

Trophic interactions and microbial-derived carbon in porosphere of arable fields

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ABSTRACT

Soil physical properties, such as porosity, are recognized to play an important role in the formation of soil organism communities and may regulate carbon sequestration in the soil ecosystem. However, despite their eminent importance, the relation between the abundance of soil animals, microbial necromass and pore space has been rarely demonstrated empirically. In this study, soil visible macroporosity (measured using X-ray computed tomography), microbial necromass (a pool of soil organic carbon), and densities of nematode groups were measured in the topsoil layer at a depth of 10 cm in four arable fields in southern Finland (clay and loam soils). Bacterial necromass was positively correlated with visible macroporosity smaller than 428 μm in size. Fungal necromass was marginally correlated ($p = 0.059$) with pores $<233 \mu\text{m}$ in size. The abundance of bacterial feeding nematodes (and unknown juveniles) scaled positively with microbial necromasses, visible macropores smaller than 700 μm and the total visible macroporosity. The abundance of other feeding groups was independent of soil visible macroporosity. However, trophic interactions between feeding groups of nematodes appeared to be weak in this soil layer. Results indicate strong bottom-up regulation between microbes and microbial feeding nematodes. Microbial necromass, as an important organic fraction in soil, was clearly related to small soil macropores ($<428 \mu\text{m}$).

These findings provide novel insights into how soil architecture, particularly macroporosity below 700 μm , influences the spatial ecology of soil organisms — an aspect that has received limited attention in boreal agroecosystems.

1. Introduction

Soil physical properties, such as porosity, have been recognized to have an important role on the formation of the community structure of decomposers (Erktan et al., 2020) and regulation of the function of the soil ecosystem (Ettema and Wardle, 2002), including soil organic carbon (SOC) accumulation (Rabot et al., 2018; Kravchenko et al., 2019). Evidently, moist surfaces of soil particles and water filled pores are typical habitats for the soil microfauna (such as nematodes) and microbes (see Erktan et al., 2020). However, despite its eminent significance, the relationship between nematode density and pore space has been rarely demonstrated empirically (see Young and Ritz, 2000; Martin and Sprunger, 2021; Schlüter et al., 2022a; Wu et al., 2025).

Soil micro- and meso-organisms are forced to select and inhabit soil pores; this choice is based on their size and subsequent ability to penetrate a pore (Geisen et al., 2019; Erktan et al., 2020). Such micro-structural compartmentalisation of organisms' habitats can be based on the 1) measurement of the size of soil aggregates (with internal pores) and estimating intra-aggregate pore space or 2) directly measuring soil pore sizes and geometry (Young et al., 2001; Rilling and Mummey, 2006; Maaß et al., 2015; Wang and Zhang, 2024).

Microbial community structure, which influences the availability of resources for nematodes, varies among different pore size classes (see Ruamps et al., 2011). Moreover, functional responses of the microbial community to the soil structural variability may affect soil decomposition processes (Baveye et al., 2018) and SOC sequestration (Kravchenko

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et al., 2019; Zhang et al., 2023).

Tillage activities in arable fields may affect the size distribution and topology of the network of soil pores (Araya et al., 2022). Hence, tillage indirectly influences trophic interactions of soil organisms and their habitat choice through a spectrum of physical-chemical conditions in the soil (Young and Ritz, 2000; Vonk et al., 2013; Sechi et al., 2018). Moreover, tillage practices affect soil microenvironments and pore size-related correlation exists in the spatial deviation of various microbial strains (Kravchenko et al., 2014; Naveed et al., 2016; Xia et al., 2023). Concomitantly, pools of organic carbon are redistributed by physical factors (e.g. water) and utilised by microorganisms in this network of pores (Kravchenko et al., 2019; Liang et al., 2019; Schlüter et al., 2022b).

In their meta-analysis of soil aggregate size, total SOC, and nematode densities, Martin and Sprunger (2021) found only a limited number of articles about the soil porosity and nematode-SOC relationship (total of 11 articles). Empirical studies on the link between soil animal densities (in any size class) in soils with different pore structures have been scarce (see also responses of microarthropods on soil porosity e.g., van Amelsvoort et al., 1988; Vreeken-Buijs et al., 1998). In addition to study by Wu et al. (2025), X-ray scanning based images on the architecture of nematode's habitat have only been conducted by Schlüter et al. (2022a). Hence, our study may fill the gap on the role of soil architecture in the life of soil organisms and interactions among them.

We investigated variations in microbial necromass and nematode density in relation to soil porosity in four fields in Southern Finland. The soils had a clayey or silty texture where experimental studies were conducted to investigate the effects of (1) deep ploughing and organic paper and pulp mill sludge amendments, and (2) ploughing of long-term grasslands on soil carbon stocks, soil structure, and growth conditions. Soil macroporosity and pore size distribution in the plough layer (at a depth of 10 cm) were determined using X-ray computed tomography (μ CT) methods (the voxel size was 39 μ m after binning). Amino sugar concentration, biomarker of microbial necromass, was determined to indicate microbial-based SOC storage. These residues of dead fungal and bacterial cells are also a source of energy for living microbes and their predators in the porosphere (Jiang et al., 2018a, 2018b; Liang et al., 2019; Kennedy and Maillard, 2023).

Our hypotheses were: 1) Increasing soil visible macroporosity in small poresize classes increase the abundance of soil organisms (microbes and microfauna) in arable fields, and 2) the size distribution of soil visible macropores influences the abundance of predators and their prey, thereby modulating density-dependent trophic interactions within the soil food web (see Erktan et al., 2020). To test these hypotheses, microbial necromass, and the total and feeding group-specific density of nematodes were determined. Correlative analysis enabled the identification of critical porosity and pore size distribution that influence the abundance of organisms and density-dependent trophic interactions among trophic groups of nematodes, as well as, between microbes and nematodes in arable fields. In addition, soil gravimetric moisture was used as an indicator of the pore water status. We addressed the following research questions: 1) Is the abundance of soil organisms at adjacent trophic levels interdependent in the arable fields? 2) How does soil visible macroporosity and different pore size classes influence the abundance and trophic interactions of organisms? The research sought additional evidence on the effect of soil porosity on the densities of nematodes and microbial necromass distribution in the pores.

2. Materials and methods

2.1. Study sites

This study was based on four field experiments located in Southern Finland. The primary purposes of experiments were to study (1) the effects of deep ploughing combined with the addition of organic soil amendment on soil carbon stocks and soil structure (two separate

experiments) and (2) the changes in soil organic carbon and soil structural properties after a land-use change from long-term grassland to cropland (two separate experiments both containing converted and grassland treatments). The ploughing depth in deep ploughing was 35–40 cm, whereas the ordinary ploughing depth was 20 cm. The used organic amendment was wood-fiber-based lime-stabilised pulp mill sludge derived from the process water treatment plant of the mill [see Rasa et al. (2021) for further details of the amendment]. The treatments were conducted in autumn 2021, two years before the sampling. The fields were cultivated with conventional machinery using mouldboard ploughing with ordinary ploughing depth in autumn and harrowing for seedbed preparation in spring after the treatments. In both experiment types, soil nematode densities, bacterial and fungal necromasses, and soil pore size distributions were determined to measure effects of treatments on the soil properties. These analyses were utilised in the present study. The experimental fields and basic soil properties are summarised in Table 1. Results related to the actual experimental setups at field experiments will be reported elsewhere. Data are deposited in the IDA repository [dataset] (Salminen et al., 2025).

2.2. CT-scanning and porosity analysis

The sampling was conducted in the study field in September 2023 after harvesting. The soil samples for μ CT were taken from ca. 5–12 cm depth using aluminium cylinders (inner diameter 46 mm, height 70 mm). Immediately after sampling, the cylinders were wrapped with a plastic film to preserve the natural moisture and stored at +5 °C until imaging in October–December 2023. The total number of samples was 58 (see Table 1). Tomography was performed using a home-built X-ray tomograph (J-Tomo) with an X-ray tube energy of 150 kV and a 6 mm glass filter was placed between the X-ray source and the sample. During each scan, 2940 radiographs were captured while the sample was rotated 360°. The tomographs were reconstructed with the Feldkamp-Davis-Kress filtered backprojection algorithm (Feldkamp et al., 1984). Noise was reduced using bilateral filtering and 2x2 binning, increasing the voxel size used in the analysis to 39 μ m. Sample collection created disturbance in the sample and regions near the cylinder edge were excluded from the analysis. Similarly, the top and bottom parts were cropped to analyse only the undisturbed soil. Next, simple manual thresholding was used to segment voids from the soil. Segmentation of samples using thresholding presented challenges in distinguishing organic matter due to the variability of particulate organic matter (POM) grey values that could misclassify certain POM regions. Threshold values for the samples were selected so that the vast majority of the POM would be treated as void.

Pore size distribution was determined using the local thickness map of void space (Hildebrand and Ruegsegger, 1997) by binning the thickness values into a pore diameter distribution. The image analysis process is visualised in Fig. 1. Pore space was divided into four pore size classes (<233 μ m, 272–428 μ m, 467–661, and >700 μ m) and porosity was calculated separately for each size class by dividing the total number of voxels in the class by the total number of voxels in the sample. Preliminary analysis revealed that different size range options of size classes (within resolution limits around size ranges) did not substantially change the correlations.

In the following sections, the quantity total visible macroporosity refers to the porosity visible in μ CT images, i.e., porosity larger than the imaging resolution that is the sum of porosity in each size class. Similarly, the pore size class <233 μ m only included pores visible within the imaging resolution. Tomographic reconstruction and image analysis were performed with pi2 and Fiji software packages (Schindelin et al., 2012) (available at <https://github.com/arttumienninen/pi2> and <https://www.fiji.sc>). After imaging, the same samples were used for microbial necromass analyses.

Table 1

Texture and carbon (C) content of soils at study sites and plants grown in 2023. The experiment type refers to the purpose of the original experiment conducted in fields where soil samples were acquired. Acronyms for study sites are shown.

Field and experimental treatment	C (%)	pH	Clay (%)	Silt (%)	Sand (%)	Plant	Abbreviation	Number of μ CT samples
Jokioinen, Deep ploughing	3.9	5.2	52	30	18	Barley	DeepJ	20
Loppi, Deep ploughing	2.5	6.6	16	55	29	Pea	DeepL	19
Tammela, Grassland ploughing	3.9	5.6	60	31	9	Oat/Grass	GrassT	10
Loppi, Grassland ploughing	3.6	5.7	18	47	35	Oat/Grass	GrassL	9

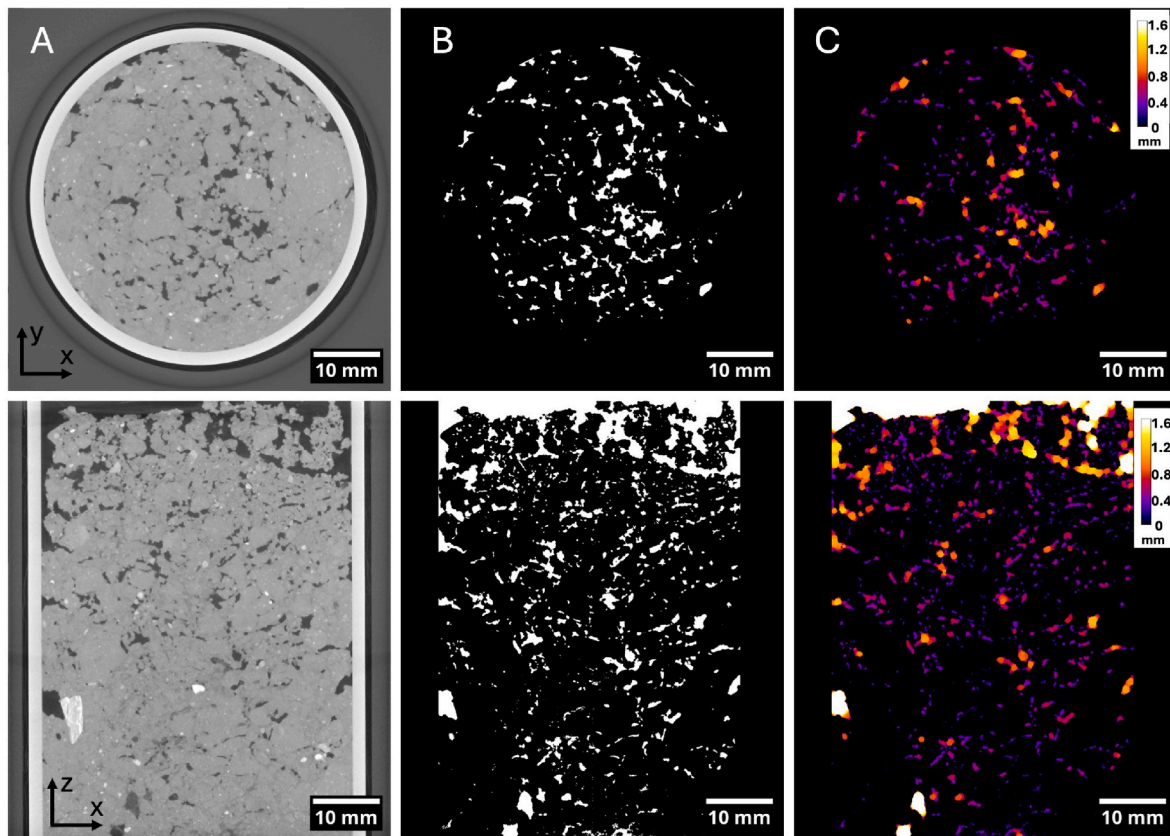


Fig. 1. Example of the image analysis process. A) Cross sections of a reconstructed tomogram of a sample from the Jokioinen deep ploughing field. Bright areas attenuate more X-rays than the dark ones. B) A segmented cross section of the same sample depicting solid (black) and void (white) and C) local thickness map showing the pore size colour-coded such that bright colours indicate large pore diameter.

2.3. Nematodes, microbial necromasses and soil moisture

To measure the density of nematodes in the topsoil level, three additional soil samples were taken from the immediate vicinity of each cylinder location at a depth of 10 cm. These samples were gently mixed in a plastic bag and pooled into a 30 g (fresh mass) sample used in the nematode extraction. Extraction was done using the wet funnel method (24 h and no additional heating of samples). Nematodes were preserved in 97 % ethanol. The total number and number of nematodes in different feeding groups (according to Yeates et al., 1993) were counted using a stereomicroscope and a microscope, respectively. The dry mass of soil samples was determined by drying the soil in an oven (90 °C, until constant weight, i.e. 8h) to indicate soil gravimetric moisture.

Microbial necromass was studied using its marker, the aminosugar glucosamine for fungal necromass and muramic acid for bacterial necromass (Adamczyk et al., 2024). Briefly, soil samples were washed with 0.2 M NaOH to remove unbound amino acids and aminosugars. Then samples were washed with water to remove NaOH and hydrolysed with 6 M HCl. Released amino sugars were derivatised with 9-fluorenylmethylloxycarbonyl (FMOC) and concentrations of amino sugars were

measured with high-performance liquid chromatography (Arc HPLC, Waters, USA) equipped with a fluorescence detector as described by Adamczyk et al. (2024) after separation in the Hewlett Packard ODS Hypersil (5 μ m, 250 mm \times 4.6 mm) column.

2.4. Statistical analysis

Differences between the four field soils were analysed using Analysis of Variance (ANOVA). Post-hoc comparisons between field sites were conducted using Tukey's HSD test. Pearson correlation analysis was applied to detect possible trophic relationships between different feeding groups of nematodes and nematodes and microbial necromasses. In addition, Pearson correlation analysis was applied to detect possible relationships between microbial necromasses, nematode densities, and soil visible macroporosity in four size classes of soil pores. Furthermore, Pearson's correlation between the densities of nematode feeding groups and soil moisture was calculated. All statistical analyses were conducted using JMP version 16.2 (SAS).

3. Results

3.1. Edaphic and biotic parameters in four fields

The total visible macroporosity of the soil did not differ between the fields (Figs. 2 and 3). Instead, there were differences among the fields in the porosity of different size classes. The density of bacterial-feeders, fungal-feeders and omnivorous nematodes had statistically significant differences between fields (Fig. 4). Moreover, microbial necromasses (Fig. 5A and B) and soil moisture differed among the fields (Fig. 5C; Supporting information; Table S1; Fig. S1).

3.2. Nematodes, microbial necromass and soil moisture

The densities of feeding groups of nematodes were mainly positively correlated with each other's density in soil (Table 2). Predators had no statistically significant correlation with any other group. Microbial necromass biomarkers correlated positively with densities of total and bacterivorous nematodes and fungal necromass correlated positively with densities of juvenile nematodes (Table 3). Both total numbers and bacterial-feeding nematodes were negatively correlated with gravimetric soil moisture (Table 3).

The results show that the soil visible macroporosity correlated positively with the total numbers of nematodes, bacterial feeding nematodes (individuals from orders Areolaimida, Monhysterida and Rhabditida) and unknown juveniles (Table 4; Fig. 6A and B). When porosity data were divided into four pore size classes, a significant relationship was found only with three smaller pore size groups (Table 4). A correlation was not found between soil porosity and abundance of fungal feeders (suborder Aphelenchida), omnivores (Dorylaimida), plant feeding nematodes (Tylenchida) or predators (Mononchida) in any pore size classes (Table 4). Bacterial and fungal ($p = 0.059$) necromass in the soil were positively correlated with the two smallest pore size class (Table 4; Fig. 7A–C). Concomitantly, the dominant nematode group, the bacterivores, seemed to be more numerous in soil with a higher amount of microbial necromass (Figs. 4 and 5). No direct correlation between fungivores and fungal necromass was found (Table 3).

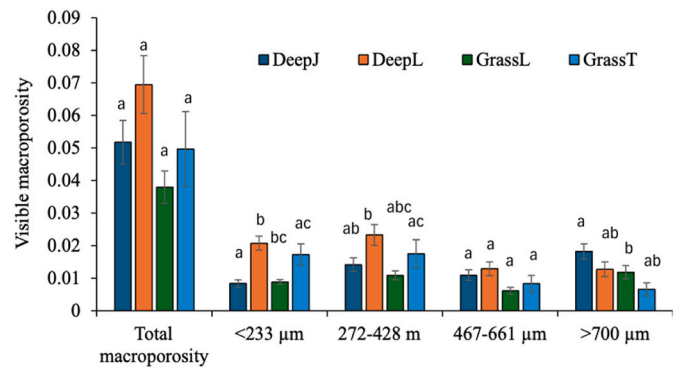


Fig. 3. Soil porosity characteristics (mean and standard error of the mean) in four arable fields. Different letters indicate statistically significant differences at $p < 0.05$ between the fields (ANOVA and Tukey's HSD test). DeepJ = deep ploughing Jokioinen, DeepL = deep ploughing Loppi, GrassL = Grassland ploughing Loppi, GrassT = Grassland ploughing Tammela.

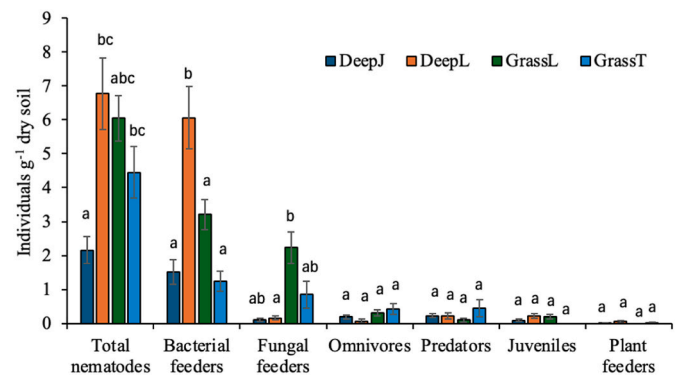


Fig. 4. Number of nematode feeding groups (mean and standard error of the mean) in four arable fields. Different letters indicate statistically significant differences at $p < 0.05$ between the fields (ANOVA and Tukey's HSD). DeepJ = deep ploughing Jokioinen, DeepL = deep ploughing Loppi, GrassL = Grassland ploughing Loppi, GrassT = Grassland ploughing Tammela.

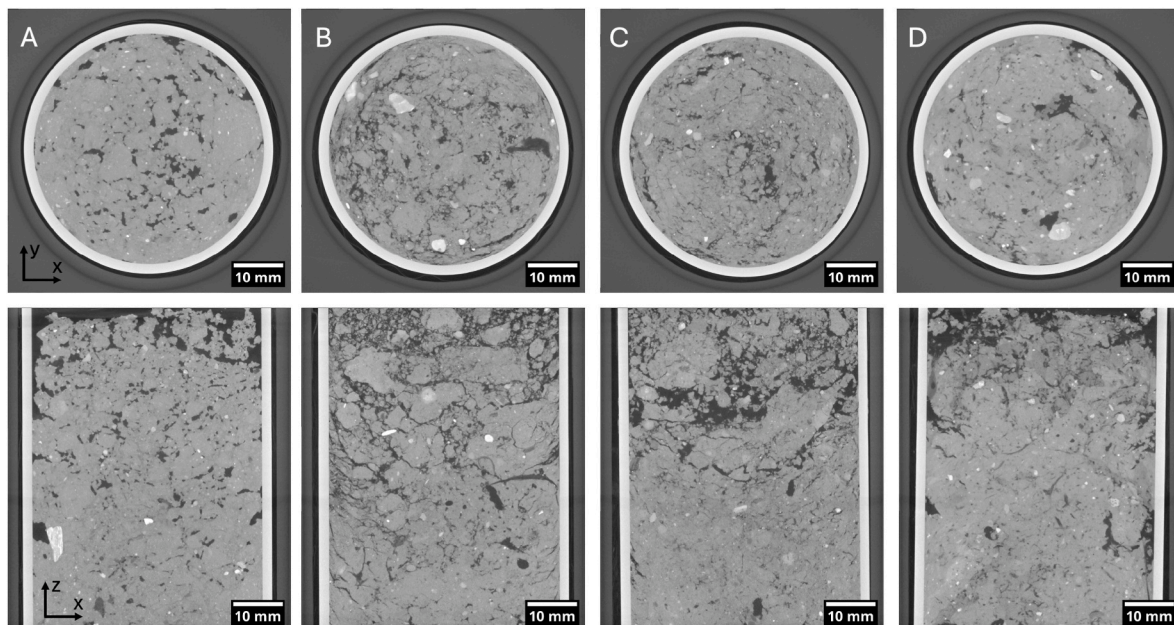


Fig. 2. Representative examples of tomographic cross-sections from each study site: A) Jokioinen deep ploughing, B) Loppi deep ploughing, C) Loppi grassland, and D) Tammela grassland.

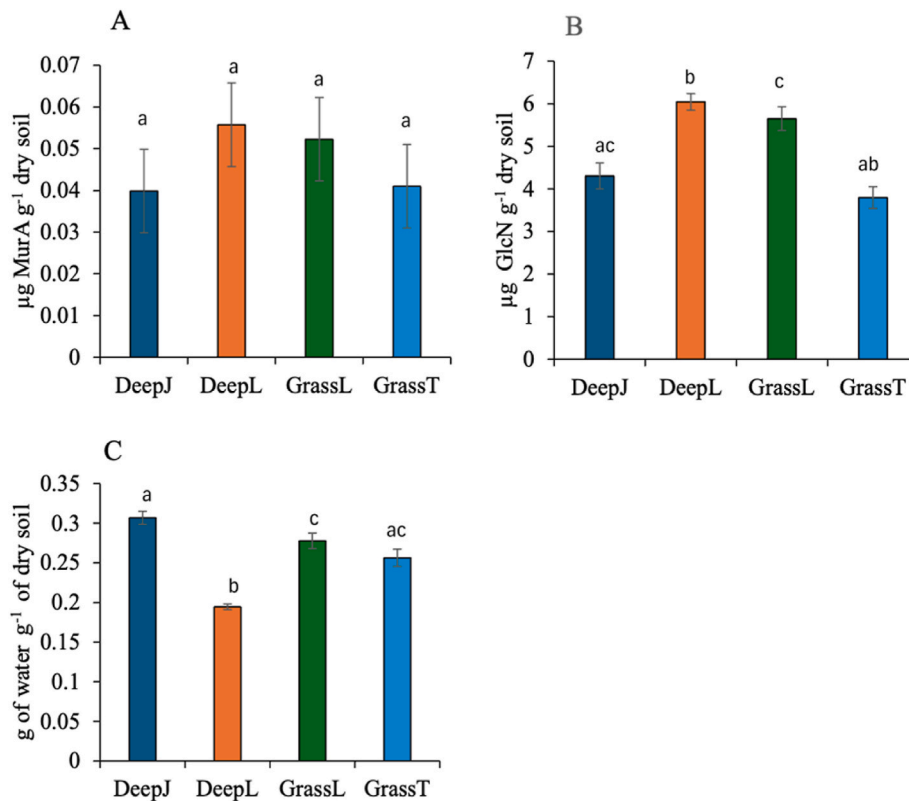


Fig. 5. Biomarkers of microbial necromass. Muramic acid for bacteria (A) and glucosamine for fungi (B), and soil moisture (C) (mean and standard error of the mean) in four arable fields. Different letters indicate statistically significant differences at $p < 0.05$ between the fields (ANOVA and Tukey’s HSD test). DeepJ = deep ploughing Jokioinen, DeepL = deep ploughing Loppi, GrassL = Grassland ploughing Loppi, GrassT = Grassland ploughing Tammela.

Table 2

Pearson’s correlations between feeding groups of nematodes. Statistically significant r-values bolded ($p < 0.001^{***}$, $p = 0.084^{\circ}$).

	Bacterial feeders	Fungal feeders	Omnivores	Predators	Juveniles	Plant feeders
Bacterial feeders	1	-0.016	-0.003	0.001	0.596***	0.490***
Fungal feeders		1	0.229[°]	0.042	0.106	-0.095
Omnivores			1	-0.125	0.080	-0.040
Predators				1	-0.079	0.138
Juveniles					1	0.457***
Plant feeders						1

Table 3

Pearson’s correlations between feeding groups of nematodes and bacterial and fungal necromasses and soil moisture. Statistically significant r-values bolded ($p < 0.001^{***}$; $p < 0.01^{**}$; $p < 0.05^{*}$ and $p = 0.063^{\circ}$).

	Fungal necromass	Bacterial necromass	Soil moisture
Total nematodes	0.327*	0.246[°]	-0.373**
Bacterial feeders	0.351**	0.272*	-0.506***
Fungal feeders	0.203	0.096	0.215
Omnivores	-0.011	0.146	0.069
Predators	-0.113	-0.0701	-0.113
Juveniles	0.376**	0.198	-0.153
Plant feeders	-0.025	-0.107	-0.211
Fungal necromass	1	0.758***	-0.174
Bacterial necromass		1	-0.196

4. Discussion

4.1. Soil pores as a habitat for nematodes

The results of our study (with μ CT scanned porosity data) are in line with those of earlier studies, indicating that an increase in water-filled

soil porosity within the habitable size range increases the abundance of soil organisms (Hassink et al., 1993; Quénehervé and Chotte, 1996; Briar et al., 2011; Jiang et al., 2018a) and support our hypothesis 1. A comparison of these previous results to our results is complex because of the fundamental differences in measured parameters. The soil aggregate size (with intra and inter-aggregate spaces) did not correspond directly to pore volumes observed through direct imaging techniques as a habitat characteristic of soil organisms. Comparison was more successful with recent studies in which visible soil porosity was measured using X-ray scanning. The total abundance of nematodes was especially correlated with soil porosity in the diameter range of 20–220 μ m (and with total visible porosity) (Schlüter et al., 2022a). Moreover, soil visible macroporosity was positively correlated with the abundance of bacterial and fungal feeders; however, it was negatively correlated with predatory and omnivorous nematodes (Wu et al., 2025). Similarly, Wu et al. (2025) noted a seasonal variation in the correlation between edaphic factors and nematode abundances. Such seasonal variation is common in nematode communities (see, e.g., Siebert et al., 2020). We performed sampling once after harvesting, and such seasonal variation in nematode abundances was not analysed. However, considerable variation was observed between study fields in the numbers of individuals across

Table 4

Pearson's correlations of soil visible macroporosity with densities of nematodes and microbial necromasses in four size classes. Bolded r-values are statistically significant at levels $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$ and $p = 0.059^\circ$.

	Pore size class (μm)				Total macroporosity
	<233	272–428	467–661	>700	
Total nematodes	0.504***	0.417**	0.278*	0.007	0.348**
Bacterial feeders	0.449***	0.387**	0.305*	0.061	0.347**
Fungal feeders	-0.166	-0.179	-0.212	-0.096	-0.186
Omnivores	0.016	0.012	-0.010	0.054	0.027
Predator	-0.101	-0.107	-0.090	-0.145	-0.128
Juveniles	0.264*	0.264*	0.282*	0.113	0.277*
Plant feeders	0.013	0.077	0.146	-0.007	0.063
Bacterial necromass	0.389**	0.286*	0.158	0.051	0.256
Fungal necromass	0.250$^\circ$	0.178	0.098	0.104	0.181

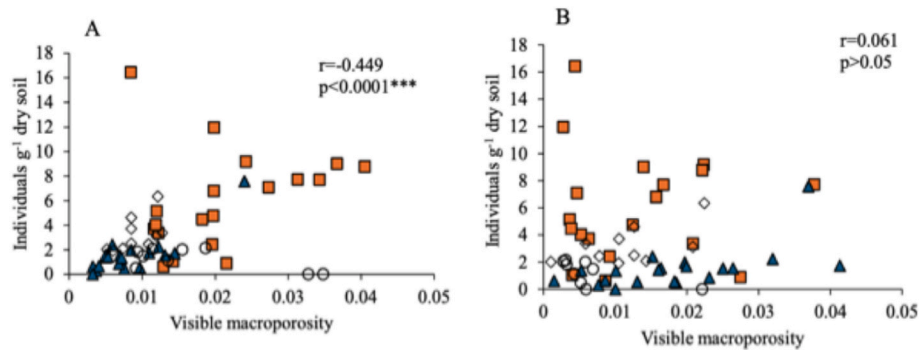


Fig. 6. Relationship between soil visible macroporosity and densities of bacterial feeding nematodes in the smallest (<233 μm , A) and largest (>700 μm , B) pore size classes. Symbols: Orange square = deep ploughing Jokioinen (DeepJ), Blue triangle = deep ploughing Loppi (DeepL), Circle = Grassland ploughing Loppi (GrassL), Diamond = Grassland ploughing Tammela (GrassT).

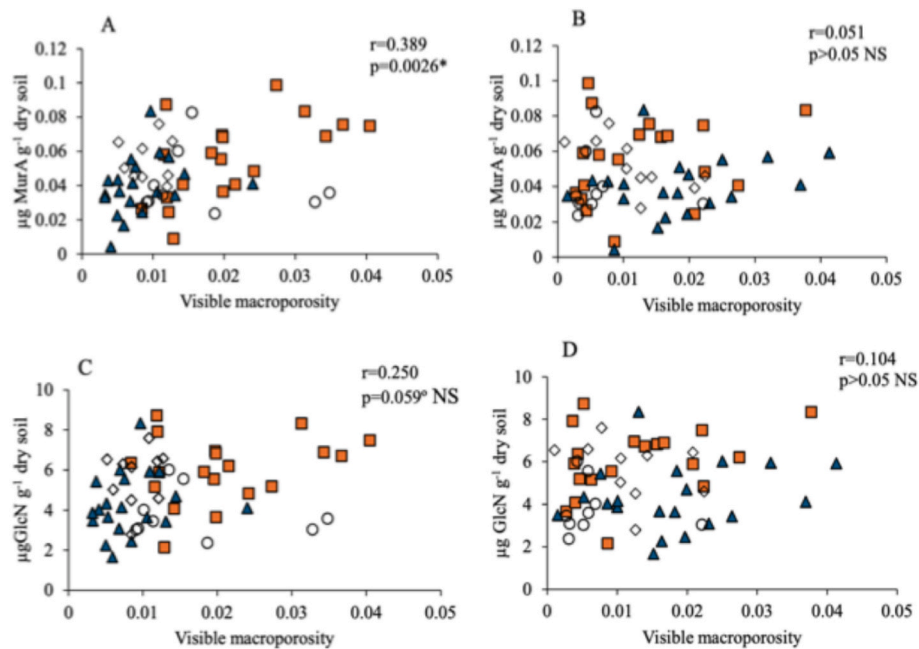


Fig. 7. Relationship between soil visible macroporosity and microbial necromass biomarkers. Bacterial origin aminosugars in the smallest (<233 μm , A) and largest (>700 μm , B) pore size classes. Fungal origin aminosugars in the smallest (<233 μm , C) and largest (>700 μm , D) pore size classes. Symbols: Orange square = deep ploughing Jokioinen (DeepJ), Blue triangle = deep ploughing Loppi (DeepL), Circle = Grassland ploughing Loppi (GrassL), Diamond = Grassland ploughing Tammela (GrassT).

different feeding groups (see Fig. 3). Consequently, the importance of density-dependent trophic interactions and pore-based regulation in these interactions could be assessed. Our results revealed that it is not

straightforward that nematodes tend to prefer smaller soil pores. However, it is clear that nematodes did not prefer pores larger than 700 μm , possibly due to air-dry conditions, strong predation pressure from larger

fauna, or the relatively small volume of these pores (see also Wu et al., 2025). This habitat distribution confirmed our hypothesis 2.

There were differences between feeding groups in their response to the porosity and pore sizes. Hence, other factors can affect the outcome of inhabiting soil pores by microfauna and microbes (e.g. season, moisture and/or pH, see Wu et al., 2025). The role of other edaphic factors was supported by a negative correlation between soil moisture and densities of bacterial-feeding nematodes.

Our results support the significance of water-filled pore space as a major habitat for soil nematodes (e.g., Hassink et al., 1993) and that moisture conditions are vital for nematodes (Quénéhervé and Chotte, 1996). The correlation between soil moisture and microbial necromass was statistically insignificant. Hence, the moisture conditions were not always optimal in our study sites for bacterial-feeding nematodes. It is possible that the water saturation (due to autumn rains) and oxygen depletion may directly regulate the well-being of soil organisms in this particular soil layer (Schlüter et al., 2022b). Finally, two simultaneous mechanisms may underlie the negative response of bacterial-feeding nematodes to increasing soil moisture: (1) the swelling of soil components reduces the pore space available to nematodes, and (2) the resulting atmospheric conditions, particularly oxygen depletion, within soil pores may become lethal. Such habitat changes may have occurred in soil pores smaller than 428 μm (see Table S1), which were also preferred by bacterial feeders. These weather-induced alterations in soil conditions can vary between seasons and sites, leading to seasonal and geographical variation in the abundance of nematodes within soil pores.

4.2. Link between microbial necromasses and nematodes in the porosphere

A positive correlation between bacterial-feeding nematodes and bacterial necromass (Table 3) aligns with the stimulative effect of nematodes on bacteria, or vice versa, as a bottom-up effect. Nematodes have a vital position in soil food webs (Ferris, 2010) and the grazing of nematodes usually stimulates bacterial growth and biomass (Jiang et al., 2018a). On the contrary, no direct correlation between fungivores and fungal necromass was found. This underlines the fact that microbial predation is mainly directed at living microbes, not their remains. However, a significant positive correlation was noted with bacterivorous nematodes (the most abundant nematode group) and bacterial and fungal necromasses indicating that the dynamics of nematode communities have a tight connection with SOC dynamics in the porosphere (Jiang et al., 2018a). The relationship of other feeding groups on the soil microbial necromass remains less straightforward. Soil microbes may feed on both soil organic matter fractions, i.e. POM (particulate organic matter) and MAOM (mineral associated organic matter) (Tang et al., 2023). Although it is widely believed that MAOM is a very stable C pool, oxalic acid and other simple organic acids released by plant roots and microorganisms liberate organic C compounds from protective associations of minerals (Keiluweit et al., 2015; Tang et al., 2023). As MAOM has a greater amount of microbially derived compounds than POM (Williams et al., 2018), we could expect a greater number of nematodes feeding on dead microbes bound to minerals, however, POM contains fresh, not very modified and thus more available organic matter, which attracts microbes. Thus, we cannot expect clear correlations between the feeding behaviour of soil fauna and SOM fractions, i.e. POM and MAOM. However, we found that bacterial-feeding nematode densities and abundance of microbial necromass correlated positively with the soil porosity. Hence, as an edaphic characteristic of soil habitat, porosity has a cause-effect relationship with the abundance of soil microbes and microfauna. Martin and Sprunger (2021) revealed in their meta-analysis that nematode-feeding groups did not react to the variations in soil aggregate size and that SOC was negatively correlated with total nematode densities. Machine learning-based methods have been developed recently for segmenting different POM classes from tomography images (Phalempin et al., 2025). Such an approach provides interesting

possibilities for future research combining imaging with nematode abundance at the sample level.

4.3. Trophic regulation in the porosphere

No correlation was found between soil macroporosity and predatory nematodes. As members at the highest trophic level in the microbial-nematode food web, the orders Mononchida (predators) and Dorylaimida (omnivores) have significantly larger body sizes (exact dimensions not measured here) compared to other nematodes found (Vonk et al., 2013; Sechi et al., 2018). Hence, it might be hypothesized that an increase in visible macroporosity would lead to a higher number of individuals. However, the abundance of worms from these feeding groups did not correlate with soil porosity across all pore size classes. The lack of correlation may indicate that other edaphic factors than porosity can also be important for nematodes in these soil habitats (see Li et al., 2023), however, it was not the soil moisture level. The fact that there were no correlations between predators and omnivores with other nematodes indicates that trophic interactions between feeding groups of nematodes are weak in this soil layer (e.g. compared to Mikola and Setälä, 1998a, b; Erktan et al., 2020). Positive correlations between microbial necromasses and density of bacterial feeding nematodes may support the idea that the bottom-up regulation is a major force in the food web of microorganisms (Wu et al., 2025). Wu et al. (2025) found strong bottom-up regulation of bacterivore and fungivore abundances, mediated by edaphic factors such as soil porosity and water content. However, this regulation did not affect nematode abundance at higher trophic levels (omnivore-predators) and was most pronounced in the intensively used cropland soil. Our findings from four intensively managed agricultural soils show that soil macroporosity positively affects only the abundance of bacterial-feeding and juvenile nematodes in pores smaller than 700 μm .

Results showed that the production of both bacterial and fungal necromass was favoured by increasing porosity (e.g. Six et al., 2000; Nunan et al., 2003; Kravchenko et al., 2019) but also dependent on the size-class of visible pores. Positive relationship existed only with smaller visible pores and the correlation disappeared in the case of large pores and total porosity values. However, the correlations with soil porosity were similar between bacterial and fungal necromasses. Hence, no evidence was found for the idea that the fungal compartment of the soil food web is more vulnerable to predation (if expected that denser microflora produces more necromass) whereas bacteria are better protected from the predators by their capability to inhabit small soil pores as refugia (Erktan et al., 2020). Due to this capability of bacteria, it has been expected that bacteria have a more significant role in the turnover of SOC (Jiang et al., 2018a, 2018b). In addition, finer soil texture (particle size varied from 100 to 630 μm) significantly reduced the predation pressure of a tardigrade predator against nematodes (Hohberg and Traunspurger, 2005). Altogether, the fate of nematodes as a predator of microbes or a prey of other soil animals depends on the soil aggregate and pore structure. Furthermore, more empirical evidence is needed on the consequences of porosity and pore size distribution on trophic interactions in the porosphere (Erktan et al., 2020).

In conclusion, this research provides additional evidence over the previous studies on the effect of soil porosity on the densities of nematodes and microbial necromass spatial distribution. Microbial-feeding nematodes do not consistently prefer smaller-scale soil pores, indicating that their distribution is not always directly linked to pore size. However, it is clear that nematodes did not prefer pores larger than 700 μm , possibly due to air-dry conditions, strong predation pressure from larger fauna, or the relatively small share of these pores. In addition, microbial necromass as part of SOC is more related to the small size classes of soil pores.

These findings offer novel insights into how soil architecture, particularly macroporosity below 700 μm , influences the spatial ecology of soil organisms — an aspect that has received limited attention in

boreal agroecosystems.

CRedit authorship contribution statement

Janne Salminen: Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Jari Hyväluoma:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Bartosz Adamczyk:** Writing – review & editing, Methodology, Formal analysis. **Sylwia Adamczyk:** Writing – review & editing, Methodology, Formal analysis. **Petri Niemi:** Writing – review & editing, Formal analysis. **Sami Kinnunen:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Arttu Miettinen:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Data curation, 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

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