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Changes in organic carbon, structure and nematode density in boreal soils following conversion from grassland to cropland

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ABSTRACT

Grasslands are known to be beneficial for increasing carbon stocks in soils as well as enhancing a range of essential soil ecosystem functions. Conversion of grassland to cropland can lead to loss of these benefits. The purpose of this study was to consider how the soil properties are altered after such land-use change in the boreal climate. Our study setup consisted of three fields which had been under extensive grassland management from 10 to over 30 years. Part of each field was ploughed and taken to cereal production and the rest was left as grassland. Carbon dioxide (CO2) fluxes from soil were measured during two growing seasons, and after the two years, the soil carbon stock, structure, and nematode densities were determined from both ploughed and undisturbed soils. Our results showed a practically and statistically significant land use change-induced reduction in soil carbon stock after two years. A significant reduction in the particulate organic carbon fraction was detected after the change. However, neither soil structural measures determined with X-ray tomography nor nematode density showed systematic alteration after the land-use change. Our results suggest that slow accumulation of carbon in soil leading to elevated carbon stocks can be easily lost if the favourable soil management ceases, which calls for long-term commitment to carbon conservation practices if lasting impacts are strived for.

1. Introduction

There is an ongoing land use change from natural vegetation to cropland and further a change in the soil management and agricultural practices on croplands (Foley et al., 2005). Land-use changes lead to modifications of ecosystems and a range of environmental impacts. For example, land use changes affect the carbon (C) cycle (Ramesh et al., 2019), soil hydraulic properties and hydrological cycles (Jarvis et al., 2013; Robinson et al., 2022), and biodiversity (Tsiafouli et al., 2015). Conversion of natural vegetation to cropland generally depletes soil C stocks (Wang et al., 2011; Sanderman et al., 2017), consequently affecting the soil structure, functions, and ecosystem services. However, land use change and intensification of agricultural practices can also directly affect soil structure and functions (Lal, 2014; Ngatia et al., 2021; Hyväluoma et al., 2024).

Soil structure formation is driven by many natural processes such as biopore formation by earthworms and plant roots, wetting-drying and freezing-thawing cycles, and aggregation of primary mineral particles due to electrochemical interactions, soil organic matter and microbe-derived compounds, and plant roots and hyphae (Vogel et al., 2022). In addition to natural processes, anthropogenic activities such as tillage (Pires et al., 2017; Schlüter et al., 2020) and compaction due to field traffic (Keller et al., 2021) can notably affect the soil structure. Soil structure controls numerous soil processes including water infiltration and retention, gas exchange, and the dynamics of soil organic matter and nutrients (Rabot et al., 2018). Thereby, it strongly influences the plant growth and C storage as well as erosion and nutrient leaching from agricultural fields.

Grasslands can have positive impacts on a range of ecosystem services provided by soils including water retention and flow regulation, C storage, and erosion control (Bengtsson et al., 2019). Further, improved soil structure and functions (Ajayi et al., 2019) can lead to benefits in the agricultural productivity and C accrual (Persson et al., 2008; Lugato et al., 2015; Prade et al., 2017). It has been shown that when

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structurally degraded cropland is converted into grassland, the soil structure improves with increasing age of sward (Ajayi and Horn, 2016). However, the structure evolution of degraded soil may require a decadal time scale to result in significant structural improvement after conversion to grassland (Bacq-Labreuil et al., 2021). Grasslands have also been found to be favourable for soil C sequestration due to high organic matter inputs and reduced soil disturbance slowing the degradation of organic matter (Vertes et al., 2007; Poeplau and Don, 2013; Conant et al., 2017). Such a positive impact has also been noted in crop rotation with perennial grass phases (Kostensalo et al., 2024). Contrariwise, conversion of land use from grassland to cropland can lead to structural degradation and reduced C stocks (Poeplau et al., 2011a; Poeplau and Don, 2013; Hebb et al., 2017; Singh et al., 2021), and even a single ploughing event in a grass-to-grass renovation can significantly reduce C stocks (Linsler et al., 2015; Reinsch et al., 2018).

After an abrupt change in soil management, soil structure and C content are carried towards a new stationary state with the direction of change depending on how the management practices are altered. The time required to reach a new equilibrium is highly variable and depends on the climatic conditions. For example, while in the tropics the so-called sink saturation can be less than 10 years, in boreal regions the required time can be centuries (Smith, 2005). The response time to the management change is typically asymmetric such that changes in soil occur a way faster in the conversion of grassland to cropland than in the reverse process (Soussana et al., 2004; Or et al., 2021). Thus, the benefits in C accrual and soil structure that are slowly built up with advantageous soil management practices, such as, e.g., grasslands or crop rotations including perennial grass phases, may be easily lost by unconsidered management decisions. Thereby, achieving lasting gains with soil management changes aiming at, e.g., C sequestration requires multi-generational commitment.

The purpose of the present work was to study the changes occurring in soil after a land-use change from long-term grassland to cropland in a boreal climate. More generally, our work was motivated by the question of how a land use change from a soil management practice known to be effective to accrue C to soil to conventional management affects the C storage and soil properties. We considered three fields that had been under continuous grassland management from one to over three decades. At the beginning of the study period, the experimental fields were partly ploughed and taken for cereal production. This allowed us to consider the short-term changes in soil properties on a time scale of two years.

2. Materials and methods

2.1. Experimental setup

The study setup consisted of three experimental sites located in the Häme region in Southern Finland (Table 1). One of the fields had been under extensive grassland management for 10 years and two of them for over 30 years. One of the fields had a clayey and two had silty texture, and the soils are classified as Stagnosol and Regosols according to the WRB system, respectively (Lilja et al., 2017). In autumn 2021, at each site a strip of the grassland was ploughed and taken into cereal production and the rest of the field was left as grassland. Thus, the setup had two treatments: the undisturbed long-term grassland and the ploughed grassland in cereal production. Due to practical constraints (sites were in private farms), the field trials at a single location did not have randomized replication. However, replicate measurements and samplings were carried out within the treatments and measurement results were considered independent observations, since all sites were situated on a flat terrain, had homogeneous properties in the initial sampling (cf., e.g., Willems et al., 2011; Schlüter et al., 2020), and the distance between the measurement points across treatment boundary was shorter than that between the sampling points within the treatments. Poeplau et al. (2022) noted that C-related parameters have relatively high variability even within distances less than 1 m. The soil structural properties have been reported to vary notably even at a distance of 10 cm (Koszinski et al., 1995). Our sampling points had clearly larger spacings than these distances.

Table 1

The sward age, soil texture, and coordinates of the study sites. The textural classification is $<2\,\mu m$ for clay, 2–63 μm for silt, and 63 μm – 2 mm for sand.

Site	Sward age [years]	Clay	Silt	Sand	Coordinates
Mustiala	>30[a]	60	31	9	60°49′ N, 23°47′ E
Loppi 1	>30[a]	20	49	31	60°40′ N, 24°29′ E
Loppi 2	10	18	47	35	60°41′ N, 24°37′ E

[a] These grasslands can be older than 30 years as exact age was not known.

All study sites are in the southern boreal vegetation zone. For the meteorological normal period 1991–2020 (Jokinen et al., 2021), the annual mean precipitation in the area was 621 mm and the annual mean temperature was 5.2 °C according to the long-term averages from the nearest weather station of the Finnish Meteorological Institute (Jokioinen Ilmala). The highest and lowest monthly average temperatures were 17.0 °C (July) and − 5.4 °C (February), respectively, and the highest and lowest monthly precipitations were 74 mm (July) and 31 mm (March).

2.2. Soil sampling

The study sites were sampled twice during the experiment. The first sampling occasion was before the initiation of the experiment in October 2021. Soil core samples were taken from six locations at each study site, three of which were in the area that was ploughed after the sampling and three were taken from the adjacent area that remained as grassland. Sampling was done down to 20 cm depth in two 10 cm segments with an auger of 4.8 cm in diameter. The second sampling was conducted in September 2023, i.e., two years after the experiment was started. In this sampling, disturbed composite samples were collected for C fractioning from the topsoil layer corresponding to the ploughing depth (0–18 cm in Loppi1, 0–20 cm in Mustiala and Loppi2) by bulking five soil core samples of ca. 2 cm in diameter in each of the six sampling plots. In addition, soil cores were taken also to a depth of 18–20 cm with a similar auger as in the first sampling (diameter of 4.8 cm). The sampling depth was matched with the ploughing depth to avoid the possibility that partly non-ploughed soil would have been mixed with the samples of the treatment layer.

In the second sampling, undisturbed soil cores were sampled in aluminium cylinders with an inner diameter of 46 mm and a height of 70 mm for X-ray tomography imaging. Five samples were taken for imaging both from ploughed and grassland areas from Mustiala and Loppi2 (but not from Loppi1) sites, from the depth of ca. 5–12 cm. Additional soil was sampled from the immediate vicinity around each imaging cylinder for nematode analyses.

2.3. Laboratory analyses

The C concentration and bulk density were determined from the soil core samples. The soil segment with known volume was dried at +37 °C and weighed. Samples were ground to pass a 2-mm sieve, and the total C was determined via dry combustion (Leco 628 CHN Determinator). In the acidic soil the total C can be taken to represent organic C (Nelson and Sommers, 1996).

C stocks in topsoil were determined from C concentrations and bulk densities for the plough layer using two different approaches. First, the stocks were determined for the plough layer with the depth varying between 18 and 20 cm at different sites. At all sites, the C stocks were scaled to a 20 cm soil layer to make results from all fields comparable despite the slightly different ploughing depths. Second, the equivalent soil mass method was used to calculate the C stocks representing the soil layer with the weight of mineral soil of $100\,\mathrm{kg\,m^{-2}}$.

The soil C reserves in the plough layer were size and density fractionated into mineral-associated organic C (MOC) and free particulate organic C (POC) following the working scheme presented by Keskinen et al. (2019). Fresh samples of 50 g were gently passed through a 5-mm sieve and thereafter dispersed by shaking in 400 ml of deionized water with 15 glass beads for 18 h. The obtained suspensions were wet sieved to size fractions of <0.063 mm and 0.063–2 mm, which were oven dried at 80 °C. The coarser fraction was then further density separated in sodium polytungstate adjusted to 1.8 g cm^{-3} to differentiate the heavy MOC and light POC pools. The initial finer fraction (<0.063 mm) was assumed to contain merely MOC. Total C concentration of the three separate fractions was analysed by dry combustion (Leco 628 CHN Determinator) and taken to consist of organic C due to soil acidity (Nelson and Sommers, 1996).

2.4. CO_2 measurements

The CO_2 fluxes were measured during the two growing seasons considered in this study (2022 and 2023) with closed opaque chambers. The measurement interval was two weeks and measurements were done in the daytime. The measurements were started in spring after the ploughed sites were sown and continued until moldboard ploughing in autumn. In each site, three measurement points were on the ploughed area and three on the grassland. At each measurement point, a cylindrical collar with a diameter of 50 cm was installed to a depth of approximately 10 cm. The distance between the soil surface and the top of the collar was measured to determine the total air volume inside each collar. The aboveground vegetation was removed inside the collars to prevent autotrophic respiration in the opaque chambers. During the sample collection, a cylindrical chamber with a height of 35 cm was placed on the top of a groove in the collar and the joint between the collar and chamber was sealed by filling the groove with water. The chambers were closed for 45 min and during this time a total of four gas samples were collected with a syringe into pre-vacuumized vials. The first gas sample was taken immediately after closing the chamber and three additional samples were taken in 15 min intervals.

The collected gas samples were analysed with an Agilent 7890 gas chromatograph that was equipped with a flame ionization detector (FID). Nitrogen was used as the carrier gas and standard gas mixtures of known concentration of CO_2 were used for calibration. The peak areas produced by the gas chromatograph for calibration samples were converted to gas concentrations by fitting a linear regression model to the data obtained for calibration samples. The CO_2 fluxes were calculated from the observed linear growth of CO_2 concentration in the chamber over time by using the ideal gas law.

2.5. X-ray tomography

The macropore structure of intact soil samples was imaged using computed tomography (CT), which enables the determination of soil pore structure from the 3D tomograms within the resolution limits. The X-ray tomography imaging was conducted with an in-house-built JTomo X-ray tomograph, which consists of an L12161 X-ray tube (Hamamatsu Photonics, 40–150 kV, max. 75 W) and a Shad-o-box 6 k HS flat panel detector (Teledyne) in cone-beam geometry. Imaging was performed using a 150 kV source voltage and 30 W power with a 6 mm glass filter between the sample and the source. Images were acquired with a 19 μm pixel size and 500 ms exposure time. Samples were scanned at two vertical positions to image the whole sample. The number of projections was 2940 over a full rotation of 360°.

The tomographic scans were reconstructed using the filtered back-projection algorithm (Feldkamp et al., 1984) in the pi2 software (github.com/arttumiettinen/pi2). Tomograms scanned at the two vertical positions were then stitched into a single 3D volume using NRStitcher software (Miettinen et al., 2019).

Noise was reduced from images using bilateral filtering and 2 × 2 binning, which increased the pixel size used in subsequent analysis to 39 μm. A global threshold value was selected to yield the visually most accurate separation of pore and solid phases. The top and bottom of the sample were excluded to remove regions damaged due to sample collection from image analysis.

The soil pore structure was quantified using three parameters, which were calculated from the segmented binary images: porosity, critical pore size, and median pore diameter determined from pore diameter distribution. Pores smaller than the resolution (39 μm) are not visible and therefore only porosity larger than the resolution can be accounted for. Local thickness maps of the pore space (Miettinen et al., 2025) were first created from the binary images for the calculation of pore diameter distribution and critical pore size. Pore sizes were determined by binning the thickness values into a pore diameter distribution. The critical pore size is defined as the diameter of the largest spherical particle that can pass through the pore network from top to bottom (Katz and Thompson, 1986; Koestel et al., 2018). The critical pore size was calculated using an iterative flood fill process. First, an initial guess for the critical pore diameter was selected as the largest value in the local thickness map. A flood fill operation was initiated from the top of the sample, and it was allowed to proceed only to voxels with a local thickness value greater than the selected guess. The process was repeated with a decreasing diameter value. The critical pore diameter was the first diameter value, which resulted in the flood fill progressing through the sample.

2.6. Nematodes

Soil samples (100 g) were collected to assess nematode (Nematoda) densities. In the laboratory, each sample was gently homogenized, and a subsample of 30 g (fresh weight) was taken for nematode extraction using the wet funnel method. The extraction was conducted over 24 h without additional heating. Nematodes were preserved in 97% ethanol, and total counts were performed under a stereomicroscope. Nematode density was expressed as individuals per gram of dry soil.

2.7. Data analysis

The experimental design included two treatments replicated across three study sites, with 3–5 observations per treatment per field (n = 18–48). For the analysis of CO₂ fluxes, twenty measurement days between 22 June 2022 and 11 January 2023 were included, and repeated measurements from the same plot were modelled using a compound symmetry (CS) covariance structure.

Fourteen response variables were analysed using generalized linear mixed models (GLMMs) fitted with the GLIMMIX procedure in SAS software (Version 9.4, SAS Institute Inc., Cary, NC). A Gaussian distribution was assumed when appropriate, while gamma or lognormal distributions were used for skewed variables. Fixed effects included treatment, field, and their interaction, and Tukey's method was applied for pairwise comparisons of these fixed effects. The results of F-tests for all response variables and fixed effects are presented in Supplementary Table S1 to clarify the modelling framework. The level of statistical significance was set at $\alpha = 0.05$. Degrees of freedom were estimated using the Kenward–Roger method. Residual analysis, such as assessing the normality of conditional Pearson residuals, was used to evaluate the appropriateness of the models. These diagnostics were performed for all models to verify that model assumptions were adequately met. Given the relatively small sample sizes in some analysis, the interpretation of diagnostics was done with caution. Based on these diagnostics, three extreme outliers were excluded from the CO₂ model.

Replicates within each treatment were located in the same field strip (see Section 2.1). To account for potential spatial correlation of these replicates, we modelled this correlation using a repeated measures covariance structure (CS or unstructured, UN) in the model. This approach accounts for non-independence of observations within plots and thereby addresses potential pseudoreplication in the data. Alternative specifications including plot as a random effect (G-side) yielded similar results for fixed effects, but the estimation of degrees of freedom did not always reflect potential pseudoreplication. In most models, this variance component was estimated to be zero, even after removing boundary constraints to allow negative estimates. This approach can be useful when estimates are near zero or when a theoretical justification for this exists. The random structure for the CO_2 model also included field × row and field × row × day effects. The row effect, representing a pair of treatments located adjacently in the field, was also tested for C concentration and C stock in the 0–20 cm layer, although convergence issues were encountered.

3. Results

3.1. Carbon

3.1.1. Carbon concentration and stock

Initial sampling and C analyses confirmed at each study site that there were no notable differences between the two treatments before the experiment started. However, after the two experimental years, the C concentrations showed statistically significant differences between the ploughed and grassland treatments over all sites ($p = 0.017$). At each site, the C concentration was lower in the ploughed treatment. On the field level, a statistically significant difference was detected at Mustiala and a marginally significant difference at Loppi1, while the difference in the Loppi2 field was not statistically significant (Fig. 1a).

C stocks showed similar trends to C concentrations. C stocks determined for the 20 cm layer showed a statistically significant treatment effect ($p = 0.035$) and C stock in the ploughed treatment was 2.1 kg C m^{-2} (18%) lower than in the grassland. C stock was also lower in the ploughed treatments than in the undisturbed grassland when all sites were assessed combined (Fig. 1b). However, due to the high variance in the bulk densities, the differences at the individual field level were not statistically significant. The C stocks determined with the equivalent soil mass method also had a statistically significant treatment effect ($p = 0.030$) over all sites and at individual sites the differences were marginally significant at Mustiala and Loppi2 sites (Fig. 1c). The differences between C stocks determined by two different methods were minor, as there was a difference in bulk densities of the treatments only at the Loppi2 site (marginal significance, see Supplementary Table S2).

3.1.2. Mass and density fractions

At all sites, the majority of C was in mineral-associated form, contributing over 70% of total C in Loppi1 and over 90% in Mustiala and Loppi2, respectively. Across all sites, ploughing significantly reduced POC content (Fig. 2a). However, when the sites were assessed individually, a statistically significant difference in POC between the grassland and ploughed treatments was observed only in Mustiala with the lowest POC content within all fields. The amount of carbon associated with >0.063 mm mineral particles (MOC > 0.063) that accounted only 3 to 7% of the total C also tended to decrease under ploughing compared to the grassland, but due to high within-treatment variability at individual site level this difference was significant only in Loppi1 (Fig. 2b). Similarly, MOC in <0.063 mm particles (MOC < 0.063) was lower under ploughing in Loppi1 site (Fig. 2c) with the highest total C content.

When comparing carbon pool sizes, the largest relative difference between the grassland and plough treatments was observed in the POC fraction, which was 33% lower in the ploughed treatment, the absolute mean difference being 0.27 g C (100 g soil)$^{-1}$. In the MOC > 0.063 fraction, the difference was 24%, however, the absolute mean values differed only 0.08 g C (100 g soil)$^{-1}$. In the MOC < 0.063 fraction, the mean MOC < 0.063 content in grasslands was 4.7 g C (100 g soil)$^{-1}$ whereas for ploughed soils it was 4.2 g C (100 g soil)$^{-1}$, however, although the absolute difference was large, it was not statistically significant. Thus, only about one-third of the reduction in C was attributed to the POC fraction.

3.2. CO_2 fluxes

Regarding the CO_2 fluxes, a significant treatment effect was observed ($p = 0.0001$). The fluxes were mostly higher in the grassland treatments with some exceptions as shown in Fig. 3. Significant differences were detected repeatedly during the two-year experimental period at each field.

3.3. Soil structure and nematode density

The soil structural properties quantified from X-ray tomography images showed only slight differences between the two treatments. Over all sites, critical pore diameter exhibits a marginally significant difference ($p = 0.071$), whereas porosity and median pore diameter did not exhibit significant differences. In the Loppi2 site, porosity was higher in the ploughed treatment than in the grassland, and in the Mustiala site, critical pore diameter was lower in the ploughed treatment than in the grassland, but otherwise no statistically significant differences could be detected at the individual field level (Fig. 4).

Regarding the nematode density, no differences between treatments

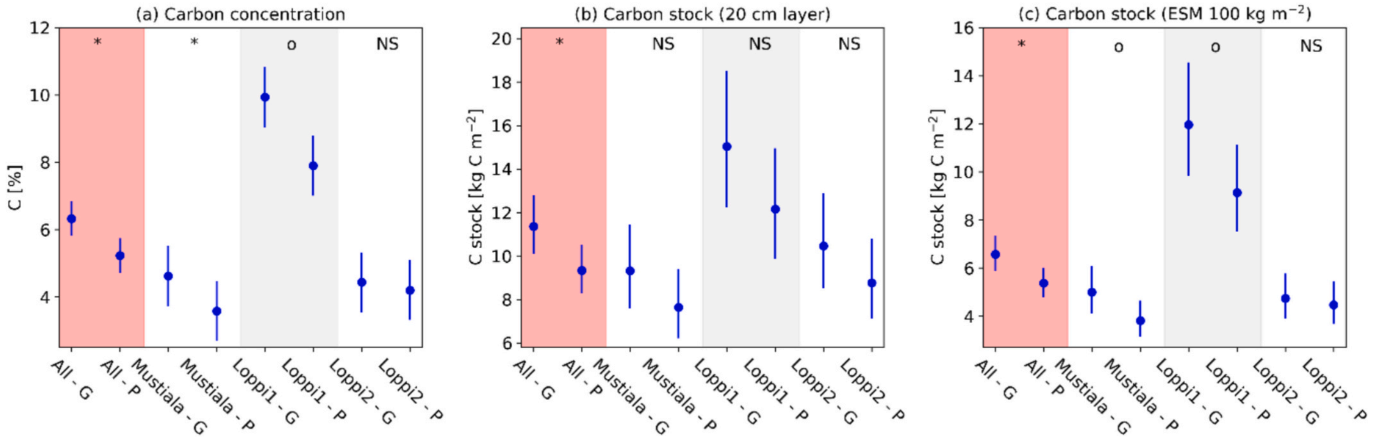

Fig. 1. (a) Carbon concentrations, (b) carbon stocks determined for the 20 cm topsoil layer, and (c) carbon stocks determined with the equivalent soil mass method for a 100 kg m^{-2} mineral soil layer in the three field sites. The red background colour indicates estimates determined over all fields. Error bars denote the 95% confidence interval. Asterisk denotes statistically significant difference between treatments ($p < 0.05$), open circle marginally significant difference ($0.05 < p < 0.1$), and NS stands for a non-significant difference. G = grassland and P = plough treatment.

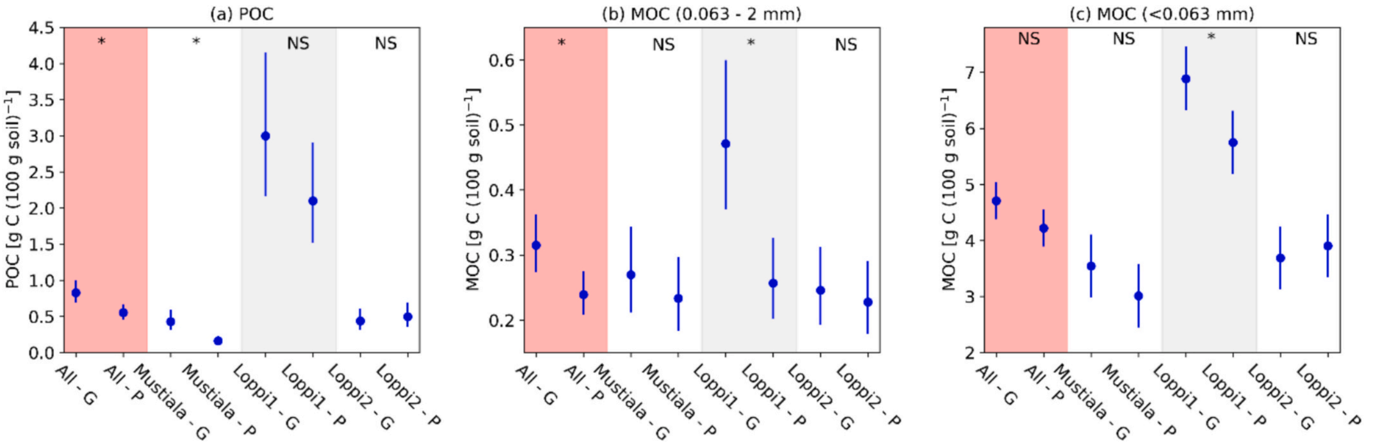

Fig. 2. (a) Free particulate organic carbon (POC), and mineral-associated organic carbon (MOC) in the (b) coarse, and (c) fine size fraction of the 0–18/20 cm topsoil layer of three field sites. The red background colour indicates estimates determined over all fields. Error bars denote the 95% confidence interval. Asterisk denotes statistically significant difference between treatments ($p < 0.05$) and NS stands for a non-significant difference. G = grassland and P = plough treatment.

were observed (Fig. 5).

4. Discussion

4.1. Carbon

The change in C stocks following a land-use change can vary largely between different locations due to contrasting environmental conditions including soil type, climate conditions, soil productivity and management practices (Poeplau et al., 2011b). Our study showed that ploughing of the long-term grasslands led to a reduction of C concentration and C stocks in the topsoil layer. This finding is not surprising as the previous research shows that increasing tillage intensity has a negative impact on C stocks in the topsoil layers, although the effect in the full soil profile is not that clear (Haddaway et al., 2017). Perennial crops (Ledo et al., 2020) and grassland are favourable for C accrual (Conant et al., 2017) and perennial vegetation is especially efficient in accumulating soil C due to high and persistent root-derived C input (Rasse et al., 2005; Anderson-Teixeira et al., 2013). However, the high organic matter accumulation can also result in high C loss risk when management is changed and, for example, an Irish study reported a 22% reduction in topsoil C stock due to renovation of a permanent grassland (Necpálová et al., 2014), which is comparable to our observation (18%).

Generally, the response time to land-use change is longer in colder climate (Smith, 2005) as elevated temperatures are expected to accelerate the decomposition of organic matter (Davidson and Janssens, 2006; Li et al., 2017). Under a tropical climate, the C loss has been reported to be particularly rapid after the clearance of natural vegetation (Powlson et al., 2022). Our results showed that even in colder boreal conditions a notable change in C storage occurs following the considered land use change, even at the time scale of two years. Thus, the land-use change considered here, i.e., from long-term grassland to intensively tilled cereal production, can be considered remarkable.

Traditionally, POC has been regarded as the fraction of SOC most sensitive to land-use change and environmental variation (Ellerbrock and Gerke, 2013; Rocci et al., 2021). In line with these studies, our results showed a significant reduction in the POC fraction within just a few years following an abrupt land-use change from grassland to cereal cultivation. However, recent studies indicate that MOC, traditionally considered stable, can also be a highly dynamic pool (Schiedung et al., 2025; Yeasmin et al., 2023). Yeasmin et al. (2023) observed variable C losses from the MOC fraction in soils with differing properties after land-use change and proposed that the higher saturation level of mineral surfaces may contribute to increased C losses from MOC. In this study, the significant loss of MOC due to the ploughing of long-term grassland was detected at the site with the highest MOC content. In addition, this site showed the greatest exceedance of the estimated maximum capacity of mineral particles to protect organic carbon, as calculated for Finnish mineral soils by Salonen et al. (2024). In soils with higher C loading, organic molecules may no longer bind directly to mineral surfaces, but instead, they may form multilayered associations on mineral particles (Kaiser and Guggenberger, 2003; Kleber et al., 2007). Our results support the previous findings that a part of the operationally defined MOC fraction can be relatively labile and sensitive to land-use change (Krull et al., 2003; Yeasmin et al., 2023) and therefore challenge the assumption that increasing MOC would enable long-term SOC storage.

The magnitude of the observed C stock reduction is practically significant. The observed difference of 2.1 kg m^{-2} between the treatments after two growing seasons indicates a large reduction in C stock in comparison to the possibilities to accrue new C into soil. As an example, the global meta-analysis of Poeplau and Don (2015) showed that C stock was higher in cover crop treatment than in reference soil, and the annual growth rate of the stock was 0.032 kg C m^{-2}. Regarding the northern conditions, Poeplau et al. (2015) observed an identical C accrual rate for ryegrass cover crops in southern Sweden. With this growth rate, it would take almost 70 years to recover the C stock reduction observed in our study. Another Swedish study based on 4–5 decades-long field experiments reported that the difference in topsoil C stock between ley rotation and cereal monoculture increased over time at a rate of 0.043 kg C m^{-2} yr^{-1}, although this difference primarily resulted from the C loss associated with the cereal monoculture (Bukombe et al., 2026). In general, the annual growth rates of C stocks with a variety of management practices appear to be of the same magnitude (see, e.g., the syntheses in Merante et al. (2017) and Minasny et al. (2017)), whereby the recovery of the quick reduction of C observed in our experiments can be expected to take decades with management practices that are known to re-accumulate the lost C. Also, if soils managed with favourable C management practices have reached the equilibrium and the accumulation of C has ceased, conservation of C stock requires that management which led to C accumulation is maintained (Soussana et al., 2004).

4.2. CO_2 fluxes

Our CO_2 flux measurements showed that during the two growing seasons after ploughing of grassland, the cultivated treatment had lower CO_2 fluxes than the grassland at all three sites. At first glance, it might appear contradictory with the C stock results, which indicated a clear reduction in C stocks due to ploughing and cultivation. Previous research has shown that CO_2 losses peak immediately after the tillage event, whereafter there is a rapid decline in the CO_2 flux on a time scale

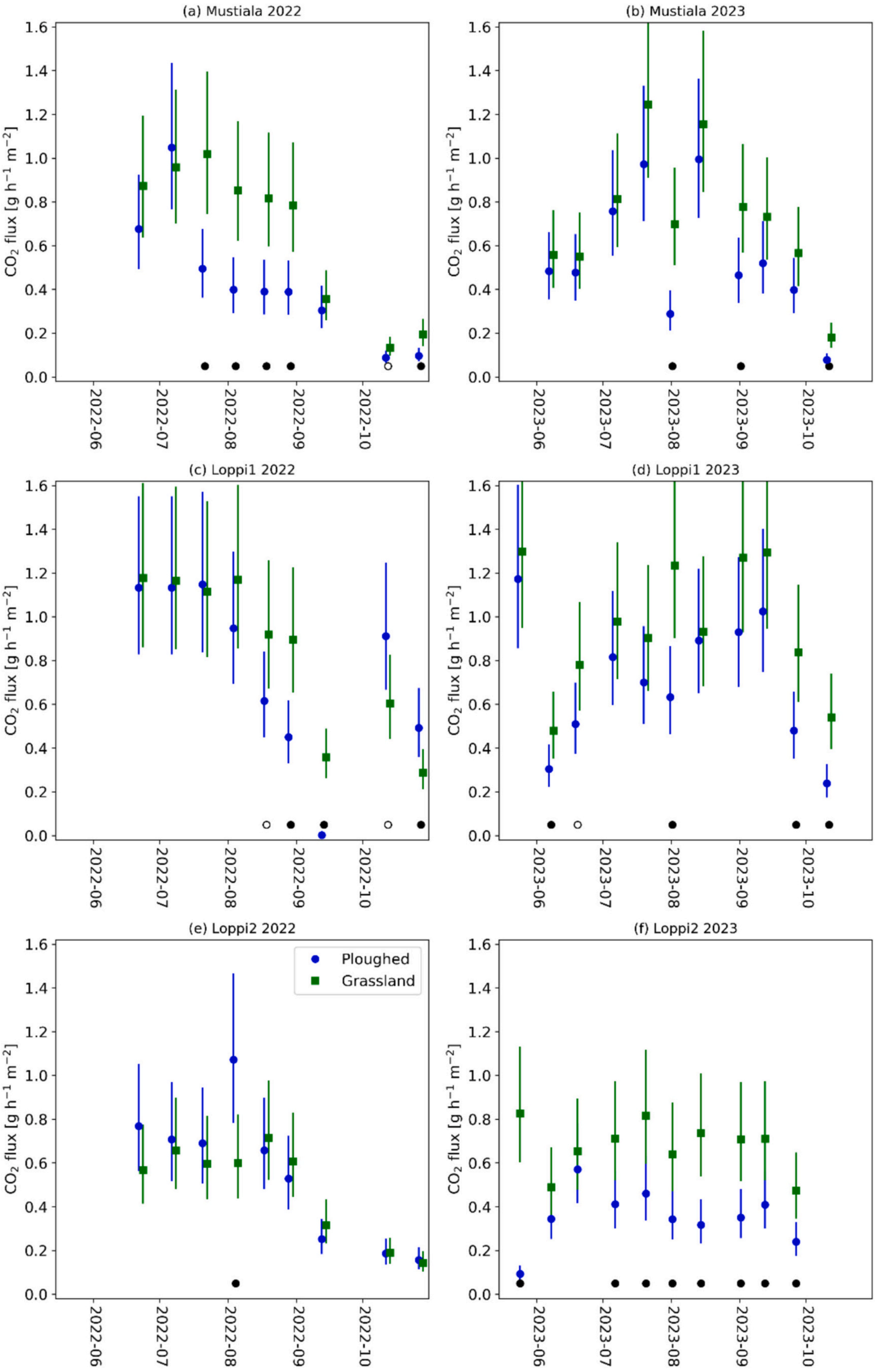

Fig. 3. Measured CO_2 fluxes from plough and grassland treatments for all three sites and both growing seasons. Error bars denote the 95% confidence interval. The filled black circles at the bottom of each panel indicate a statistically significant difference between the treatments ($p < 0.05$) and open circles a marginally significant difference ($0.05 < p < 0.1$). For clarity, data points have been slightly displaced horizontally to avoid overlaps.

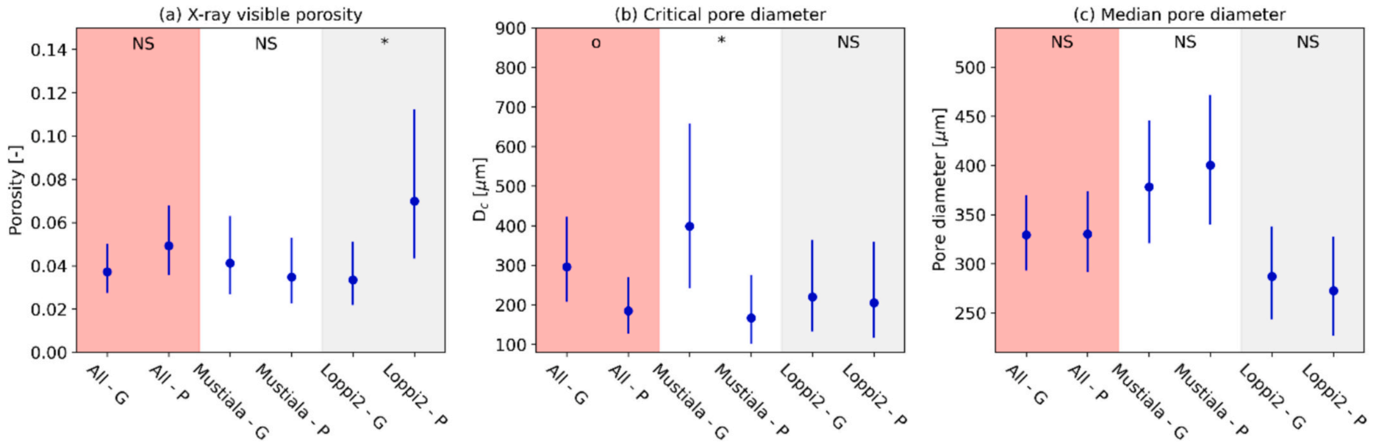

Fig. 4. Soil structural properties at Mustiala and Loppi2 study sites: (a) X-ray visible porosity, (b) critical pore diameter, (c) median pore diameter. The red background colour indicates estimates determined over both fields. Error bars denote the 95% confidence interval. Asterisk denotes statistically significant difference between treatments ($p < 0.05$), open circle marginally significant difference ($0.05 < p < 0.1$), and NS stands for a non-significant difference. G = grassland and P = plough treatment.

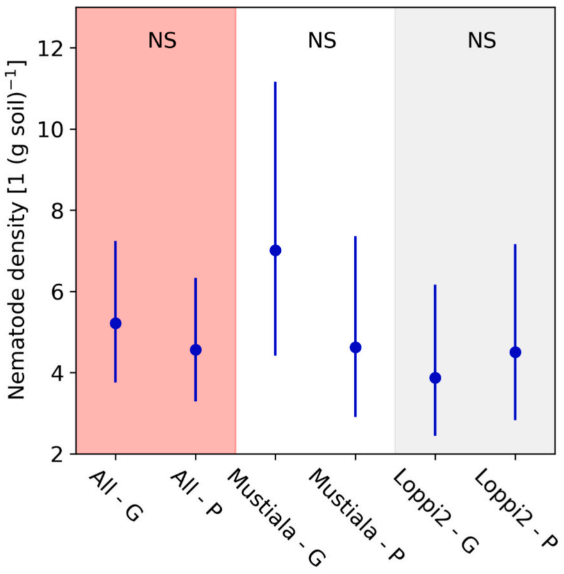

Fig. 5. Nematode density at Mustiala and Loppi2 sites. The red background colour indicates estimates determined over both fields. Error bars denote the 95% confidence interval. NS stands for a non-significant difference. G = grassland and P = plough treatment.

of hours or days (Reicosky and Archer, 2007; Willems et al., 2011; Reinsch et al., 2018; Shurpali et al., 2025). However, on longer time scales, the results are less consistent, and several studies have indicated reduced CO_2 fluxes from the tilled fields and fields under cereal production compared to grassland (Lohila et al., 2003; Willems et al., 2011; Holland et al., 2024).

The apparent contradiction between the C stock and CO_2 flux results may originate from other components in the soil C balance. After the tillage event, the photosynthetic C uptake by plants is interrupted. While we did not measure biomass production at our experimental sites, visual inspection of the plant growth suggested poor cereal growth at the ploughed treatments after the long extensive grassland period. Higher C inputs through primary production in grass plots have been reported to exceed and thus compensate for the greater CO_2 losses through soil respiration from grass leys compared to cereal systems (Paustian et al., 1990). Thus, the lower C uptake to plants contributing to the C balance in cultivated treatment can lead to reduced C stock despite lower CO_2 flux. Therefore, the detected lower soil C after ploughing a long-term grassland for cereal cultivation was most likely a combination of high initial C losses immediately after ploughing and reduced primary production in the cereal plots compared to the permanent grass plots.

4.3. *Soil structure*

The X-ray tomography imaging of soil structure showed some differences between the treatments, but these were not clear and systematic. The soil structural properties are influenced by soil management (Pagliai et al., 2004; Bronick and Lal, 2005; Skaalsveen et al., 2019; Schlüter et al., 2020) and grasslands have been reported to lead to positive impacts on soil structure and functions (Schwartz et al., 2003; Bodhinayake and Si, 2004; Kodesova et al., 2011). Continuous biopores are formed in long-term grassland soils due to root and earthworm actions (Schlüter et al., 2022).

While tillage in the renovation of grassland may have detrimental impacts on soil structure, there is evidence of a legacy effect where the positive structural effects of grassland are passed to the following crop production (Hoeffner et al., 2021). In addition to its disruptive effects, tillage also increases the macroporosity of soil (Oliveira et al., 2024). Recently, it was observed that long-term grassland had higher macroporosity than adjacent long-term no-till soil, but no differences were observed between long-term grassland and conventional tillage with crop rotation including perennial grasses (Hyväluoma et al., 2024), which suggests that also shorter grass phases in crop rotation may lead to similar structural effects as long-term grassland. Thus, when considering the present comparison between long-term grassland and ploughed grassland taken into cereal production, legacy effects from the preceding long grass phase and macropore formation due to tillage may explain why no clear trends between the treatments were observed. After a change in the soil tillage practices, soil structure is known to change on a time scale of several years (Reichert et al., 2016). Also, tillage results in temporal variation in soil structure during the growing season due to soil settling after tillage (Sandin et al., 2017; Keskinen et al., 2019). These processes could affect the comparisons between the treatments, which limits the generalization of our results.

4.4. *Nematodes*

Our results did not show differences in nematode density due to plough treatment. Soil biota in general respond to the tillage system (van Capelle et al., 2012), but there are indications that the negative effects of tillage are directed more to larger-sized biota than smaller-sized ones, such as nematodes (Postma-Blaauw et al., 2010). Regarding short-term impacts, larger-sized soil biota have been found to be primarily affected by conversion tillage, while smaller soil biota are affected by long-term consequences (Postma-Blaauw et al., 2010). One plausible explanation for this biota size-dependent effect relates to soil structure. Nematodes do not burrow like, e.g., earthworms, but use existing pores for their movement (Hassink et al., 1993) and the soil macroporosity has been found to correlate with nematode density (Salminen et al., 2025). The X-ray tomography analyses at our study sites did not show remarkable structural differences between the treatments, which is consistent with the absence of differences in nematode density. Also, a recent meta-analysis by Betancur-Corredor et al. (2022) found no significant tillage effect on total nematode density, which is in line with our result. However, tillage intensity can affect the soil nematode community structure (Arseneault et al., 2024), which was not considered in our study.

5. Conclusions

Our field experiment focused on the changes that occur in soil after a land-use change from long-term grassland to cropland in a boreal climate. While we found clear indications of C losses, no systematic effects on soil structure or nematode density were observed. Our results showed that in boreal conditions the loss of C happens rapidly after the land use change, which suggests that there is notable temporal asymmetry such that soil C stocks react considerably faster to land use change from grassland to cropland than to the reverse change. While this study focused on land use change from grassland to cropland, similar concerns about soil C stocks and structure can be extended to, for example, soil management practices aimed at increased C storage. The desired increases in C stocks are slowly achieved but can be easily lost if the favourable management practices cease. Therefore, profitable investment in increasing soil C stocks demands that the management that led to C accumulation, be it grassland or other means, is maintained, which in practice requires multigenerational commitment to C management practices.

CRediT authorship contribution statement

Jari Hyväluoma: Writing – review & editing, Writing – original draft, Visualization, Investigation, Data curation, Conceptualization. **Riikka Keskinen:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Petri Niemi:** Writing – review & editing, Methodology, Investigation. **Janne Salminen:** Writing – review & editing, Methodology, Investigation. **Sami Kinnunen:** Writing – review & editing, Investigation, Formal analysis. **Arttu Miettinen:** Writing – review & editing, Software, Methodology. **Janne Kaseva:** Writing – review & editing, Writing – original draft, Formal analysis. **Helena Soinne:** Writing – review & editing, Writing – original draft, Project administration, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geodrs.2026.e01099.

Data availability

Data will be made available on request.

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