

# Organic soils can be CO<sub>2</sub> sinks in both drained and undrained hemiboreal peatland forests

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**Abstract.** Drainage of organic soils is associated with increasing soil carbon dioxide (CO<sub>2</sub>) efflux, which is typically linked to losses in soil C stock. In previous studies, drained organic forest soils have been reported as both CO<sub>2</sub> sinks and sources depending on, e.g., soil nutrient and moisture regime. However, most of the earlier research was done in the boreal zone, and both the magnitude of CO<sub>2</sub> efflux and the impact of soil moisture regime on soil C stock are likely to vary across different climatic conditions and ecosystems, depending further on vegetation. A two-year study was conducted in hemiboreal forest stands with nutrient-rich organic soil (including current and former peatlands) and a range of dominant tree species (black alder, birch, Norway spruce, Scots pine) in the Baltic states (Estonia, Latvia, Lithuania). In this study, we analyzed the CO<sub>2</sub> balance of organic soil in drained (19) and undrained (7) sites. To assess the CO<sub>2</sub> balance, soil respiration was measured along with evaluation of CO<sub>2</sub> influx into the soil through aboveground and belowground litter. To characterize the sites and factors influencing the CO<sub>2</sub> fluxes, we analysed soil temperature, soil water-table level, and physical and chemical parameters of soil and soil water. Irrespective of drainage status, the soils functioned as both CO<sub>2</sub> sinks and sources. On average, close-to-neutral soil CO<sub>2</sub> balance ( $+0.45 \pm 0.50$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) was observed in drained sites dominated by black alder, birch, or Norway spruce, while drained Scots pine sites showed soil CO<sub>2</sub> removals with a mean rate of  $+2.77 \pm 0.36$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>. In undrained birch- and spruce-dominated sites, soil functioned as mean CO<sub>2</sub> sink at  $+1.33 \pm 0.72$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>, while the undrained black alder stands showed an uncertain CO<sub>2</sub> balance of  $+1.12 \pm 2.47$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>. Variation in the soil CO<sub>2</sub> balance was related to soil macronutrient concentrations and pH: forest types characterized by lower nutrient availability showed greater soil CO<sub>2</sub> sink. The reported soil CO<sub>2</sub> balance values may be used as regional emission factors.

## 1 Introduction

Soil in peatlands, characterised by its high content of partially decomposed plant matter, is a major terrestrial organic carbon (C) stock, estimated to range from 504 to 3000 Gt C (Scharlemann et al., 2014). Although northern peatlands make up only 2-4% of the global land area, they contain a substantial amount of soil C, estimates ranging from around 500 to 1,055 Gt C (Nichols and Peteet, 2019; Yu, 2012), highlighting the significance of these lands in the global C budget. About 28% of the pristine (undrained) peatlands globally are inherently covered by forest (Zoltai and Martikainen, 1996), and those peatland forests in the boreal biome can accumulate C into the soil at similar rates to non-forested peatlands; the faster decomposition rates observed in peatland forests (Beaulne et al., 2021) can be compensated by higher litter inputs (Straková et al., 2010). To enhance tree growth, peatland drainage for forestry has been common in the past. Drainage facilitates oxygen access to deeper peat layers, thereby promoting tree root survival and function, but also the mineralization of organic matter and the release of C into the atmosphere in the form of CO<sub>2</sub>. Therefore, the conservation of organic soil C stocks in managed current and former peatlands has attracted attention in the context of climate change.

42 The approximately 13 million ha of forestry-drained organic soils in Europe have been estimated to emit 17 million tons of  
43 CO<sub>2</sub> per year (European Environment Agency, 2023). Despite the temperate zone being characterized by wide climatic  
44 gradients, currently, only a single default emission factor (EF) by the Intergovernmental Panel on Climate Change (IPCC) is  
45 available for the entire temperate zone, to which the Baltic states correspond according to the IPCC (Hiraishi et al., 2013). The  
46 EF was developed using study results from 8 drained sites (Hiraishi et al., 2013), which were published in 5 articles (Von  
47 Arnold et al., 2005; Glenn et al., 1993; Minkinen et al., 2007; Yamulki et al., 2013). These studies employed different CO<sub>2</sub>  
48 estimation methods, complicating the comparability of the aggregated results (Jauhiainen, 2019; Jauhiainen et al., 2023). None  
49 of the sites are in the Baltic states. Given that the soil emissions in the boreal zone are smaller than in the temperate zone  
50 (Jauhiainen et al., 2023), and Baltic states are situated in the hemiboreal vegetation zone (Ahti et al., 1968) – in transition  
51 between the temperate and boreal zones – the IPCC's default temperate EF may not be suitable for application in this region.  
52 The same issue arises on a broader geographic scale, where the use of unharmonized country-specific and default EFs creates  
53 challenges in comparing the estimated emissions both within and across different countries and climate zones. Discrepancies  
54 in CO<sub>2</sub> emissions between regions can be expected due not only to climate gradient (Ojanen et al., 2010) but also to site  
55 productivity (Janssens et al., 2001). While higher ecosystem productivity is associated with increased soil respiration rates  
56 (Janssens et al., 2001) it also facilitates higher CO<sub>2</sub> influx through litter (Krasnova et al., 2019). Therefore, EFs are most  
57 appropriately used when applied to areas with similar environmental conditions, rather than being limited by national  
58 boundaries or applied too broadly across diverse geographic regions.

59 In the Baltic states (Estonia, Latvia, and Lithuania), organic soils (Eggleston et al., 2006) are current or former peatlands where  
60 a peat layer is still identifiable, or, due to high decomposition, no longer meets the typical characteristics of peat. However,  
61 these soils by definition contain at least a 20 cm thick layer rich in organic matter (organic layer). In the region, the total area  
62 of drained organic forest soils is reported to be 0.8 million ha, with estimated emissions of 1.8 million tons of CO<sub>2</sub> per year  
63 (Konstantinavičiūtė et al., 2023; Ministry of the Environment of Republic of Estonia, 2021; Skrebele et al., 2023). Thus,  
64 countries with a relatively small total land area yet a substantial proportion of organic soil can have a considerable role in  
65 organic soil management. This underscores the importance of acquiring precise estimates of the CO<sub>2</sub> emissions from organic  
66 forest soils in this region. However, despite the Baltic States being located next to each other and thus expectedly showing  
67 similar soil CO<sub>2</sub> emissions from comparable sites and land uses, the emission estimation approach is currently not harmonized  
68 as the countries use different EFs to estimate and report emissions (Konstantinavičiūtė et al., 2023; Ministry of the Environment  
69 of Republic of Estonia, 2021; Skrebele et al., 2023). According to National Greenhouse Gas Inventories submissions of 2023,  
70 the CO<sub>2</sub> emissions of drained organic forest soil in Estonia and Lithuania were estimated using the default EF provided by  
71 IPCC for the temperate zone (Calvo Buendia et al., 2019), while Latvia applied a country-specific EF. Due to similarities in  
72 biogeography, climate, and land-use practices, common EFs based on regionally representative, congregated data could be a  
73 better option.

74 A recent synthesis evaluated whether default IPCC EFs can be improved by compiling results from the most recent studies  
75 (Jauhiainen et al., 2023). Still, only modest and insignificant changes judging by confidence intervals (CI) of IPCC EFs could  
76 be introduced for the temperate climate zone as a whole, due to limited data (Jauhiainen et al., 2023). Although the general  
77 driving factors of CO<sub>2</sub> emissions are known, the number and geographical representation of studies on drained soils,  
78 particularly in the temperate zone, remain too limited for stratification of EFs based on local conditions. It is widely known  
79 that soil temperature is the primary factor influencing gross CO<sub>2</sub> emissions. However, while temperature can explain variations  
80 in emissions, it does not fully account for their magnitude. The extent of CO<sub>2</sub> emissions is affected by soil properties (Basiliko  
81 et al., 2007), incorporating complex interactions between a soil's physical, chemical, and biological characteristics, including  
82 the impact of the litter quality (Berger et al., 2010). The recent synthesis confirmed that key factors influencing the magnitude  
83 of CO<sub>2</sub> emissions include soil C concentration, carbon-to-nitrogen (C:N) ratio, and bulk density, as well as stand type  
84 (Jauhiainen et al., 2023). Yet, the list likely remains quite incomplete, as individual studies in different site types using various  
85 methods can provide unharmonized results making it difficult to identify the relationships influencing CO<sub>2</sub> emissions. Varying

86 and often insufficient reporting of study site conditions in previous studies (Jauhiainen, 2019) further hampers the ability to  
87 compile the results for effective synthesis and meta-analysis (Jauhiainen et al., 2023). This limitation may have hindered the  
88 identification of emission-impacting factors and the ability to quantify their relationships, underscoring the need for more  
89 localized studies to address these gaps, particularly in the hemiboreal vegetation zone which overlaps with the Cool Temperate  
90 Moist climate zone (Calvo Buendia et al., 2019) - a subregion of temperate zone as defined by the IPCC.

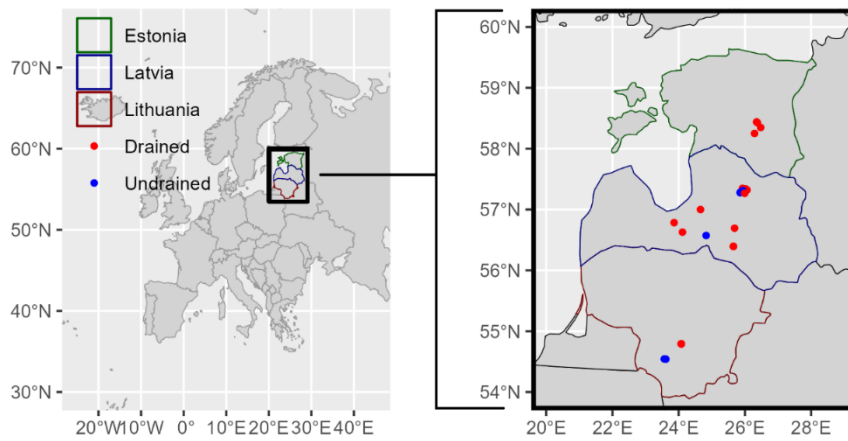
91 In the few studies on drained and undrained soil C or CO<sub>2</sub> balance conducted in the Baltic states, using both chamber and soil  
92 inventory methods, findings have been inconsistent (Butlers et al., 2022; Lazdiņš et al., 2024; Bārdule et al., 2022). Drained  
93 organic soils have been identified as both C sinks and sources, with no decisive conclusions reached regarding the factors  
94 driving such variation. Soil C loss of nutrient-rich organic soil has been identified using the soil inventory method (Lazdiņš et  
95 al., 2024) but not confirmed by the chamber method (Butlers et al., 2022; Bārdule et al., 2022) that, unlike the inventory  
96 method, targets the current situation (Jauhiainen et al. 2019). Given that nutrient-rich organic forest soils can make up to 72 %  
97 of total organic forest soils (Līcīte et al., 2019) and are associated with a higher risk of soil C loss, there is a need to enhance  
98 our understanding of the underlying drivers to improve the accuracy of CO<sub>2</sub> balance estimates in Baltic states. Therefore,  
99 studies using harmonised data collection methods are necessary, covering a variety of nutrient-rich forest soils, recording or  
100 monitoring essential environmental conditions, and accounting for both soil CO<sub>2</sub> efflux and influx from various litter sources.

101 This study aimed to quantify the soil CO<sub>2</sub> balance in hemiboreal forests with nutrient-rich organic soil and different dominant  
102 tree species. The research was carried out in 26 forest stands with organic soil in Estonia (EE), Latvia (LV), and Lithuania  
103 (LT), including both undrained and drained sites, over two years. We analysed soil CO<sub>2</sub> emissions as well as CO<sub>2</sub> influx by  
104 tree fine roots, ground vegetation (below- and aboveground) and fine foliar litter. We examined factors contributing to soil  
105 CO<sub>2</sub> balance by directly or indirectly influencing soil processes, such as site type, dominant tree species, soil and soil water  
106 properties, and soil water-table level (WTL). Mean annual soil CO<sub>2</sub> balance values were estimated for potential use as EFs.  
107 For this purpose, we also assessed whether the CO<sub>2</sub> fluxes differed between countries. To facilitate the use of the results in  
108 future syntheses or meta-analyses, the data used for CO<sub>2</sub> balance estimation have been openly published.

## 109 2 Materials and methods

### 110 2.1 Study sites

111 In total, 26 study sites (Figure 1) were established in stands dominated by black alder (*Alnus glutinosa* (L.) Gärtner), birch  
112 (*Betula pendula* Roth, *Betula pubescens* Ehrh.), Scots pine (*Pinus sylvestris* L.), or Norway spruce (*Picea abies* (L.) Karst.) of  
113 different ages (Table S1). The study sites included both drained (n=19) and undrained (n=7) organic soils (Eggleston et al.,  
114 2006), with the organic layer thickness ranging from 27 cm to over 2 meters, measured by a rod insertion. According to forest  
115 type classification, all sites were characterised as nutrient-rich based on ground vegetation and stand productivity (Bušs, 1981).  
116 Drained sites were represented by two site types: *Oxalidosa turf. mel.* (Oxalis), which has relatively higher nutrient availability  
117 (pH, macronutrients), and *Myrtillosa turf. mel.* (Myrtillus). Undrained sites were represented by the *Dryopterioso-caricosa*  
118 site type. Soil drainage status was determined based on the presence of drainage ditches within or along the respective forest  
119 compartment (a rectangular forest area of 50 ± 25 ha used as a management unit).



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

Despite the greater variation in stand characteristics among the more numerous drained sites compared to the undrained sites, the two groups were overall comparable. (Table 1). The mean stand age of both groups was 74 years, with a range of 26-162 years for 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, respectively. More information on stand characteristics, including mean WTL and coordinates, is provided in Table S1. The projective cover of the most common ground vegetation species in the study sites is presented in Table S2. All comparisons will be done at group level, since pairwise comparison, even of closely located sites that belong to the same site type, is hampered by the inherent variation in soil characteristics (see Laiho and Pearson 2016).

Both groups represent historically naturally forested lands that have undergone active forest management. While the exact time since drainage is unknown, active drainage of the forests was initiated in the mid-19th century and resumed in the mid-20th century. Drainage ditches were dug to depths of 0.8 to 1.2 m, with distances between them ranging from 100 to 400 m, and they are maintained to remain functional (Zālītis, 2012).

**Table 1: Range (minimum; maximum) 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

At each study site, three subplots (Figure S1) for data collection were selected, with a minimum distance of 30 m, in an area representing typical ecosystem characteristics of the floristically defined site type, as classified under the local forest site type system (Bušs, 1981). The subplots were arranged along a transect positioned perpendicular to the closest ditch in drained areas and perpendicular to stand border in undrained areas. In the drained sites, the first subplot was located about 20 m from the nearest drainage ditch. In the undrained sites, the first subplot was located at least 20 m from the forest border.

Empirical data was gathered from January 2021 to December 2022 in Estonia and Latvia, and from July 2021 to June 2023 in Lithuania. The sites were visited monthly in Latvia and Lithuania, and biweekly in Estonia. The meteorological conditions during the study were typical for the region (Table S3).

## 143 2.2 Respiration

144 Measurements of forest floor respiration, which we will hereafter refer to as total respiration ( $R_{tot}$ ), included both soil  
145 heterotrophic respiration and autotrophic dark respiration of ground vegetation (above and below-ground) as well as tree roots  
146 extending to the measurement locations. Gas samples were collected from manual closed static dark (opaque) chambers (PVC,  
147 volume  $0.0655 \text{ m}^3$ ) as described in the literature (Hutchinson and Livingston, 1993) for subsequent laboratory analysis.  $R_{tot}$   
148 monitoring included five to six monitoring locations, divided over 3 subplots, at each site. Ring-shaped chamber collars (area  
149  $0.196 \text{ m}^2$ ) were permanently installed in the soil at a depth of five cm at least one month before the first sampling to avoid the  
150 installation effect on fluxes. Collar locations reflected local diversity in vegetation and potential WTL gradient at each subplot  
151 and the encircled soil surface and vegetation were kept intact. Thus, the soil heterotrophic respiration component in  $R_{tot}$   
152 includes  $\text{CO}_2$  emissions caused by the decomposition of both fresh litter and soil organic matter.

153 Gas samples were collected by obtaining four air samples from a closed chamber into pre-evacuated ( $0.3 \text{ mbar}$ ) glass vials  
154 ( $100 \text{ cm}^3$ ). The air samples were taken from the chamber outlet, equipped with a valve attached in the sampling tube reaching  
155 approximately the centre of the airspace. The air within the chamber was not artificially mixed during sampling. Air sampling  
156 was done by first removing the residual air left from the sampling tube (to avoid potential impact on the concentration readout)  
157 by a syringe, and thereafter pre-evacuated glass vial was attached into the outlet. The first sample was taken immediately after  
158 attaching the chamber on the collar, and subsequent samples were taken at either 10 (Latvia) or 20 (Estonia and Lithuania)  
159 minute intervals over 30- or 60-minute monitoring periods, respectively (Butlers et al., 2022; Vigricas et al., 2024).

160 The gas samples were analysed using a Shimadzu GC-2015 gas chromatograph (Shimadzu USA Manufacturing, Inc., Canby,  
161 OR, USA) equipped with an electron capture detector (ECD). The uncertainty of the method used was estimated to be 20 ppm  
162 of  $\text{CO}_2$  (Magnusson et al., 2017). Linear regression was applied to relate the  $\text{CO}_2$  concentrations with the time elapsed since  
163 chamber closure for each measurement. Subsequently, the measurement data was screened to identify deviations from the  
164 recognized trend, considering the removal of measurements with identified errors. All measurements were discarded if the  
165 regression coefficient of determination ( $R^2$ ) was less than 0.9 ( $p < 0.01$ ), except for cases where the difference between the  
166 highest and lowest measured  $\text{CO}_2$  concentration in the chamber was less than the uncertainty of the method (specifically  
167 applicable during non-vegetation periods). Consequently, a small amount of data ( $< 5\%$ ) was discarded.

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

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

170 where  $R_{tot}$  is the instantaneous total respiration,  $\text{mg CO}_2\text{-C m}^2 \text{ h}^{-1}$ ;  $M$  is the molar mass of  $\text{CO}_2\text{-C}$ ,  $12.01 \text{ g mol}^{-1}$ ;  $R$  is the  
171 universal gas constant,  $8.314 \text{ m}^3 \text{ Pa K}^{-1} \text{ mol}^{-1}$ ;  $P$  is the assumption of air pressure inside the chamber,  $101.300 \text{ Pa}$ ;  $T$  is the air  
172 temperature in the chamber,  $\text{K}$ ;  $V$  is the chamber volume,  $0.0655 \text{ m}^3$ ; the slope is the  $\text{CO}_2$  concentration change over time,  
173  $\text{ppm h}^{-1}$ ; and  $A$  is the collar area,  $0.19625 \text{ m}^2$ .

174 We also conducted measurements of heterotrophic respiration ( $R_{het}$ ) for comparison, as described in the Supplementary text.

## 175 2.3 Environmental variables

176 Manual WTL measurements were carried out using nylon-mesh-coated, perforated piezometer tubes (5 cm in diameter)  
177 installed down to a 140 cm depth in all subplots. Manual soil temperature measurements were done at depths of 5, 10, 20, and  
178 40 cm in all subplots by Comet data logger (COMET SYSTEM, s.r.o., 756 61 Roznov pod Radhostem, Czech Republic)  
179 equipped with Pt1000 temperature probes. All manual measurements were carried out at the same time as the  $\text{CO}_2$  flux  
180 measurements. Continuous soil temperature measurements at depths of 10 and 40 cm were carried out at 30-minute interval in  
181 the centermost subplot (Maxim Integrated DS1922L2F, iButtonLink Technology, Whitewater, WI 53190 USA).

Once per month, soil water samples were collected from perforated tubes (7.5 cm in diameter) explicitly installed for water sampling for chemical analysis. Water chemical parameters including pH, electrical conductivity (EC), and concentrations of dissolved organic carbon (DOC), total nitrogen (N), and nitrate ( $\text{NO}_3^-$ ), ammonium ( $\text{NH}_4^+$ ) and phosphate ( $\text{PO}_4^{3-}$ ) ions were determined. Soil samples were taken down to a depth of 75 cm (0-10; 10-20; 20-30; 30-40; 40-50; 50-75cm) at two locations in each subplot during the establishment of the study sites. Two separate sample sets were collected, one for the determination of bulk density, and another for ash content and chemical parameters (pH, concentrations of total carbon (TC), nitrogen (N), and  $\text{HNO}_3$  extractable phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg)). The samples were collected with a volumetric 100  $\text{cm}^3$  cylinder (Cools and De Vos, 2010) at 10 cm intervals to a depth of 50 cm. Two additional samples were taken from soil depths of 50-75 and 75-100 cm with a soil auger. Soil samples collected for determination of bulk density were oven-dried (105 °C) and weighed, while soil samples for chemical analyses were prepared by air drying ( $\leq 40$  °C), sieving and homogenizing (LVS ISO 11464:2006). Organic carbon (Corg) content was calculated by multiplying soil organic matter content derived from the ash content measurement result by factor 0.5, thus assuming that organic matter is 50% Corg (Pribyl, 2010). All soil and water analyses were done in an ISO 17025-certified laboratory using ISO standard methods (Table S4).

## 2.4 Litter input

Annual litter inputs to be used in  $\text{CO}_2$  balance estimation were either measured (foliar litter) or estimated based on biomass components measured (ground vegetation, fine roots).

Foliar fine litter (fLF) was collected with conical litter traps (area 0.5  $\text{m}^2$ ) set one meter above ground (Latvia, Lithuania), or with square mesh frames (0.5 x 0.5 m) placed on the ground (Estonia). In each study site, five replicate litter traps were placed in the centremost subplot of the transect. It included all fine fractions of litter, such as needles, leaves, and branches with a diameter up to 1 cm and a length up to 10 cm. Branches with larger dimensions were collected from coarse woody litter (cLF) traps (square mesh frames, 0.5 x 0.5 m) placed on the ground. The litter samples were collected from the traps once every four weeks. Due to the heterogenous nature and large dimensions of cLF, respective decomposition emissions could not be representatively included in  $R_{\text{tot}}$  measurements. Therefore, we considered only fLF as the litter input source, and the cLF results are presented only as indicative of the site conditions.

Ground vegetation (GV) aboveground (aGV) and belowground (bGV) biomass samples were collected at the end of the growing season (August) in 2021 in five replicates per subplot, from square sampling locations with an area of 0.0625  $\text{m}^2$ . Aboveground biomass was separated into herbaceous (aGV) species and dwarf shrubs. bGV was collected from the top soil layer, extending down to 20 - 30 cm from the same location and area as aGV. Herbaceous ground vegetation roots (bGV) were separated from tree and shrub roots by wet sieving based on root morphological properties. We assumed that the measured herbaceous ground vegetation aboveground (aGV) and belowground (bGV) biomasses were equal to annual ground vegetation litter inputs. The contribution of shrub litter was thus not included but was assumed to be minor (see Table S5).

Moss biomass was measured by collecting samples from 0.01  $\text{m}^2$  square areas, with four replicates per subplot, and visually removing any dead parts. Collections were conducted concurrently with moss production sampling. Moss production (MP) samples in four replicates per subplot were collected by anchoring a square mesh (0.01  $\text{m}^2$ ) on the moss at the end of the growing season and harvesting the moss biomass grown through the mesh by the end of the next growing season. Including moss litter in the  $\text{CO}_2$  balance estimation by aligning  $\text{CO}_2$  influx and efflux from areas with and without moss cover, without increasing uncertainty, would however have required doubling the number of spatial replicates in chamber measurements. Therefore, we did not consider moss as a litter source, which causes underestimation of litter inputs to a varying extent. The moss results are presented only as indicative of site conditions (see Table S5).

Tree fine-root production (FRP) was estimated with the ingrowth core method (Laiho et al., 2014; Bhuiyan et al. 2017). Five replicate ingrowth cores (cylindrical mesh bags with diameter 2.5 cm, mesh size 2 mm) per subplot, filled with soil collected from the subplot, were installed in autumn or spring and removed after two growing seasons. In the laboratory, the biomass of

the ingrown fine roots was determined after wet sieving, and ground vegetation roots were separated from tree roots by morphological properties. We assumed that tree fine-root biomass was essentially not changing over the study years, and thus we could assume that FRP equalled litter production. Since the ingrowth cores were removed from the soil after two growing seasons, the FRP estimate was calculated by dividing the fine-root biomass in the cores by two (Bhuiyan et al., 2017).

All litter and biomass samples were oven-dried (70 °C), weighed and milled before further analysis. Chemical analyses were performed according to ISO standard methods (Table S4). To estimate the annual CO<sub>2</sub> influx to be used in the CO<sub>2</sub> balance estimation (section 1.5), the estimated annual litter inputs on a unit area were transformed to CO<sub>2</sub> influx by using C content values measured for each component (Table 2).

**Table 2: Mean C and N content (% of dry matter) in foliar litter from trees and biomass components used for estimating other litter inputs.** The values are means ± standard deviation including both drained and undrained sites. Abbreviations: aGV and bGV – above- and belowground biomass of herbaceous vegetation, FR – tree fine roots, M – moss, fLF – foliar fine litter, cLF – coarse woody litter.

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

## 2.5 Estimation of annual soil CO<sub>2</sub> balance

We estimated the annual soil CO<sub>2</sub> balance of the sites by combining annualized CO<sub>2</sub> influx (section 1.4) and efflux data. In exceptional cases where the CO<sub>2</sub> influx from specific source was not estimated in certain countries, such as bGV and FRP in EE and FRP in some sites in LT and LV (Table S10), we assumed the CO<sub>2</sub> influx to be equivalent to the average results from sites with the same drainage status in the other countries. While we directly measured R<sub>het</sub>, we utilized the estimated R<sub>het</sub> derived from R<sub>tot</sub> as the efflux value (marked from here onwards as R<sub>het</sub><sup>'</sup>). Such an approach was necessary because, at all sites, our R<sub>het</sub> values were significantly higher (by mean 5.8±3.1 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) than R<sub>tot</sub>, which would be logically impossible if the conditions in the measurement locations were the same. This pattern was probably mostly due to the high and variable CO<sub>2</sub> efflux from roots killed by the trenching, noted also in other studies (e.g., Hermans et al., 2022). This discrepancy could not be remedied with the root data at hand (for more details, please refer to the Supplementary text and Discussion section).

To estimate annual CO<sub>2</sub> efflux, at first, site-specific relationships between instantaneous R<sub>tot</sub> fluxes and soil temperatures were established. To identify the best approach for to express the relationship, we compared the suitability of exponential regression on untransformed data and linear regression on logarithmically or Box-Cox transformed data. The performance of these models for flux data interpolation based on continuous soil temperature data was evaluated by using the root mean square error (RMSE) of prediction. It was found that the Box-Cox approach achieved the best conformity of flux data to a normal distribution and provided the best fit for the models. Previous studies also indicate that this method effectively addresses the typical underestimation of fluxes caused by their nonlinearity (Box and Cox, 1964; Liaw et al., 2021; Wutzler et al., 2020). Interpolation was performed by evaluating the relationship between R<sub>tot</sub> and soil temperature (at 10-cm depth) measured at each study site and constructing site-specific linear regression equations (Table S6) after applying Box-Cox transformation to the flux data for normalization (Box and Cox, 1964). This approach, compared to alternative methods, more successfully (lower RMSE of prediction) accounted for the exponential nature of the relationship between flux and temperature, and prevented underestimation (Liaw et al., 2021; Wutzler et al., 2020). Hourly R<sub>tot</sub> estimates were then formed by using the hourly recorded soil temperatures (logger data) for each study site. Consecutively, site-specific annual R<sub>tot</sub> estimate was calculated by summing the interpolated hourly emission estimates of the year.

We derived site-specific annual R<sub>het</sub><sup>'</sup> from estimated annual R<sub>tot</sub> empirically. To avoid potential bias introduced by using a single fixed factor, we instead used Equation (2), accounting for the observed pattern of decreasing R<sub>het</sub> proportion as soil surface respiration (R<sub>s</sub>) increases (Bond-Lamberty et al., 2004; Subke et al., 2006). The equation characterizes the relationship between R<sub>s</sub> and R<sub>het</sub>, and was created using results of previous studies (Jian et al., 2021) in the boreal zone (Figure S2). We

assumed  $R_{tot}$  is equal to  $R_s$ , i.e., that aboveground autotrophic respiration has a minor role in  $R_{tot}$  (Hermans et al., 2022; Munir et al., 2017), and applied the equation to annual  $R_{tot}$  directly.

$$R_{het}' = -0.70 + 0.78 \times R_{tot} \quad (2)$$

Neglecting aboveground autotrophic respiration leads to a minor overestimation of  $R_{het}$ .

We will use the + sign to denote positive soil  $CO_2$  balance (soil  $CO_2$  sink), and – sign to denote net loss of  $CO_2$  from soil to the atmosphere.

## 2.6 Statistical analysis

Statistical analyses were performed and figures prepared using the software R version 4.3.1 (packages ‘MASS’, ‘stats’, ‘nlme’, ‘Hmisc’, ‘lmerTest’, ‘lme4’, ‘vegan’, ‘pls’, and ‘caret’), using  $p=0.05$  as the limit for statistical significance. The compliance of the data with the normal distribution was checked with the Shapiro-Wilk normality test and visually by density and quantile-quantile (Q-Q) plots. To calculate the uncertainty of the study results when combining multiple data sources, we used the root sum of the squares method to aggregate the individual uncertainties (95 % confidence interval). Therefore, for the  $CO_2$  influx, for instance, we combined the uncertainties from various influx (fLF, GV, FRP) sources. The uncertainty of Equation (2) used for the calculation of  $R_{het}'$  was expressed as the root mean square error (RMSE) of the corresponding regression model. The soil  $CO_2$  balances were calculated by summing the  $CO_2$  influx and efflux for individual sites. The uncertainties of the averaged  $CO_2$  balances, categorized by drainage status, country, site type, or dominant tree species, are expressed as standard error. Figures were prepared by using packages ‘ggplot2’, ‘corplot’, ‘ggbiplot’.

Correlations between the sample groups were expressed with the Pearson correlation coefficient ( $r$ ). We compared differences between two sample groups using pairwise Wilcoxon rank sum tests with continuity correction and adjusted the  $p$ -values using Bonferroni correction. The method was used to compare soil parameters and instantaneous or annualized  $R_{tot}$  data segregated by site type, drainage status, country or dominant tree species. In the same way, soil characteristics were compared between drained and undrained sites. Multivariate testing of flux and impacting factor relationships involved assessing the significance of these factors on the relationship between soil temperature and  $R_{tot}$  using mixed-effects linear models. As flux impacting factors, we considered country, dominant tree species, drainage status, WTL, and a 30 cm WTL threshold distinguishing shallow and deep drainage in the IPCC guidelines. In this analysis, Box-Cox transformed flux data was fitted to linear models using the study site as a random effect. In addition, multivariate relationships were observed through Principal Component Analysis (PCA) to visualize covariation and seek observational confluences with the results of other analyses. To assess the contribution of influencing factors on the soil  $CO_2$  balance, Redundancy Analysis (RDA) and Partial Least Squares Regression (PLSR) were conducted.

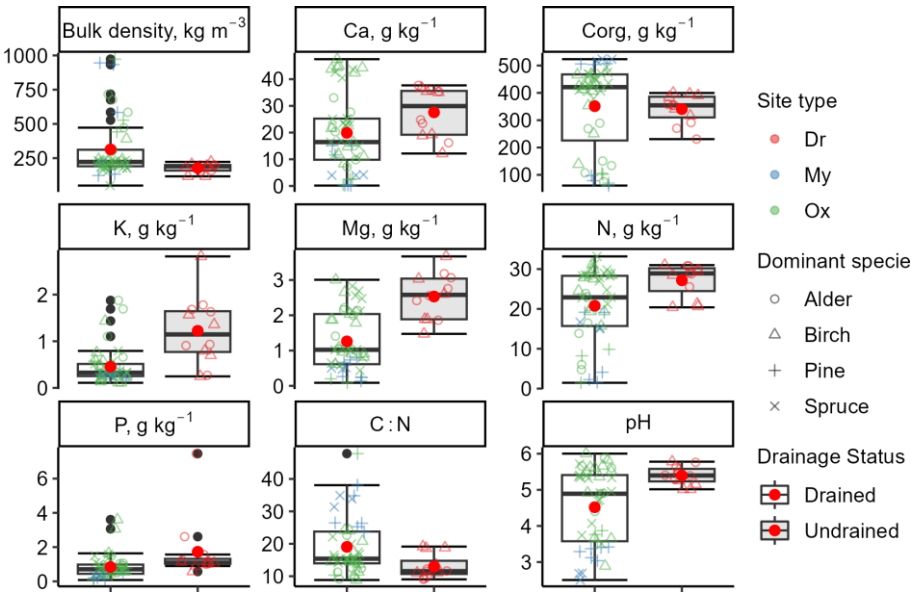
## 3 Results

### 3.1 Soil and soil water characteristics

The organic layer depth in the drained sites ranged from 27 to 212 cm (mean  $81 \pm 47$  cm) and in undrained sites from 100 to 230 cm (mean  $167 \pm 49$  cm). Soil bulk density (0-30 cm depth) in the drained sites (mean  $314 \pm 215$  kg  $m^{-3}$ ) was characterized by both higher variation and higher mean density ( $p=0.003$ ) compared to undrained sites (mean  $168 \pm 32$  kg  $m^{-3}$ ) (Table S7). Soil drainage status had no impact on Corg content in the 0-30 cm soil layer ( $p=0.11$ , total mean  $416 \pm 130$  g  $kg^{-1}$ ). However, drained soils had a higher mean C:N ratio ( $22 \pm 7$ ;  $p=0.01$ ) than the undrained soils ( $17 \pm 3$ ). A trend could be observed that undrained soils had higher nutrient concentrations and higher pH than the drained soils. Soil analysis confirmed that site types classified based on ground vegetation composition served as an indicator of nutrient availability (Figure 2). In drained Oxalis sites, mean macronutrient concentrations in the 0–30 cm soil layer was higher compared to Myrtillus sites. Notably, N, Mg,

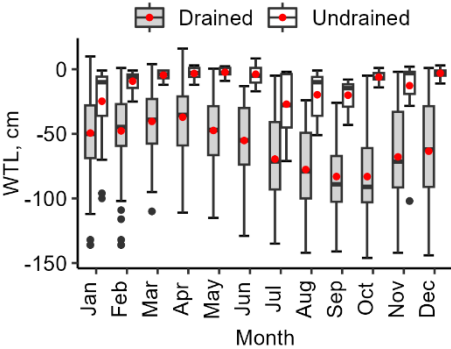


Ca, and P showed statistically significant differences ( $p < 0.05$ ). Additionally, soil pH values in the Oxalis sites were, on average, 1.89 units higher ( $p = 0.018$ ).



**Figure 2: Variation of soil chemical and physical properties at soil depth 0-30 cm.** The clear box represents the drained, and the grey-shaded box the undrained sites. Data points represent individual subplots. 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 whiskers extend to the smallest and largest values within 1.5 × IQR from the 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 values, respectively. Corg – organic carbon; N – total nitrogen. Site types: Dr - *Dryopteris-caricosa*; Ox - *Oxalis turf. mel.*; My - *Myrtilla turf. mel.*

The range of mean WTL over the study period was from -23 to -112 cm (mean -60±25 cm) in the drained sites and from -7 to -17 cm (mean -13±4 cm) in the undrained sites, respectively. In the undrained sites, the WTL was mainly rather high (see interquartile range in Figure 3) and had comparably smaller variation (mean standard deviation 16 cm) than in the drained sites (mean standard deviation 23 cm); however, in all sites except LTC108, WTLs below 30 cm were also observed (Figure 4). In the undrained sites, the range of min-max WTL was from 3±3 cm to -63±27 cm, while the WTL in drained sites had a greater absolute variation ranging from -14±19 cm to -104±28 cm.



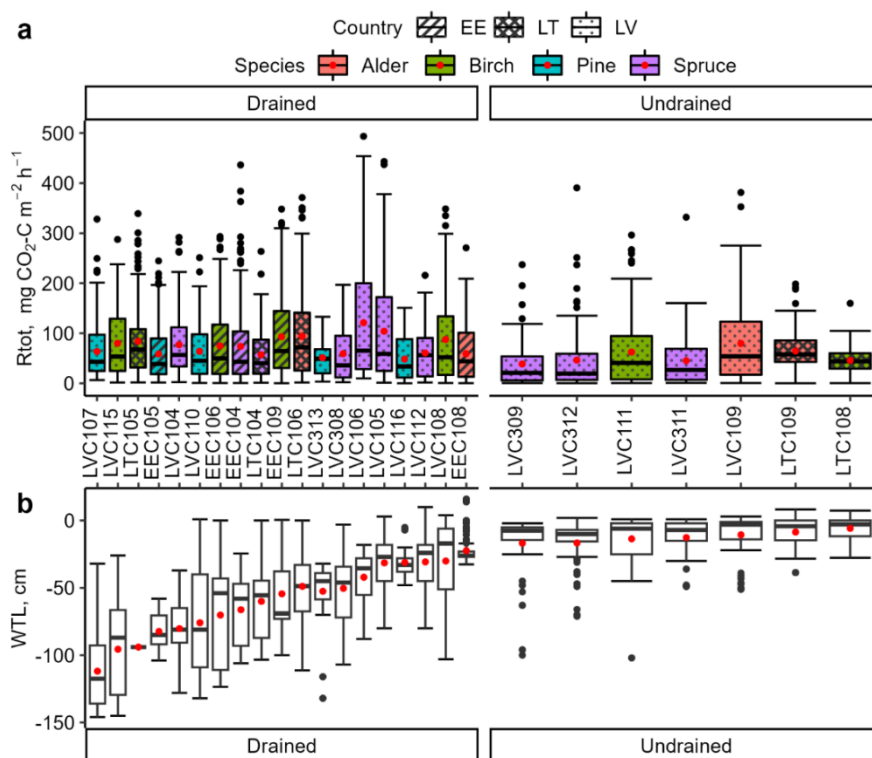
**Figure 3: Yearly variation of soil water-table level (WTL) in the study sites.** The edges of the box represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles, encapsulating the interquartile range (IQR). The whiskers extend to the smallest and largest values within 1.5 \* IQR from the 25<sup>th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

The concentrations of all measured chemical parameters in the soil water, except for NH<sub>4</sub><sup>+</sup>, were, on average, higher in the drained sites (Figure S3). However, the results were highly variable (Table S8).

### 3.2 Instantaneous total respiration

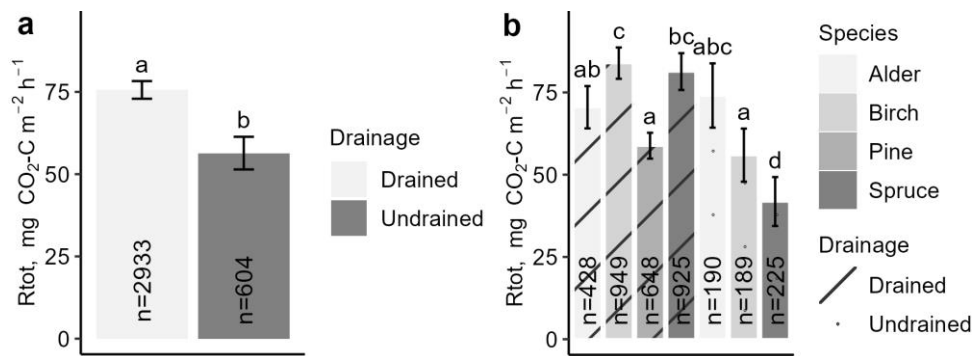
In the drained sites, the mean instantaneous R<sub>tot</sub> varied from 48 to 125 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup>, and in the undrained sites from 38 to 80 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup> (Figure 4). In all sites combined, during the summer months (June, July, August), the interquartile

range of  $R_{\text{tot}}$  varied from 111 to 198 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup> with a mean of 160±78 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup>. In contrast, during the winter (December, January, February), it ranged from 8 to 24 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup> with a mean of 17±14 mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup>. The relative standard deviations of the instantaneous  $R_{\text{tot}}$  in drained (90±9%) and undrained (106±29%) sites were comparable. Although the study sites represented a broad soil WTL gradient, no significant impact of the site mean WTL on the mean instantaneous  $R_{\text{tot}}$  emission was observed ( $r=0.16$ ,  $p>0.05$ ). Furthermore, no significant correlations were found between instantaneous  $R_{\text{tot}}$  and soil water parameters.



**Figure 4: Variation of instantaneous total respiration (R<sub>tot</sub>, a) and soil water-table level (WTL, b) in the study sites.** 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 whiskers extend to the smallest and largest values within  $1.5 \times \text{IQR}$  from the 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 values, respectively.

The instantaneous  $R_{\text{tot}}$  in drained sites (mean  $76 \pm 3 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ ) was overall higher ( $p < 0.05$ ) than  $R_{\text{tot}}$  in undrained sites (mean  $56 \pm 5 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ ) (Figure 5a).  $R_{\text{tot}}$  was the lowest at undrained sites dominated by spruce and the highest at drained sites dominated by birch (Figure 5b).  $R_{\text{tot}}$  was significantly different ( $p < 0.05$ ) between coniferous forest sites with different dominant tree species and/or soil moisture regime, with  $R_{\text{tot}}$  ranging from mean  $42 \pm 7 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$  in undrained spruce forests to  $59 \pm 4$  and  $81 \pm 6 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$  in drained pine and spruce forests, respectively. In deciduous stands, the moisture regime and dominant tree species had less impact on the mean flux;  $R_{\text{tot}}$  was higher ( $p < 0.05$ ) in drained birch stands (mean  $84 \pm 5 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ ) than in undrained birch stands ( $56 \pm 8 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ ), while in alder stands the mean  $R_{\text{tot}}$  was similar regardless of the soil moisture regime (total average  $67 \pm 9 \text{ mg CO}_2\text{-C m}^{-2} \text{ h}^{-1}$ ) (Figure 5b). In drained coniferous and deciduous sites, on average, the mean  $R_{\text{tot}}$  was similar, but in undrained sites, emissions in deciduous forests were about 40% higher. Mean  $R_{\text{tot}}$  in sites with the same drainage status did not differ ( $p > 0.05$ ) between countries (Figure S4, g).



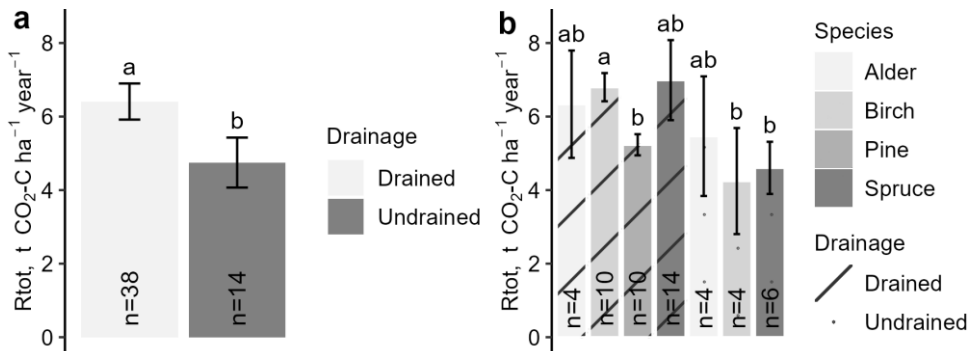
**Figure 5: Mean instantaneous total respiration (R<sub>tot</sub>) throughout the study period, categorized by drainage status (a) or dominant tree species and drainage status (b).** Error bars indicate confidence interval. A shared letter indicates that differences are not significant.

The impact of WTL is reflected in the mean R<sub>tot</sub>, which was  $87 \pm 3$  mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup> when WTL was below 30 cm and  $57 \pm 3$  mg CO<sub>2</sub>-C m<sup>-2</sup> h<sup>-1</sup> when WTL was closer to soil surface. However, when evaluating the effect of WTL on R<sub>tot</sub> variation in mixed-effects models predicting R<sub>tot</sub> based on soil temperature, WTL was found to have an insignificant impact on R<sub>tot</sub> variation. Similarly, the contribution of country and dominant tree species to R<sub>tot</sub> prediction was marginal (Table S9). The inclusion of dominant species provided minimal model improvement ( $\Delta AIC = +5$ ,  $\Delta \log Lik = 0$ ), while country effects captured some additional variability in R<sub>tot</sub>. However, the increase in R<sup>2</sup> due to country variables was minor (from 0.77 to 0.78), indicating limited explanatory power.

### 3.3 Annual total respiration

Soil temperature at 10 cm depth (Figure S5) was used in constructing R<sub>tot</sub> prediction models and for emission interpolation needed for annualizing R<sub>tot</sub>. The 10 cm depth was chosen because it showed the strongest correlation between instantaneous R<sub>tot</sub> and soil temperatures measured at different depths, with a mean Pearson correlation coefficient (r) of  $0.86 \pm 0.04$  across the study sites. For the other soil depths (5, 20, 30, 40 cm), r ranged from  $0.71 \pm 0.07$  to  $0.79 \pm 0.05$ . Linear models developed using Box-Cox transformed data provided the best R<sub>tot</sub> prediction power. A lambda value of 0.3411 was used for all data transformations, as individual data transformations for each site resulted in comparatively less successful data normalization. With this approach, the RMSE of instantaneous R<sub>tot</sub> predictions for individual sites decreased by an average of  $16 \pm 14\%$ , compared to linear models with logarithmically transformed data or non-linear models with untransformed data (Table S6).

Annualized R<sub>tot</sub> indicated similar mutual relationships among the study site dominant tree species and drainage status categories as the instantaneous R<sub>tot</sub>. Pooled estimated annual emissions from drained sites (overall mean  $6.41 \pm 0.49$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) and undrained sites (overall mean  $4.75 \pm 0.68$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) differed significantly (Figure 6, a). However, when the data were further stratified by country, the differences were no longer statistically significant due to wider confidence intervals (Figure S4, h).



**Figure 6: Annualized total respiration (R<sub>tot</sub>) in study sites stratified by drainage status (a) or dominant tree species (b).** Error bars indicate confidence interval. A shared letter indicates that differences are not significant.

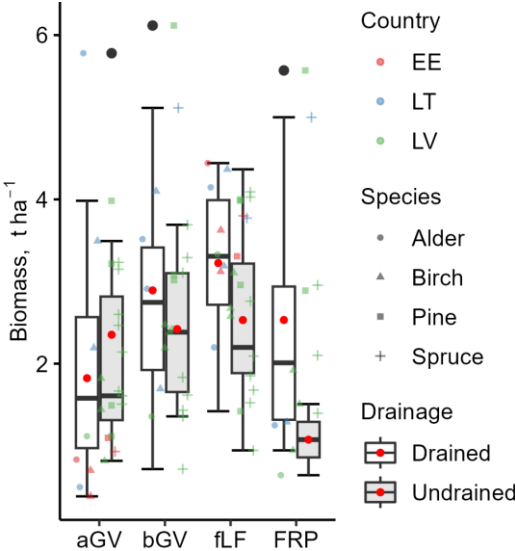
When categorizing data according to drainage status and dominant tree species, fewer differences were found in the annualized  $R_{tot}$  than in the instantaneous  $R_{tot}$  (Figure 6, b). For instance, among the drained sites, the lowest mean annual  $R_{tot}$  was estimated for pine forests ( $5.23 \pm 0.29 \text{ t CO}_2\text{-C ha}^{-1} \text{ year}^{-1}$ ), while in spruce, birch, and alder forests, the means were similar ( $p > 0.05$ ) ( $6.71 \pm 0.31 \text{ t CO}_2\text{-C ha}^{-1} \text{ year}^{-1}$ ). Emissions from undrained soils in alder, birch, and spruce forests were similar to each other and lower than from drained sites, ranging from  $4.6 \pm 0.71$  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  $4.86 \pm 0.71$ ).

The correlation between  $R_{tot}$  and WTL was low; however, a drainage status (drainage ditch presence) impact on  $R_{tot}$  is indicated by the PCA results, where undrained sites tend to have more similar characteristics while drained sites show greater diversity concerning  $R_{tot}$ . However, clear covariation of dominant tree species and  $R_{tot}$  are not recognized by PCA (Figure S6 and Figure S7). When comparing the chemical and physical properties of different soil layers with the estimated annual  $R_{tot}$ , as well as the measured mean  $R_{het}$ , the mean measured  $R_{het}$  consistently showed a higher correlation with evaluated soil parameters (Figure S8). The only exception is Corg, for which no correlation was observed between Corg in different soil layers and neither  $R_{tot}$  or  $R_{het}$  ( $r$  around  $-0.1$ ). Excluding Corg, the other soil chemical parameters generally had a low to moderate correlation (mean  $r = 0.4$ ) with respiration. The highest correlation was with pH, K, Mg, and P (mean  $r = 0.5 \pm 0.07$ ,  $p < 0.05$ ), and it was consistent across all evaluated soil layers, while the correlation with BD (mean  $r = -0.2$ ,  $p > 0.05$ ) tends to increase with deeper soil layers reaching the highest correlation ( $r = -0.3$ ) in layer 20-30 cm. In addition, a higher C:N ratio is associated with lower  $\text{CO}_2$  emissions (mean  $r = -0.4$ ,  $p < 0.05$ ).

### 3.4 Annual litter inputs

The estimated mean litter inputs at the subplot level were mostly similar between drained and undrained sites (Table S10 and S11), typically differing by less than 20%. Only fLF and FRP tended to be considerably higher in the drained sites, FRP on average even more than twice as high. Compared to undrained sites, bGV in drained sites was about 20% higher on average, while aGV was about 20% lower on average (Figure 7). However, regardless of the soil drainage status, the proportion of aGV in the total GV biomass was  $54 \pm 18\%$  (Table 3).

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**Figure 7: Variation in the biomass components used as litter input estimates.** Abbreviations: aGV and bGV – above- and belowground biomass of herbaceous vegetation, fLF – fine foliar litter (needles, leaves, fine woody litter), FRP – tree fine root production. 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 whiskers extend to the smallest and largest values within  $1.5 \times \text{IQR}$  from the 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 values, respectively.

**Table 3: Biomass (mean $\pm$ CI, t dm. ha<sup>-1</sup>) components used as litter input estimates, stratified by drainage status.** Abbreviations: aGV and bGV – above- and belowground biomass of herbaceous vegetation; respectively; FRP – tree fine root production; fLF – fine foliar litter (needles, leaves, fine woody litter).

Category	Drained	Undrained
aGV	1.82±0.52	2.35±1.61
bGV	2.89±0.85	2.42±0.84
FRP	2.53±0.77	1.08±0.57
fLF	3.22±0.44	2.53±1.06

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Both bGV ( $r=|0.6|$ ) and FRP ( $r=|0.7|$ ) had a significant negative correlation with soil pH but a positive with the C:N ratio in soil layer 0-30 cm. Additionally, FRP had a significant negative correlation ( $r=|0.7|$ ) with the contents of N, Ca, and Mg in the soil. No explanatory factors for aGV could be identified. Moderate correlation ( $r=0.5$ ,  $p<0.05$ ) was found between stand age and fLF.

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### 3.5 Annual soil carbon balance

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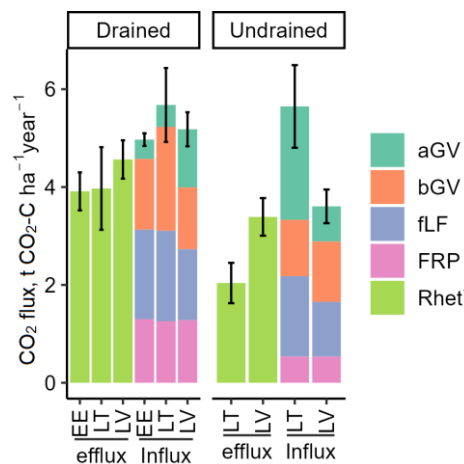
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The estimated  $R_{het}$  (Table S10) proportion of  $R_{tot}$  varied between 54 and 71% (mean 65%). Consequently, the estimated annual gross C losses from drained soils in the form of  $R_{het}$  emissions ranged from 2.36 to 7.49 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup> (mean 4.30±1.20), while for undrained soils the range was from 1.63 to 4.68 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup> (mean 3.00±0.99). According to the RMSE of the model (Equation 2, Figure S2) prediction, the  $R_{tot}$  to  $R_{het}$  calculation introduced an uncertainty of approximately 0.32 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>. In drained and undrained sites, the total estimated CO<sub>2</sub> influx ranged from 3.81 to 7.03 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup> (mean 5.20±0.91) and 2.89 to 5.98 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup> (mean 4.19±1.10), respectively (Figure 8). The uncertainties (relative CI) in CO<sub>2</sub> efflux and influx in both drained and undrained soils were relatively uniform, with a mean uncertainty of 36±14% for the estimated individual annual CO<sub>2</sub> fluxes. The largest source of uncertainty was CO<sub>2</sub> influx in undrained soils (49±13%), while the uncertainty of individual CO<sub>2</sub> fluxes in drained sites averaged 27±6% (Figure 8).



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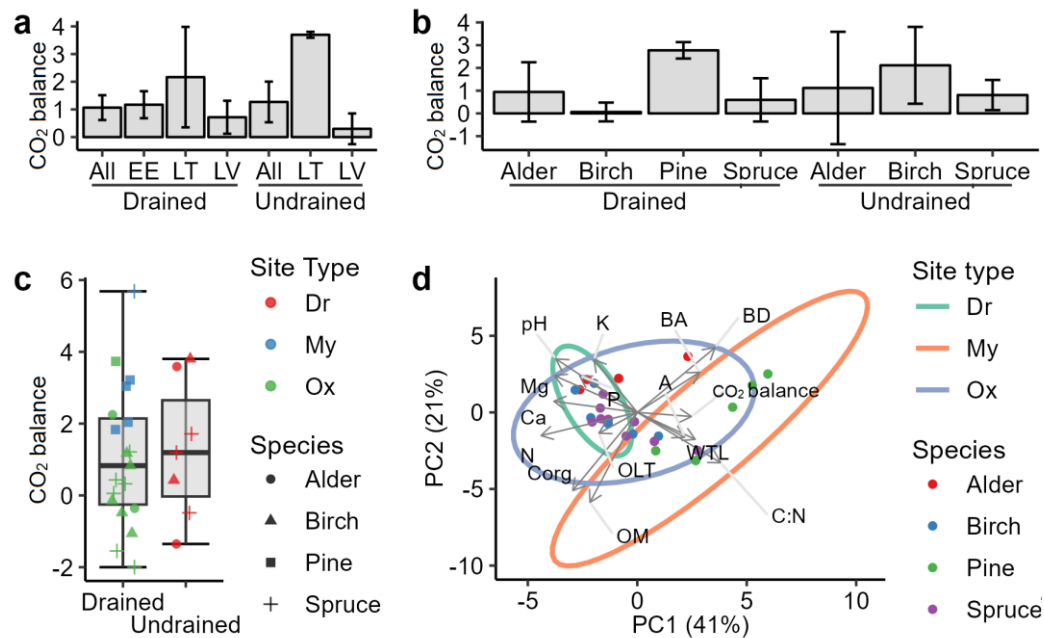
**Figure 8: Components of the estimated soil CO<sub>2</sub> balance (sum±combined CI).** Efflux is soil heterotrophic respiration ( $R_{het}$ ) calculated from  $R_{tot}$ , and influx is the estimated litter input; both are expressed as C. Thus, efflux indicates soil C losses and influx soil C gains. Abbreviations: aGV and bGV – above- and belowground biomass of herbaceous vegetation; respectively; fLF – fine foliar litter; FRP – tree fine root production.

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The mean soil CO<sub>2</sub> balance during the study period was +1.06±0.45 and +1.27±0.73 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup> for the drained and undrained sites, respectively (Figure 9, a). These results indicate that long-term drainage reduced soil CO<sub>2</sub> sequestration capacity by an average of 0.20 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>.

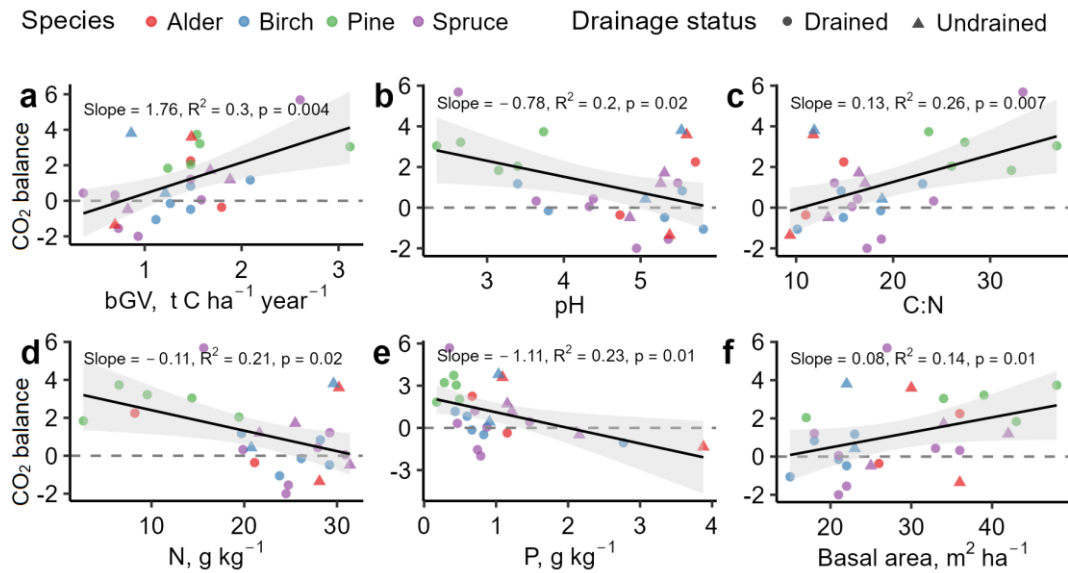


**Figure 9: Soil CO<sub>2</sub> balance (a, b, c: mean t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>±SE) and impacting factors (d: PCA biplot). Positive values indicate soil CO<sub>2</sub> sink, i.e., CO<sub>2</sub> removals from the atmosphere.** Abbreviations: A – stand age; BA – basal area, BD – bulk density; C:N – ratio between organic carbon and nitrogen in soil; OLT – soil organic layer thickness; WTL – water table level; pH – soil pH value; K, Ca, Mg, P, OM, Corg, N represent the content of potassium, calcium, magnesium, phosphorus, organic matter, organic carbon and nitrogen in the top 0-30 cm layer of soil, respectively. Site types: Dr - Dryopterioso-caricosa (undrained sites); Ox - Oxalidososa turf. mel. (drained); My - Myrtillosa turf. mel. (drained).

The soil CO<sub>2</sub> balance stratified by dominant tree species (Figure 9, b) indicates that the drained sites were skewed towards CO<sub>2</sub> removals due to significantly higher CO<sub>2</sub> removals in pine stands. Pine sites (n=5) showed high CO<sub>2</sub> removals with low uncertainty (mean +2.77±0.36 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>), in contrast to the other drained sites (n=19), where the mean soil CO<sub>2</sub> balance was estimated at +0.45±0.50 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>, suggesting that soils in drained alder, birch and spruce sites were in near CO<sub>2</sub> equilibrium during the study period. The soil CO<sub>2</sub> removals identified for undrained birch and spruce stands (+1.33±0.72 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>, n=5) were consistent, while in alder stands, the CO<sub>2</sub> balance of +1.12±2.47 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup> was highly uncertain due to the number of sites being just two.

A trend of higher soil CO<sub>2</sub> removals was observed in site types associated with relatively lower nutrient availability (Figure 9, c). In Oxalis sites, the mean soil CO<sub>2</sub> balance was +0.32±0.40 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>, while in Myrtillosa sites, it was +3.16±0.69 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>. Thus, drained nutrient-rich soils were approximately at CO<sub>2</sub> equilibrium, whereas comparably nutrient-poorer soils acted as a CO<sub>2</sub> sink. The observed tendency is supported by PCA (Figure 9, d) which indicates that higher soil CO<sub>2</sub> removals are associated with lower nutrient concentrations and pH levels. In addition, the PCA reveals that the risk of soil CO<sub>2</sub> source is reduced in stands with higher basal area and age, as well as with a higher soil C:N ratio, which in our study likely reflects the variability in peat quality and decomposability under different vegetation types.

According to correlation analysis, soil parameters such as pH, C:N ratio, N, and P showed the strongest correlations with the soil CO<sub>2</sub> balance (Figure 10). Basal area was the tree stand characteristic with the strongest correlation with CO<sub>2</sub> balance, while, among the CO<sub>2</sub> flux components, bGV demonstrated the most consistent role in CO<sub>2</sub> balance. No meaningful relationship was identified between soil CO<sub>2</sub> balance and soil organic matter or C content, nor with the depth of the WTL or organic layer thickness.



**Figure 10: Relationships between soil CO<sub>2</sub> balance (t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) and impacting factors.** Positive values indicate soil CO<sub>2</sub> removals. The figures include impacting factors showing the highest correlations found in the study dataset. Data points represent individual study sites.

Soil nutrient availability as CO<sub>2</sub> balance affecting factor is confirmed by RDA and PLSRS models. RDA and PLSRS models ( $p < 0.05$ ) explained 78% and 70% of the soil CO<sub>2</sub> balance variance, respectively. After excluding variables introducing multicollinearity, the models included WTL, organic layer thickness, pH, N, K, Ca, Mg, P, organic matter content of the soil, stand age, and basal area. The variables pH, K, and Mg showed significant contributions ( $p < 0.05$ ) in the RDA model explaining the variation of soil CO<sub>2</sub> balance. The variable N was not significant ( $p = 0.087$ ) but was close to the threshold of significance. PLSR model indicated that pH, K, Mg and N explained 45% of the CO<sub>2</sub> balance variance; however, the VIP values for all potential explanatory variables were below 0.4, suggesting limited predictive power for CO<sub>2</sub> balance with the current dataset.

## 4 Discussion

### 4.1 Soil CO<sub>2</sub> balance

The soil CO<sub>2</sub> balance of the studied drained and undrained organic forest soils fluctuated around equilibrium, demonstrating both CO<sub>2</sub> sink and source dynamics. The reason for the uncertain CO<sub>2</sub> balance in undrained alder stands could not be determined, as site characteristics were consistent with the patterns observed in other undrained sites showing soil CO<sub>2</sub> removals. However, we identified soil properties as the likely reasons for why the soil in drained pine stands showed CO<sub>2</sub> removals, in contrast to the C-neutral soils observed at other drained sites.

Although observing a CO<sub>2</sub> sink in drained nutrient-rich soils may seem somewhat unexpected, given that these soils have generally been estimated to on average act as net CO<sub>2</sub> sources in both boreal and temperate zones (Jauhiainen et al. 2023), it is not entirely novel. Both soil CO<sub>2</sub> sinks and sources have also been observed in earlier studies under a wide range of site conditions (e.g., Ojanen et al. 2013; Minkinen et al., 2018; Bjarnadottir et al., 2021; Hermans et al., 2022). Many of the soil CO<sub>2</sub> sink sites may be classified as nutrient-poor, but not all (e.g., Ojanen et al. 2013). In soil inventory studies carried out in Latvia, the soil C stocks of forestry-drained peatlands were found to be stable in all but the most nutrient-rich soil conditions, under which the C stock was reduced in the long term (Dubra et al., 2023; Lazdiņš et al., 2024). However, interpretation of soil CO<sub>2</sub> balances solely based on the nutrient status of a forest site should be approached with caution, as it is typically derived from indirect indicators such as vegetation or stand productivity, rather than a quantitative assessment of soil nutrient concentrations. Consequently, sites with variable conditions may be classified under a given nutrient status category. Similarly, drainage status does not guarantee specific WTL levels (Figure 4). This may be the reason for varying findings on soil CO<sub>2</sub>



486 balances across studies that allegedly target the same soil type and drainage status, i.e. the category of drained, nutrient-rich  
487 soils may be too broad, encompassing varying nutrient and moisture regimes, which prevents the expectation of similar CO<sub>2</sub>  
488 balances, especially in different climates. In our study, this aspect was evident, as the soil CO<sub>2</sub> balance, regardless of drainage  
489 status, appeared to be influenced by the composition and relative proportions of the dominant tree species in combination with  
490 variation in soil nutrient conditions and organic matter quality, as indicated by the C:N ratio, across the study sites.

491 The soils at our study sites represented a wide range, from highly mineralized soils close to the threshold of organic soil  
492 definition (Hiraishi et al., 2013) to deep peat (Figure 2). Similarly, the WTLs varied widely, with sites ranging from an average  
493 WTL close to the soil surface to depths exceeding one meter (Figure 4). However, no meaningful relationship was identified  
494 between WTL variation and soil CO<sub>2</sub> efflux, nor between mean WTL and soil CO<sub>2</sub> balance. Also, soil C and organic matter  
495 contents, or the depth of the organic layer were poor predictors of soil CO<sub>2</sub> balance. Probably the importance of these factors  
496 decreases over time since initial disturbance by drainage system implementation. Rhet has been found to decrease over time  
497 following drainage (Qiu et al., 2021), except for the initially wettest, waterlogged hollow surfaces (Munir et al., 2017). There  
498 are few long-term monitoring or chronosequence studies, but those suggest that the most intensive period of soil C loss  
499 following drainage is the first decade/decades (Hargreaves et al. 2003; Vanguelova et al., 2019). During that period, also peat  
500 subsidence following drainage is highest (Lukkala 1949), and labile substances in peat that due to lowering WTL and peat  
501 subsidence becomes exposed to oxic decomposition are largely lost, leaving more decomposition-resistant substrates behind  
502 (e.g., Jayasekara et al., 2025). Simultaneously, major changes in litter inputs and their decomposability take place (Straková  
503 et al., 2010, 2012). Considering the long period since drainage of our sites, dating back to around a century ago and potentially  
504 even to the mid-19th century (Zālitis, 2012), the initially high soil C loss due to drainage-induced increase in gross soil CO<sub>2</sub>  
505 emissions has likely been offset by enhanced biomass growth and the resulting increased litter inputs (Hommeltenberg et al.,  
506 2014). However, a comparison of soil CO<sub>2</sub> balances between drained and undrained sites still shows a negative impact of  
507 historical drainage (Table S11). To more accurately assess the impact of drainage on soil CO<sub>2</sub> balance and its evolution in  
508 time, long-term studies would be required.

509 Soil nutrient conditions explained the observed CO<sub>2</sub> balances better than WTL and soil C characteristics did. In our study,  
510 drained nutrient-rich soils were represented by *Oxalis* (*Oxalidosa turf. mel.*) and *Myrtillus* (*Myrtillosa turf. mel.*) site types.  
511 All our drained birch and alder sites and most of drained spruce sites belonged to *Oxalis* site type, but most of the pine sites  
512 belonged to the *Myrtillus* site type. While the soil CO<sub>2</sub> balance under the other species in drained sites was practically neutral  
513 during the study period, pine stands showed relatively high CO<sub>2</sub> removals. In the *Myrtillus* site type nutrient concentrations  
514 were, on average, 1.5 to 5.4 times lower compared to *Oxalis* sites. In addition, *Myrtillus* sites had significantly lower pH levels  
515 and a higher C:N ratio (Figure 2). The distinctive CO<sub>2</sub> balance patterns between the site types suggest that, in addition to lower  
516 nutrient concentrations, increased soil acidity and differences in soil organic matter and litter input quality (decomposability)  
517 had a role in the observed CO<sub>2</sub> removals in these sites. Previous studies have also reported a negative correlation between pH  
518 and soil C content (Zhou et al., 2019) and have linked soil acidification with increasing soil C stocks (Madsen et al., 2025;  
519 Marinos and Bernhardt, 2018). The relevance of soil chemical parameters in determining soil CO<sub>2</sub> balance was supported by  
520 RDA and PLSR analysis, revealing that soil pH and macronutrient concentrations were key parameters determining soil CO<sub>2</sub>  
521 balance. Both soil pH and macronutrient concentrations may be influenced by the tree species (Reich et al., 2005; Dawud et  
522 al., 2016). Conifers, especially Scots pine, are linked with lowered soil pH (Reich et al., 2005), which may be a way to engineer  
523 the ecosystem to its own favour, as Scots pine unlike the other tree species found in our sites can also thrive in nutrient-poor  
524 peatland forests (e.g., Ohlson, 1995). The soil acidification in coniferous stands can be attributed to litter quality (Reich et al.,  
525 2005; Brock et al., 2019). However, in undrained coniferous stands, soil pH was clearly higher compared to drained sites, and  
526 similar to that of undrained broadleaf sites (Figure 2). This is likely because undrained sites may receive more groundwater  
527 inputs that neutralize soil acidity than the drained sites. Our drained sites mostly had more acid soils than the undrained ones,  
528 a pattern that has previously been recorded for boreal drained peatland forests (Laiho & Laine, 1990). Apart from the reduced  
529 groundwater influence, the phenomenon has been explained by a reduction in soil buffering capacity resulting from leaching



and tree uptake of base elements such as Ca and Mg, as well as increased oxidation of both organic and inorganic compounds following drainage, contributing to a gradual increase in soil acidity over time (Laine et al., 2006).

Among the drained sites, pine stands had the lowest mean soil CO<sub>2</sub> efflux (Figure 6, b). Additionally, nutrient availability correlated negatively with belowground biomass (bGV, FRP) confirming previous observations that greater belowground biomass is associated with reduced nutrient availability (Zhang et al., 2024). Higher CO<sub>2</sub> efflux observed in Oxalis sites were consistent with the previous observations of higher organic matter decomposition rates typically observed in sites with high nutrient availability (Hiraishi et al., 2013; Shahbaz et al., 2022). However, an increased total soil CO<sub>2</sub> influx from litter was also observed in these sites during the study period, effectively offsetting soil C loss from Rhet. Another potential contributor to the positive CO<sub>2</sub> balance in drained soils was soil compaction induced by drainage, as the increased BD of drained soil was found to be associated with lower Rhet emissions. The reason may be reduced soil porosity limiting gas exchange between the soil and the atmosphere (Ball, 2013; Novara et al., 2012). Thus, while drained soil may be prone to a higher decomposition rate, flux-driving processes seem to be countered by increased soil compaction.

In any case, the mean CO<sub>2</sub> removals we estimated are uncertain and remain indicative, preventing a definitive conclusion that the soil functions as a CO<sub>2</sub> sink. Some uncertainty in the results arises from the inherent variation of study sites categorised into different forest site types and drainage statuses; such variation is natural and cannot be considered erroneous (see, e.g., Westman & Laiho, 2000; Ojanen et al., 2010). However, based on the observed patterns, we consider site stratification by drainage status and site type to be an appropriate approach for interpreting soil CO<sub>2</sub> balance. This stratification captures key ecological differences that are relevant to C dynamics and supports meaningful comparisons across site conditions. The results obtained reflect CO<sub>2</sub> balances only for the study period, specific to the respective stands in their specific developmental stages and site conditions. They do not represent average CO<sub>2</sub> balance over a longer timeframe, such as an entire forest management cycle. In similar conditions, organic soils have been found to be a CO<sub>2</sub> source following regenerative felling (Butlers et al., 2022; Korkiakoski et al., 2023). Therefore, if the impact of management practices were considered, the soil CO<sub>2</sub> balance would likely shift towards reduced CO<sub>2</sub> sequestration.

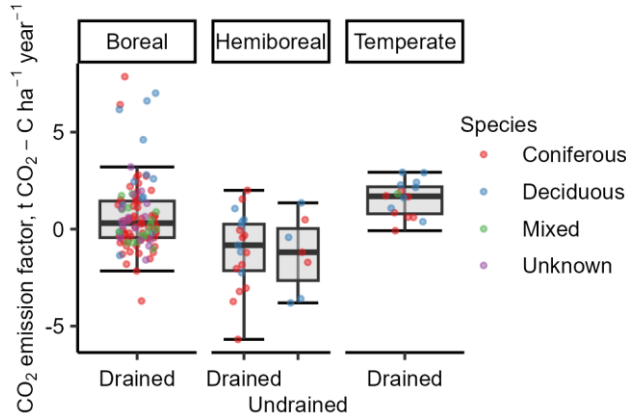
Our CO<sub>2</sub> balance estimate does not include the impacts of dissolved organic carbon (DOC) leaching and methane (CH<sub>4</sub>) emissions. DOC leaching occurs from both drained and undrained organic soils; however, in drained sites, related C losses can be increased by 0.43 to 0.78 t C ha<sup>-1</sup> yr<sup>-1</sup> (Hiraishi et al., 2013). While CH<sub>4</sub> emissions from drained organic soils, including emissions from drainage ditches in temperate zone, are generally minor, averaging around 5.9 kg CH<sub>4</sub>-C ha<sup>-1</sup> year<sup>-1</sup>, C losses by CH<sub>4</sub> emissions from undrained soils are highly variable and uncertain, ranging from 0 to 856 kg CH<sub>4</sub>-C ha<sup>-1</sup> year<sup>-1</sup> (Hiraishi et al., 2013). Consequently, not accounting for DOC and CH<sub>4</sub> when comparing the C balance of drained and undrained organic soils increases the uncertainty, while these impacts potentially offset each other.

## 4.2 Soil CO<sub>2</sub> emission factors

The reported soil CO<sub>2</sub> balance values can be directly used as EFs (Table 4). Considering the lack of sufficient evidence for differences in drained soil CO<sub>2</sub> efflux (Table S9) or balance (Figure S4) between countries (see the Supplementary text), the use of regional soil CO<sub>2</sub> EFs is recommended over country-specific values. For example, the mean soil CO<sub>2</sub> balance for drained soils can be treated as EF of  $-1.06 \pm 0.45$  t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>, which falls within the range of boreal forest organic soils CO<sub>2</sub> EFs reported by previous studies (Table 4, Figure 11). The highest values observed in this study fall within the range reported in temperate-zone studies. The greater discrepancy with the temperate emission factors may be explained by the limited number of temperate studies available and their focus on a narrower range of site conditions compared to those represented in the Baltic countries.

**Table 4: Organic soil CO<sub>2</sub> emission factors (t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) of this study compared to those reported in previous studies.** Values for the boreal and temperate zones are synthesised from the results of previous studies on nutrient-rich organic soils (Jauhiainen et al., 2023), while values for the hemiboreal zone reflect the EFs derived in this study. Abbreviations: NR – nutrient rich; NP – nutrient poor; Min and Max refer to the minimum and maximum values reported; C<sub>l</sub>min and C<sub>l</sub>max represent the lower and upper 95% confidence limits for the mean; N – number of estimates.

Climate zone	Drainage status	Mean	Min	Max	CImin	CImax	N
Boreal	Drained	0.71	-3.70	7.86	0.34	1.08	103
Hemiboreal	Drained	-1.06	-5.69	2.00	-1.51	-0.61	19
	Undrained	-1.27	-3.80	1.35	-2.00	-0.54	7
Temperate	Drained	1.61	-0.08	2.93	1.15	2.07	16



**Figure 11: Organic soil CO<sub>2</sub> emission factors of this study compared to those reported in previous studies.** Values for the boreal and temperate zones are synthesised from the results of previous studies on nutrient-rich organic soils (Jauhiainen et al., 2023), while values for the hemiboreal zone reflect the EFs derived in this study.

### 4.3 Total respiration

No significant differences in R<sub>tot</sub> were observed between the countries, likely because the gradient in the mean air temperature from Estonia to Lithuania, ranging from 6.4 to 8.5 °C, was not substantial enough to introduce distinguishable differences. Nevertheless, while temperature is generally recognised as a strong factor influencing soil respiration and its variation, it should not be regarded as the sole predictor of respiration. Relationships observed in one region may not directly apply to another, as differences in soil moisture (Jovani-Sancho et al., 2018) or nutrient status, as discussed earlier, can significantly alter the respiration dynamics. Similarly, no clear impact of dominant tree species on R<sub>tot</sub> was found. This points to a minor role of dominant tree species on emissions. However, there is some evidence that emissions in undrained sites tended to be higher in deciduous stands, particularly alder stands, according to the measured instantaneous emissions. The enhanced soil CO<sub>2</sub> efflux observed in the presence of alder can probably be attributed to the symbiotic nitrogen fixation associated with these trees (Warlo et al., 2019), which increases nitrogen availability in the soil. Nitrogen availability, in turn, can stimulate decomposition processes, leading to a higher rate of CO<sub>2</sub> release. However, we did not observe increased nitrogen levels in neither the soil nor soil water of alder sites. Although statistically unconfirmed, a tendency can be noticed that in drained sites R<sub>tot</sub> emissions tend to be higher in birch stands, but lower in pine forests. Also, previous studies indicated that deciduous stands show higher CO<sub>2</sub> emissions (Jauhiainen et al., 2023).

While it was found that both drainage status and WTL threshold above or below 30 cm can be used as a predictor of R<sub>tot</sub>, a meaningful correlation between WTL and R<sub>tot</sub> was not found. Furthermore, although the absolute variation of the WTL was higher in drained sites, the relative variation in both WTL level and R<sub>tot</sub> was indifferent to the drainage status. The observations suggest that higher WTL conditions in undrained sites, while decreasing R<sub>tot</sub> emissions, do not guarantee higher resilience to moisture regime disturbances, i.e., more stable emissions. The main reason is that the presence of drainage ditches is not the only factor constraining WTL both spatially and temporally, and in undrained sites too, WTL frequently falls below 30 cm (Butlers et al., 2023) ensuring oxic conditions in soil layers containing labile organic matter. Furthermore, this typically happens in summer (Butlers et al., 2023) when increased temperatures further promote organic matter mineralization. The role of WTL dynamics is reflected also in PCA, showing higher dispersion of drained sites likely due to higher variation in WTL depths. This may be the reason complicating the quantification of relationships between R<sub>tot</sub> and the affecting factors,

604 especially in drained sites. The wide range of mean WTL measured at the drained sites also helps explain why  $R_{tot}$  at these  
605 sites is not necessarily significantly higher compared to undrained sites.

606 To achieve accurate  $R_{tot}$  annualization using data from periodic flux measurements, data interpolation through modelling  
607 approaches was applied. For  $R_{tot}$  interpolation we compared nonlinear models and linear models after logarithmic or Box-  
608 Cox transformation. Both the advantages and shortcomings of these data transformation methods and modelling approaches  
609 have been reported in previous studies. (Box and Cox, 1964; Khomik et al., 2009; Liaw et al., 2021; Moulin et al., 2014;  
610 Wutzler et al., 2020; Yueqian, 2020). Although the bias in predicted annual  $R_{tot}$  varied among study sites, the overall impact  
611 of different flux modelling approaches on estimated mean annual  $R_{tot}$  of drained and undrained sites was minimal.  
612 Specifically, the mean bias of results obtained through the implementation of the Box-Cox transformation compared to other  
613 approaches was  $-2\pm 9\%$ . Thus, while such an impact has been observed in previous studies, the skewing of results due to the  
614 annualization of respiration was not identified in our study.

#### 615 **4.4 Soil heterotrophic respiration**

616 We used a  $R_{het}$  value derived from  $R_{tot} - R_{het}'$  as the soil  $CO_2$  efflux.  $R_{het}'$  was derived from  $R_{tot}$  empirically using the  
617  $R_{het}/R_s$  data from a large dataset (Jian et al. 2021), thereby reducing the effect of potential systematic and random errors in  
618 individual studies. Such empirical derivation of  $R_{het}$  has been acknowledged to be an applicable approach and has been utilized  
619 in previous studies (Jauhiainen et al., 2019, 2023). To elaborate the recalculation model we used  $R_{het}$  and  $R_s$  values from  
620 the database (Jian, J. et al., 2021) on forest soil flux in the boreal zone, as existing experience suggests that organic soil  
621 emissions in hemiboreal forests are more likely to align with boreal rather than temperate conditions (Bårdale et al., 2022;  
622 Butlers et al., 2022; Dubra et al., 2023; Heikkinen et al., 2023; Jauhiainen et al., 2023; Krasnova et al., 2019; Lazdiņš et al.,  
623 2024). The choice of using only boreal data tends towards estimating higher  $R_{het}'$ , compared to the use of temperate data, as  
624 illustrated in Figure S2. This approach aimed to avoid the underestimation of soil  $CO_2$  efflux. The mean share of  $R_{het}$  acquired  
625 using boreal data was  $0.65\pm 0.04$  while using temperate data -  $0.60\pm 0.15$ , or around 10% difference. Accordingly, the  $R_{het}$   
626 proportion values we applied were higher than the typically observed range of 0.5 to 0.6 (Bond-Lamberty et al., 2004; Hanson  
627 et al., 2000), demonstrating that our approach avoided underestimating  $R_{het}$ .

628 The role of ground vegetation autotrophic respiration in  $R_{tot}$  increases with its biomass (Munir et al., 2017). Therefore, the  
629 risk of underestimating  $R_{het}$  by using  $R_{het}'$  is further reduced because the  $R_{het}/R_s$  ratio used to recalculate  $R_{tot}$  to  $R_{het}'$  does  
630 not account for the impact of autotrophic respiration from aboveground vegetation, consequently, the approach tends to rather  
631 overestimate the  $R_{het}$ . This aspect should be considered when assessing our results. When estimating the impact of historical  
632 drainage on the soil  $CO_2$  balance by comparing sites by drainage status, this bias was likely negligible, because the mean  
633 ground vegetation biomass did not significantly differ between drained and undrained sites ( $\Delta=0.53$  t dm. ha<sup>-1</sup>).

634 The applicability of the approach is supported by the comparability of the estimated  $R_{het}'$  values with  $R_{het}$  reported in previous  
635 studies (Bond-Lamberty and Thomson, 2010). We estimated  $R_{het}'$  of drained soil to be mean  $4.30\pm 1.20$  t  $CO_2$ -C ha<sup>-1</sup> year<sup>-1</sup>,  
636 which is slightly higher than both mean  $R_{het}$  of forest organic soil found in the boreal zone ( $4.09$  t  $CO_2$ -C ha<sup>-1</sup> year<sup>-1</sup>) (Ojanen  
637 et al., 2010) and in a broader regional scale ( $3.71\pm 0.53$  t  $CO_2$ -C ha<sup>-1</sup> year<sup>-1</sup>) (Jian, J. et al., 2021). When attempting to correct  
638 for the approximated overestimation of  $R_{het}$  introduced by trenching (see the Supplementary text), the resulting mean  $R_{het}$   
639 would be  $2.4$  t  $CO_2$ -C ha<sup>-1</sup> year<sup>-1</sup>, which is considerably lower than the  $R_{het}'$  values we used in the  $CO_2$  balance estimates.

#### 640 **4.5 Carbon influx by litter inputs**

641 In the estimation of  $CO_2$  influx, we considered data only for fLF, aGV, bGV, and FRP, excluding cLF, MP and dwarf shrubs.  
642 This approach was chosen because the  $CO_2$  emissions produced in decomposition of these litter types was directly included in  
643 the measured  $R_{tot}$ . For instance, cLF due to its dimensions and scarce coverage could not be objectively included in chamber  
644 measurements. Furthermore, while fLF is relatively uniform in forest areas, the coverage of mosses and dwarf shrubs is not

always so, therefore it is necessary to know their area of projection to be included in the CO<sub>2</sub> balance estimation. One solution for incorporating the “missing” litter inputs would be to use modelling approaches (Alm et al., 2023). However, we did not attempt to include those litter sources in the soil CO<sub>2</sub> balance estimation, as doing so would have introduced additional uncertainty. We estimated that annual moss production was 22±10% of the average total moss biomass of 0.50±0.09 kg dry matter (dm.) m<sup>-2</sup> measured for moss patches in our sites. Thus, mosses could potentially provide annual litter inputs reaching up to 0.98±0.25 t dm. ha<sup>-1</sup> if their cover was 100%. The mean annual cLF was 0.74±0.23 t dm. ha<sup>-1</sup>. Therefore, the litter input estimates (mean 4.70±1.43 t CO<sub>2</sub>-C ha<sup>-1</sup> year<sup>-1</sup>) used in the calculation of soil CO<sub>2</sub> balance likely led to overestimated soil C loss. This highlights the need to consider all litter input components in further studies, even though that may clearly increase the workload.

## 5. Conclusions

Although all soils in our study sites were classified as nutrient-rich based on forest site type taxonomy, they included a wide variety, ranging from those near the threshold of organic soil definition to soils with deep peat layers. Consequently, the soils exhibited broad variability in pH, macronutrient concentrations, and C:N ratio. That in turn contributed to the observed behaviour of the soils demonstrating both CO<sub>2</sub> sink and source dynamics under both drained and undrained conditions. During the study period, drained soils under birch, black alder, and Norway spruce remained CO<sub>2</sub> neutral, while in pine stands the soils were CO<sub>2</sub> sinks, presumably due to the significantly lower nutrient availability limiting mineralization of the organic matter. The disparity in soil nutrient conditions also explains why some undrained soils, characterized by relatively high nutrient availability, acted as CO<sub>2</sub> sources. These findings highlight the potential to improve predictions of soil CO<sub>2</sub> balance by complementing the broad “nutrient-rich” soil classification - typically assigned using site vegetation as a proxy - with quantitative measurements of soil nutrient status.

The study provides a notable contribution through both the plot-level summary and raw data on soil CO<sub>2</sub> influx and efflux. The spatial coverage of the study sites, along with the variability in stand characteristics, soil properties, and water-table level dynamics, provides input for synthesising dynamic empirical soil CO<sub>2</sub> balance models that depend on drainage status, meteorological conditions, soil chemistry, and stand-related parameters. The reported soil CO<sub>2</sub> balance values can be directly used as emission factors. Additional research is still needed to expand the dataset for establishing robust quantitative relationships that can be used to reliably identify and predict whether organic soils function as CO<sub>2</sub> sinks, sources, or remain in neutral balance, depending on site-specific conditions and annual weather variations.

## Data availability

Data used for carbon balance estimations is available at <https://doi.org/10.5281/zenodo.14968843>

## Author contributions

KS, JJ, RL, AL and KA developed a harmonised methodology. ABu, DČ, TS and MKS managed and processed the study data. ABu wrote the original manuscript, with significant reviewing contributions from RL, JJ, TS, ABā, IL, VS, HV, IL, AH and AJ provided critical reviews and edits to the manuscript.

## Competing interests

The authors declare that they have no conflict of interest.

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685 VRIILA-2024/2-0002).

## 686 References

- 687 Ahti, T., Hämet-Ahti, L., and Jalas, J.: Vegetation zones and their sections in northwestern Europe, *Ann. Bot. Fenn.*, 5, 169–211, 1968.
- 688 Alm, J., Wall, A., Myllykangas, J. P., Ojanen, P., Heikkinen, J., Henttonen, H. M., Laiho, R., Minkkinen, K., Tuomainen, T., and Mikola, J.: A new method for  
689 estimating carbon dioxide emissions from drained peatland forest soils for the greenhouse gas inventory of Finland, *Biogeosciences*, 20, 3827–3855,  
690 <https://doi.org/10.5194/bg-20-3827-2023>, 2023.
- 691 Estonian Environment Agency. Climate normals: <https://www.ilmateenistus.ee/kliima/kliimanormid/sademed/?lang=en>, last access: 25 April 2024.
- 692 Latvian Environment, Geology and Meteorology Centre. Climate normals: <https://data.gov.lv/dati/dataset/noverojumu-stacijas>, last access: 25 April 2024.
- 693 Lithuanian Hydrometeorological Service. Climate normals: <https://www.meteo.lt/en/climate/lithuanian-climate/standard-climate-normals/>, last access: 25  
694 April 2024.
- 695 Von Arnold, K., Nilsson, M., Hånell, B., Weslien, P., and Klemetsson, L.: Fluxes of CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O from drained organic soils in deciduous forests, *Soil*  
696 *Biol. Biochem.*, 37, 1059–1071, <https://doi.org/10.1016/j.soilbio.2004.11.004>, 2005.
- 697 Ball, B. C.: Soil structure and greenhouse gas emissions: A synthesis of 20 years of experimentation, *Eur. J. Soil Sci.*, 64, 357–373,  
698 <https://doi.org/10.1111/ejss.12013>, 2013.
- 699 Bārdule, A., Gerra-Inohosa, L., Kļaviņš, I., Kļaviņa, Z., Bitenieks, K., Butlers, A., Lazdiņš, A., and Libiete, Z.: Variation in the Mercury Concentrations and  
700 Greenhouse Gas Emissions of Pristine and Managed Hemiboreal Peatlands, *Land*, 11, 1414, <https://doi.org/10.3390/land11091414>, 2022.
- 701 Basiliko, N., Blodau, C., Roehm, C., Bengtson, P., and Moore, T. R.: Regulation of decomposition and methane dynamics across natural, commercially mined,  
702 and restored northern peatlands, *Ecosystems*, 10, 1148–1165, <https://doi.org/10.1007/s10021-007-9083-2>, 2007.
- 703 Beaulne, J., Garneau, M., Magnan, G., and Boucher, É.: Peat deposits store more carbon than trees in forested peatlands of the boreal biome, *Sci. Rep.*, 11,  
704 1–11, <https://doi.org/10.1038/s41598-021-82004-x>, 2021.
- 705 Berger, T. W., Inselsbacher, E., and Zechmeister-Boltenstern, S.: Carbon dioxide emissions of soils under pure and mixed stands of beech and spruce, affected  
706 by decomposing foliage litter mixtures, *Soil Biol. Biochem.*, 42, 986–997, <https://doi.org/10.1016/j.soilbio.2010.02.020>, 2010.
- 707 Bhuiyan, R., Minkkinen, K., Helmisaari, H. S., Ojanen, P., Penttilä, T., and Laiho, R.: Estimating fine-root production by tree species and understorey functional  
708 groups in two contrasting peatland forests, *Plant Soil*, 412, 299–316, <https://doi.org/10.1007/s11104-016-3070-3>, 2017.
- 709 Bond-Lamberty, B. and Thomson, A.: A global database of soil respiration data, *Biogeosciences*, 7, 1915–1926, <https://doi.org/10.5194/bg-7-1915-2010>,  
710 2010.
- 711 Bond-Lamberty, B., Wang, C., and Gower, S. T.: A global relationship between the heterotrophic and autotrophic components of soil respiration?, *Glob.*  
712 *Chang. Biol.*, 10, 1756–1766, <https://doi.org/10.1111/j.1365-2486.2004.00816.x>, 2004.
- 713 Box, G. E. P. and Cox, D. R.: An Analysis of Transformations, *J. R. Stat. Soc. Ser. B*, 26, 211–243, <https://doi.org/10.1111/j.2517-6161.1964.tb00553.x>, 1964.
- 714 Brock, O., Kooijman, A., Nierop, K. G. J., Muys, B., Vancampenhout, K., and Jansen, B.: Disentangling the effects of parent material and litter input chemistry  
715 on molecular soil organic matter composition in converted forests in Western Europe, *Org. Geochem.*, 134, 66–76, 2019.
- 716 Bušs, K.: Forest Ecology and Typology, Zinātne, Rīga, Latvija, 64 pp., 1981.
- 717 Butlers, A., Lazdiņš, A., Kalēja, S., and Bārdule, A.: Carbon Budget of Undrained and Drained Nutrient-Rich Organic Forest Soil, *Forests*, 13, 1790,  
718 <https://doi.org/10.3390/f13111790>, 2022.
- 719 Butlers, A., Lazdiņš, A., Kalēja, S., Purviņa, D., Spalva, G., Saule, G., and Bārdule, A.: CH<sub>4</sub> and N<sub>2</sub>O Emissions of Undrained and Drained Nutrient-Rich Organic  
720 Forest Soil, *Forests*, 14, <https://doi.org/10.3390/f14071390>, 2023.
- 721 Calvo Buendia, E., Tanabe, K., Kranjc, A., Baasansuren, J., Fukuda, M., Ngarize, S., Osako, A., Pyrozhenko, Y., Shermanau, P., and Federici, S.: 2019 Refinement  
722 to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories, Switzerland, 2019.
- 723 Chin, M. Y., Lau, S. Y. L., Midot, F., Jee, M. S., Lo, M. L., Sangok, F. E., and Melling, L.: Root exclusion methods for partitioning of soil respiration: Review and  
724 methodological considerations, *Pedosphere*, 33, 683–699, <https://doi.org/10.1016/j.pedsph.2023.01.015>, 2023.
- 725 Comstedt, D., Boström, B., and Ekblad, A.: Autotrophic and heterotrophic soil respiration in a Norway spruce forest: Estimating the root decomposition and  
726 soil moisture effects in a trenching experiment, *Biogeochemistry*, 104, 121–132, <https://doi.org/10.1007/s10533-010-9491-9>, 2011.
- 727 Cools, N. and De Vos, B.: Sampling and analysis of soil, Manual Part X, in: Manual on methods and criteria for harmonized sampling, assessment, monitoring  
728 and analysis of the effects of air pollution on forests, 208, 2010.
- 729 Dawud, S.M., Raulund-Rasmussen, K., Domisch, T. et al.: Is Tree Species Diversity or Species Identity the More Important Driver of Soil Carbon Stocks, C/N  
730 Ratio, and pH?. *Ecosystems* 19, 645–660, <https://doi.org/10.1007/s10021-016-9958-1>, 2016
- 731 Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change,  
732 <https://doi.org/10.1038/nature04514>, 2006.

Denmead, O. T.: Approaches to measuring fluxes of methane and nitrous oxide between landscapes and the atmosphere, *Plant Soil*, 309, 5–24, <https://doi.org/10.1007/s11104-008-9599-z>, 2008.

Díaz-Pinés, E., Schindlbacher, A., Pfever, M., Jandl, R., Zechmeister-Boltenstern, S., and Rubio, A.: Root trenching: A useful tool to estimate autotrophic soil respiration? A case study in an austrian mountain forest, *Eur. J. For. Res.*, 129, 101–109, <https://doi.org/10.1007/s10342-008-0250-6>, 2010.

Dubra, S., Samariks, V., Līcīte, I., Butlers, A., Purviņa, D., Lupiķis, A., and Jansons, Ā.: Effects of Drainage on Carbon Stock in Hemiboreal Forests: Insights from a 54-Year Study, *Sustainability*, 15, 16622, <https://doi.org/10.3390/su152416622>, 2023.

Eggleston, H. ., Buendia, L., Miwa, K., Ngara, T., and Tanabe, K. (Eds.): 2006 IPCC Guidelines for National Greenhouse Gas Inventories, Prepared by the National Greenhouse Gas Inventories Programme, IGES, Japan, 2006.

Epron, D.: Separating autotrophic and heterotrophic components of soil respiration: Lessons learned from trenching and related root-exclusion experiments, *Soil Carbon Dyn. An Integr. Methodol.*, 157–168, <https://doi.org/10.1017/CBO9780511711794.009>, 2010.

European Environment Agency: Annual European Union greenhouse gas inventory 1990–2021 and inventory report 2023, Copenhagen, 2023.

Fuss, R. and Hueppi, R.: Greenhouse Gas Flux Calculation from Chamber Measurements: R Package, 2024.

Glenn, S., Heyes, A., and Moore, T.: Carbon dioxide and methane fluxes from drained peat soils, Southern Quebec, *Global Biogeochem. Cycles*, 7, 247–257, 1993.

Hanson, P. J., Edwards, N. T., Garten, C. T., and Andrews, J. A.: Separating root and soil microbial contributions to soil respiration: A review of methods and observations, *Biogeochemistry*, 48, 115–146, <https://doi.org/10.1023/A:1006244819642>, 2000.

Heikkinen, J., Clarke, N., He, H., Dalsgaard, L., Ojanen, P., Vesterdal, L., Alm, J., Butlers, A., Callesen, I., Lohila, A., Sigurdsson, B. D., Soosaar, K., Bjarnadottir, B., Lazdins, A., Laiho, R., and Management, N. R.: Reviews and syntheses : Greenhouse gas emissions from drained organic forest soils – synthesizing data for site-specific emission factors for boreal and cool temperate regions, *Biogeosciences*, 2023.

Hermans, R., Mckenzie, R., Andersen, R., Teh, Y. A., Cowie, N., and Subke, J. A.: Net soil carbon balance in afforested peatlands and separating autotrophic and heterotrophic soil CO<sub>2</sub> effluxes, *Biogeosciences*, 19, 313–327, <https://doi.org/10.5194/bg-19-313-2022>, 2022.

Hiraishi, T., Krug, T., Tanabe, K., Srivastava, N., Fukuda, M., Troxler, T., and Jamsranjav, B.: 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands, IPCC, Switzerland, 2013.

Hommeltenberg, J., Schmid, H. P., Drösler, M., and Werle, P.: Can a bog drained for forestry be a stronger carbon sink than a natural bog forest?, *Biogeosciences*, 11, 3477–3493, <https://doi.org/10.5194/bg-11-3477-2014>, 2014.

Hutchinson, G. L. and Livingston, G. P.: Use of chamber systems to measure trace gas fluxes, *ASA Spec. Publ.*, 1993.

Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E. J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Guomundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, *Glob. Chang. Biol.*, 7, 269–278, <https://doi.org/10.1046/j.1365-2486.2001.00412.x>, 2001.

Jauhiainen, J.: Report on current situation – applied emission factors and projections of greenhouse gas emissions from organic soils, *Salaspils*, 65 pp., <https://doi.org/10.13140/RG.2.2.35701.93927>, 2019.

Jauhiainen, J., Alm, J., Bjarnadottir, B., Callesen, I., Christiansen, J. R., Clarke, N., Dalsgaard, L., He, H., Jordan, S., Kazanavičiūtė, V., Klemetsson, L., Lauren, A., Lazdins, A., Lehtonen, A., Lohila, A., Lupikis, A., Mander, Ü., Minkinen, K., Kasimir, Å., Olsson, M., Ojanen, P., Öskarsson, H., Sigurdsson, B. D., Sogaard, G., Soosaar, K., Vesterdal, L., and Laiho, R.: Reviews and syntheses: Greenhouse gas exchange data from drained organic forest soils - a review of current approaches and recommendations for future research, *Biogeosciences Discuss.*, 1–26, <https://doi.org/10.5194/bg-2019-261>, 2019.

Jauhiainen, J., Heikkinen, J., Clarke, N., He, H., Dalsgaard, L., Minkinen, K., Ojanen, P., Vesterdal, L., Alm, J., Butlers, A., Callesen, I., Jordan, S., Lohila, A., Mander, Ü., Öskarsson, H., Sigurdsson, B. D., Sogaard, G., Soosaar, K., Kasimir, Å., Bjarnadottir, B., Lazdins, A., and Laiho, R.: Reviews and syntheses: Greenhouse gas emissions from drained organic forest soils – synthesizing data for site-specific emission factors for boreal and cool temperate regions, *Biogeosciences*, 20, 4819–4839, <https://doi.org/10.5194/bg-20-4819-2023>, 2023.

Jian, J., R., Vargas, K. J., Anderson-Teixeira, E. Stell, V., Herrmann, M., Horn, N., Kholod, J., Manzon, R., Marchesi, D., Paredes, and Bond-Lamberty., B. P.: A Global Database of Soil Respiration Data, Version 5.0., Oak Ridge, Tennessee, USA., <https://doi.org/doi.org/10.3334/ORNLDAAC/1827>, 2021.

Jovani-Sancho, A. J., Cummins, T., and Byrne, K. A.: Soil respiration partitioning in afforested temperate peatlands, *Biogeochemistry*, 141, 0–1, <https://doi.org/10.1007/s10533-018-0496-0>, 2018.

Khomik, M., Altaf Arain, M., Liaw, K. L., and McCaughey, J. H.: Debut of a flexible model for simulating soil respiration-soil temperature relationship: Gamma model, *J. Geophys. Res. Biogeosciences*, 114, 1–11, <https://doi.org/10.1029/2008JG000851>, 2009.

Konstantinavičiūtė, I., Byčėnienė, S., Kavšinė, A., Juška, R., Žiukelytė, I., Lenkaitis, R., Karlonienė, D., Politika, L., Mačiulskas, M., Armolaitis, K., Ozarinskienė, M., Matelytė, D., Merkelienė, J., Kairienė, E., and Šulinskas, K.: Greenhouse Gas Emissions in Lithuania. 1990–2021. Lithuania’s national inventory report, 2023.

Korkiakoski, M., Ojanen, P., Tuovinen, J. P., Minkinen, K., Nevalainen, O., Penttilä, T., Aurela, M., Laurila, T., and Lohila, A.: Partial cutting of a boreal nutrient-rich peatland forest causes radically less short-term on-site CO<sub>2</sub> emissions than clear-cutting, *Agric. For. Meteorol.*, 332, <https://doi.org/10.1016/j.agrformet.2023.109361>, 2023.

Krasnova, A., Kukumägi, M., Mander, Ü., Torga, R., Krasnov, D., Noe, S. M., Ostonen, I., Püttsepp, Ü., Killian, H., Uri, V., Lohmus, K., Söber, J., and Soosaar, K.: Carbon exchange in a hemiboreal mixed forest in relation to tree species composition, *Agric. For. Meteorol.*, 275, 11–23, <https://doi.org/10.1016/J.AGRFORMET.2019.05.007>, 2019.

Kupka, D. and Gruba, P.: Effect of pH on the sorption of dissolved organic carbon derived from six tree species in forest soils, *Ecol. Indic.*, 140, 108975, <https://doi.org/10.1016/j.ecolind.2022.108975>, 2022.

Kutzbach, L., Schneider, J., Sachs, T., Giebel, M., Nykänen, H., Shurpali, N. J., Martikainen, P. J., Alm, J., and Wilmking, M.: CO<sub>2</sub> flux determination by closed-chamber methods can be seriously biased by inappropriate application of linear regression, *Biogeosciences*, 4, 1005–1025, <https://doi.org/10.5194/bg-4-1005-2007>, 2007.

- 794 Kuzyakov, Y., Friedel, J. K., and Stahr, K.: Review of mechanisms and quantification of priming effects, *Soil Biol. Biochem.*, 32, 1485–1498, 2000.
- 795 Laiho, R., Bhuiyan, R., Straková, P., Mäkiranta, P., Badorek, T., and Penttilä, T.: Modified ingrowth core method plus infrared calibration models for estimating  
796 fine root production in peatlands, *Plant Soil*, 385, 311–327, <https://doi.org/10.1007/s11104-014-2225-3>, 2014.
- 797 Laiho, R. & Pearson, M. : Surface peat and its dynamics following drainage - do they facilitate estimation of carbon losses with the C/ash method? *Mires  
798 and Peat*, 17(08), 1- 19. (Online: <http://www.mires-and-peat.net/pages/volumes/map17/map1708.php>); 10.19189/Map.2016.OMB.247, 2016
- 799 Laiho, R. & Laine, J.: Post-drainage nutrient stores in peat. In: Hånell B (ed) *Biomass production and element fluxes in forested peatland ecosystems*. Swedish  
800 University of Agricultural Sciences, Umeå, 81–91, 1990
- 801 Laine, J., Laiho, R., Minkinen, K., and Vasander, H.: Forestry and Boreal Peatlands. In: Wieder, R.K., Vitt, D.H. (eds) *Boreal Peatland Ecosystems*. Ecological  
802 Studies, vol 188. Springer, Berlin, Heidelberg . [https://doi.org/10.1007/978-3-540-31913-9\\_15](https://doi.org/10.1007/978-3-540-31913-9_15), 2006
- 803 Lazdiņš, A., Lupiķis, A., Polmanis, K., Bārdule, A., Butlers, A., and Kalēja, S.: Carbon stock changes of drained nutrient-rich organic forest soils in Latvia, *Silva  
804 Fenn.*, 58, 1–21, <https://doi.org/10.14214/sf.22017>, 2024.
- 805 Liaw, K. L., Khomik, M., and Arain, M. A.: Explaining the Shortcomings of Log-Transforming the Dependent Variable in Regression Models and Recommending  
806 a Better Alternative: Evidence From Soil CO<sub>2</sub> Emission Studies, *J. Geophys. Res. Biogeosciences*, 126, <https://doi.org/10.1029/2021JG006238>, 2021.
- 807 Ličite, I., Lupiķis, A., Peters, J., Butlers, A., Armolaitis, K., Soosaar, K., Laiho, R., Čiudlienė, D., and Jauhiainen, J.: Report on the identified climate change  
808 mitigation targeted management practices on organic soils, *Salaspils*, 119 pp., 2019.
- 809 Madsen, R. L., Asplund, J., Nybakken, L., Biong, R., and Kj, O. J.: Harvesting history affects soil respiration and litterfall but not overall carbon balance in  
810 boreal Norway spruce forests, *Forest Ecology and Management*, 578, 0–2, <https://doi.org/10.1016/j.foreco.2024.122485>, 2025.
- 811 Magnusson, B., Näykki, T., Hovind, H., Krysell, M., and Sahlin, E.: Handbook for Calculation of Measurement Uncertainty in Environmental  
812 Laboratories, Nordtest Report TR 537, Nord. Rep. TR 537 (ed. 4) 2017, 51, 2017.
- 813 Marinos, R. E. and Bernhardt, E. S.: Soil carbon losses due to higher pH offset vegetation gains due to calcium enrichment in an acid mitigation experiment.,  
814 *Ecology*, 99, 2363–2373, <https://doi.org/10.1002/ecy.2478>, 2018.
- 815 Ministry of the Environment of Republic of Estonia: Greenhouse Gas Emissions in Estonia 1990–2019. National Inventory Report Submission to the UNFCCC  
816 Secretariat, 1990–2021 pp., 2021.
- 817 Minkinen, K., Laine, J., Shurpali, N. J., Mäkiranta, P., Alm, J., and Penttilä, T.: Heterotrophic soil respiration in forestry-drained peatlands, *Boreal Environ.  
818 Res.*, 12, 115–126, 2007.
- 819 Moore, T. R., Trofymow, J. A., Taylor, B., Prescott, C., Camiré, C., Duschene, L., Fyles, J., Kozak, L., Kranabetter, M., Morrison, I., Siltanen, M., Smith, S., Titus,  
820 B., Visser, S., Wein, R., and Zoltai, S.: Litter decomposition rates in Canadian forests, *Glob. Chang. Biol.*, 5, 75–82, 1999.
- 821 Moulin, A. P., Glenn, A., Tenuta, M., Lobb, D. A., Dunmola, A. S., and Yapa, P.: Alternative transformations of nitrous oxide soil flux data to normal  
822 distributions, *Can. J. Soil Sci.*, 94, 105–108, <https://doi.org/10.4141/CJSS2013-008>, 2014.
- 823 Munir, T. M., Khadka, B., Xu, B., and Strack, M.: Partitioning forest-floor respiration into source based emissions in a boreal forested bog: Responses to  
824 experimental drought, *Forests*, 8, 1–17, <https://doi.org/10.3390/f8030075>, 2017.
- 825 Nakano, T., Sawamoto, T., Morishita, T., Inoue, G., and Hatano, R.: A comparison of regression methods for estimating soil-atmosphere diffusion gas fluxes  
826 by a closed-chamber technique, *Soil Biol. Biochem.*, 36, 107–113, <https://doi.org/10.1016/j.soilbio.2003.07.005>, 2004.
- 827 Ngao, J., Longdoz, B., Granier, A., and Epron, D.: Estimation of autotrophic and heterotrophic components of soil respiration by trenching is sensitive to  
828 corrections for root decomposition and changes in soil water content, *Plant Soil*, 301, 99–110, <https://doi.org/10.1007/s11104-007-9425-z>, 2007.
- 829 Nichols, J. E. and Peteet, D. M.: Rapid expansion of northern peatlands and doubled estimate of carbon storage, *Nat. Geosci.*, 12, 917–921,  
830 <https://doi.org/10.1038/s41561-019-0454-z>, 2019.
- 831 Nomura, K., Yamasaki, Y., Takada, A., Sago, Y., Yasutake, D., and Kitano, M.: A new method of evaluating gas fluxes in a closed chamber system with  
832 theoretical consideration for dynamic characteristics of a concentration sensor, *Environ. Control Biol.*, 57, 53–59, <https://doi.org/10.2525/ecb.57.53>, 2019.
- 833 Novara, A., Armstrong, A., Gristina, L., Semple, K. T., and Quinton, J. N.: Effects of soil compaction, rain exposure and their interaction on soil carbon dioxide  
834 emission, *Earth Surf. Process. Landforms*, 37, 994–999, <https://doi.org/10.1002/esp.3224>, 2012.
- 835 Ohlson, M.: Growth and nutrient characteristics in bog and fen populations of Scots pine (*Pinus sylvestris*). *Plant and Soil*, 172(2), 235–245.  
836 <http://www.jstor.org/stable/42947484>, 1995.
- 837 Ojanen, P., Minkinen, K., Alm, J., and Penttilä, T.: Soil-atmosphere CO<sub>2</sub>, CH<sub>4</sub> and N<sub>2</sub>O fluxes in boreal forestry-drained peatlands, *For. Ecol. Manage.*, 260,  
838 411–421, <https://doi.org/10.1016/j.foreco.2010.04.036>, 2010.
- 839 Ojanen, P., Minkinen, K., Lohila, A., Badorek, T., and Penttilä, T.: Chamber measured soil respiration: A useful tool for estimating the carbon balance of  
840 peatland forest soils?, *For. Ecol. Manage.*, 277, 132–140, <https://doi.org/10.1016/j.foreco.2012.04.027>, 2012.
- 841 Pribyl, D. W.: A critical review of the conventional SOC to SOM conversion factor, *Geoderma*, 156, 75–83, <https://doi.org/10.1016/j.geoderma.2010.02.003>,  
842 2010.
- 843 Qiu, C., Ciais, P., Zhu, D., Guenet, B., Peng, S., Petrescu, A. M. R., Lauerwald, R., Makowski, D., Gallego-Sala, A. V., Charman, D. J., and Brewer, S. C.: Large  
844 historical carbon emissions from cultivated northern peatlands, *Sci. Adv.*, 7, 1–10, <https://doi.org/10.1126/sciadv.abf1332>, 2021.
- 845 Ryhti, K., Kulmala, L., Pumpanen, J., Isotalo, J., Pihlatie, M., Helmisaari, H. S., Leppälampi-Kujansuu, J., Kieloaho, A. J., Bäck, J., and Heinonsalo, J.: Partitioning  
846 of forest floor CO<sub>2</sub> emissions reveals the belowground interactions between different plant groups in a Scots pine stand in southern Finland, *Agric. For.  
847 Meteorol.*, 297, <https://doi.org/10.1016/j.agrformet.2020.108266>, 2021.
- 848 Reich, P. B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S. E., Eissenstat, D. M., Chorover, J., Chadwick, O. A., Hale, C. M., Tjoelker, M. G.: Linking litter  
849 calcium, earthworms and soil properties: a common garden test with 14 tree species, *Ecology Letters*, 8(8), 811 - 818, <https://doi.org/10.1111/j.1461-0248.2005.00779.x>, 2005
- 850
- 851 Savage, K. E., Davidson, E. A., Abramoff, R. Z., Finzi, A. C., and Giasson, M. A.: Partitioning soil respiration: quantifying the artifacts of the trenching method,  
852 *Biogeochemistry*, 140, 53–63, <https://doi.org/10.1007/s10533-018-0472-8>, 2018.

853 Scharlemann, J. P. W., Tanner, E. V. J., Hiederer, R., and Kapos, V.: Global soil carbon: Understanding and managing the largest terrestrial carbon pool,  
854 Carbon Manag., 5, 81–91, <https://doi.org/10.4155/cmt.13.77>, 2014.

855 Shahbaz, M., Bengtson, P., Mertes, J. R., Kulesa, B., and Kljun, N.: Spatial heterogeneity of soil carbon exchanges and their drivers in a boreal forest, Sci.  
856 Total Environ., 831, 154876, <https://doi.org/10.1016/j.scitotenv.2022.154876>, 2022.

857 Silva, J. P., Lasso, A., Lubberding, H. J., Peña, M. R., and Gijzen, H. J.: Biases in greenhouse gases static chambers measurements in stabilization ponds:  
858 Comparison of flux estimation using linear and non-linear models, Atmos. Environ., 109, 130–138, <https://doi.org/10.1016/j.atmosenv.2015.02.068>, 2015.

859 Skrebele, A., Treija, S., Lupkina, L., Cakars, I., Siņics, L., Lazdāne- Mihalko, J., Puļķe, A., Štelce, V., Klāvs, G., Gračkova, L., Bārdule, A., Butlers, A., Līcīte, I.,  
860 Lazdiņš, A., Bērziņa, L., Gancone, A., and Dansone, B.: Greenhouse Gas Emissions in Latvia 1990–2021. Latvia's National Inventory Report, Riga, 2023.

861 Straková, P., Niemi, R. M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., Fritze, H., and Laiho, R.: Litter type affects the activity of aerobic  
862 decomposers in a boreal peatland more than site nutrient and water table regimes, Biogeosciences, 8, 2741–2755, [https://doi.org/10.5194/bg-8-2741-](https://doi.org/10.5194/bg-8-2741-2011)  
863 2011, 2011.

864 Straková, P., Penttälä, T., Laine, J., and Laiho, R.: Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter  
865 decomposition: Consequences for accumulation of organic matter in boreal peatlands, Glob. Chang. Biol., 18, 322–335, <https://doi.org/10.1111/j.1365-2486.2011.02503.x>, 2012.

867 Subke, J. A., Inglisma, I., and Cotrufo, M. F.: Trends and methodological impacts in soil CO<sub>2</sub> efflux partitioning: A metaanalytical review, Glob. Chang. Biol.,  
868 12, 921–943, <https://doi.org/10.1111/j.1365-2486.2006.01117.x>, 2006.

869 Vanguelova, E. I., Crow, P., Benham, S., Pitman, R., Forster, J., Eaton, E. L., and Morison, J. I. L.: Impact of Sitka spruce (*Picea sitchensis* (Bong.) Carr.)  
870 afforestation on the carbon stocks of peaty gley soils- A chronosequence study in the north of England, Forestry, 92, 242–252,  
871 <https://doi.org/10.1093/forestry/cpz013>, 2019.

872 Vigras, E., Čiuldienė, D., Armolaitis, K., Valujeva, K., Laiho, R., Jauhiainen, J., Schindler, T., Bārdule, A., Lazdiņš, A., Butlers, A., Kazanavičiūtė, V., Belova, O.,  
873 Kamil-Sardar, M., and Soosaar, K.: Total Soil CO<sub>2</sub> Efflux from Drained Terric Histosols, Plants, 13, <https://doi.org/10.3390/plants13010139>, 2024.

874 Warlo, H., von Wilpert, K., Lang, F., and Schack-Kirchner, H.: Black alder (*Alnus glutinosa* (L.) Gaertn.) on compacted skid trails: A trade-off between  
875 greenhouse gas fluxes and soil structure recovery?, Forests, 10, <https://doi.org/10.3390/f10090726>, 2019.

876 Westman, C.J., Laiho, R. Nutrient dynamics of drained peatland forests. Biogeochemistry 63, 269–298 (2003). <https://doi.org/10.1023/A:1023348806857>

877 Wutzler, T., Perez-Priego, O., Morris, K., El-Madany, T. S., and Migliavacca, M.: Soil CO<sub>2</sub> efflux errors are lognormally distributed -implications and guidance,  
878 Geosci. Instrumentation, Methods Data Syst., 9, 239–254, <https://doi.org/10.5194/gi-9-239-2020>, 2020.

879 Yamulki, S., Anderson, R., Peace, A., and Morison, J. I. L.: Soil CO<sub>2</sub> CH<sub>4</sub> and N<sub>2</sub>O fluxes from an afforested lowland raised peatbog in Scotland: Implications  
880 for drainage and restoration, Biogeosciences, 10, 1051–1065, <https://doi.org/10.5194/bg-10-1051-2013>, 2013.

881 Yu, Z. C.: Northern peatland carbon stocks and dynamics: A review, Biogeosciences, 9, 4071–4085, <https://doi.org/10.5194/bg-9-4071-2012>, 2012.

882 Yueqian, M.: Analysis and modelling of soil CO<sub>2</sub> emissions within temperate coniferous and deciduous forests, McMaster University, 133 pp., 2020.

883 Zālītis, P.: Mežs un ūdens, Latvijas Valsts mežzinātnes institūts “Silava,” Salaspils, 356 pp., 2012.

884 Zhang, X., Wang, Y., Wang, J., Yu, M., Zhang, R., Mi, Y., Xu, J., Jiang, R., and Gao, J.: Elevation Influences Belowground Biomass Proportion in Forests by  
885 Affecting Climatic Factors, Soil Nutrients and Key Leaf Traits, Plants, 13, <https://doi.org/10.3390/plants13050674>, 2024.

886 Zhou, W., Han, G., Liu, M., and Li, X.: Effects of soil pH and texture on soil carbon and nitrogen in soil profiles under different land uses in Mun River Basin,  
887 Northeast Thailand, PeerJ, 2019, <https://doi.org/10.7717/peerj.7880>, 2019.

888 Zoltai, S. C. and Martikainen, P. J.: Estimated extent of forested peatlands and their role in the global carbon cycle, For. Ecosyst. For. Manag. Glob. Carbon  
889 Cycle, 1, 47–58, [https://doi.org/10.1007/978-3-642-61111-7\\_5](https://doi.org/10.1007/978-3-642-61111-7_5), 1996.

890