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Under the lens: Carbon and energy channels in the soil micro-food web

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ABSTRACT

While carbon flow through soil decomposition channels is well studied, the associated energy fluxes are less considered. In particular, how microbial substrate and energy turnover are linked to higher trophic levels has hardly been investigated to date. Soil nematode communities can serve as a model group to address this knowledge gap. As important microbial grazers nematodes hold a central position in soil food webs. The present study relates the structure and function of the micro-food web to microbial carbon and energy use efficiency. Microbial biomass (phospholipid fatty acids), activity (substrate-induced growth) and energy flow (substrate-induced heat release) are linked with the nematode fauna, i.e. population density, ecological indices and metabolic footprints. Soils from four agricultural sites in central Europe were compared, either long-term unfertilized or fertilized with farmyard manure.

Environmental conditions (e.g. soil nutrients, moisture) influenced microbial biomass, nematode population density and decomposition channels more than fertilization. While all arable soils were dominated by bacteria, at sites with moderate nutrient status fungi also contributed to carbon and energy flow. The life strategies of microorganisms and nematodes showed a comparable pattern: nutrient-poor unfertilized soils comprised more *K*-strategists, characterized by an efficient but slow metabolism. Conversely, nutrient-rich soils represented fast cycle systems, dominated by copiotrophic microorganisms and strong *r*-strategists among nematodes. Across soils, microbial energy use efficiency was quite balanced compared to carbon use efficiency. Remarkably, nematode functional groups were closely linked to microbial substrate turnover efficiency, suggesting nematode faunal analysis as a useful proxy. The nematode Channel Index, a measure for soil decomposition channel activity, is proposed as a tool for mapping microbial carbon and energy turnover.

1. Introduction

Soil microbial and faunal communities interact in complex food webs, driving the carbon, nutrient and energy flows central to biogeochemical cycles (Gessner et al., 2010; Grandy et al., 2016; Schimel and Schaeffer, 2012). In the soil decomposer system, the detrital food chain forms two main pathways for carbon and energy, which are based on bacteria and fungi (Crotty et al., 2014; Morriën, 2016). The dynamics therein differ due to the basal food web resources, such as nutrient content and availability of substrates. Soil systems with bacteria as the main decomposers represent “fast cycles”. They show a high turnover of organic matter and a rapid transfer of nutrients to plants. In contrast, pathways dominated by fungi are “slow cycles”, based on the decomposition of complex organic resources, which leads to lower metabolic rates (Ruess and Ferris, 2004; Scheu et al., 2005).

These turnover processes at the food web base can be addressed by microbial carbon use efficiency (CUE) and energy use efficiency (EUE), with low CUE and EUE indicating loss of carbon and energy via respiration and heat (Del Giorgio and Cole, 1998). Microbial community composition determines CUE, e.g. in fungal-rich soils efficiency is

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generally higher than in bacterial-dominated soils (Domeignoz-Horta et al., 2021). CUE and EUE are often in a linear relationship, but the nominal oxidation state of carbon and respiration type (aerobic/anaerobic) can decouple this link (Chakrawal et al., 2020; Wang and Kuzyakov, 2023). While soil microbial CUE is well investigated (e.g. Geyer et al., 2016; Manzoni et al., 2012; Sinsabaugh et al., 2013), EUE has only recently come into focus.

Through its interconnectedness, the entire soil trophic network determines the fluxes of carbon and energy (Grandy et al., 2016; Kou et al., 2018; Nielsen et al., 2011). Nematodes are a central group in soil food webs with life strategies ranging from *r*-to *K*-strategists. Their ecological indices are well-established tools for analyzing soil ecosystem condition and health (du Preez et al., 2022; Ferris, 2010a; Melakeberhan et al., 2021). The major soil decomposition pathways can be assigned using the ratio of fungal-to bacterial-feeding nematodes (f/b) as well as the Channel Index (CI), a weighted index linking trophic groups with life strategies (Ferris et al., 2001; Freckman and Ettema, 1993). These ecological tools are frequently applied as indicators of soil conditions in arable fields differing in management (e.g. tillage, fertilizer), resource quality and quantity or crop type (Ewald et al., 2020; Glavatska et al., 2017; Scharroba et al., 2012, 2016; Zhong et al., 2017).

Nematode metabolic footprints assign the production and activity of higher trophic levels in the micro-food web using trait-based measurements of morphological (body mass) and physiological (respiration) characteristics. They are based on the lifetime amount of carbon used for growth and egg production and carbon lost by metabolic activity. Metabolic footprints thus reveal patterns and relative sizes of the herbivore, bacterivore and fungivore mediated carbon and energy channels in soils (Ferris, 2010b; Mulder and Maas, 2017). In arable land, metabolic footprints were used to indicate changes in soil carbon and energy channels in relation to management practice or resource amendment (Ewald et al., 2020, 2022; Zhong et al., 2017). Mulder and Maas (2017) investigated 200 sites, ranging from arable fields over managed grasslands to forests, and proposed nematode metabolic footprints as functional descriptors of land use. More recently, metabolic footprints were employed to describe the energetic structure of nematode food webs (Barnes et al., 2018). A recent study indicated that mature and complex soil communities support high energy flux across soil food webs (Zheng et al., 2023). Moreover, soil amendment with organic fertilizer or biochar was shown to increase the flow uniformity of energy across trophic levels, thereby enhancing ecosystem functions (Wan et al., 2022b; Wan et al., 2022a; Zhu et al., 2023).

Besides biotic interactions, soil environment (e.g. soil type, organic matter content, moisture, temperature) affects microbial diversity and activity as well as carbon and energy flow to higher trophic levels. Soil physical structure (e.g. aggregation and pore size) shapes microbial community structure and diversity (Bach et al., 2018) and in turn trophic interactions (Erktan et al., 2020). For example, pore size determines access of nematodes to bacterial prey, which affects the impact of grazing on bacterial community dynamics (Jiang et al., 2018) and the overall microbial metabolic quotient qCO_2 (Jiang et al., 2013). Moreover, resource amendment with organic fertilizers, e.g. farmyard manure, fosters the bacterial community (Wang et al., 2022; Watts et al., 2010). Following these dynamics, nematode population density, particularly that of bacterial feeders, is increased by organic enrichment (Griffiths et al., 1994; Leroy et al., 2009; van Eekeren et al., 2009; Villenave et al., 2003).

The close association between microorganisms and their nematode grazers was frequently observed in arable soils (Ewald et al., 2020; Glavatska et al., 2017; Scharroba et al., 2012). The related decomposition pathways in the micro-food web are well studied in regard to the organisms' abundance, biomass and assemblages (Ruess and Ferris, 2004). However, carbon and energy are often used interchangeably; while energy flow is mentioned in soil food web studies, the work itself refers to material flows, mainly carbon and nitrogen (Moore and de Ruiter, 2012). Few attempts have been made to link carbon and energy fluxes across the soil micro-food web (Barnes et al., 2018), which highlights the need for more empirical studies relating CUE and EUE of microbial decomposers with higher trophic levels.

The aim of the present study was to investigate the relationship between soil micro-food web structure and function and soil carbon and energy pathways. The microbial and nematode communities of four long-term arable field sites, either fertilized with farmyard manure (FYM) or unfertilized (UF), were investigated. Decomposition channels were analysed using the fungal to bacterial ratios of phospholipid fatty acids and the respective nematode trophic groups as well as the nematode Channel Index. Micro-food web activity and carbon allocation were determined by microbial CUE, EUE and nematode metabolic footprints. We hypothesized that: *i)* site-specific environmental filtering leads to micro-food webs with similar patterns in abundance and main type of decomposers, *ii)* long-term FYM application increases carbon and energy flow to bacteria and the metabolic footprints of their grazers, and *iii)* nematode ecological indices (e.g. channel index) are a proxy for microbial resource and energy use efficiency.

2. Materials and methods

2.1. Field sites

Soils were derived from four arable field sites in Mid-Europe: two sandy loams —Dikopshof (DI) and Reckenholz (RE), a loamy sand —Thyrow (TH) and a silt loam —QualiAgro (QA). All sites are long-term field experiments investigating effects of different management practices. TH is close to the village Thyrow (Brandenburg, Germany), DI is located near Wesseling (North Rhine-Westfalia, Germany). The RE site is an arable field near Zurich (Switzerland), established as the Zurich Organic Fertilization Experiment. The QA soil originates from an experimental field close to the village Davron (Île-de-France, France). For information on soil properties, climate and arable management of sites see Table 1.

At these four long-term field experiments two treatments were chosen for this study: unfertilized (UF) and fertilized with farmyard manure (FYM). Soil was sampled with a spade from the upper 20 cm after harvest of crops in August (DI), September (QA and RE) and October (TH) 2021.

2.2. Nematodes

Nematodes were extracted from 40 g field fresh soil (n = 4 for each soil type) by a modified wet funnel method (Ruess, 1995). Extraction started with 20 °C for 24 h, followed by 6 h of heat with a stepwise temperature increase (+5 °C h^{-1}) from 20 to 45 °C. Nematodes were fixed in 4 % formaldehyde and stored at 4 °C until analysis. Using a light microscope, the total number of individuals was counted, and 10% were determined to family level. Feeding groups were assigned according to Yeates et al. (1993). The life strategy was ascribed to colonizers (*c*) and persisters (*p*), representing extremes on a *c/p* scale from 1 to 5 (Bongers, 1990). Colonizers are comparable to *r*-strategists, with a short life-cycle, high reproduction rate and positive response to resource enhancement. In contrast, persisters are *K*-strategists characterized by a long life-cycle, low reproduction rate and sensitivity to disturbance.

The Channel-Index (CI) provides information about the soil decomposition pathways (Ruess and Ferris, 2004). Values range between 0 and 100, with a high CI assigning a dominance of fungal and low CI of bacterial decomposition. The CI was calculated according to Ferris et al. (2001) as:

$$CI = 100 * \frac{0.8 * Fu_2}{3.2 * Ba_1 + 0.8 * Fu_2} \quad (1)$$

where Ba_1 represents the bacterial feeder with a *c-p* value of 1 and Fu_2 the fungal feeder with a *c-p* value of 2. Further, the f/b-ratio was

Table 1
Location, climate, agricultural management and soil properties at the long-term experimental field sites at Dikopshof, Thyrow, QualiAgro, and Reckenholz. Data derived from: Thyrow - Ellmer and Baumecker (2016), Kroschewski et al. (2022); Dikopshof - Ahrends et al. (2018), Rueda-Ayala et al. (2018); QualiAgro - Chalhoub et al. (2013), Van den Nest et al. (2015); and Reckenholz - Cagnarini et al. (2021), Weisskopf et al. (2010). UF – unfertilized, FYM - farmyard manure, TOC – total organic carbon, TN – total nitrogen.

Field site	Thyrow		Dikopshof		QualiAgro		Reckenholz	
Location	52°16′N, 13°12′E		50°81′N, 6°95′E		48°87′ N, 1°95′ E		47°43′ N, 8°52′ E	
Height above sea level (m)	40		62		120		438	
Climate	semi-continental		temperate oceanic		temperate oceanic		oceanic	
Annual mean temperature (°C)	9.2		10.5		10.8		9.5	
Annual mean rainfall (mm)	510		688		644		1050	
Soil texture	loamy sand		silt loam		silt loam		sandy loam	
Soil type	haplic retisol		haplic luvisol		haplic luvisol		haplic luvisol	
Aggregation	weak		moderate		moderate-strong		moderate	
Crop rotation	*Zea mays* L. *Secale cereale* L.		*Beta vulgaris* L. *Triticum aestivum* L. *Secale cereale* L. *Trifolium resupinatum* L. *Solanum tuberosum* L.		*Hordeum vulgare* L. *Avena sativa* L. *Hordeum vulgare* L. *Zea mays* L.		*Triticum aestivum* L. *Zea mays* L. *Solanum tuberosum* L. *Triticum aestivum* L. *Zea mays* L. *Hordeum vulgare* L. 2 years lay	
Fertilization since	1938		1904		2014		1949	
Application rate (t ha^{-1})	20		60		2		2.5	
Fertilization	**FYM**	**UF**	**FYM**	**UF**	**FYM**	**UF**	**FYM**	**UF**
Clay (%)	5.6	5.5	15.1	16.2	13.7	15.7	15.1	14.0
Silt (%)	11.1	11.1	68.9	67.3	80.9	79.8	33.8	33.2
Sand (%)	83.3	83.3	15.9	16.4	5.4	4.5	51.1	52.9
TOC (%)	0.68	0.28	0.74	0.69	1.42	0.71	1.05	0.81
TN (%)	0.06	0.03	0.08	0.08	0.14	0.07	0.11	0.09
pH ($CaCl_2$)	5.0	4.2	6.3	6.1	6.4	5.7	5.2	4.7

assigned, which describes the ratio of fungal-to bacterial-feeders based on their number (Freckman and Ettema, 1993).

Food web conditions were analysed by the enrichment (EI) and structure (SI) index using the following equations:

$$EI = 100 * \frac{e}{e+b}, SI = 100 * \frac{s}{s+b} \quad (2)$$

where b is the basal, s the structure and e the enrichment component (Ferris et al., 2001). The EI gives information on nutrient enrichment and the SI on stability and complexity of the soil food web. v

Nematode metabolic footprints translate nematode biomass and metabolic activity into carbon and energy flow in the food web (Ferris, 2010b). They are the sum of the production component (P) and the respiration component (R). P is the lifetime amount of carbon used for growth and egg production, and R expresses the carbon lost through metabolic activity. The metabolic footprint (F) is the sum of these two components ($F = P + R$) and was calculated as:

$$\mathrm{F} = \sum \left(N_t\left(0.1\left(W_t / m_t\right) + 0.237\left(W_t^{0.75}\right)\right)\right), \quad (3)$$

where N_t is the number of nematodes, W_t is the nematode body weight and m_t is the *c-p* value of the taxon *t*. The value *0.1* estimates the nematodes' carbon content in fresh matter, *0.237* is the fraction of the molecular weight of carbon in CO_2 and *0.75* describes the allometric power dependence of basal metabolism and body weight. For the calculation of nematode footprints, body weights (W_t) based on the nematode information system (see http://nemaplex.ucdavis.edu/ecology/nematode_weights.htm) were used.

Each footprint is an estimator for the contribution of the respective nematode functional group to soil ecosystem processes. According to Ferris (2010b) the following metabolic footprints were assessed to characterise the carbon and energy flow in the food web.

- enrichment footprint — nematodes responsive to resource enrichment
- structure footprint — higher trophic levels with regulatory function in the food web
- bacterivore, fungivore and herbivore footprint — indicators for carbon end energy entering the soil food web through the respective channel
- omnivore and predator footprint — longer food chains with higher trophic levels

The enrichment and structure footprints can be visualized by a faunal analysis diagram based on EI and SI. Both footprints are added in rhomboid shapes around the group averages. The four edges of the rhomboid were calculated with *SI - Fs/k* and *SI + Fs/k* for the x-axis coordinates and *EI - Fe/k* and *EI + Fe/k* for the y-axis coordinates. F_s is the structure and F_e is the enrichment footprint (Ferris, 2010b). The scalar $k = 0.15$ was chosen to best visualize the data set. The overall food web response is maximized when the rhomboid area becomes a square, i.e. the system is in metabolic balance and stability.

2.3. PLFA

Phospholipid fatty acids (PLFA) and heat release (see 2.5.) analyses were performed with air-dried and re-wetted soil, which afterwards was incubated for 10 days at a water pressure of pF 2.5. The PLFAs were extracted from 4 g soil (n = 3 for each soil type) according to the method of Bligh and Dyer (1959). In a fractionation step following the procedure of Frostegard et al. (1993), glycolipids, neutral lipids and PLFAs were separated using silica gel SPE cartridges (Bond Elut SI, 500 mg, 3 ml^{-1}, Agilent Technologies, Santa Clara, CA, USA). Subsequent methanolysis was carried out with 0.2 mol l^{-1} methanolic KOH according to Ruess et al. (2007). The resulting fatty acid methyl esters (FAMEs) were quantified by gas chromatography-mass spectrometry (GC/MS; Agilent 5977B GC/MSD, Santa Clara, California, USA).

The total PLFA concentration per sample was determined by summing up all predominant soil PLFAs. Groups were assigned based on marker fatty acids characteristic for Gram + bacteria (i15:0, a15:0, i16:0, i17:0), Gram-bacteria (cy17:0, cy19:0), saprotrophic fungi (18:2ω6,9c) and microfauna (20:4ω6,9,12,15) (Frostegård and Bååth, 1996; Ruess and Chamberlain, 2010). The f/b-ratio for PLFA was calculated using the marker 18:2 ω6 for saprotrophic fungi divided by the sum of fatty acid markers for Gram+ and Gram-bacteria.

2.4. Substrate induced microbial growth

Microbial growth parameters were determined in 25 g (dry weight) of field fresh soil (n = 3 for each soil type) amended with a solution of glucose (5 mg g^{-1}) and mineral salts ($(NH_4)_2SO_4$ - 0.95 mg g^{-1}, KH_2PO_4 - 1.5 mg g^{-1}; $MgSO_4$ * 7 H_2O - 1.9 mg g^{-1}. The rate of CO_2 emission was detected hourly by a respirometer (Respicond V, Sweden) at 22 °C.

Microbial activity ($R_{CO_2}(t)$) was characterized through the kinetic analysis of respiratory curves by fitting the model (Eq. (4))

$$R_{CO_2}(t) = A + B \cdot exp(\mu t) \quad (4)$$

to the experimental rates of CO_2 release during the lag and exponential growth phase after glucose addition (Panikov, 1995). Here, A is the initial respiration rate independent of growth, B denotes the initial rate of respiration associated with growth, μ denotes the maximal specific growth rate of soil microorganisms and t is incubation time. The theoretical background of kinetic respiration analysis and the derivation of Eqn. (4) has been described in detail in previous publications (Blagodatsky et al., 2000; Wutzler et al., 2012). The parameters were optimized using Origin (OriginPro 2022b; OriginLab Corporation, Northampton, MA, USA).

Total microbial biomass was calculated based on initial value of substrate induced respiration (A + B in Eq. (4)), which was multiplied by conversion factor 60.15 based on Kaiser et al. (1992). The initial active fraction of microorganisms (r_0) was estimated from the parameters as

$$r_0 = \frac{0.1 \cdot B}{A + 0.1 \cdot B}. \quad (5)$$

The carbon use efficiency (CUE) of microbial growth on glucose was estimated from CO_2 release according to

$$CUE = 1 - \frac{C_{CO_2}}{C_{glucose}}, \quad (6)$$

where C_{CO_2} denotes the cumulative CO_2 emission after 60 h of incubation (mol C g^{-1}) and $C_{glucose}$ denotes the total amount of carbon added to the soil as glucose (mol C g^{-1}). Assuming that all glucose was consumed by the end of the experiment, this provides a simple estimate of the carbon incorporated into newly formed biomass during microbial growth (Hagerty et al., 2018).

2.5. Energy release

For energy release measurements, the same substrate and mineral solutions as for respiration measurement were used (see 2.4.; n = 3 for each soil type). Heat flow (μW g^{-1} s^{-1}) during microbial glucose degradation was determined using a TAMAIR (UB TA Instruments, New Castle, USA) isothermal conduction calorimeter with eight dual channels at an internal temperature of 20 °C. The mean heat (J g^{-1}) was determined by approximating the integral with the following equation:

$$\int_{x_0}^{x_n} f(x)\mathrm{d}x = h \sum_{i=0}^{n-1} y_{i+\frac{1}{2}}, \quad (7)$$

where h is the step size, given by $h = x_{i+1} - x_i$ (uniform spacing), $y_{i+\frac{1}{2}}$ is the value of the curve at the midpoint of the interval $[x_i, x_{i+1}]$. This can be calculated using linear interpolation between the points y_i and y_{i+1}: $y_{i+\frac{1}{2}} = \frac{1}{2}(y_i + y_{i+1})$.

To compare the dynamics of the cumulative heat release at the sites, a logistic model $C = C_0 * \left(1 - \frac{1}{(1-f_k) * e^{k_1 * t} + f_k}\right)$ (Wirsching et al., 2023) was fitted to the mean heat and the inflection point as the time of maximum heat release $rate_{max} = \frac{1}{k_1} * \ln\left[\frac{1}{1-f_k} + 1\right]$ was determined.

Energy use efficiency (EUE) was estimated from measured heat release using the energy balance approach corresponding to the estimation of CUE (see 2.4.):

$$EUE = 1 - \frac{Q}{\Delta E_{glucose}}. \quad (8)$$

Here, Q denotes the cumulative heat release (kJ g^{-1}) after the rate of heat release first returned to the level observed in unamended controls and $\Delta E_{glucose}$ denotes the total energy content in added glucose (kJ g^{-1}). Eqns. (6) and (8) rely on the assumption that all glucose has been metabolized by the time of estimation (Wang and Kuzyakov, 2023).

2.6. Statistics

Statistical analyses of data were performed using RStudio® for Windows (PBC, Version 1.4.1106). Normality of distribution was checked with the Shapiro-Wilk Test. The proportional f/b-ratio was arcsin transformed before analysis of the normality of distribution. Given normal distribution, effects of the factors fertilizer (UF, FYM) and site (TH, DI, QA, RE) as well as their interactions were determined by two-way ANOVA. The significance of group differences was then analysed using Tukey HSD Post-Hoc tests ($p < 0.05$). Non-parametric data (e.g. nematode metabolic footprints; nematode trophic groups; PLFA biomarkers) were analysed by Kruskal-Wallis and Dunn-Bonferroni ($p < 0.05$) tests. Correlations between means were performed using Pearson's correlation, using ($p < 0.05$) as significance-threshold.

Statistical analysis of CUE, EUE and SIGR data as well as linear regressions were performed with the *stats* module of the *scipy* package (Version 1.11.0) in Python (Version 3.9.7). Significant differences between means were assessed using pairwise t-tests ($p < 0.05$) adjusted for multiple testing using the Benjamini-Hochberg method (Benjamini and Hochberg, 1995) as implemented in the *scipy.stats.false_discovery_control* function.

3. Results

3.1. Effects of environmental conditions and fertilizer amendment on microbial and nematode communities

Nematode population densities across the investigated arable field sites ranged from 5 to 22 Ind. g^{-1} DW and increased from TH over DI and QA to RE (Fig. 1a). Nematode numbers were higher in fertilized (FYM) soil at RE and QA, compared to TH and DI or TH, respectively. Fertilization had a significant positive impact on population densities at all field sites (Table S1) and increased nematode numbers by 29–52%. Nematode densities also differed between sites, yet there was no significant interaction between site and fertilization. In all soils bacterial feeders were most abundant (~60%), followed by plant feeders (~24%) and fungal feeders (~12%; Table S2).

Total PLFAs ranged from 11 to 48 nmol g^{-1} DW (Fig. 1c). Comparable to nematode population densities, PLFA concentration increased from TH over DI and RE to QA. Lowest concentrations were detected in unfertilized (UF) soil at TH (significant compared to QA and RE) and highest in fertilized QA soil (significant compared to DI and RE-UF). In sum, PLFA concentration was significantly affected by site and fertilizer application, with no interaction between site and fertilization (Table S1). Nematode population densities and total PLFAs correlated significantly and positively (Fig. S1).

Generally, the fungal to bacterial (f/b) ratios of microbial and nematode populations were low across sites, suggesting mainly bacterial driven decomposition processes (Fig. 1b–d). However, in TH and DI, nematode communities indicated a higher fungal contribution in unfertilized than in fertilized plots, which was significant for TH. In contrast, nematode f/b-ratios in QA and RE were not altered by fertilization. Both f/b-ratios were affected by site and fertilization, with a tendency towards an interaction in nematodes (Table S1). The f/b-ratios

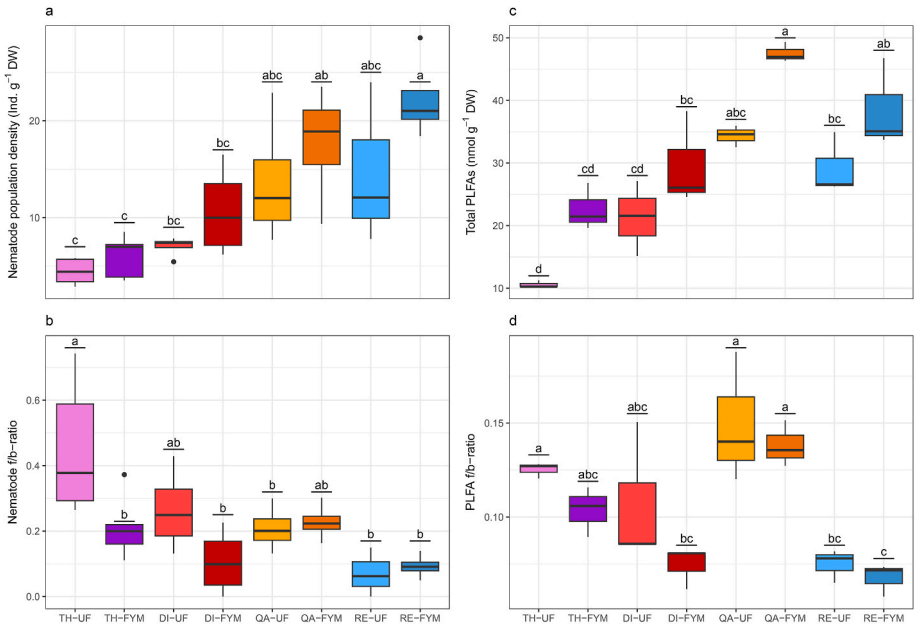

Fig. 1. Impact of site and fertilization on the population density of nematodes, biomass of microorganisms and major decomposition pathways. Investigated were the field sites Thyrow (TH), Dikopshof (DI), QualiAgro (QA) and Reckenholz (RE), either unfertilized (UF) or fertilized with farmyard manure (FYM). Box plots show: a) Nematode population density (Ind. g^{-1} DW ± s.d.), b) Nematode fungal-to bacterial-feeder (f/b) ratio (±s.d.), c) Total phospholipid fatty acids (PLFAs in nmol g^{-1} DW ± s.d.) and d) PLFA fungi to bacteria (f/b) ratio (±s.d.). One-way ANOVA followed by Tukey HSD, bars with the same or no letters are not significantly different at $p < 0.05$.

of microorganisms and their nematode grazers tended to correlate positively ($r = 0.65, p = 0.082$). While fungal feeder densities correlated significantly with the concentration of fungal PLFAs (Fig. S2d), bacterial feeders and bacterial PLFAs did not (Fig. S2b).

Microbial and nematode community responses were partly linked to soil physical and chemical properties and to local climate (Table S3). Nematode population densities and total PLFAs correlated significantly and positively with total organic carbon and total nitrogen. Further significant positive correlations were observed for nematode population densities with mean annual precipitation and for total PLFAs with soil water content. In contrast, no link to soil texture, i.e. clay, silt and sand, was assigned (Table S3). For f/b-ratios only one significant negative correlation was detected, between nematode grazers and mean annual precipitation.

3.2. Response of nematode metabolic footprints

Nematode metabolic footprints represent the sum of the standardized carbon utilization of the respective indicator taxa, with the enrichment footprint (F_e) assigning the contribution of nematodes responsive to resource enrichment. The F_e showed that food webs were moderately enriched at TH and DI and highly enriched at RE, while they occupied an intermediate position in QA (Fig. 2a). This food web enrichment was significant for TH compared to RE–FYM. The structure footprint (F_s), reflecting the contribution of higher trophic levels to carbon utilization, was generally low. As for the F_e, the F_s differed between sites (Table S4) and was highest at RE (Fig. 2a). The multifunctionality of both footprints, given by the area of the rhomboid, displays low structure (horizontal axis) paired with considerable enrichment (vertical axis), indicating unbalanced micro food-web conditions irrespective of site.

Carbon and energy entering the food web via the respective channels can be assigned by the corresponding metabolic footprints (Fig. 2b). The bacterivore footprint (F_b), i.e. the metabolic activity of bacterial feeders, was the largest contributor to these processes. Their functional role was most prominent at the fertilized sites in RE and QA, where the F_b was

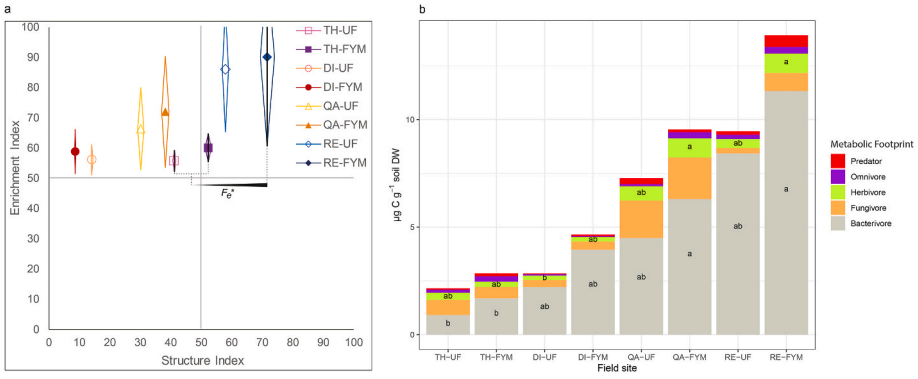

Fig. 2. Impact of site and fertilization on nematode metabolic footprints. Investigated were the field sites Thyrow (TH), Dikopshof (DI), QualiAgro (QA) and Reckenholz (RE), either unfertilized (UF) or fertilized with farmyard manure (FYM). a) Nematode fauna profile depicting Enrichment and Structure Indices (axes) and enrichment and structure footprints (rhomboids), b) metabolic footprints (µg C g^{-1} soil DW) of predators, omnivores, herbivores, fungivores and bacterivores. F_e – enrichment footprint, * with $p < 0.05$.

significantly higher than in TH. These site effects on the activity of the bacterial channel were significant (Table S4). Further, the F_b correlated significant and positively with the concentration of bacterial PLFAs (Fig. S2a).

The fungivore (F_f), herbivore (F_h), omnivore (F_o) and predator (F_p) footprints did not follow the same pattern as the F_b (Fig. 2b). The magnitudes of carbon and energy flow through the fungal channel, represented by the F_f, were significantly affected by site (Table S4) and positively correlated to the concentration of fungal PLFAs (Fig. S2c). The contribution of the herbivore channel, indicated by the F_h, was also significantly affected by site. Most carbon and energy via the root pathway were retained in fertilized soils at QA and RE, and least in unfertilized DI soil (Fig. 2b). The functional activity of higher trophic levels was low, with the F_o and F_p combined contributing in average 12 % to nematode carbon utilization at TH, but only 4 % at all other field sites. The F_o was affected by site and tended to respond positively to fertilization, while the F_p only showed a trend for a site effect (Table S4).

3.3. Substrate induced growth and heat release in the soil microbiome

Substrate-induced growth respiration (SIGR) of the different field sites displayed two different patterns in response dynamics (Fig. 3). In the fertilized soils of TH and DI, SIGR peaked ~6 h earlier than in the unfertilized variant (Fig. 5c). In the nutrient-rich soils of QA and RE, maximum SIGR was achieved after 27–29 h and 36 h, respectively (Fig. 3), with no differences between fertilized and unfertilized variants (Fig. 5c).

This pattern, separating TH and DI from QA and RE, was also visible in respiration based microbial characteristics. Generally, microbial biomass carbon estimated by SIGR was greater in the nutrient-rich soils of QA and RE (Fig. S4b). The specific growth rate of microorganisms was significantly lower in fertilized than unfertilized soils at QA and RE, yet no fertilizer effect was apparent in the less rich soils at TH and DI (Fig. S4c). While fertilization did not alter microbial biomass carbon in any field site (Fig. S4b), it significantly increased active biomass at RE and TH, with a trend at QA ($p = 0.078$, Fig. S4a). Basal respiration was only significantly influenced by fertilization in DI (Fig. S4d). The microbial metabolic quotient qCO_2 was not affected by fertilization (Fig. S4e).

The same mean cumulative heat release of 19 J g^{-1} soil was achieved at all sites during the incubation period, regardless of fertilization (Fig. 4). The dynamics of heat release generally differed between unfertilized and fertilized soils, with the maximum heat release calculated from the function fitted to the cumulative heat curve reached earlier in fertilized (~7 h) compared to unfertilized soils ($p < 0.01$), which was significant for all sites except RE.

3.4. Links in carbon and energy processing in the micro-food web

The nematode Channel Index (CI) is a measure for functional group contribution and a predictor of dynamics in soil decomposition channels (Fig. 5a). The CI assigned differences in carbon and energy flow based on site and fertilization, without interactions of these factors (Table S1). Moreover, the CI was higher in unfertilized TH soils than at QA and RE ($p < 0.05$). This higher fungal participation in unfertilized TH soil (and to a lesser extent DI) indicated by the CI, mirror the time lag in SIGR responses (Fig. 5c), overall reflecting slower decomposition processes. In contrast, the sites QA and RE were characterized by a low CI, i.e. bacterial based decomposition with high turnover rates, irrespective of fertilizer amendment. Correspondingly, no differences in SIGR due to fertilization were detected.

Carbon use efficiency (CUE) spanned from 0.27 to 0.56, with TH soil showing high, DI and RE intermediate, and QA low values (Fig. 5c). Fertilization reduced CUE in TH and DI, whereas no effects were apparent for QA and RE. Energy use efficiency (EUE) was quite homogenous across sites, with values ranging between 0.72 and 0.76 (Fig. 5d). Similar to CUE, EUE appears to be higher in unfertilized than in fertilized soils of TH and DI, but neither site nor fertilization had a significant impact. In general, EUE was higher and less variable than CUE, with both metabolic measures of microbial activity correlating significant and positively (Fig. S3a).

The links in process dynamics were supported by significant, positive correlations with time until maximum SIGR with CUE (Fig. S3b) as well as with EUE (Fig. S3c). Furthermore, the CI tended to correlate positively with EUE ($r = 0.70$, $p = 0.053$). Overall, the pattern of the nematode CI, microbial response time in SIGR, CUE and EUE at the four different field sites were quite similar.

4. Discussion

4.1. Environmental conditions shape micro-food web structure and function

The patterns of nematode population densities and microbial biomass were comparable, increasing from TH over DI to QA and RE. This connection indicates a distinct link between functional levels of the micro-food web, which is in line with other studies in arable land (Briar

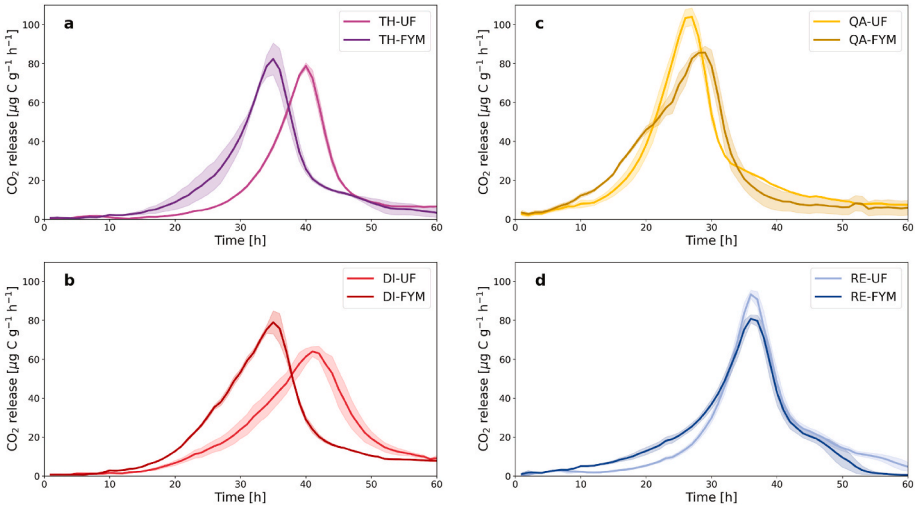

Fig. 3. Substrate induced growth respiration (CO_2 release in µg C g^{-1} h^{-1} ± s.d.). Incubated were soils from the field sites: a) Thyrow (TH), b) Dikopshof (DI), c) QualiAgro (QA) and d) Reckenholz (RE), either unfertilized (UF) or fertilized with farmyard manure (FYM).

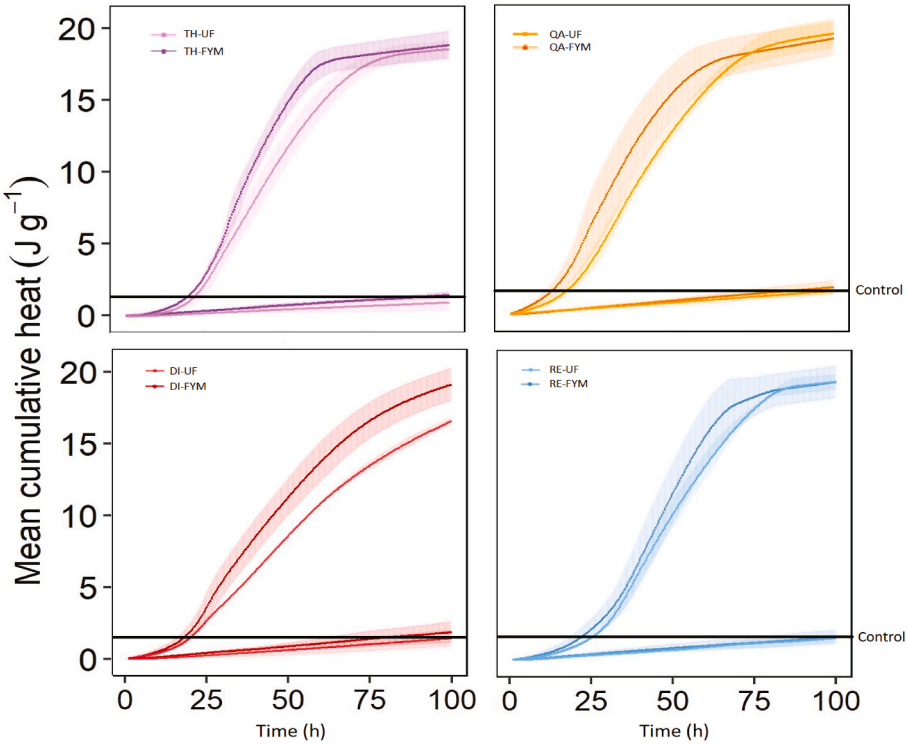

Fig. 4. Energy release as cumulative heat (J g^{-1}) after addition of glucose as substrate. Incubated were soils from the field sites: a) Thyrow (TH), b) Dikopshof (DI), c) QualiAgro (QA) and d) Reckenholz (RE), either unfertilized (UF) or fertilized with farmyard manure (FYM).

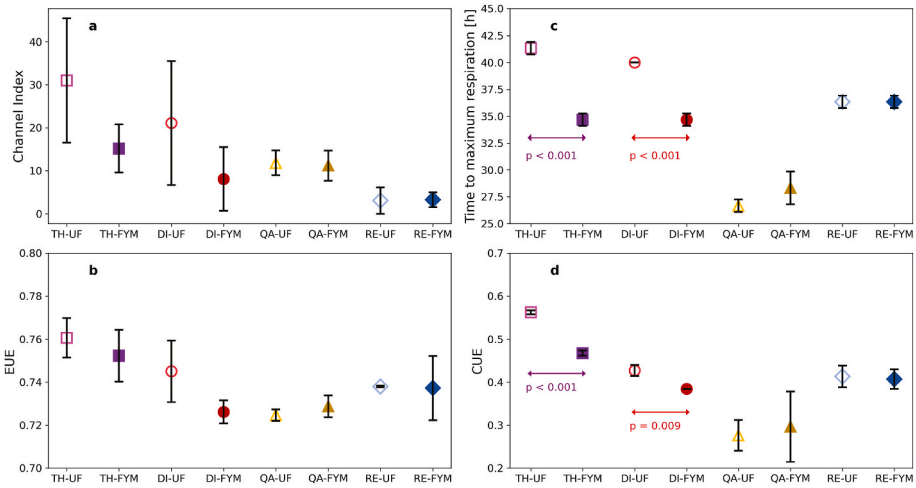

Fig. 5. Pattern in carbon and energy flow across microbiota in the soils from the field sites Thyrow (TH), Dikopshof (DI), QualiAgro (QA) and Reckenholz (RE), either unfertilized (UF) or fertilized with farmyard manure (FYM). Given are means ± s.d. for: a) Nematode Channel Index, b) Time to maximum substrate induced respiration, c) Carbon use efficiency (CUE) and d) Energy use efficiency (EUE). The *p*-values indicating differences between UF (empty symbols) and FYM (filled symbols) soils are obtained from Bonferroni-corrected pairwise t-tests.

et al., 2011; Glavatska et al., 2017; Scharroba et al., 2016). While the field site pattern was distinct, the positive impact of long-term FYM fertilization on nematode population densities and microbial biomass was less pronounced. However, this promotion of microorganisms and their grazers is in line with other studies on long-term organic amendment (van Eekeren et al., 2009; Villenave et al., 2003; Wang et al., 2022; Watts et al., 2010). Likely, differences in soil nutrient status (e.g. nitrogen), altered microbial growth and in turn the development of higher trophic levels (Krivtsov et al., 2007; van Eekeren et al., 2009). In addition, sandy soils with low water storage capacity, as in TH, negatively affect size and structure of nematode and bacterial populations (Kaiser et al., 2016; Richter et al., 2018, 2023). Low moisture restricts grazer movement by disconnecting soil pores (Neher, 2010; Otobe et al., 2004). It is well acknowledged that microbial and nematode communities are strongly influenced by the abiotic soil environment, e.g. water content, temperature, humus content, pH value, and C and N content (Foley et al., 2023; Kitagami et al., 2018; Richter et al., 2018, 2023; Xiong et al., 2021). The similar pattern observed in the population development further reveals a distinct biotic filtering by interactions between microorganisms and their grazers (Xu et al., 2023).

This strong link across trophic levels was also reflected by the functional composition of the different micro-food webs. With moderate

soil nutrient content (TH and DI), organic fertilization increased nutrients and shifted decomposition in favor of bacteria (Cui et al., 2018; Villenave et al., 2010; Wang et al., 2022). Such nutrient supply fosters the growth of opportunistic bacterial species, outcompeting slower-growing fungi (Grabau et al., 2019; Mulder and Maas, 2017). However, in nutrient-enriched micro-food webs (QA and RE), carbon and energy channeling were already dominated by bacteria and their grazers; these decomposition channels were therefore not responsive to long-term organic fertilization. Sustained organic enrichment can therefore halt heterotrophic succession, resulting in a consistent structure of functional groups in the soil microbiome (Ferris and Bongers, 2006). In sum, site-specific environmental filtering resulted in micro-food webs differing in functional groups and main decomposition pathways. This provided a good basis for analysing the pattern of the relative magnitude of carbon and energy channels as well as their usage in the microbiomes across sites.

4.2. Carbon and energy flux assigned by metabolic footprints

The enrichment footprint revealed a high nutrient supply at QA and especially at RE, indicating that food web processes in the nutrient-enriched sites were mainly driven by *r*-strategists, a common feature of arable soil (Ewald et al., 2022; Neher, 2010). These taxa are characterized by high rates of metabolic and respiratory activity, efficiently exploiting available bacterial resources and quickly turning over carbon and nutrients (Ruess and Ferris, 2004). Related bottom-up forces can induce long food chains with sufficient matter transfer to higher trophic levels (Scheu et al., 2005), as reflected by the structure footprint at RE. However, also in the sandy soils at TH, the structure footprint assigned a considerable activity of higher trophic levels with regulatory function in the food web. Here, likely the combination of low soil moisture and nutrient availability resulted in competition for resources at the food web base, fostering top-down control (Ferris et al., 2001; Richter et al., 2023).

The bacterivore footprint was the largest contributor to resource flow across sites. Using metabolic footprints Ciobanu et al. (2015) showed the general dominance of bacterial-based energy channels in different types of soil ecosystems, i.e. forests, grasslands and shrublands. Based on the herbivore footprint, less plant carbon entered the micro-food web at soils with moderate nutrient content compared to nutrient-rich, fertilized soils. This can be caused by differences in crop rotation at the long-term field experiments (see Table 1), e.g. presence of suitable host plants (Biswal, 2022; Thurau et al., 2010). Further, nutrient enrichment positively affects root biomass and rhizodeposition, enhancing the plant carbon transfer into belowground food webs (Bonkowski et al., 2009; Hemmerling et al., 2022). Finally, compared to the other functional footprints, the omnivore and predator footprints were low across sites. This is likely due to the disturbance of omnivores and predators by agricultural practices such as tillage or pesticides (Ewald et al., 2020, 2022; Okada and Harada, 2007; Zhang et al., 2012), resulting in a low abundance and thus a low contribution to the carbon flow in the food web.

The divergent energy distribution among functional groups suggests that energetic food webs are impacted by environmental conditions such as soil properties (e.g. texture, pH) and climate. The functional footprints of nematodes were mainly affected by site, likely reflecting the overall energetic status of the soil (Moore and de Ruiter 2012). Thus, at a regional scale, interacting environmental factors have distinct effects on energy pathways (Ciobanu et al., 2015). In contrast, the impact of long-term resource enhancement via fertilization was only partly visible in the detritivore food chain; only the bacterivore footprint tended to increase with fertilization. This supports recent ideas, that organic amendment promotes a uniform energy flow through different trophic levels of the nematode food web, which is maintained by respective alterations in community composition (Wan et al., 2022b; Zhu et al., 2023).

4.3. Nematode indices as proxy for resource and energy use efficiency

Fertilization decreased microbial carbon use efficiency (CUE) and the time to maximum CO_2 release in substrate induced growth respiration (SIGR) only in soils with moderate nutrient status. Considering the impact of fertilization on soil PLFA concentration, this could be related to higher microbial biomass in fertilized soils, yet neither the microbial biomass C nor the metabolic quotient were impacted by organic amendment. However, in nutrient-rich, fertilized soils active microbial biomass displayed lower maximum specific growth rates, indicating increased competition between microorganisms involved in substrate utilization (Blagodatskaya et al., 2014). Additionally, substrate turnover was faster in nutrient-rich, fertilized soils, as indicated by the larger active biomass. Similar effects were shown in earlier work for other long-term fertilization experiments (Blagodatsky et al., 1994).

A striking observation are the matching patterns of CUE and CI across sites and fertilizer treatments, indicating similar life strategies of microorganisms and nematodes in the respective micro-food webs. Microbial *K*-strategists with efficient slow growth (Blagodatskaya et al., 2007; Fierer et al., 2007) likely were frequent in soils with a lower nutrient status, particularly when unfertilized, which is in line with the slower decomposition processes indicated by the nematode fauna (CI; Ferris et al., 2001). Conversely, copiotrophic microorganisms, with a shorter lag-period and faster growth on available substrate, flourished under high resource availability irrespective of fertilization, utilizing easily available carbon resources quickly, but inefficiently (Arcand et al., 2017; Blagodatskaya et al., 2014). Correspondingly, the nematode communities were dominated by strong *r*-strategists, which have high energy-transfer rates and less efficiency (Schiemer, 1983). This coherence of microbial and nematode carbon and energy processing suggests that the CI is a valuable tool to determine these dynamics in the soil microbiome.

Microbial energy use efficiency (EUE) and CUE showed a positive linear relationship. This was also described by other theoretical and experimental approaches (Chakrawal et al., 2021; Manzoni et al., 2018), indicating that mass (carbon and nutrients) and energy exchanges were closely linked (Kästner et al., 2024). Arcand et al. (2017) observed similar thermodynamic efficiencies when comparing long-term organic and conventionally managed arable land, likely due to differences in soil organic matter and additional heat released thereof. According to the current understanding, the dynamic balance between the CUE and EUE is mainly dependent on the quality of decomposed substrate (Kästner et al., 2021), energy and matter stabilization within necromass (Joergensen and Wichern, 2018), community composition and physiological state of microorganisms (Endress et al., 2024). Wang and Kuzyakov (2023) suggested that CUE is generally higher than EUE, as energy restricts microbial growth more than carbon. However, compared to CUE, EUE was higher, indicating that microorganisms were not energy limited in the range of the investigated arable soils.

Remarkably, EUE was more balanced across sites compared to CUE. This homogenisation of EUE in microbial populations could be related to trophic interactions. Grazers alter microbial community structure, thereby changing maintenance requirements and metabolic capacity, which in turn can affect community level EUE (Wang and Kuzyakov, 2023). Grazing induces stress and defence responses, and the related synthesis of macromolecules is carbon and energy dependent (Feist and Palsson, 2010). However, nematode predation further affects microbial cell-maintenance, cell-growth and dormancy, changing the energy balance of the microbial prey, as some processes are energy-dependent but do not require carbon. Carbon-independent cell-maintenance processes include the recycling of macromolecular compounds (Nunan et al., 2015), while cell-growth involves the maintenance of chemical gradients (Estrada et al., 2016; Paerl et al., 2000) and dormancy that of energized membranes (Van Bodegom, 2007). For nematodes it has been shown that the energy flux, i.e., energy consumption by different trophic groups, increases in uniformity across food web levels (Wan et al.,

2022b; Zheng et al., 2023; Zhu et al., 2023). The present study indicates that this may also apply to the entire micro-food web, including the microorganisms at its base.

5. Conclusion

This study is the first to establish a link between the structure and function of the soil micro-food web with carbon and energy use efficiency in an arable field soil. The trophic networks were highly connected and fueled the flow of carbon and energy along the same microbial and microfaunal channels. This link allows the use of higher trophic levels such as nematodes for mapping changes in microbial resource processing. The observed differences in the response of carbon and energy utilization highlights the shortcoming of using these terms interchangeably. Regardless of soil properties and organic amendment, energy use efficiency was quite balanced across field sites, providing empirical evidence that the flow of energy within the micro-food web is homogenized. In future studies, the combination of an energetic micro-food web approach with ecological indices and metabolic footprints of nematodes will better allow deciphering the mechanisms behind energy flow in soil systems.

CRediT authorship contribution statement

Miriam van Bommel: Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Karoline Arndt:** Investigation. **Martin-Georg Endress:** Visualization, Validation, Formal analysis, Data curation. **Fatemeh Dehghani:** Investigation. **Johannes Wirsching:** Writing – review & editing, Visualization, Investigation, Formal analysis. **Evgenia Blagodatskaya:** Writing – review & editing, Supervision, Funding acquisition. **Sergey Blagodatsky:** Writing – review & editing, Visualization, Supervision, Funding acquisition. **Ellen Kandeler:** Writing – review & editing, Supervision, Funding acquisition. **Sven Marhan:** Writing – review & editing. **Christian Poll:** Writing – review & editing. **Liliane Ruess:** Writing – review & editing, Supervision, Project administration, Funding acquisition, 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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2024.109575.

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