

1 **Spatial variation of surface soil carbon in a boreal forest – the role of historical**
2 **fires, contemporary vegetation, and hydro-topography**

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12 Abstract

13 Knowledge about the spatial variation of boreal forest soil carbon (C) stocks is limited, but
14 crucial for establishing management practices that prevent losses of soil C. Here, we
15 quantified the surface soil C stocks across small spatial scales, and aim to contribute to an
16 improved understanding of the drivers involved in boreal forest soil C accumulation. Our
17 study is based on C analyses of 192 soil cores, positioned and recorded systematically
18 within a forest area of 11 ha. The study area is a south-central Norwegian boreal forest
19 landscape, where the fire history for the past 650 years has been reconstructed. Soil C
20 stocks ranged from 1.3 to 96.7 kg m⁻² and were related to fire frequency, ecosystem
21 productivity, vegetation attributes, and hydro-topography. Soil C stocks increased with soil
22 nitrogen concentration, soil water content, *Sphagnum*- and litter-dominated forest floor
23 vegetation, and proportion of silt in the mineral soil, and decreased with fire frequency in site
24 1, feathermoss- and lichen-dominated forest floor vegetation and increasing slope. Our
25 results emphasize that boreal forest surface soil C stocks are highly variable in size across
26 fine spatial scales, shaped by an interplay between historical forest fires, ecosystem
27 productivity, forest floor vegetation, and hydro-topography.

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29 Key words: Organic surface carbon stocks, forest fire history, hydro-topography, spatial fine-
30 scale variation

31 1. Introduction

32 Boreal forest soils store approximately 20% of the terrestrial carbon (C) stock (Scharlemann
33 et al., 2014), and thus play an important role in the global C dynamics (Pan et al., 2011). The
34 large build-up of C in boreal forest soils are mainly due to low temperatures that lead to low
35 decomposition rates (Malhi et al., 1999; DeLuca & Boisvenue, 2012). Even so, these stocks
36 can be highly variable on fine spatial scales (Kristensen et al. 2015), which imply that
37 additional drivers are involved. Specifically, boreal forest soil C stocks are controlled by: I)
38 Temperature and humidity which drives primary production, decomposition and respiration
39 (Jobbágy & Jackson, 2000; Pan et al., 2011); II) Fire regimes which impact the soil structure,
40 nutrient pools and biochemistry (Andrieux et al., 2018; McLauchlan et al., 2020; Palviainen
41 et al., 2020; Mack et al., 2021); III) Climate- and fire interactions, which alter boreal forest
42 vegetation composition and hence litter quality, root distribution, and above-belowground
43 allocation patterns (Zackrisson et al., 1996; Jobbágy & Jackson, 2000; Nilsson & Wardle,
44 2005); and IV) Soil texture and topography that determine hydrological conditions and build-
45 up of organic matter, where coarse-texture soils favour faster organic matter decomposition
46 (Harden et al., 1997; Harden et al., 2000; Olsson et al., 2009; Zajícová & Chuman, 2020).

47 Forest ecosystems are experiencing alterations in fire regimes as climate is changing
48 (Flannigan et al., 2000; Whitlock et al., 2003; Seidl et al., 2020). This will impact the boreal
49 forest soil C stocks significantly as the proportion of fire-consumed C is determined by both
50 fire intensity and frequency (Williams et al., 2016). Typically, higher fire intensities and
51 increased frequencies result in larger C losses and longer soil C stock recovery times
52 (Alcaniz et al., 2018; Pellegrini et al., 2018), which both have been found to be variable in
53 boreal forests (Hume et al., 2016; Palviainen et al., 2020; Li et al., 2021). Yet, a general
54 trend in the boreal forest C stock recovery process is that an initial period with fast
55 accumulation of organic matter is followed by slow and continuous increases of the soil C
56 stocks. This can go on for several hundreds, or even thousands of years, related to
57 vegetation attributes of the forest ecosystem (Wardle et al., 2012; Andrieux et al., 2018;
58 Mack et al., 2021). However, despite a growing body of research on how fire impacts soil C
59 stocks in boreal forests, we lack information about relationships between occurrences of
60 historical fires and contemporary soil C stock sizes, as both figures are known to be spatially
61 variable in boreal forests (Zackrisson, 1977; Niklasson & Granström, 2000; Pellegrini et al.,
62 2018; McLauchlan et al., 2020).

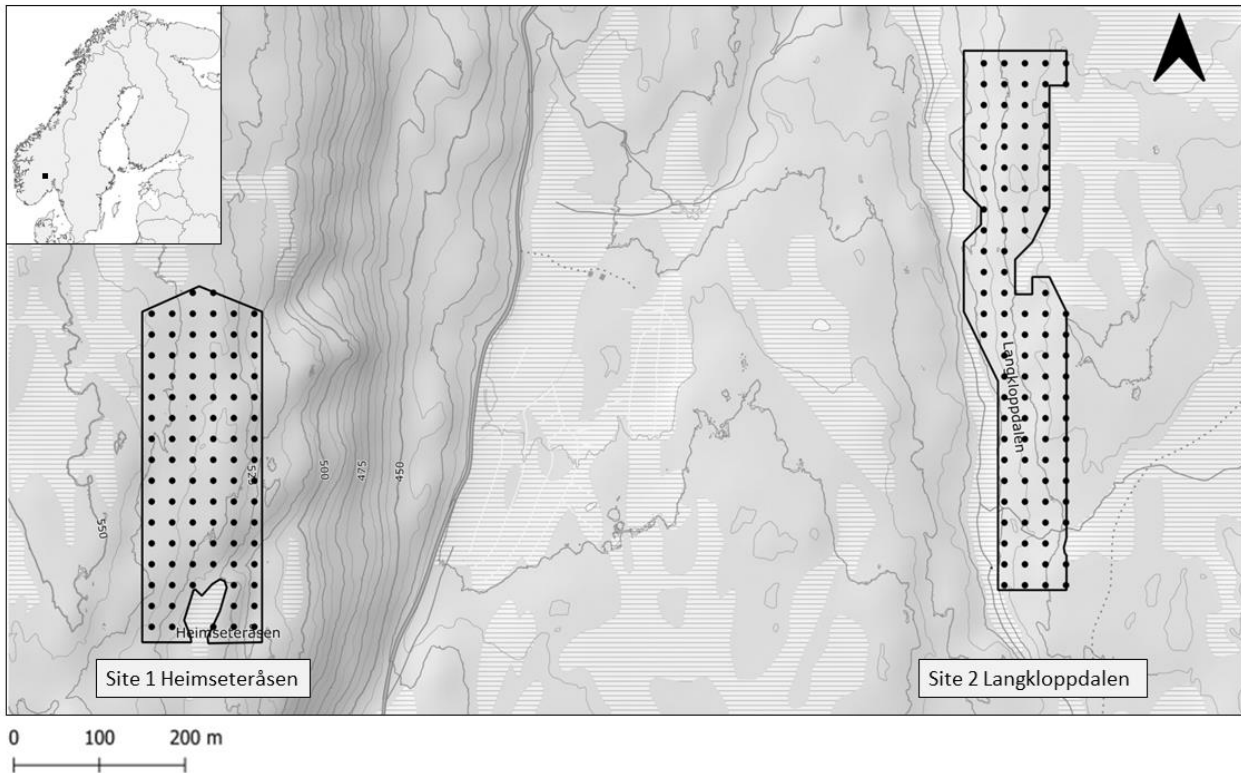
63 Here we focus on the interplay between contemporary and historical drivers of forest organic
64 surface soil C stock sizes (hereafter termed soil C). Our main aim is to increase the
65 understanding of processes involved in forest soil C dynamics and improve the knowledge

66 about size variation over fine spatial scales. To do this, we utilized a detailed
67 dendrochronology-based study of fire history (Storaunet et al., 2013) to establish a study
68 design that allow us to investigate if and how the size of boreal forest soil C stocks varies
69 across different historical fire regimes. We used this set up to address the following
70 questions. (I) To which extent does historical high-resolution fire data (i.e., time since last fire
71 and fire frequency) relate to present soil C stock sizes? (II) Does hydro-topography and
72 contemporary vegetation attributes play a more important role than fire history in shaping the
73 spatial variation in soil C stock sizes? We focused on the organic surface soil C layer since it
74 is strongly affected by forest fires (Li et al., 2021; Hanes et al., 2022), and a key determinant
75 of the C dynamics in the boreal forest soil (Högberg et al., 2001; Lindahl et al., 2007).

76 2. Materials and methods

77 2.1 *Study sites*

78 The study area consisted of two forest sites located in Trillemarka-Rollagsfjell Nature
79 Reserve in south-central Norway (60°2'N, 9°25'E). With an area of 147 km², Trillemarka-
80 Rollagsfjell Nature Reserve is one of the largest forested areas in south-central Norway with
81 little influence of modern clearcutting practices. It belongs to the mid-boreal vegetation zone,
82 with an intermediate oceanic and continental climate, experiencing mean annual
83 precipitation of 800-900 mm and mean annual temperature of 5°C, with monthly means
84 varying from -5.6°C in January to 16.3°C in July. Climate data are averages from Veggli,
85 located 15 km W of the study area, 275 m a.s.l., and Sigdal – Nedre Eggedal, located 11 km
86 NNE from the study area, 143 m a.s.l. (<https://seklima.met.no/observations/>). The
87 topography is characterized by north-south ridges of Precambrian rocks that constitute a
88 bedrock of acid granites and gneisses, as well as east-facing slopes of rich moraine
89 material.



90 **Fig. 1** Location of the two study sites (site 1 and site 2) and positions of plots for soil sampling and
 91 vegetation analyses in Trillemarka-Rollagsfjell Nature Reserve, south-central Norway. Topographic
 92 contour line distance=5 m. Data retrieved from The Norwegian Mapping Authority (2017).

93 Two approximately 5.5 ha study sites were selected within a 360-ha area of the Nature
 94 Reserve at elevations ranging from 400 (site 2, Langkloppdalen) to 550 m a.s.l. (site 1,
 95 Heimseteråsen) (Fig. 1). The forests were nutrient-poor and dominated by Scots pine (*Pinus*
 96 *sylvestris*), with sparse occurrences of Norway spruce (*Picea abies*), downy birch (*Betula*
 97 *pubescens*), and rowan (*Sorbus aucuparia*). The two study sites were placed in order to
 98 represent a broad range of differences in time since last fire and fire frequency (Fig. 2) as
 99 outlined in Storaunet et al. (2013) (see below / Section 2.2.2), while avoiding open
 100 unforested peatland areas.

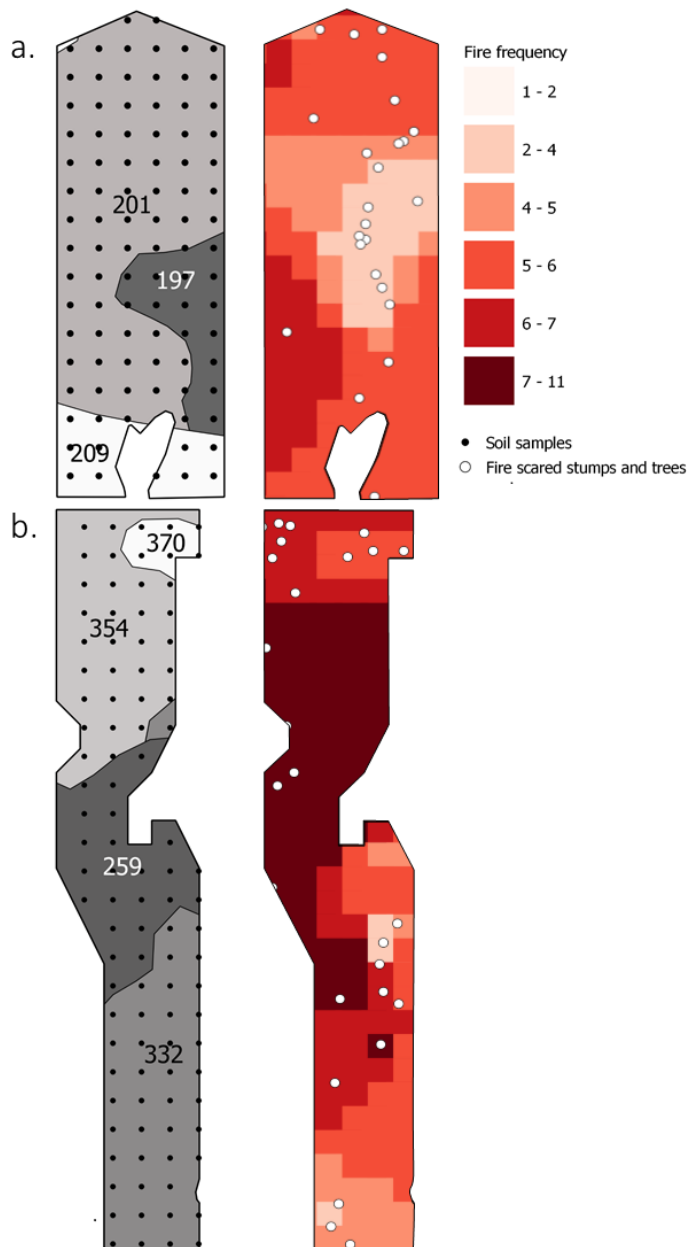
101 2.2 Data collection

102 2.2.1 Organic surface soil sampling

103 In September-October 2020 we collected a total of 195 soil samples at plots that were
104 located systematically 24 m apart across both sites (Fig. 1). At each soil sample plot, we
105 sampled the entire organic surface soil horizon including a few centimetres of the
106 underlying mineral layer with a sharp-edged cylindrical soil corer (\varnothing 58 mm). The soil
107 samples were divided in the field into organic layer and mineral layer and stored in separate
108 sealed plastic bags. We used soil depth and corer inner area to calculate sample volume.
109 Hence, soil sample depth and volume varied with thickness of the organic surface soil. We
110 relocated plots on bare bedrock ($n=8$, starting one meter north and moving 90 degrees
111 clockwise until a suitable location was achieved) and used a metal rod to measure the
112 thickness of the organic surface soil in a few plots ($n=18$), where the depth of the organic soil
113 exceeded the length of the soil corer (40 cm). Thus, our estimates cover organic soil depths
114 ranging from 2 to 110 cm, averaging 21.3 ± 1.6 cm (\pm SE). All soil samples were brought back
115 to the lab, weighed, and dried at 40°C until mass was constant. Prior to further analyses, the
116 dry soil was weighed, and the organic soil homogenized by a rotary mill (Brabender Rotary
117 Mill, Germany).

118 2.2.2 Fire history

119 The fire history data originated from Storaunet et al. (2013), who delineated 57 individual
120 forest fires in the landscape over the past 650 years by their high-resolution sampling and
121 cross-dating of fire scars. A strong anthropogenic signal was found in the fire regime from
122 1600 and onwards, with an increased fire frequency during 16-1700s and an almost
123 cessation of fires after 1800. From these fire historical data, we extracted the variables “Time
124 since last fire” and “Fire frequency” for each soil sample plot across our study sites (Fig. 2)
125 (see Storaunet et al. 2013 for methodological details).



126 **Fig. 2** Fire history characteristics of the study sites 1 and 2 (a. and b.). Numbers in left panels denote
 127 number of years since the last fire. Right panels depict number of recurring fires since AD 1350. Data
 128 extracted from Storaunet et al. (2013). Black dots in left panels denote soil sample locations, whereas
 129 white dots in right panels denote fire scarred wooden samples.

130 2.2.3 Vegetation

131 Quadrat vegetation sampling plots of 50x50 cm were located around the center of all soil
 132 sampling positions. We recorded percentage forest floor vegetation cover according to these
 133 vegetation categories: *Sphagnum* mosses; feather mosses (mainly *Pleurozium schreberi*
 134 and *Hylocomium splendens*); lichens (mostly *Cladonia* species and *Cetraria islandica*); litter
 135 (field layer vegetation, but no forest floor vegetation); naked (bare ground without any
 136 vegetation), plots on bare bedrock were relocated in the sampling procedure ($n=8$). In

137 addition, we estimated the forest stand basal area of *P. sylvestris*, *P. abies* and deciduous
138 trees using a relascope (factor 1) at every soil sample plot.

139 2.2.4 Topography and wetness

140 We defined microtopography of the 50x50 cm sample plot as convex (i.e., well drained hills),
141 concave (i.e., terrain depressions), or flat, and registered aspect and slope using a compass
142 and a clinometer (referred to as 'plot' in analyses). We also derived topography for the soil
143 sampling plots from a 0.25x0.25 m resolution digital terrain model (DTM) (The Norwegian
144 Mapping Authority, 2017). We retrieved elevation, slope and aspect using QGIS 3.16.7
145 (QGIS.org, 2022), and averaged slope and aspect over a 24x24 m area around each
146 sample plot (referred to as 'terrain' in analyses). Further, we defined soil water content as
147 sample dry weight divided by sample wet weight, subtracted from one. As rainfall conditions
148 varied prior to sampling, the soil wetness variable was centred and scaled by subtracting the
149 mean and dividing by the SD per sampling date.

150 2.3 Soil analyses

151 Total C and nitrogen (N) concentrations (%) of the organic surface soil were determined by
152 automated dry combustion in an elemental analyser (vario MICRO cube, Elementar,
153 Germany). The dry matter mass was used to determine bulk density (BD; g cm^{-3}) of the
154 organic and mineral soil fraction. C and N stocks (kg m^{-2}) in the soil were thereafter
155 calculated by multiplying C (%) or N (%) with BD (g cm^{-3}) and soil depth (cm) and scaled to
156 kg m^{-2} . Soil texture of 21 mineral soil samples were determined. The 21 samples were
157 chosen based on a stratified random procedure where samples first were grouped by soil C
158 stock size (i.e., largest, median, and smallest). For each category, we included the 14 top-
159 ranked samples from which we randomly drew 7 samples. Samples without mineral soil
160 were excluded. The selected samples were carefully sieved through a 2 mm sieve before
161 they were analysed by a laser diffraction particle size analyzer (Beckman Coulter LS 13 320,
162 United States).

163 2.4 Data analyses

164 Prior to statistical analyses, data were explored visually by boxplots, dotplots, and pairplots
165 to identify patterns in the data, potential outliers, and covariation. We identified three outliers
166 using a Bonferroni outlier test. These samples had unrealistically low C% values due to
167 contamination with mineral soil, and were thus removed, reducing the sample size to 192. A
168 principal component analysis (PCA) was performed on the 5 forest floor vegetation
169 categories outlined above (Appendix A, Fig. A.1). We did this to identify forest floor

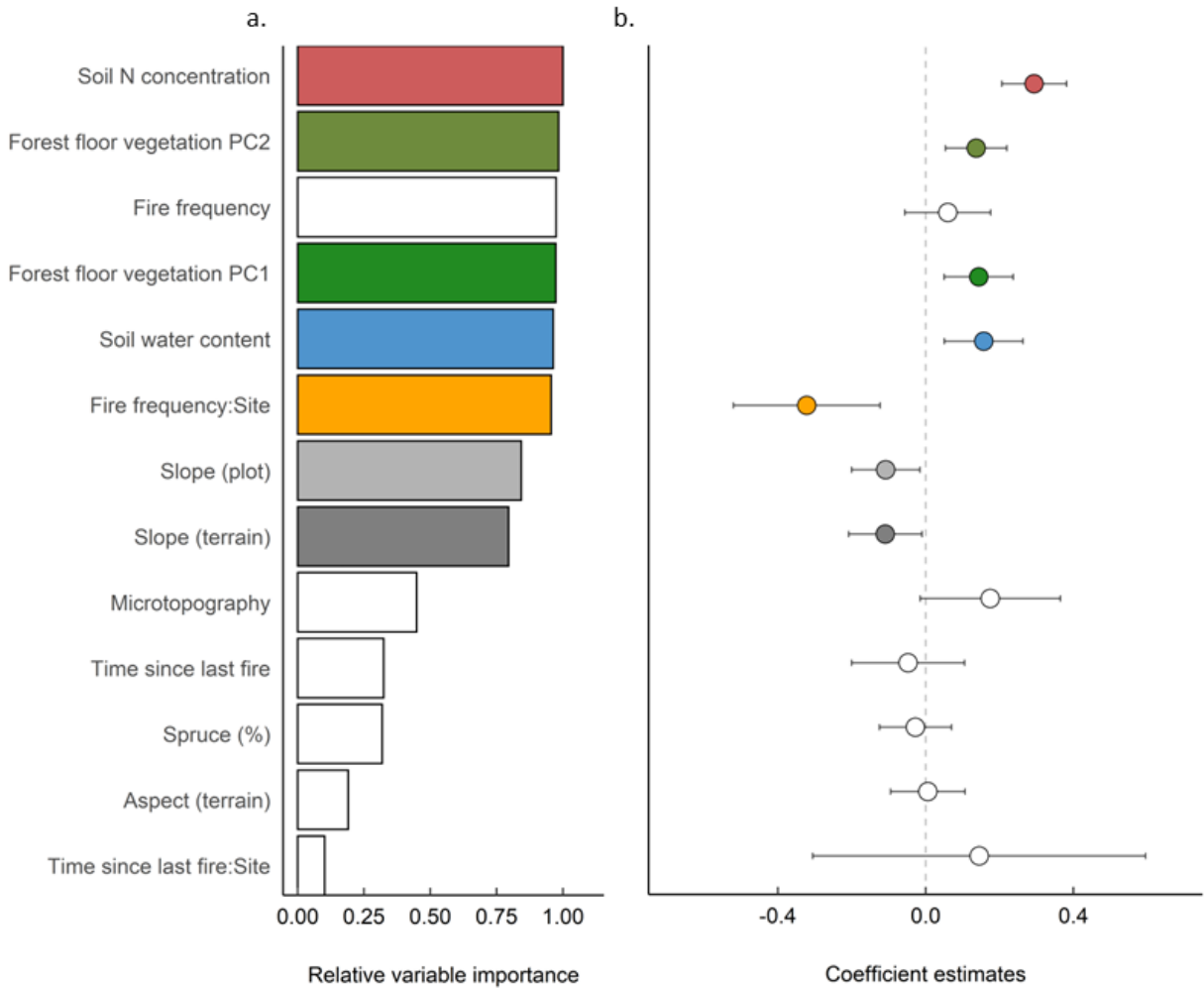
170 vegetation gradients with contrasting properties. We give an overview of all response- and
171 predictor variables in Appendix A, Table A.1.

172 To test the effects of predictor variables, we used linear mixed effect models. The two sites
173 were included as random effects to deal with potential site-specific difference introduced by
174 the study design. However, site was not significant in explaining overall soil C stock
175 variation. As we selected the study sites to cover a range of differences in fire history,
176 interaction terms between site and fire frequency as well as site and time since last fire were
177 included in the models. The model assumptions of normality and homoscedasticity of
178 residuals were visually inspected. As the normality assumption was violated, we applied a
179 \log_e -transformation of soil C stocks to improve the fit of the data.

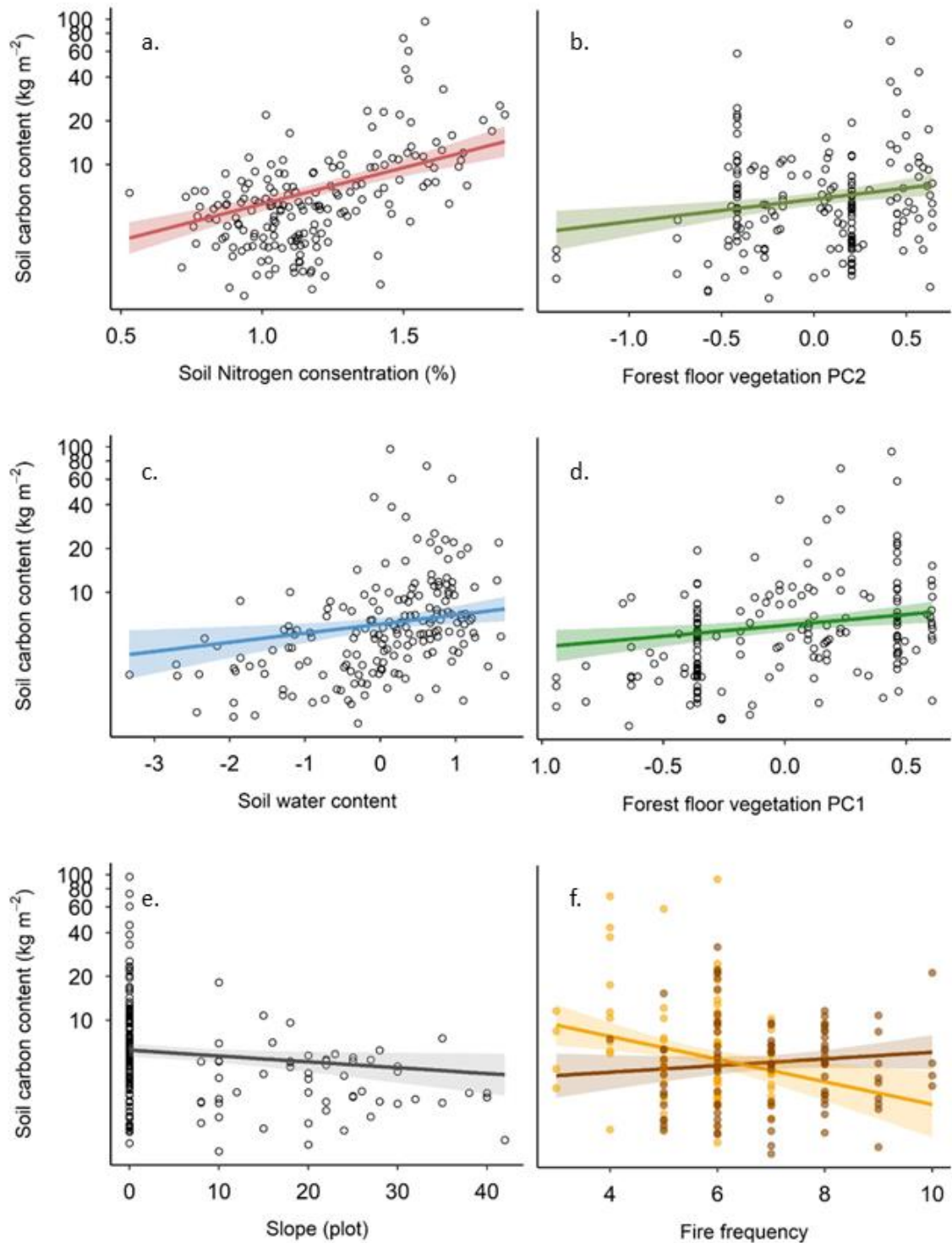
180 We used information-theoretic model averaging based on Akaike information criterion (AIC)
181 to assess the relative importance of each predictor variable in relation to soil C stocks
182 (Burnham & Anderson, 2002). Strongly correlated variables ($|r| \geq 0.5$) were not allowed in
183 the same model (see Appendix A Fig. A.2 for covariation plot). We calculated variable
184 importance score of each predictor variable by summing the Akaike weights over all models
185 including the relevant term. Corresponding estimated coefficients were averaged over the
186 same models and weighted according to the probability of each model. Soil texture (i.e.,
187 sand, silt, and clay) in relation to soil C stocks were modelled in separate mixed effect
188 models due to small sample size ($n=21$). We did all statistical analyses in R version 4.1.1
189 (RStudio Team, 2020), using the packages 'vegan', 'emmeans', 'nlme' and 'MuMIN'. All
190 maps were created using QGIS 3.16.7 (QGIS.org, 2022).

191 3. Results

192 C stocks in the organic layer ranged from 1.3 kg m⁻² to 96.7 kg m⁻² across the study sites
193 and averaged 9.1±0.9 kg m⁻². The relative importance of the different drivers of C soil stocks
194 are given in Fig. 3a, and the predictor variables included in the best model explained half of
195 the variation in soil C stocks (marginal R²=0.51, see Appendix B, Table. B.1 for all models
196 with $\Delta AIC < 2$). N-rich organic surface soil had larger C stocks (Fig. 3b, Fig. 4a). Further, soil
197 C varied with vegetation attributes. Plots with a larger proportion of litter compared to lichen
198 (forest floor vegetation PC2) and peatmoss compared to feathermoss (forest floor vegetation
199 PC1) had larger soil C stocks (Fig. 3b, Fig. 4b, d, see Appendix A Fig. A.1 for PCA plot).
200 Fine-scale spatial variation in hydro-topography (i.e., soil water content and slope) also
201 influenced the soil C stocks. Wetter areas had larger soil C stocks compared to drier, and
202 soil C stocks decreased with increasing slope (Fig. 3b, Fig. 4c, e). Lastly, a significant
203 interaction term between fire frequency and site implied that soil C decreased with
204 increasing fire frequency at site 1: areas with a low fire frequency (i.e., 3-4 fires) during the
205 past 650 years had larger soil C stocks compared to areas with a high fire frequency (i.e., 6-
206 7 fires). There was no effect of fire frequency at site 2 (Fig. 4f). In addition, areas with a
207 higher proportion of silt in the mineral soil had larger soil C stocks (separate mixed effect
208 model estimate: 0.16, CI: 0.02-0.31, $n=21$). Proportion of silt in the mineral soil varied from
209 13% to 61% across our study sites and was highly correlated with sand content ($r=-0.99$).



210 **Fig. 3** (a) Relative variable importance scores, and (b) corresponding significant coefficient estimates
 211 from model average analysis of predictors of boreal forest soil C stocks. The variable importance
 212 scores can be interpreted as the probability of that variable being a part of the best model and can
 213 therefore be used to rank the predictors in order of importance. Model average coefficients were
 214 averaged across all models and means, 95% CI are shown where CI's crossing zero are non-
 215 significant. All continuous predictor variables are centered and scaled to be directly comparable.
 216 Forest floor vegetation PC1 is a vegetation gradient going from feathermoss- to peatmoss-dominated
 217 sampling plots, and forest floor vegetation PC2 a vegetation gradient going from lichen- to litter-
 218 dominated sampling plots. Interacting terms between site and fire history have site 1 as reference
 219 level.



220 **Fig. 4** (a) Soil N concentration (%), (b) forest floor vegetation PC2, (c) soil water content, (d) forest
 221 floor vegetation PC1, (e) slope of the plot, and (f) fire frequency per site, site 1 is in light orange
 222 (significant) and site 2 in dark orange (non-significant), as drivers of boreal forest soil C stocks (log_e-
 223 scale). Significant model fits from the best model based on the model average analysis are shown for
 224 each driver as a solid line with 95% CI. Soil C data are presented as open black dots in all panels
 225 except for f, where soil C data are coloured according to site.

226 4. Discussion

227 We show that soil C stocks are highly variable across fine spatial scales in boreal Scots pine
228 forests, averaging $9.1 \pm 0.9 \text{ kg m}^{-2}$. This is higher than averages from other comparable study
229 areas in Sweden ($2.8 \pm 0.1 \text{ kg m}^{-2}$, Olsson et al. (2009)) and Denmark ($3.9 \pm 0.7 \text{ kg m}^{-2}$, Vejre
230 et al. (2003)). However, both these studies report shallower organic surface soil layers than
231 what we found across our study area, which is a key-explanation for the discrepancy. Our
232 study provides evidence that the variation in soil C stock sizes is partly attributed to historical
233 forest fires, but even more to contemporary ecosystem productivity, vegetation composition,
234 and fine-scale hydro-topography.

235 4.1 *Role of historical fires*

236 Typically, increased fire frequency results in larger C losses (Alcaniz et al., 2018; Pellegrini
237 et al., 2018). A significant interaction term revealed that the effect of fire frequency on soil C
238 was not consistent between the two study sites. At the western site 1, soil C expectedly
239 decreased with fire frequency, whereas no such effect was present at the eastern site 2. We
240 propose that the lack of impact of forest fires at site 2 may be explained by: I) low intensity
241 fires; II) organic soil recovery due to long time since last fire events; and III) discrepancies in
242 spatial precision between soil C stock estimates and fire history data.

243 First, many of the fires in the area may have been low-intensity and anthropogenic
244 prescribed burns, especially after AD 1600 (Storaunet et al., 2013; Rolstad et al., 2017).
245 Historically, summer dairy farmers were known to set fires in spring and early summer to
246 remove old field vegetation while leaving the organic soil layer intact (Larsson, 1995;
247 Niklasson & Drakenberg, 2001). This fire management was to enhance the quality of forest
248 pastures without reducing the long-term productivity of the land. Likewise, a Finnish
249 experimental study, reporting raw humus layers to be remarkably resistant to drought due to
250 strong water-holding capacity (Lindberg et al., 2021). Therefore, many of the fires at site 2
251 may have had negligible effect on soil C, whereas several large, natural fires may have
252 depleted more of the soil C at site 1.

253 Second, no fires have been recorded at site 2 over the past 250-300 years, and in addition,
254 after AD 1600 the fire sizes and intensity went significantly down (Storaunet et al., 2013).
255 This suggests that the forest soil C stocks were only lightly depleted and thereafter partly or
256 fully recovered in the time period after last fires. Our finding is consistent with previous
257 studies on soil C recovery time, which have been investigated across chronosequences
258 (Harden et al., 2012; Hume et al., 2016; Palviainen et al., 2020) and differences in fire
259 frequencies in boreal forests (Pellegrini et al., 2018).

260 On the other hand, studies have also found the recovery of boreal forest soil C stocks to be
261 impacted by historical fire regimes for hundreds to several thousands of years (Wardle et al.,
262 2012; Andrieux et al., 2018). As our record of fires was limited to the last 650 years, soil C
263 stocks may have been more influenced by earlier Holocene fire activity, masking possible
264 effects of more recent fires. Furthermore, besides a direct effect of fire, i.e., that fire
265 consumes organic matter, and removes soil C stocks partly or totally, these studies also
266 found that fire had indirect effects on soil C stocks, through fire driven changes in plant
267 diversity, composition (Wardle et al., 2012), and soil pH (Andrieux et al., 2018).

268 Third, and possibly most likely, the lack of influence of past fire events at site 2 can be
269 attributed to a mismatch in terms of spatial resolution. Even though Storaunet et al. (2013)
270 have documented the spatiotemporal fire history of the study sites in detail, we have a
271 considerably higher spatial resolution in the present study. Many of the fires may also have
272 burnt the ground vegetation only partially, resulting in a fine-scaled mosaic pattern of burnt
273 and unburnt areas. Such spatial discrepancies could obscure potential relationships between
274 fire occurrences in the past and contemporary soil C stock sizes as the impact of historical
275 fires may be overshadowed by other variables that operate on finer spatial scales. In
276 addition, the dendroecological records of fire events may have missed several low-intensity
277 fires that did not produce fire scars in the trees. Likely, the fire history of our study sites, as
278 well as of most boreal forests, is more spatially complex than can be revealed by standard
279 dendrochronological studies as their spatial precision is directly dependent on the number
280 and distribution of fire scarred trees, see e.g. (Parisien & Moritz, 2009; Rolstad et al., 2017).

281 *4.2 Role of nitrogen and soil texture*

282 Boreal forests are strongly N limited (Tamm, 1991; DeLuca et al., 2008; Maaroufi et al.,
283 2015), and soil N availability is thus an important indicator of productivity. Our soil total N
284 measures do not necessarily reflect availability. Nonetheless, total N concentration in the soil
285 samples was clearly the most important driver of soil C stock sizes in our study. Results from
286 a long-term N addition experiment give support for a positive relationship between N
287 availability and amount of C in the organic surface soil as N treatments resulted in increasing
288 C pools in the soil O-horizon (Maaroufi et al., 2015). However, the relationship between N
289 availability and C sequestration in boreal forest soils is complex (Hume et al., 2016; Högberg
290 et al., 2017; Mayer et al., 2020), and it is worth noting that the N treatment levels in Maaroufi
291 et al. (2015) was generally high, with yearly doses of 12.5 or 50 kg N ha⁻¹, over 16 years.

292 Productivity and soil C stocks of the boreal forest was also mediated by soil drainage, which
293 have for long been considered a primary control on boreal forest soil C stocks (Harden et al.,
294 1997). In-depth investigation of soil drainage was beyond the scope of this study. Even so,

295 our results suggest that differences in soil texture, especially proportion of silt in the mineral
296 soil, constitutes an important regulator of build-up of organic matter. Moreover, we found
297 differences in slope of each sampling plot to be more important than the slope of the general
298 terrain, highlighting how fine-scale differences need to be accounted for in soil C stock
299 estimations.

300 *4.3 Role of contemporary vegetation and hydro-topography*

301 It is well known that vegetation composition is important in shaping forests and soil C
302 accumulation on wide forest type spatial scales (Jobbágy & Jackson, 2000; Nilsson &
303 Wardle, 2005; Jonsson & Wardle, 2010). Our study adds a further perspective to this context
304 by revealing a strong fine-scale spatial relationship between vegetation composition and soil
305 C stock size within a single and widely distributed boreal forest type, i.e., nutrient poor Scots
306 pine forests with feathermosses and ericaceous dwarf shrubs as dominants in the field- and
307 forest floor vegetation (see Kielland-Lund (1981) for forest type definition).

308 Whether the forest floor was dominated by feathermosses or *Sphagnum* peatmosses turned
309 out as an important driver of the soil C stocks across fine spatial scales, and peatmoss
310 dominated areas stored the largest amounts of soil C. We attribute this to hydro-topography,
311 and the habitat preferences and ecophysiological characteristics of the different functional
312 groups of mosses. Feathermosses generally prefer drier habitats and have a relatively high
313 decomposability and low productivity compared to peatmosses (Lang et al., 2009), resulting
314 in less C accumulation. In contrast, peatmosses prefer waterlogged habitats, in which they
315 outcompete other vegetation (Van Breemen, 1995; Bisbee et al., 2001). Such wet habitats
316 create an anoxic soil environment with low decomposition rates, resulting in accumulation of
317 organic matter, and thereby C (Ohlson & Halvorsen Økland, 1998). The importance of moss
318 cover and water availability for the C stocks in boreal forests is known from previous studies
319 e.g., (Olsson et al., 2009; Andrieux et al., 2018; Zajícová & Chuman, 2020) and our results
320 underline the general importance of the forest floor vegetation as a driver of the spatial
321 variation in C stocks across fine scales.

322 Nitrogen availability, which is an important driver soil C stocks (Maaroufi et al., 2015), is also
323 known to be significantly affected by hydro-topographic variability. For example, Woo and
324 Kumar (2017) have shown that both the distributions of concentrations and age of different
325 inorganic nitrogen species including nitrate, ammonia, and ammonium in the soil is linked to
326 micro-topographic variability.

327 *4.4 Conclusion*

328 We conclude that boreal forests soil C stocks, which appear homogenous on large spatial
329 scales, are highly heterogenous across fine spatial scales. Variation in soil C stocks was
330 partly attributed to historical forest fires, but more so to contemporary ecosystem
331 productivity, vegetation composition, and fine-scale hydro-topography. These results
332 highlight the importance of high spatial resolution, as well as controlling for various edaphic
333 and biotic factors when investigating soil C stocks and its drivers.

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339 Declaration of interest

340 The authors report there are no competing interests to declare.

341 Data statement

342 Data associated with this manuscript are deposited in the NMBU Open Research Data
343 database <https://doi.org/10.18710/FJWV6X>.

344 References

- 345 Alcaniz, M., Outeiro, L., Francos, M., & Ubeda, X. (2018). Effects of prescribed fires on soil properties:
 346 A review. *Science of The Total Environment*, *613*, 944-957.
 347 doi:10.1016/j.scitotenv.2017.09.144
- 348 Andrieux, B., Beguin, J., Bergeron, Y., Grondin, P., & Paré, D. (2018). Drivers of postfire soil organic
 349 carbon accumulation in the boreal forest. *Global Change Biology*, *24*(10), 4797-4815.
- 350 Bisbee, K. E., Gower, S. T., Norman, J. M., & Nordheim, E. V. (2001). Environmental controls on
 351 ground cover species composition and productivity in a boreal black spruce forest.
 352 *Oecologia*, *129*(2), 261-270.
- 353 Burnham, K. P., & Anderson, D. R. (2002). A practical information-theoretic approach. *Model
 354 selection and multimodel inference*, *2*.
- 355 DeLuca, T. H., & Boisvenue, C. (2012). Boreal forest soil carbon: distribution, function and modelling.
 356 *Forestry*, *85*(2), 161-184.
- 357 DeLuca, T. H., Zackrisson, O., Gundale, M. J., & Nilsson, M.-C. (2008). Ecosystem feedbacks and
 358 nitrogen fixation in boreal forests. *Science*, *320*(5880), 1181-1181.
- 359 Flannigan, M. D., Stocks, B. J., & Wotton, B. M. (2000). Climate change and forest fires. *Science of
 360 The Total Environment*, *262*(3), 221-229.
- 361 Hanes, C. C., Wotton, M., Woolford, D. G., Martell, D. L., & Flannigan, M. (2022). Mapping organic
 362 layer thickness and fuel load of the boreal forest in Alberta, Canada. *Geoderma*, *417*,
 363 115827.
- 364 Harden, J., Manies, K. L., O'Donnell, J., Johnson, K., Froking, S., & Fan, Z. (2012). Spatiotemporal
 365 analysis of black spruce forest soils and implications for the fate of C. *Journal of Geophysical
 366 Research: Biogeosciences*, *117*(G1).
- 367 Harden, J., O'Neill, K., Trumbore, S. E., Veldhuis, H., & Stocks, B. (1997). Moss and soil contributions
 368 to the annual net carbon flux of a maturing boreal forest. *Journal of Geophysical Research:
 369 Atmospheres*, *102*(D24), 28805-28816.
- 370 Harden, J., Trumbore, S. E., Stocks, B., Hirsch, A., Gower, S., O'Neill, K., & Kasischke, E. (2000). The
 371 role of fire in the boreal carbon budget. *Global Change Biology*, *6*(S1), 174-184.
- 372 Hume, A., Chen, H. Y. H., Taylor, A. R., Kayahara, G. J., & Man, R. Z. (2016). Soil C:N:P dynamics
 373 during secondary succession following fire in the boreal forest of central Canada. *Forest
 374 ecology and management*, *369*, 1-9. doi:10.1016/j.foreco.2016.03.033
- 375 Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F., Ekblad, A., Högberg, M. N., . . . Read, D. J.
 376 (2001). Large-scale forest girdling shows that current photosynthesis drives soil respiration.
 377 *Nature*, *411*(6839), 789-792.
- 378 Högberg, P., Näsholm, T., Franklin, O., & Högberg, M. N. (2017). Tamm Review: On the nature of the
 379 nitrogen limitation to plant growth in Fennoscandian boreal forests. *Forest ecology and
 380 management*, *403*, 161-185.
- 381 Jobbágy, E. G., & Jackson, R. B. (2000). The vertical distribution of soil organic carbon and its relation
 382 to climate and vegetation. *Ecological applications*, *10*(2), 423-436.
- 383 Jonsson, M., & Wardle, D. A. (2010). Structural equation modelling reveals plant-community drivers
 384 of carbon storage in boreal forest ecosystems. *Biology letters*, *6*(1), 116-119.
- 385 Kielland-Lund, J. (1981). Die Waldgesellschaften SO-Norwegens. *Phytocoenologia*, 53-250.
- 386 Lang, S. I., Cornelissen, J. H., Klahn, T., Van Logtestijn, R. S., Broekman, R., Schweikert, W., & Aerts, R.
 387 (2009). An experimental comparison of chemical traits and litter decomposition rates in a
 388 diverse range of subarctic bryophyte, lichen and vascular plant species. *Journal of Ecology*,
 389 *97*(5), 886-900.
- 390 Larsson, B. (1995). *Svedjebruk och röjningsbränning i Norden: terminologi, datering, metoder:*
 391 Nordiska museet.
- 392 Li, J., Pei, J., Liu, J., Wu, J., Li, B., Fang, C., & Nie, M. (2021). Spatiotemporal variability of fire effects
 393 on soil carbon and nitrogen: a global meta-analysis. *Global Change Biology*.

394 Lindahl, B. D., Ihrmark, K., Boberg, J., Trumbore, S. E., Högberg, P., Stenlid, J., & Finlay, R. D. (2007).
395 Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest.
396 *New phytologist*, 173(3), 611-620.

397 Lindberg, H., Aakala, T., & Vanha-Majamaa, I. (2021). Moisture content variation of ground
398 vegetation fuels in boreal mesic and sub-xeric mineral soil forests in Finland. *International*
399 *Journal of Wildland Fire*, 30(4), 283-293.

400 Mack, M. C., Walker, X. J., Johnstone, J. F., Alexander, H. D., Melvin, A. M., Jean, M., & Miller, S. N.
401 (2021). Carbon loss from boreal forest wildfires offset by increased dominance of deciduous
402 trees. *Science*, 372(6539), 280-283.

403 Malhi, Y., Baldocchi, D., & Jarvis, P. (1999). The carbon balance of tropical, temperate and boreal
404 forests. *Plant, Cell & Environment*, 22(6), 715-740.

405 Mayer, M., Prescott, C. E., Abaker, W. E., Augusto, L., Cécillon, L., Ferreira, G. W., . . . Laclau, J.-P.
406 (2020). Tamm Review: Influence of forest management activities on soil organic carbon
407 stocks: A knowledge synthesis. *Forest ecology and management*, 466, 118127.

408 McLauchlan, K. K., Higuera, P. E., Miesel, J., Rogers, B. M., Schweitzer, J., Shuman, J. K., . . .
409 Adalsteinsson, S. A. (2020). Fire as a fundamental ecological process: research advances and
410 frontiers. *Journal of Ecology*.

411 Maaroufi, N. I., Nordin, A., Hasselquist, N. J., Bach, L. H., Palmqvist, K., & Gundale, M. J. (2015).
412 Anthropogenic nitrogen deposition enhances carbon sequestration in boreal soils. *Global*
413 *Change Biology*, 21(8), 3169-3180.

414 Niklasson, M., & Drakenberg, B. (2001). A 600-year tree-ring fire history from Norra Kvills National
415 Park, southern Sweden: implications for conservation strategies in the hemiboreal zone.
416 *Biological conservation*, 101(1), 63-71.

417 Niklasson, M., & Granström, A. (2000). Numbers and sizes of fires: long-term spatially explicit fire
418 history in a Swedish boreal landscape. *Ecology*, 81(6), 1484-1499.

419 Nilsson, M.-C., & Wardle, D. A. (2005). Understorey vegetation as a forest ecosystem driver: evidence
420 from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, 3(8),
421 421-428.

422 Ohlson, M., & Halvorsen Økland, R. (1998). Spatial variation in rates of carbon and nitrogen
423 accumulation in a boreal bog. *Ecology*, 79(8), 2745-2758.

424 Olsson, M. T., Erlandsson, M., Lundin, L., Nilsson, T., Nilsson, Å., & Stendahl, J. (2009). Organic
425 carbon stocks in Swedish Podzol soils in relation to soil hydrology and other site
426 characteristics. *Silva Fennica*, 43(2), 209-222.

427 Palviainen, M., Laurén, A., Pumpanen, J., Bergeron, Y., Bond-Lamberty, B., Larjavaara, M., . . . Chen,
428 H. (2020). Decadal-Scale Recovery of Carbon Stocks After Wildfires Throughout the Boreal
429 Forests. *Global Biogeochemical Cycles*, 34(8), e2020GB006612.

430 Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., . . . Canadell, J. G. (2011). A
431 large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988-993.

432 Parisien, M.-A., & Moritz, M. A. (2009). Environmental controls on the distribution of wildfire at
433 multiple spatial scales. *Ecological Monographs*, 79(1), 127-154.

434 Pellegrini, A. F., Ahlström, A., Hobbie, S. E., Reich, P. B., Nieradzik, L. P., Staver, A. C., . . . Randerson,
435 J. T. (2018). Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem
436 productivity. *Nature*, 553(7687), 194-198.

437 QGIS.org. (2022). QGIS Geographic Information System. *QGIS Association*. Retrieved from
438 <http://www.qgis.org>

439 Rolstad, J., Blanck, Y. I., & Storaunet, K. O. (2017). Fire history in a western Fennoscandian boreal
440 forest as influenced by human land use and climate. *Ecological Monographs*, 87(2), 219-245.

441 RStudio Team. (2020). RStudio: integrated development for R. RStudio, PBC, Boston. In.

442 Scharlemann, J. P., Tanner, E. V., Hiederer, R., & Kapos, V. (2014). Global soil carbon: understanding
443 and managing the largest terrestrial carbon pool. *Carbon Management*, 5(1), 81-91.

- 444 Seidl, R., Honkaniemi, J., Aakala, T., Aleinikov, A., Angelstam, P., Bouchard, M., . . . Gauthier, S.
445 (2020). Globally consistent climate sensitivity of natural disturbances across boreal and
446 temperate forest ecosystems. *Ecography*, 43(7), 967-978.
- 447 Storaunet, K. O., Rolstad, J., Toeneiet, M., & Blanck, Y.-I. (2013). Strong anthropogenic signals in
448 historic forest fire regime: a detailed spatiotemporal case study from south-central Norway.
449 *Canadian Journal of Forest Research*, 43(9), 836-845.
- 450 Tamm, C. O. (1991). *Nitrogen in terrestrial ecosystems: questions of productivity, vegetational*
451 *changes, and ecosystem stability*: Springer Science & Business Media.
- 452 The Norwegian Mapping Authority. (2017). NDH Modum-Sigdal 5pkt 2017 (DTM). Retrieved from
453 <https://hoydedata.no/LaserInnsyn/>. <https://hoydedata.no/LaserInnsyn/>
- 454 Van Breemen, N. (1995). How Sphagnum bogs down other plants. *Trends in ecology & evolution*,
455 10(7), 270-275.
- 456 Vejre, H., Callesen, I., Vesterdal, L., & Raulund-Rasmussen, K. (2003). Carbon and nitrogen in Danish
457 forest soils—contents and distribution determined by soil order. *Soil Science Society of*
458 *America Journal*, 67(1), 335-343.
- 459 Wardle, D. A., Jonsson, M., Bansal, S., Bardgett, R. D., Gundale, M. J., & Metcalfe, D. B. (2012).
460 Linking vegetation change, carbon sequestration and biodiversity: insights from island
461 ecosystems in a long-term natural experiment. *Journal of Ecology*, 100(1), 16-30.
- 462 Whitlock, C., Shafer, S. L., & Marlon, J. (2003). The role of climate and vegetation change in shaping
463 past and future fire regimes in the northwestern US and the implications for ecosystem
464 management. *Forest ecology and management*, 178(1-2), 5-21.
- 465 Williams, C. A., Gu, H., MacLean, R., Masek, J. G., & Collatz, G. J. (2016). Disturbance and the carbon
466 balance of US forests: A quantitative review of impacts from harvests, fires, insects, and
467 droughts. *Global and Planetary Change*, 143, 66-80. doi:10.1016/j.gloplacha.2016.06.002
- 468 Woo, D. K., & Kumar, P. (2017). Role of micro-topographic variability on the distribution of inorganic
469 soil-nitrogen age in intensively managed landscape. *Water Resources Research*, 53(10),
470 8404-8422.
- 471 Zackrisson, O. (1977). Influence of forest fires on the North Swedish boreal forest. *Oikos*, 22-32.
- 472 Zackrisson, O., Nilsson, M.-C., & Wardle, D. A. (1996). Key ecological function of charcoal from
473 wildfire in the Boreal forest. *Oikos*, 10-19.
- 474 Zajícová, K., & Chuman, T. (2020). Spatial variability of forest floor and topsoil thicknesses and their
475 relation to topography and forest stand characteristics in managed forests of Norway spruce
476 and European beech. *European Journal of Forest Research*, 1-14.
- 477 Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and*
478 *extensions in ecology with R*: Springer Science & Business Media.