., 2023) However, our estimates  
577 of C balance by species may be influenced by the random effects associated with the study sites, as suggested by mixed-effects  
578 modeling. Such data segregation approach is not unequivocally most appropriate if considering that the study did not find a  
579 definite proof of country or dominant tree species impact on  $R_{\text{tot}}$ . Therefore, we should interpret these specific study results  
580 with caution. We believe that estimating the C balance based on drainage status, without further stratification of results,  
581 provided a more accurate assessment. Furthermore, it is evident that utilizing  $R_{\text{tot}}$  as the soil C output value leads to an  
582 overestimation of soil carbon losses. Therefore, the focus should primarily be on analyzing the results of C balance estimation  
583 by incorporating  $R_{\text{het}}$ , assessing the capacity of litter to offset soil C losses. Additionally, it is crucial to examine the factors  
584 influencing soil C influx and efflux to aim towards an accurate assessment of changes in soil C stocks of both drained and  
585 undrained soils.

586 There are observations that soil  $\text{CO}_2$  emissions are determined by soil nutrient status of the site (Meyer et al., 2013; Korkiakoski  
587 et al., 2023), supporting assumption that nutrient-rich soils are likely a C source. However, such interpretation should be  
588 exercised cautiously, considering complexity of forest floor C balance components and interactions. Some aspects noticed in  
589 this study are a negative correlation found between nutrient availability and belowground biomass (bGV, FRP) confirming  
590 previous observations that greater belowground biomass is associated with reduced nutrient availability (Zhang et al., 2024).  
591 At the same time increased ground vegetation belowground biomass was associated with lower WTL. Which are two  
592 countering effects in the study sites, as while WTL is increased in undrained sites, soil in these sites were nutrient richer. In  
593 general, while higher organic matter decomposition rates can be expected for nutrient rich sites (Shahbaz et al., 2022; Hiraishi  
594 et al., 2013a), also higher total soil C influx by litter can be expected by increased biomass growth, thus offsetting soil C loss  
595 by  $R_{\text{het}}$ . This is indicated by our study, as in both drained and undrained sites mean C amount of litter biomass exceeded  
596 estimated  $R_{\text{het}}$ .

597 Acquired empirical data segregated by drainage status indicated that both drained and undrained nutrient rich organic soil in  
598 Baltic states is not a C source ensuring C removals of  $0.9 \pm 1.51 \text{ t C ha}^{-1} \text{ year}^{-1}$  and  $1.19 \pm 1.48 \text{ t C ha}^{-1} \text{ year}^{-1}$ , respectively.  
599 Such results can be found controversial by the general public, but results of studies showing soil as a C sink in afforested  
600 peatlands is common (Minkinen et al., 2018; Lohila et al., 2011; Bjarnadottir et al., 2021), preventing consensus that peatland  
601 drainage is a measure associated with soil C stock loss. Preserved C stock is also indicated by similar mean estimated Corg  
602 content in the top 30 cm of soil suggesting that the Corg stock in drained soils might not be at higher risk than undrained ones.  
603 However, such an assessment, although providing indications, would not be correct for comparison because the C stock is  
604 significantly influenced by the soil bulk density, which in 30 cm topsoil was on average 1.8 times greater in the drained soils



605 at the study sites, consequently almost doubling the C stock in the corresponding soil layer and meantime suggesting a soil  
606 compaction introduced by drainage. Noteworthy that the C:N ratio in drained soils is increased compared to undrained soils,  
607 however it can give a misleading impression of the degree of ongoing mineralization if nitrogen inputs and outputs from the  
608 soil are not considered (Ostrowska and Porębska, 2015). Nevertheless, assuming that the area was drained around a century  
609 ago, as was mostly done in this region (Zālītis, 2012), then according to the IPCC default emission factor of 2.6 t CO<sub>2</sub>-C ha<sup>-1</sup>  
610 year<sup>-1</sup> (Hiraishi et al., 2013b), the Corg stock should have been already depleted in drained soils which is not the case. Drainage  
611 of peatlands does not necessarily result in a loss of soil C stocks (Minkinen and Laine, 1998). Short-term soil C loss due to  
612 drainage induced increase in gross soil CO<sub>2</sub> emissions could already been offset by enhanced biomass growth (Hommeltenberg  
613 et al., 2014), as initial soil C stock can be restored after several forest rotations (Vanguelova et al., 2019). It is observed by a  
614 local soil inventory studies that C stocks of forestry drained peatlands are stable in nutrient-poor or moderate rich soil  
615 conditions, while there is evidence that nutrient-rich organic soil can lose C stock in the long term (Lazdiņš et al., 2024; Dubra  
616 et al., 2023). However, we did not find firm proof of that in this study.

#### 617 **4 Conclusions**

618 The study indicates complex interactions between a range of factors, including water table level dynamics, soil compaction,  
619 availability of labile organic matter, and the litter sources and variation, determining the soil carbon balance. Thus, highlighting  
620 the importance of considering nutrient status and drainage status rather as proxies of the underlying factors influencing soil  
621 CO<sub>2</sub> fluxes than general predictors. While not confirmed with high certainty, indications have been observed that CO<sub>2</sub>  
622 emissions from soils in deciduous forests tend to be higher than in coniferous forests. However, estimated soil C influx and  
623 efflux did not conclusively demonstrate a loss of soil carbon stock within the study sites. The absence of a significant country  
624 impact on the estimated soil emissions suggests that a uniform approach for organic soil emissions estimation can be applied  
625 across the Baltic states.

626 Two approaches used for the carbon balance estimation provided contradictory results, with soil being estimated as a carbon  
627 sink regardless of drainage status, while the forest floor (including ground vegetation) was estimated to be a net source of CO<sub>2</sub>  
628 emissions. Likely a more accurate estimation would be to assume the carbon balance to be midway between these assessments.  
629 Consequently, during the study period, drained soils experienced a carbon loss of 0.07±1.80 t C ha<sup>-1</sup> year<sup>-1</sup>, while carbon  
630 stocks of undrained soils increased by an average of 0.36±2.0 t C ha<sup>-1</sup> year<sup>-1</sup>.

631 Despite the discrepancy in the evaluation of carbon balance in drained and undrained sites, the results regarding the impact of  
632 drainage on carbon balances were uniform. Both approaches showed a negative impact of drainage on carbon balance ranging  
633 between an average of 0.29 and 0.57 t C ha<sup>-1</sup> year<sup>-1</sup>, with a mean of 0.43±2.69 t C ha<sup>-1</sup> year<sup>-1</sup>.

#### 634 **Data availability**

635 Data used for carbon balance estimations is available at DOI: 10.5281/zenodo.11073425

#### 636 **Author contributions**

637 KS, RL, JJ, AL and KA developed a harmonized methodology. ABu, DČ, TS and MKS managed and processed the study  
638 data. ABu wrote the original manuscript, with JJ managing the writing process and incorporating insights from all team  
639 members, including significant reviewing contributions from RL. TS, ABā, IL, VS, HV, IL and AH provided critical reviews  
640 and edits to the manuscript.



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644 **Competing interests**

645 Authors have no competing interests to declare.

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