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Location in soil pores as determinant of resource accessibility for microarthropods

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ABSTRACT

Trophic interactions among soil-living organisms occur predominantly within the soil pore network and are essential for soil functioning. The access of animal consumers to microorganisms is likely determined by the dimension of soil pores in which microorganisms are located and the body size of consumers. However, experimental evidence for size segregation is lacking for many soil organisms, notably microarthropods, which are key players in the soil food web. Here, we tested how the location of microorganisms in pores with different neck diameters influences their accessibility to microarthropods, and whether this accessibility varies with the consumer's body size. By adding ^{13}C sodium pyruvate solution to intact soil cores at different matric potential, we labelled microbial communities in different pore size classes and traced their consumption by three species of Collembola (Hexapoda), which was done by measuring the ^{13}C incorporation into animal tissue after four-weeks of incubation. Collembola incorporated labelled C from each of the pore size treatments (4–13, 13–41 and 41–931 μm), indicating that microorganisms are not fully physically protected from consumption by microarthropods, even in pores that are smaller than their body width. However, the incorporation of ^{13}C into Collembola tissue increased with pore neck diameter, suggesting that the physical environment limited the access of Collembola to resources. Overall, our findings suggest that resource accessibility is constrained by the body size of consumers, potentially shaping the trophic niches of microarthropods and influencing soil element dynamics at the pore scale.

1. Introduction

Soil pores provide a range of microhabitats, that vary in size and micro-environmental conditions, where soil organisms live and feed (Foster, 1988; Ruamps et al., 2011; Erktan et al., 2020). Soil organisms, such as fungi and bacteria (microorganisms), protists and nematodes (microfauna), and microarthropods (mesofauna) live in pores, or on pore walls of different sizes (van Straalen, 2023). They are linked to each other by trophic interactions that play a key role in soil functioning (e.g., mineralization and nutrient cycling; Schaefer, 1990; van der Heijden et al., 2008; Bardgett and van der Putten, 2014). The wide range of pore sizes, coupled with the large differences in body size between microbial prey and consumers (e.g., protists, nematodes, microarthropods), suggest that trophic interactions in soil are limited by size-based segregation of resources and consumers within pores (Erktan et al., 2020). Pore-scale spatial constraints on trophic interactions have been studied experimentally in protists, nematodes and tardigrades (Jones and Thomasson, 1976; Wright et al., 1993; Hohberg and Traunspurger, 2005), and results have generally shown that predation decreases with smaller pore size. However, size segregation in larger soil animals, such as

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microarthropods, remains to be demonstrated.

Restrictions in the access to resources along trophic chains are crucial for soil functioning, as they determine the type and amount of organic matter that enters the soil food web, how organic matter is transformed and mineralized at the different trophic levels, and the amount of organic matter, including microbial biomass, that is physically protected in soil pores and therefore inaccessible to consumers (Basile-Doelsch et al., 2020). Many microarthropods are generalist feeders (Scheu and Setälä, 2002; Digel et al., 2014; Briones, 2018) and can feed on an array of resources, known as "food flexibility" (Briones, 2018). Nevertheless, when a range of resources is available, feeding preferences are apparent, suggesting that the physical access that microarthropods have to resources is likely to be a major determinant of their feeding regime (Lehmitz and Maraun, 2016; Erktan et al., 2020; Fujii et al., 2023).

Studying how the localization of food sources in soil influences their availability to soil organisms, including micro- and mesofauna, remains a methodological challenge. Soil chips, which are artificial transparent pore spaces (Aleklett et al., 2018), offer opportunities to directly observe trophic interactions and monitor changes in local chemistry at the pore scale when coupled with microspectroscopy techniques (e.g., Raman scattering; Pucetaite et al., 2021). However, this approach is primarily useful for microorganisms (bacteria, fungi) and small aquatic microfauna, such as protists and nematodes, but not for larger, non-aquatic organisms, such as microarthropods. For these organisms, a potentially useful approach is to place microbial resources (e.g., bacteria; Wright et al., 1993) or labelled organic resources (e.g., ^{13}C labelled substrates) into pores of different size using variations in matric potential and assess the effect of consumers on prey populations or the incorporation of the isotopic label into consumers. The primary rationale behind this approach is to use controlled variations in matric potential to introduce isotopically labelled, trackable food resources into pores with varying neck diameters. This method is based on the Young-Laplace law, which links soil matric potential to the neck diameter of water-filled pores. A number of studies have identified differences in microbial communities, or in their activity, residing in different pore size classes using this approach (Wright et al., 1993; Ruamps et al., 2011; Chenu et al., 2025). Despite potential inaccuracies of the approach due to hysteresis or the diffusion of the labelled material, it has been recently shown by imaging that the targeted pore size classes are broadly reached (Li et al., 2024). Therefore, we used this approach to determine how pore neck diameter and body size constrain microarthropod resource use.

The objective of this study was to determine how the location of carbon resources in pores of different neck diameter affects the access of microarthropods of different body size to these resources and how it affects the structure of microbial communities at the pore scale. We adopted the matric potential approach (Killham et al., 1993; Ruamps et al., 2011) to incorporate ^{13}C labelled sodium pyruvate into soil pores of different size classes and to trace its incorporation into microbial communities and, subsequently, into three species of Collembola of different body size. We hypothesized that (i) the access of microarthropods to microbial carbon resources increases with pore neck size and decreases with body size. We further hypothesized that (ii) the effects of microarthropods on microbial community composition increase with pore neck size and decrease with microarthropod body size.

2. Methods

2.1. Soil sampling

Intact soil cores were taken from a long-term tillage experiment on an arable field located in the south of Göttingen (51.487°N, 9.936°E). The soil is classified as Haplic Luvisol, with 12 % sand, 73 % silt and 15 % clay, and pH was 7.2 (Ehlers et al., 2000; Engell et al., 2022). The field had been under rotation of oat (*Avena sativa* L.), wheat (*Triticum aestivum* L.), peas (*Pisum sativum* L.) and rape (*Brassica napus* L.), and managed with minimum tillage (Engell et al., 2022). Shortly after harvest of the rape crop in late July 2021, 128 undisturbed soil cores were taken from a depth of 2–5 cm (beneath the litter layer) using a soil auger (∅ 7.5 cm, height 3 cm). In addition to these samples, eight undisturbed cores were taken to estimate water retention curves and another eight samples of loose soil for measuring microbial biomass. All soil samples were placed in plastic jars, transported to the lab and stored at −20 °C. Soil cores to be placed into microcosms were freeze-dried (VaCo 2, Zirbus Technology, Germany) for defaunation and stored at 4 °C.

2.2. Experimental design and the setup of microcosms

The experiment was based on the incubation of undisturbed, but defaunated soil cores in which microbial communities in different pore size classes were labelled with ^{13}C. Three pore size classes were targeted, i.e. 4 – 13, 13 – 41 and 41 – 931 μm (see below), and a control without ^{13}C label was also set up. Then, soil cores were inoculated with one of three species of Collembola. The three species of Collembola had different body sizes (body width ranging from 300 to 580 μm), and we also considered a control without Collembola. Each treatment was replicated eight times, resulting in a total of 128 microcosms [(3 pore size classes + 1 control) × (3 Collembola species + 1 control) × 8 replicates]. Each microcosm consisted of an intact soil core (∅ 7.5 cm, height 3 cm) placed in a glass jar (∅ 9.5 cm, height 10 cm).

The pore size classes were chosen to ensure that each represented a similar pore volume (8.2 % of the total pore space) and that the smallest pore class was not directly accessible to any of the three Collembola species, while the largest pore class was accessible to each of the Collembola species. Collembola species were chosen based on differences in body size and their ability to survive and reproduce under laboratory conditions. These criteria led us to choose *Proisotoma minuta* (body length 1.1 mm, body width 300 μm), *Sinella curviseta* (body length 2.0 mm, body width 500 μm) and *Heteromurus nitidus* (body length 3.0 mm, body width 580 μm; Hopkin, 2007).

The experiment was set up in a sequence of steps, starting with the ^{13}C labelling of microbial communities in different pore size classes by adding a solution of ^{13}C labelled pyruvate, followed by the incubation of the samples to let the label being incorporated into microbial biomass for 16 h (for details see Methods: Labelling of microbial communities). Then, soil moisture was adjusted to 47 % soil water holding capacity (measured by a modified percolation method; Estefan et al., 2013) which represents an inhabitable moisture level for Collembola. In addition, at this moisture level only pores smaller than ~ 8 μm (as indicated by the water retention curve) were water filled, leaving the pores to be filled with the ^{13}C label largely air-filled and thus allowing Collembola as non-aquatic organisms to access these resources unhindered by water (Fig. 1). For the small pore class, the partial filling of pores with water (up to 8 μm diameter) may have favoured the colonization by aquatic organisms (i.e., bacteria, protists), but it unlikely affected accessibility of resources by Collembola given their much larger body width. Finally, Collembola were added, and the microcosms were incubated for 4 weeks in the dark at 20 °C. During the incubation, the microcosms were opened once a week for 20 min in order to renew the atmosphere whilst avoiding changes in soil moisture.

At the end of the incubation, approximately 20 g (fresh weight) of the soil was taken and stored at −20 °C until phospholipid fatty acid (PLFA) analysis. Collembola were extracted from the remaining soil using heat (Macfadyen, 1961) and collected in 50 % diethylene glycol. They were then transferred into water for storage at −20 °C. Within two weeks, soil animals were sorted for bulk stable isotope and compound specific isotope analysis of neutral lipid fatty acids.

2.3. Labelling of microbial communities

Sodium pyruvate was used to label microbial communities in the

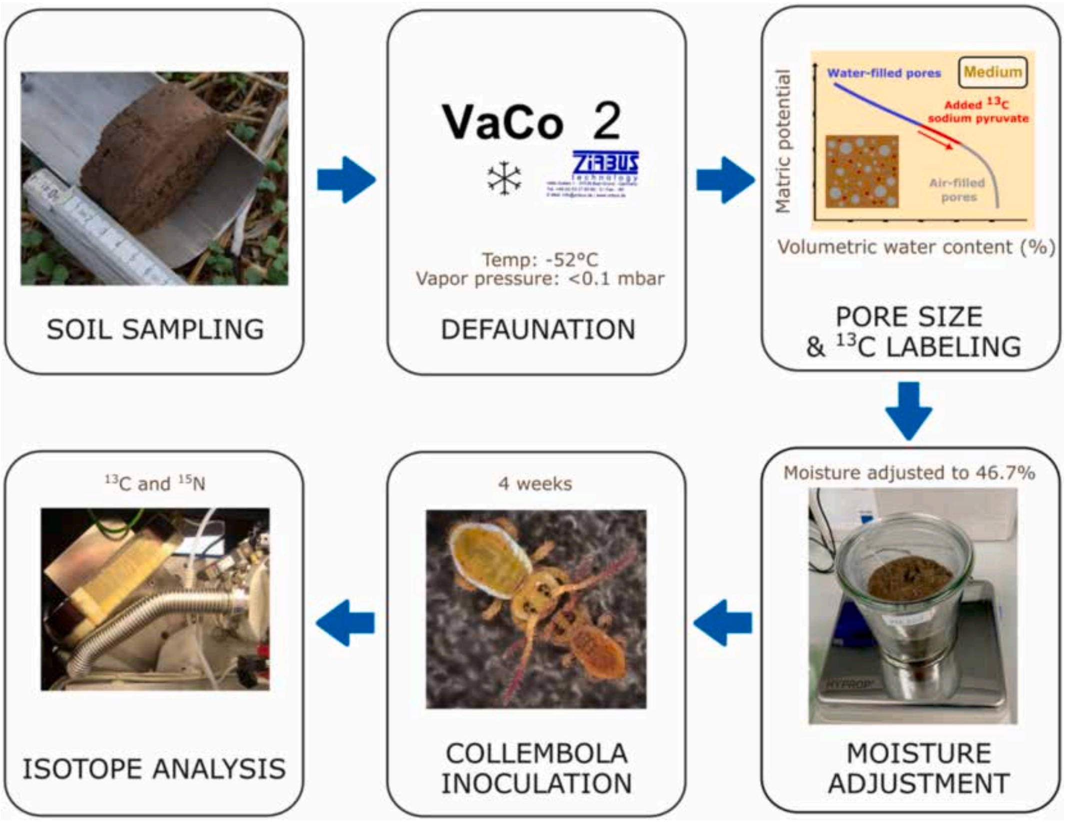

Fig. 1. Workflow chart. Workflow showing the establishment of the microcosm experiment and analyses conducted. It includes soil sampling, defaunation using freeze-drying, pore size distribution and ^{13}C labelling, adjusting moisture, Collembola inoculation and stable isotope analysis. Note that Pore size & ^{13}C labelling are shown qualitative; values are illustrative only.
Source: https://www.uni-goettingen.de/de/71205.html

different pore size classes as it is consumed by a wide range of microorganisms (Vander Heiden et al., 2009) and thus is easily incorporated and fixed in microbial biomass. The concentration of the solution was chosen to represent a small proportion of total soil C, hence limiting potential biases caused by changes in microbial community composition after the addition of larger quantities of labile C. A total of 1.54 ± 0.015 mg ^{13}C labelled sodium pyruvate equivalent to 0.50 mg ^{13}C per core was thus added, corresponding to about 7.95 ‰ of the C contained in microbial biomass (based on measurements of the microbial biomass by substrate-induced respiration; see Supplementary results) and an average addition rate of 3.13 μg C g^{-1} soil.

To determine the volume of the ^{13}C solution to be added to the three pore size classes, the soil water retention curve was established using the evaporation method (Schindler et al., 2010) implemented with a HYPROP device (Meter Group, Germany). The curves were then used to estimate the maximum equivalent diameter (D) of soil pores retaining water at any given matric potential (h) using a rearranged version of the Young-Laplace equation for the standard case of pure water at 25 °C:

$$D = \frac{3000}{|h|} \tag{1}$$

with D expressed in μm, and h in cm of H_2O. Finally, the van Genuchten equation (van Genuchten, 1980) was used to fit the relationship between the measured soil water content and matric potential, resulting in a continuous soil water retention curve with

$$\theta(h) = \theta_r + \frac{\theta_s - \theta_r}{\left[1 + (\alpha|h|)^n\right]^{1-\left(\frac{1}{n}\right)}} \tag{2}$$

where θ_s and θ_r are the saturated and residual water contents, and α and n are fitting parameters, both of which were obtained by inverse fitting.

Based on the water retention curve (Fig. 2), we identified three pore size classes of 4–13, 13–41 and 41–931 μm that corresponded to equal pore volumes (8.2 % of the total porosity). To fill the different pore size classes of the intact soil cores, labelled and unlabelled sodium pyruvate solutions were added following a series of sequential steps. First, using unlabelled sodium pyruvate, the four sets of 32 soil cores (freeze-dried) each were equilibrated at –75, –23, –7 or –0.3 kPa (the latter corresponding to the control, non-labelled treatment). This filled pores with pore neck diameters up to 4, 13, 41 and 931 μm (non-labelled treatment), respectively. In a second step the labelled ^{13}C sodium pyruvate was added to equilibrate the three first sets of 32 soil cores at –23, –7 and –0.3 kPa. This filled the soil pores up to pore neck diameters of 13, 41 and 931 μm, respectively. In a third step non-labelled sodium pyruvate was added to the two sets of 32 soil cores equilibrated at –23 and –7 kPa, bringing them to –0.3 kPa and filling the pores up to a pore neck diameter of 931 μm. The sodium pyruvate addition was conducted dropwise in a grid pattern across the soil surface to ensure homogeneous addition on the surface of the soil core. In addition, both ^{13}C labelled and unlabelled sodium pyruvate were applied at the same concentration (0.149 mg mL^{-1}) to avoid net diffusive fluxes driven by total solute concentration gradients. However, this does not prevent isotopic mixing of labelled ^{13}C between pore domains due to Brownian motion which may still occur during the fixation phase, and could lead to some degree of mixing between targeted and non-targeted pore classes. Overall, all the 128 soil cores received the same quantity of sodium pyruvate, regardless of the pore class targeted for labelling.

In order to minimize microbial consumption of the labelled substrate during transit through untargeted pores, the soils were left to equilibrate at 4 °C for 6 h between steps. This equilibration time was chosen

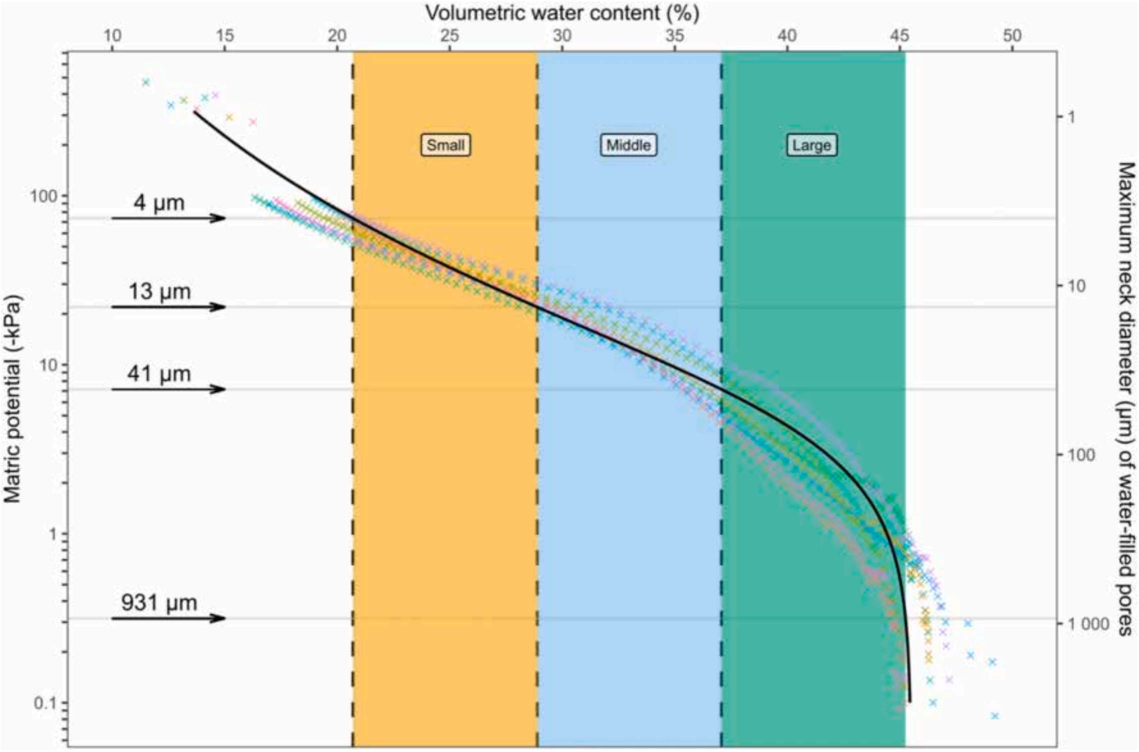

Fig. 2. Drying curve. Volumetric water content in relation to water potential (water retention curve) and maximum neck diameter of water-filled pores (pore size distribution based on Young-Laplace law). ^{13}C-labelled sodium pyruvate was used to incorporate the label into each small (4–13 μm), medium (13–41 μm) and large (41–931 μm) neck diameter pores. The black line represents the regression based on measurements from eight independent replicates (coloured scatter points).

according to Ruamps et al. (2011) who showed that it is sufficient for an even distribution of the label in the targeted soil pores. Subsequently, the samples were incubated in a closed jar at 20 °C overnight (approximately 16 h) to stimulate microbial activity and ensure that the sodium pyruvate was incorporated into microbial tissue, whilst minimizing diffusion. These two incubation steps are essential to ensure that the labelling is accurate enough to target broadly defined pore size classes (Li et al., 2024).

The potential deviations from the targeted pore size classes and the reasons for these deviations have been discussed at length elsewhere (Li et al., 2024; Chenu et al., 2025). In addition to the points raised by these authors, we note that hysteresis may also cause deviations from the targeted pore size classes, because soils were labeled by wetting while pore sizes were estimated based on a drying curve. However, the extent of the deviations is unlikely to have been sufficiently large to invalidate our treatments and likely affected all pore size classes in a similar way.

2.4. Inoculation with Collembola

For each set of 32 labelled (and non-labelled control) soil cores, eight replicates were inoculated with synchronized juveniles of *Proisotoma minuta*, *Sinella curviseta* or *Heteromurus nitidus*. To obtain juvenile Collembola, 30 adult individuals were added to Petri-dishes with a bottom layer of plaster of Paris and fed with baker's yeast (OECD, 2016). The Petri-dishes with adult Collembola were incubated at 20 °C in the dark for three days to allow them to lay eggs, then the adult Collembola were removed. Juveniles began to hatch after about ten days. Thirty 1- to 6-day-old juveniles were added to the microcosms immediately after the pore labelling and the adjustment of the moisture content (see Supplementary results).

2.5. Bulk isotope analysis

The ^{13}C/^{12}C ratio can be used to trace the origin of the C sources incorporated into consumer biomass. Higher ^{13}C contents in Collembola indicates that they fed on the ^{13}C-labelled material introduced into the pores. Trophic position of a consumer, indicated by the ^{15}N/^{14}N ratio, reflects how many steps of energy-transfer in food webs separate consumers from basal resources (e.g., plant litter). To evaluate the incorporation of ^{13}C-labelled material and the trophic position of Collembola, stable isotope ratios of carbon (^{13}C/^{12}C) and nitrogen (^{15}N/^{14}N ratio) in Collembola were determined using an elemental analyser (Flash EA 1112, Thermo Electron, Milano, Italy) coupled to a mass spectrometer (Delta XP, Thermo Electron, Bremen, Germany) adjusted for small sample size (Langel and Dyckmans, 2014). One to two individuals of *H. nitidus*, *S. curviseta* and five to ten individuals of *P. minuta* were used for stable isotope analyses (mean dry mass of 7.7 μg), and the remaining Collembola were kept for neutral lipid fatty acid analysis (see section Fatty acid analyses). Collembola were transferred into tin capsules and dried at 60 °C for 48 h. Vienna Pee Dee Belemnite was used as the primary standard and acetanilide (C_8H_9NO, Merck, Darmstadt, Germany) as the internal working standard. The variation in stable isotope ratios of carbon and nitrogen was expressed as δX (‰) $= (R_{sample} - R_{standard}) / R_{standard} \times 1000$, with R the ratio between the heavy and light isotopes (^{13}C/^{12}C or ^{15}N/^{14}N).

2.6. Fatty acid analyses

Phospholipid fatty acid (PLFA) profiles were analyzed to assess microbial community structure, and neutral lipid fatty acid (NLFA) profiles were quantified to trace energy channels from basal resources to Collembola. PLFAs were extracted from approximately 5 g soil (dry weight equivalent) and NFLAs were extracted from animals, both using a modified Bligh and Dyer method (Frostegård et al., 1993). Lipids were then fractionated into neutral lipids, glycolipids and phospholipids by elution through silica acid columns using chloroform, acetone and methanol, respectively (HF BOND ELUT-ST, Varian Inc., Darmstadt, Germany). Phospholipids were subjected to mild alkaline methanolysis (for details see Pollierer et al., 2015) and neutral lipid fatty acids were saponified and methylated following the procedures given for the Sherlock Microbial Identification System (MIDI Inc., Newark, NJ, USA; Ruess et al. 2002). Fatty acid methyl esters were identified by chromatographic retention time compared to standards (FAME CRM47885, BAME 47080-U; Sigma-Aldrich, Darmstadt, Germany) using a GC-FID Clarus 500 (PerkinElmer Corporation, Norwalk, USA) equipped with an Elite 5 column. The temperature program started at 60 °C (hold time 1 min) and was increased by 30 °C per min to 160 °C, and then by 3 °C per min to 280 °C. The injection temperature was 250 °C and helium was used as carrier gas. Linoleic acid (18:2ω6,9) was used as fungal marker and oleic acid (18:1ω9) was used as fungal or plant-associated marker (Zelles, 1997). The saturated fatty acids i15:0, a15:0, i16:0 and i17:0 were used as markers for Gram-positive bacteria (Firmicutes; Joergensen 2022), and cy17:0, cy19:0, 16:1ω7 and 18:1ω7 were used as markers for Gram-negative bacteria (Zelles, 1999; Fanin et al., 2019). In soil, these fatty acids were quantified from the phospholipid fraction (PLFAs), reflecting microbial biomass, whereas in Collembola, they were quantified from the neutral lipid fraction (NLFAs), reflecting assimilated dietary resources.

2.7. Compound-specific ^{13}C fatty acid analysis

While ^{13}C values of PLFAs reflect active incorporation of the label into microorganisms, ^{13}C values of NLFAs integrate dietary intake over time, enabling the quantification of label transfer from microorganisms to soil animals. We measured ^{13}C values in each of the PLFAs in order to trace the incorporation of the added ^{13}C label into microbial groups. To further explore the contribution of different groups of microorganisms to Collembola nutrition, we applied compound specific ^{13}C analysis of NLFAs extracted from Collembola. We measured $^{13}C/^{12}C$ ratios in individual PLFAs (microbial communities) and NLFAs (Collembola) using a Thermo Finnigan Trace GC coupled via a GP interface to a Delta Plus mass spectrometer (Finnigan, Bremen, Germany). The GC was equipped with a fused silica capillary column. The temperature program started at 60 °C and increased by 6 °C per minute to 310 °C, where it was held for 15 min. The injection temperature was 250 °C and helium was used as carrier gas. The helium flow rate was 2.2 ml min^{-1}. Fatty acid methyl esters (FAMEs) were identified by chromatographic retention time. The carbon isotope composition is reported in the δ notation (‰) relative to Vienna Pee Dee Belemnite standard (V-PDB). To obtain isotope ratios of the fatty acids, isotope ratios of FAMEs were corrected for the isotope ratio of the methyl moiety originating from methanol using the formula $\delta^{13}C_{FA} = [(C_n + 1) \times \delta^{13}C_{FAME} - \delta^{13}C_{MeOH}] / C_n$, with $\delta^{13}C_{FA}$ being the $\delta^{13}C$ of the fatty acid, C_n the number of carbon atoms in the fatty acid, $\delta^{13}C_{FAME}$ the $\delta^{13}C$ of the FAME and $\delta^{13}C_{MeOH}$ the $\delta^{13}C$ of the methanol (−52 ‰) used for methylation (Abraham et al., 1998). ^{13}C atom percent excess (APE) of individual fatty acids were calculated as $APE = 100 \times [(^{13}C_{labelled} / (^{13}C_{labelled} + ^{12}C_{labelled})) - (^{13}C_{control} / (^{13}C_{control} + ^{12}C_{control}))]$ with $C_{labelled}$ and $C_{control}$ being the abundance of corresponding isotopes in the labelled samples vs. the respective control samples (Lemanski and Scheu, 2014). Atom excess was calculated as the product of the APE and the concentration of each fatty acid. Only a few fatty acids were identified due to low animal biomass in the NLFA fraction and the results are only included in the supplementary materials (Fig. S2).

2.8. Data analyses

Differences among animal densities and bulk C isotope ratios were determined using linear models, with animal species (control, *P. minuta*, *S. curviseta* and *H. nitidus*) and pore size classes (control, small, medium and large) and their interactions as predictors. Animal abundances were log-transformed to improve normality and homoscedasticity of residual variance. We further used PERMANOVA and principal component analysis to test the effects of pore size, animal species and their interactions on ^{13}C atom excess composition of PLFA profiles based on Bray-Curtis dissimilarities. Mean and standard deviation are reported in the results unless otherwise stated. All analyses were carried out in R 4.3.0 (R Core Team, 2023).

3. Results

Compound-specific ^{13}C PLFA analyses indicated that soil microorganisms were significantly ^{13}C enriched in each of the labelled treatments. The extent of the enrichment varied with pore size class and fatty acids (PERMANOVA: $F_{2,80} = 4.6$, $P = 0.001$; Fig. 3a). In small pores, Gram-positive bacteria were more enriched in ^{13}C compared to medium and large pores (Fig. 3b). By contrast, Gram-negative bacteria in large pores were more enriched in ^{13}C compared to small pores (Fig. 3c). The ^{13}C enrichment in the plant and fungal marker PLFA (18:1ω9) was significantly higher when the ^{13}C labelled pyruvate was placed in small pores compared to when it was placed in medium and large pores (Fig. 3d).

Collembola (bulk tissue) were also significantly ^{13}C enriched in each of the labelled treatments ($F_{3,70} = 68.4$, $P < 0.001$), but the intensity of the label depended on Collembola species (interaction of animal species and pore size: $F_{6,70} = 3.1$, $P < 0.009$; Fig. 4, S1). In each of the labelled treatments, *S. curviseta* was less ^{13}C enriched than *H. nitidus* and *P. minuta* (Fig. 4). The $\delta^{13}C$ enrichment of *P. minuta* was significantly higher when the ^{13}C was added to large pores compared to medium sized pores. The $\delta^{13}C$ enrichment of *S. curviseta* did not vary significantly between the three pore size labelling treatments. By contrast, the $\delta^{13}C$ enrichment of *H. nitidus* was significantly higher when the ^{13}C label was added to large and medium than to small pores. Further, compound specific NLFA analyses showed that $\delta^{13}C$ values of the Collembola fatty acid 18:1ω9 were significantly enriched when the ^{13}C label was added to the large pores compared to the control treatment (Fig. S2).

The abundance of Collembola did not differ significantly between pore size class treatments ($F_{3,72} = 1.2$, $P = 0.30$). Generally, there were significantly more *P. minuta* individuals than *S. curviseta* and *H. nitidus* individuals at the end of the experiment (Fig. 5a). As indicated by $\delta^{15}N$ values of Collembola bulk tissue, the trophic position of *S. curviseta* was higher than that of *H. nitidus*, whereas the $\delta^{15}N$ values of *P. minuta* were not significantly different from those of the other two Collembola species (Fig. 5b). A similar pattern was found in the C/N ratio of bulk animal tissue (Fig. 5c).

Compound specific ^{13}C PLFA analyses showed that soil microbial community profiles differed between pore size classes, but were generally not affected by the inoculation of Collembola, regardless of the species inoculated (PERMANOVA: $F_{3,83} = 1.8$, $P = 0.096$; Fig. S3). Overall, the composition of the PLFA profiles indicated that Collembola did not significantly affect soil microbial community composition in the three pore size classes (pore size × animal interactions: $F_{6,83} = 1.2$, $P = 0.25$). However, in presence of *S. curviseta* the abundance of soil fungi was significantly higher than in presence of *H. nitidus* (Fig. 6a). Further, in presence of *P. minuta*, the Gram-positive to Gram-negative ratio was significantly higher than in presence of *S. curviseta* (Fig. 6c).

4. Discussion

The results showed that each of the three microarthropod species was significantly labelled, regardless of the neck diameter of the pores where the ^{13}C resources were placed, suggesting that carbon sources were not fully physically protected, even when located in small pores (4–13 μm). However, in line with our first hypothesis, labelled resource use increased with pore size in *H. nitidus*, suggesting that in this Collembola species body size modulated the access to resources in the different pore sizes.

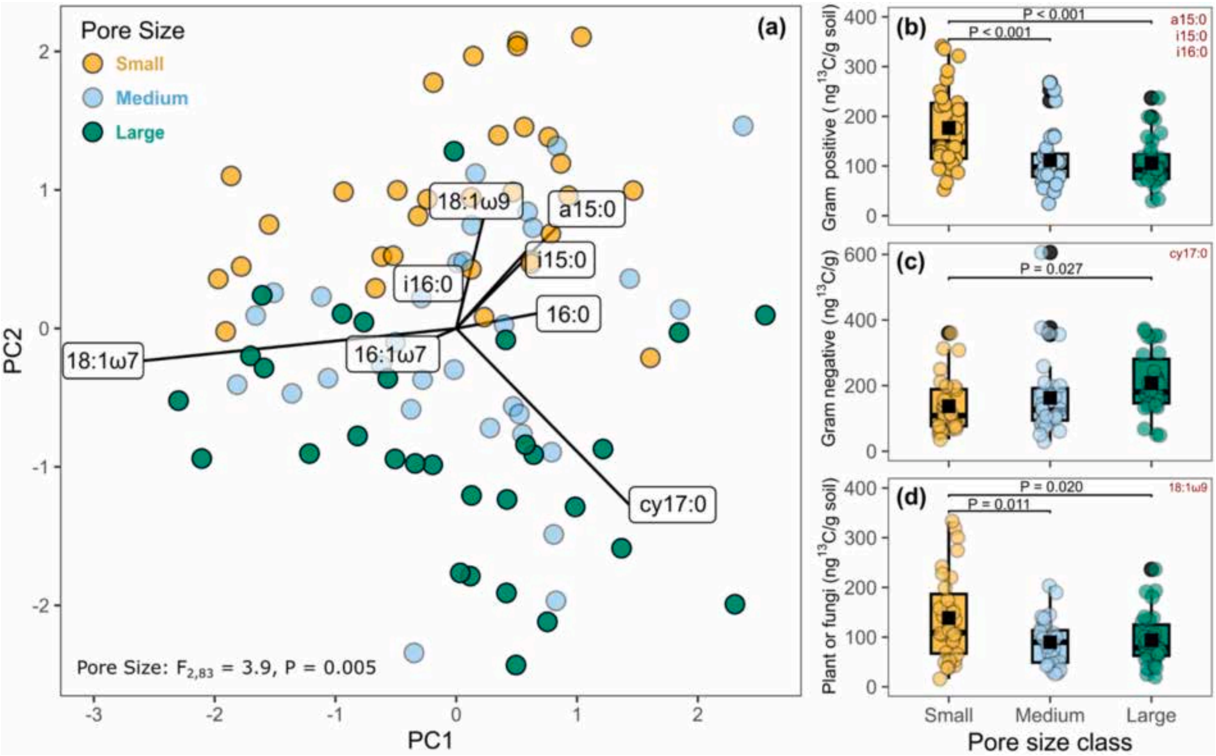

Fig. 3. ^{13}C-PLFA profile. (a) Principal component (PC) analysis of excess ^{13}C in phospholipid fatty acids (boxes) from small, medium and large pore size treatments (colour coded) at the end of the incubation period. Excess ^{13}C (ng ^{13}C g^{-1} dry weight soil) in (b) Gram-positive bacteria, (c) Gram-negative bacteria and (d) plant or fungi in small, medium and large pore size treatments (colour coded as in a). Squares in the boxplots represent means. Horizontal lines with P-values indicate significant differences between means.

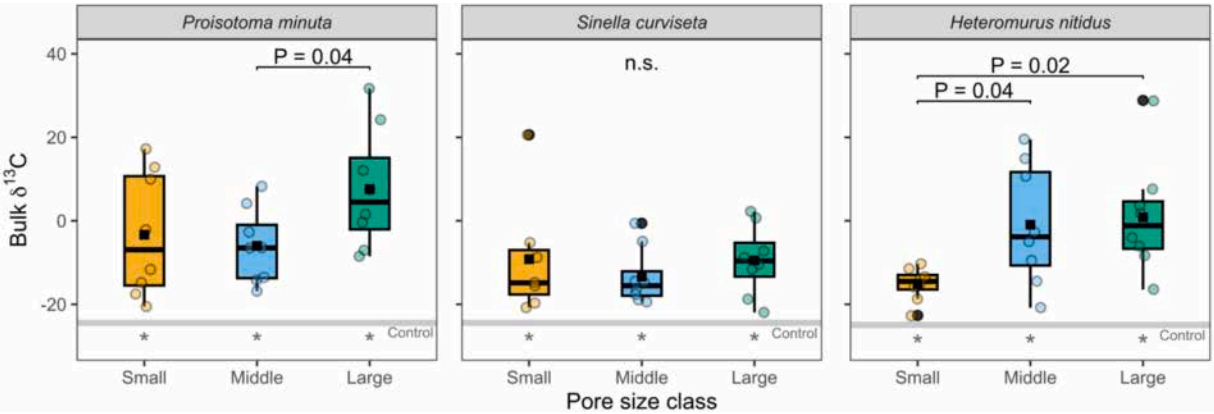

Fig. 4. Collembola ^{13}C. Bulk δ^{13}C values of three Collembola species (*Proisotoma minuta*, *Sinella curviseta* and *Heteromurus nitidus*) in small, medium and large pore size treatments. Significant differences between pore size classes are denoted by horizontal lines with P-values. Significant differences between pore treatments and the control (horizontal grey bar) are indicated by an asterisk ($P < 0.05$). Squares in the boxplots represent means.

4.1. Collembola access to resources in small pores

The results indicated that microorganisms in pores smaller than the Collembola body width may not be protected from consumption. Several mechanisms can explain this finding. First, microarthropods consume microbial food resources in small pores by ingesting soil particles containing ^{13}C labelled microorganisms. The entognathous chewing mouthparts of Collembola include mandibular molar plates within the head capsule. These mouthparts allow them to ingest food resources together with mineral soil material and thereby access resources in small pores by breaking up soil structure. This type of geophagy has been observed in Collembola in other contexts (Ponge, 2000). Second, the soil pore space forms a continuum with small pores opening into larger ones. Soil animals presumably enter large pores and graze microorganisms near the junction between small and large pores without entering them. Third, the relocation of resources by fungal hyphae bridging pores of different size (Otten et al., 2001) may also contribute to the access of labelled food resources in small pores by Collembola. In our study, the plant and fungal marker oleic acid (18:1ω9) was the most intensively labelled PLFA marker in small pores, suggesting that fungi could have transferred ^{13}C from small pores to larger ones accessible to Collembola. However, the fungal (basidiomycete, ascomycete) marker, linoleic acid (18:2ω6,9), which is common in agricultural soils (Zelles et al., 1995; Frey et al., 1999), was neither detected in soil nor in Collembola. Fourth, in addition to the role of fungi, compound specific ^{13}C analyses of Collembola suggest that bacteria played an important role in the

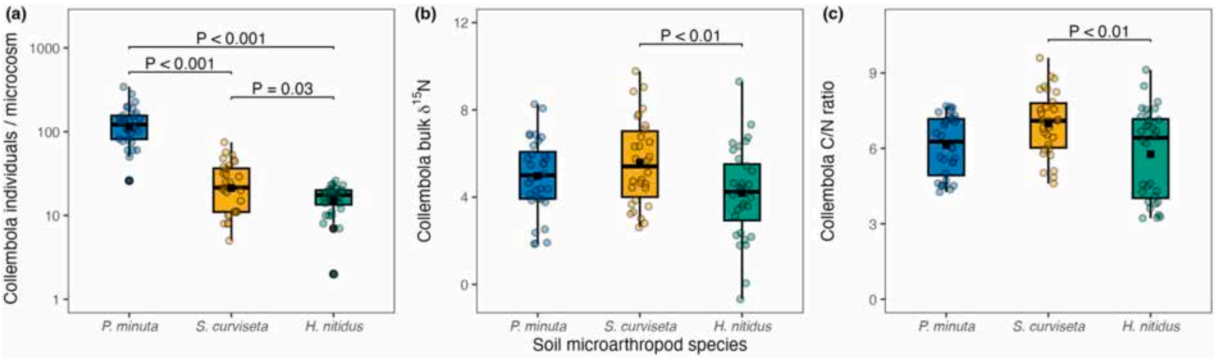

Fig. 5. Collembola ^{15}N. Abundance (a), δ^{15}N values (b) and C/N ratio (c) of *Proisotoma minuta*, *Sinella curviseta* and *Heteromurus nitidus* after four weeks of incubation. Squares in the boxplots represent means. Significant differences between pore size classes are denoted by horizontal lines with P-values.

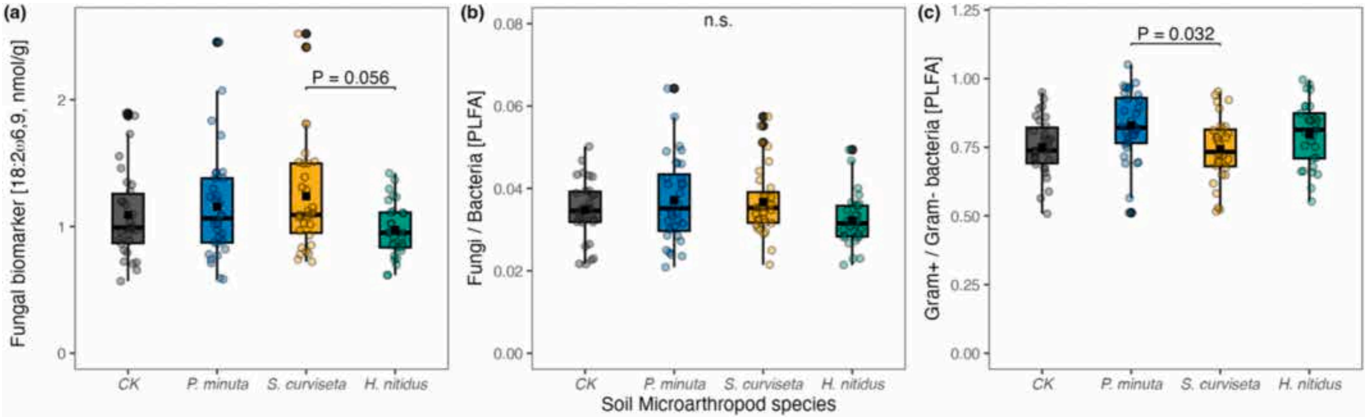

Fig. 6. PLFA concentrations. (a) Fungal biomarker concentration [nmol g^{-1} dry weight soil], (b) fungal/bacterial ratio and (c) Gram-positive to Gram-negative bacteria ratio in soil in the control (CK) and in treatments with *Proisotoma minuta*, *Sinella curviseta* and *Heteromurus nitidus*. Significant differences between Collembola species are denoted by horizontal lines with P-values. Microorganisms in different pore sizes were labelled to trace their incorporation to microarthropods. Microorganisms in small pores may not be completely protected from consumption by microarthropods. However, resource limitation is least severe in large pores and for small Collembola species. Overall, porosphere microbial location determines resources accessibility to microarthropods.

channelling of ^{13}C resources from small pores to Collembola (Fig. S2). Active bacterial motility (Yang and Van Elsas, 2018) or the movement of protists as major consumers of bacteria in soil may have redistributed the ^{13}C label, thus allowing Collembola to access the added ^{13}C from small pores without entering them. Finally, the incorporation of ^{13}C from small pores into Collembola might also partly relate to ^{13}C label that ended up in non-target pore size classes due to imperfect labelling accuracy. Further experimental evidence is needed to tease apart the various potential explanations identified here.

4.2. *Pore and body size as determinant of resource accessibility to Collembola*

Of the three Collembola species studied, the smallest, *P. minuta,* was most heavily labelled, suggesting it had higher access to the ^{13}C resources than in the other two species. Presumably, its small size contributed to its ability to acquire resources from smaller pores. In addition, *P. minuta* reproduced most in the microcosms, likely due to shorter life cycle and higher reproductive rate compared to the other two species (Hutson, 1978; Lu et al., 2025), rather than because it benefitted more from the added labelled substrate. Therefore, the higher abundance of small-sized juveniles of *P. minuta* may have contributed to the higher label in this species as they may have had greater access to smaller pores compared to adults. By contrast, the larger species *H. nitidus* and *S. curviseta* reproduced less and were less labelled. Overall, *H. nitidus* was more intensively ^{13}C labelled than *S. curviseta* likely because *H. nitidus* lives somewhat deeper in soil than *S. curviseta*, pointing to the importance of life form in driving trophic niches of Collembola (Potapov et al., 2016). Further, in *H. nitidus* the intensity of ^{13}C labelling was significantly lower when the label was placed in small pores, reflecting more pronounced restriction in accessing resources in pores of small neck size. The pore size restriction in *H. nitidus* but not in the two other species may be explained by the larger body size of this species.

Overall, variations in the incorporation of the ^{13}C label into Collembola with soil pore size provides the first experimental evidence supporting a pore size segregation restricting the access of microarthropod consumers to resources. This result is in line with the size segregation observed for bacteria, protists, nematodes and tardigrades (Jones and Thomasson, 1976; Wright et al., 1993; Hohberg and Traunspurger, 2005), evidenced by incubation experiments that manipulated the pore size distribution. In contrast to these studies, we used a novel approach tracing the incorporation of ^{13}C at the pore level into animal consumers, which allowed to investigate size segregation in larger, non-aquatic organisms.

4.3. *Microbial community composition at pore scale*

Compound-specific ^{13}C PLFA results suggest that different microorganisms consumed the labelled substrate in the different pore size treatments, confirming results of Ruamps et al. (2011) and Li et al. (2024). In our case, the differences were mainly due to variations in the incorporation of the label into Gram-positive (mainly Firmicutes) (Joergensen, 2022) and Gram-negative bacteria. Gram-negative bacteria were more heavily labelled when the ^{13}C pyruvate was placed in large pores, while Gram-positive bacteria were more heavily labelled when it was placed in small pores. This suggests that Gram-negative bacteria were more active in large pores, while Gram-positive bacteria were more active in small pores. Presumably, these differences are related to micro-gradients in abiotic conditions or different types of organic substrates available in small and large pores.

Our study also allowed us to examine whether the inoculation of Collembola influenced soil microbial composition at the pore scale. We observed that the inoculation of Collembola did not significantly affect soil bacterial (Gram-positive and Gram-negative) and fungal relative abundances, nor the microbial community composition in any of the soil pore size classes. This suggests that the consumption of soil microorganisms by Collembola did not significantly affect the structure of soil microbial communities in any of the pore size class. The findings contrast previous results from microcosm experiments using homogenized soil, where significant changes in microbial community composition (also determined by PLFAs) due to Collembola grazing (Coulibaly et al., 2019). Presumably, microorganisms are more accessible to Collembola in sieved than in intact soil, in which the proportion of large pores and their connectivity are likely to be lower, thereby restricting Collembola mobility and access to resources. Finally, despite the lack of species-specific effects of Collembola on microbial community composition at the pore level, fungal abundance and the Gram-positive to Gram-negative bacteria ratio were higher in treatments with *S. curviseta* and *P. minuta* than in those with *H. nitidus*. These variations in PLFA markers may relate to feeding preferences and/or microbial interactions in response to the consumption of microbial prey by Collembola (Chahartaghi et al., 2005). Overall, the impact of Collembola on soil microbial communities remained weak and did not vary with pore size nor with Collembola body dimensions.

5. Conclusions

We showed that even microbial resources in pores far smaller than the Collembola body width may not be fully protected from consumption. This suggests that resources in small pores are not entirely protected from consumers and can enter the soil food web. From a soil animal perspective, the access to resources even from small pores indicates that Collembola are less restricted in their access to resources than previously assumed. This apparently large access to resources across soil pores may contribute to the stability of soil food webs by improving resource supply to microarthropods. However, our results also showed that resource accessibility increases with pore size, especially for *H. nitidus*, and decreases with Collembola body size, suggesting that soil pore characteristics affect the resource spectrum and trophic niche of Collembola. From an ecosystem functioning perspective, the partial protection of carbon resources in small pores may have significant consequences for the dynamics of soil organic matter and how these dynamics are modelled at the pore scale. Using ^{13}C labelling of microbial resources in soil pores of different size, we thus provide the first experimental evidence of a size-segregation of trophic interactions between microarthropod consumers and microbial prey in undisturbed soil.

CRediT authorship contribution statement

Jing-Zhong Lu: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mohsen Zarebanadkouki:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Conceptualization. **Steffen Schlüter:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Data curation. **Melanie M. Pollierer:** Writing – review & editing, Validation, Supervision, Software, Resources, Project administration, Methodology. **Stefan Scheu:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Naoise Nunan:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Formal analysis, Conceptualization. **Amandine Erktan:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

Naoise Nunan is an Editor-in-Chief for Geoderma and was not involved in the editorial review or the decision to publish this article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2026.117810.

Data availability

Data will be made available on request.

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