

Size-trophic spectrum in soil food webs across ecto- and arbuscular mycorrhiza-dominated deciduous forests

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Article

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62 Abstract

63 Forests dominated by arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF)
 64 differ in soil biogeochemistry, but whether these basal contrasts reorganise energy
 65 channelling across soil food webs remains unclear. We combined the energy flux approach
 66 with compound-specific stable isotope analysis of amino acids (CSIA-AA) of carbon and
 67 nitrogen to reconstruct soil food webs in 24 paired AMF- and EMF-dominated deciduous
 68 forest sites. We quantified energy channelling from basal resources (plants, fungi and bacteria)
 69 to primary consumers and predators across a wide body-size spectrum: nematodes,
 70 microarthropods, macroarthropods and earthworms. Despite moderate taxon-specific
 71 differences, total energy flux, its distribution among plant, bacterial and fungal channels, and
 72 predation were similar between the forest types. Instead, energy channelling exhibited a
 73 consistent size-structured pattern: bacterial channelling and predation were highest in
 74 nematodes, fungal channelling peaked in microarthropods, plant channelling peaked in
 75 macroarthropods, and earthworms formed a terminal compartment drawing on fungal and
 76 bacterial channels. These findings show consistency of soil food web functioning across
 77 temperate deciduous forests and suggest that the size spectrum of soil fauna predicts energy
 78 channelling ('size-trophic spectrum') and, therefore, is closely linked to the ecosystem
 79 functioning of forest soils.

80 Main

81 In terrestrial ecosystems, most photosynthetically fixed energy (i.e., primary production)
 82 ultimately flows into soil and fuels belowground food webs^{1,2}. Soil food webs comprise
 83 networks of organisms spanning a wide range of body sizes, including microbes and fauna
 84 from microscopic protists to earthworms, that predominantly exploit incoming dead organic
 85 matter^{3,4}. Through their feeding activities and interactions with plants and microbes, soil
 86 fauna process plant and microbial resources and thereby influence ecosystem-level
 87 functioning⁵⁻⁷. At the food-web level, energy of basal resources flows through three principal
 88 energy channels: plant-, fungal- and bacterial-based, corresponding to the processing of plant
 89 material (living or dead), fungi and bacteria, respectively^{8,9}. The balance among these
 90 channels is therefore expected to shape key ecosystem processes, from herbivory and
 91 decomposition to nutrient mineralisation and soil carbon dynamics^{3,5}. Yet we know little on
 92 how energy flux is partitioned among these channels across ecosystems with different plant
 93 and microbial resources, and whether this partitioning follows predictable patterns across
 94 consumer communities that differ in composition and body size.

95
 96 Temperate deciduous forests provide an ideal system to address this gap, as tree resource
 97 economics can shape soil food-web functioning through litter quality and forest
 98 microclimate¹⁰. Belowground carbon and nutrient dynamics in forests are particularly
 99 strongly shaped by mycorrhizal associations¹¹⁻¹³, especially by arbuscular mycorrhizal fungi
 100 (AMF) or by ectomycorrhizal fungi (EMF), which differ fundamentally in nutrient-
 101 acquisition strategies^{12,14}. AMF-dominated systems are generally associated with relatively
 102 high-quality, rapidly decomposing litter, elevated bacterial activity and faster nutrient
 103 turnover^{15,16}, whereas EMF-dominated systems rely more strongly on fungal-mediated access
 104 to organic nutrient pools and are associated with chemically defended, slowly decomposing
 105 litter and higher fungal biomass¹⁶⁻¹⁹. These contrasting nutrient economies presumably create
 106 different resource bases for soil food webs, such that relatively fast, more plant- and

bacterial-based energy channelling could be expected in soil food webs of AMF-dominated forests, but slower and more fungal-based channelling in EMF-dominated forests^{8,9}. However, recent evidence suggests that the resource preferences of major soil fauna taxa are largely similar across forests with different dominant mycorrhizal types⁸. This apparent mismatch raises a critical question: if different animals feed on the same food, does energy channelling diverge at the entire food-web level due to shifts in the composition and body-size structure of consumer communities^{5,20,21}?

Soil-fauna communities comprise major invertebrate groups that differ systematically in body size, diet breadth, feeding mode and use of basal resources (e.g., plants, bacteria and fungi)^{22,23}. Small-bodied nematodes feed primarily on fungi and bacteria²⁴ and can strongly influence microbial community structure and composition^{25,26}. Intermediate-sized microarthropods, such as Collembola and Oribatida, exploit fungal and detrital resources and can play important roles in shaping microbial communities and decomposition processes^{27–29}. Larger detritivores, such as Diplopoda and Isopoda, primarily fragment and ingest coarse plant litter and associated soil organic matter, thereby also consuming substantial microbial biomass colonising these substrates³⁰. Predatory macroarthropods, such as Araneae and Chilopoda, feed on a broad range of prey, including both primary and secondary decomposers, and thereby integrate energy fluxes from lower trophic levels that originate from multiple basal resources^{3,31}. Earthworms have traditionally been viewed as macro-detritivores that ingest soil and dead organic matter in various stages of decay, with dead plant material constituting much of the material consumed, although associated microorganisms are also ingested^{22,32}. Together, these taxa form size-based compartments of soil food webs that exploit the same basal resources in different proportions⁴. However, the empirical data to test this quantitatively across the soil faunal size spectrum are lacking. Addressing this gap is crucial for identifying the key players in each of the major energy channels in soil food webs across the body size spectrum of soil fauna and how they are linked to energy channelling and to the functioning of soil food webs across environmental contexts^{33–35}.

Here, by reconstructing empirically parameterised soil food webs and quantifying energy fluxes, we test how energy flows through plant-, fungal- and bacterial-based channels in AMF- and EMF-dominated temperate deciduous forests (beech, oak, maple and ash stands), and how this channelling is organised across the soil-faunal size spectrum. We integrated data on the density and body size of nematodes, microarthropods, macroarthropods and earthworms across 24 forest sites with estimates of individual body mass and metabolic rate³⁶, trophic information derived from compound-specific stable isotope analysis of amino acids (CSIA-AA)³⁷, and complementary trait information³ to reconstruct soil food webs and calculate energy fluxes under a steady-state assumption (losses = gains)³⁸. This integrative approach, recently pioneered by Junggebauer et al.²⁷, enables basal resource use to be parameterised empirically rather than inferred from assumed trophic relationships, allowing more precise reconstruction of energy-channel partitioning. We tested two hypotheses: (1) following the biogeochemical differences between mycorrhizal types, plant- and bacterial-based (“fast”) energy channels are more pronounced in AMF- than in EMF-dominated forest soil food webs; (2) across forests and mycorrhizal types, the four size-based groups differ systematically in how energy is channelled: nematodes mainly via the bacterial energy channel, microarthropods via the fungal energy channel, macroarthropods via the plant energy channel, and earthworms nearly equally via all three energy channels.

Results

Energy channeling in forests dominated by AMF and EMF

Soil food-web energy fluxes did not differ significantly between AMF- and EMF-dominated forests in terms of total flux, its partitioning among plant, fungal and bacterial channels, or predation (Figs. 1 and 2; Supplementary Table 5). Mean total flux across all soil fauna was $251 \pm 42 \text{ mW m}^{-2}$ in AMF-dominated forests and $235 \pm 36 \text{ mW m}^{-2}$ in EMF-dominated forests (Linear Mixed-Effects Models (LMMs), mycorrhizal type effect: $\chi^2 = 0.7$, $P = 0.393$). The plant energy channel accounted for the largest proportion of the total flux (43–45% in both forest types), followed by the fungal (33–34%) and bacterial energy channels (15–17%); predation accounted for approximately 7% of the total flux across forests (Fig. 1).

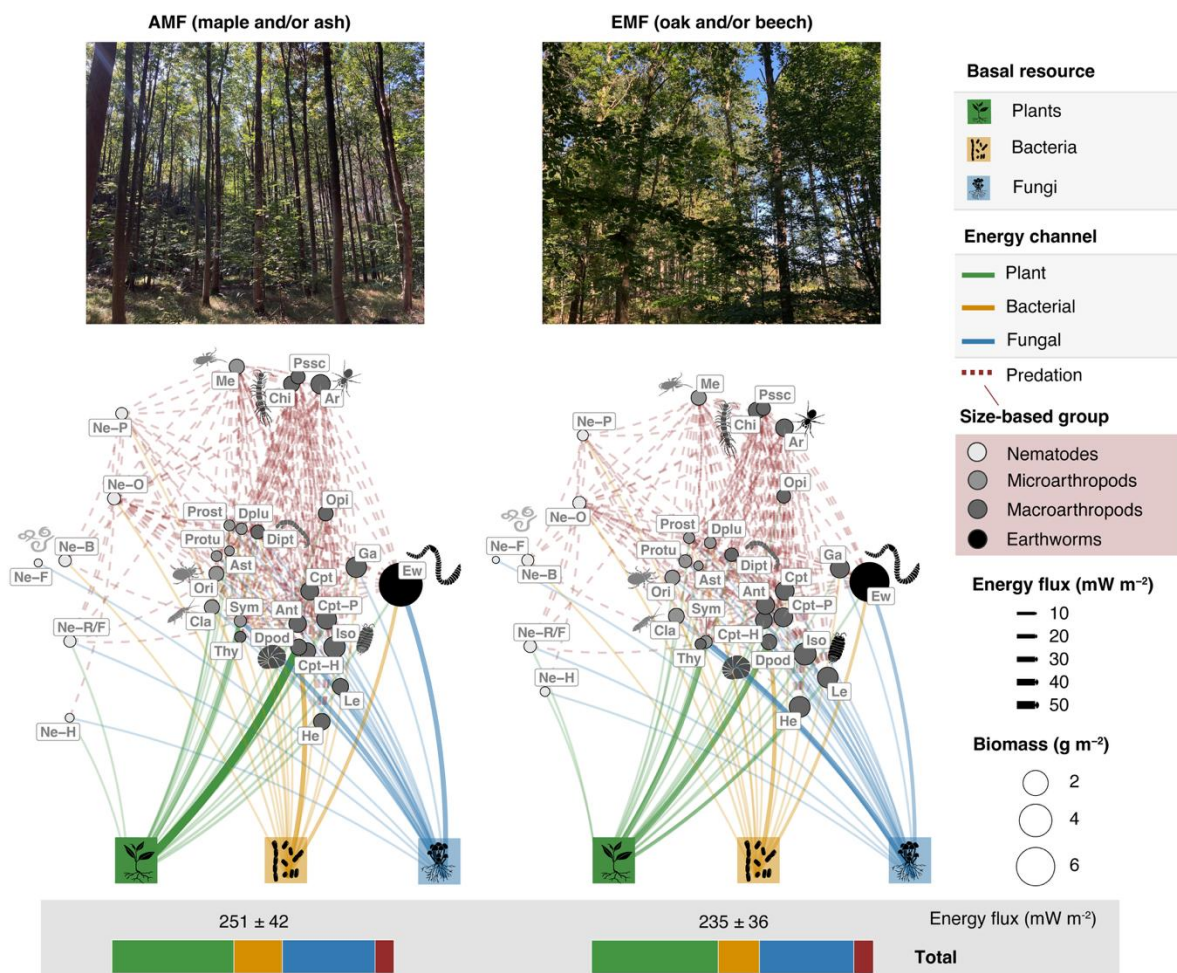


Fig. 1 | Energy fluxes in soil food webs of arbuscular mycorrhizal (AMF) and ectomycorrhizal (EMF) dominated deciduous forests. Basal resources, representing the origins of energy flux, are shown as rectangles at the base of the diagram and coloured according to the respective energy channel: plant (green), bacterial (yellow), fungal (blue). Predation across all channels is shown in red. Soil food-web nodes are shown as bubbles representing consumer trophic guilds and are positioned according to feeding preference (horizontal axis, integrating resource contribution from AA $\delta^{13}\text{C}$ Bayesian mixing models and ordered from smaller to larger body mass) and trophic level (vertical axis, calculated from feeding preferences and predator–prey traits). Nodes are grouped into four size-based categories: nematodes (light grey), microarthropods (medium grey), macroarthropods (dark grey) and earthworms (black). Node positions were slightly jittered to minimise overlap

while preserving their relative arrangement. Connecting lines indicate mean energy fluxes; line width is proportional to flux magnitude (mW m^{-2}). The relative contributions of plant, bacterial and fungal energy channels, as well as predation, to the total energy flux are shown as stacked proportional bar charts ($n = 12$ sites per mycorrhizal system). Mean total energy flux, calculated as the sum across all energy channels, is shown above the bar charts as mean $\pm$ s.e. Soil animal and basal resource icons were created by S. Meyer.

Contribution of size-based groups and taxa to total energy flux

The total energy flux varied significantly among the four size-based groups (LMM, effect of ecological group: $\chi^2 = 58.5$, $P < 0.001$; Supplementary Table 5). Macroarthropods accounted for about 53–58% of the total energy flux (AMF: 145.5 ± 36.8 ; EMF: $125.2 \pm 22.0 \text{ mW m}^{-2}$), followed by microarthropods with 24–34% (AMF: 59.8 ± 8.1 ; EMF: $78.8 \pm 25.0 \text{ mW m}^{-2}$), earthworms with 11–16% (AMF: 41.1 ± 11.1 ; EMF: $26.0 \pm 8.9 \text{ mW m}^{-2}$), and nematodes with ~2% (AMF: 4.6 ± 2.3 ; EMF: $5.1 \pm 1.1 \text{ mW m}^{-2}$; Fig. 2a,b). At the taxon level, total energy flux also differed strongly among major high-rank soil invertebrate taxa (LMM: $\chi^2 = 364.9$, $P < 0.001$), but within taxa, there were no significant effects of mycorrhizal forest type (Fig. 3; Supplementary Table 5). Diplopoda accounted for the largest share of the total energy flux (40–42%; AMF: 105.9 ± 33.2 ; EMF: $93.7 \pm 26.0 \text{ mW m}^{-2}$), which was about an order of magnitude greater than the flux of most other taxa. The second largest flux was observed for Lumbricidae (11–16%; AMF: 41.0 ± 11.1 ; EMF: $25.7 \pm 9.1 \text{ mW m}^{-2}$), followed by Isopoda (3–6%; AMF: 8.6 ± 2.0 ; EMF: $13.7 \pm 7.0 \text{ mW m}^{-2}$) and Collembola (3–5%; AMF: 8.1 ± 0.7 ; EMF: $10.6 \pm 3.0 \text{ mW m}^{-2}$). All remaining taxa displayed substantially lower fluxes, ranging from 1.9 to 5.1 mW m^{-2} across forest types.

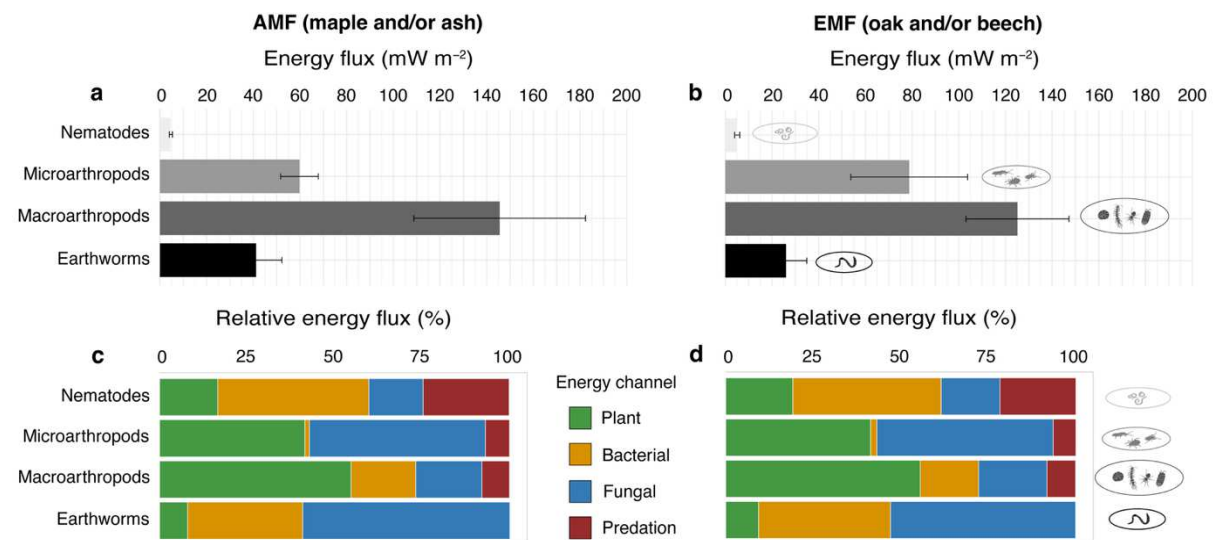


Fig. 2 | Energy flux partitioning across size-based groups of soil invertebrates in arbuscular mycorrhizal (AMF) and ectomycorrhizal (EMF) dominated deciduous forests. **a–b**, Mean energy fluxes (mW m^{-2} , mean $\pm$ s.e.) are shown for soil nematodes (light grey), microarthropods (medium grey), macroarthropods (dark grey) and earthworms (black) in AMF-dominated forests (**a**) and EMF-dominated forests (**b**). **c–d**, Relative contributions of outgoing energy fluxes from plants (green), bacteria (yellow) and fungi (blue), as well as predation (red), to total energy flux are shown for AMF-dominated forests (**c**) and EMF-dominated forests (**d**). Statistical results from linear mixed-effects models are provided in Supplementary Table 5. Soil animal icons were created by S. Meyer.

Contribution of size-based groups and taxa to energy channels

Within the four major size-based groups, nematodes received most energy through the bacterial channel (~43%), whereas plant and fungal channels and predation each contributed smaller but broadly similar proportions (16–25%) (Fig. 2c,d; Supplementary Table 5). Microarthropods received most energy through the fungal channel (49–51%), with the plant channel representing the second-largest share (40–42%). Macroarthropods received most energy through the plant channel (55–56%). By contrast, earthworms received most energy through the fungal channel (53–60%), with an additional major contribution from the bacterial channel (33–38%). Within these broad group-level patterns, the dominant higher-rank taxa showed consistent informative variation (Fig. 3b; Supplementary Table 5). In microarthropods, Oribatida received most energy through the fungal channel (70–72%), while Collembola had slightly more balanced contributions from the fungal (57–61%) and the plant channel (31–33%). Among decomposer macroarthropods, Diplopoda received most energy through the plant channel (52–57%), whereas Isopoda had broadly comparable contributions from the plant (42–45%) and fungal (43–46%) channels. Diptera exhibited the most mixed pattern, with similar contributions from the plant (26–28%) and fungal channels (35–36%) as well as predation (32–33%).

Among predators in reconstructed soil food webs, Mesostigmata received most energy through fungal (~43%) and bacterial channels (31–34%), with smaller contributions from the plant channel (22–26%) (Supplementary Fig. 4a). Araneae received most energy through plant (45–51%) and fungal channels (39–43%), and Chilopoda through fungal (47–50%) and plant channels (33–36%); bacterial inputs were comparatively low in both groups (10–12% and ~17%, respectively) (Supplementary Fig. 4b,c). Overall, predator energy channels reconstructed from food-web topology broadly corresponded with empirically measured (CSIA-AA-derived) feeding preferences in Araneae and Chilopoda, whereas correspondence was weaker in Mesostigmata (Supplementary Fig. 4).

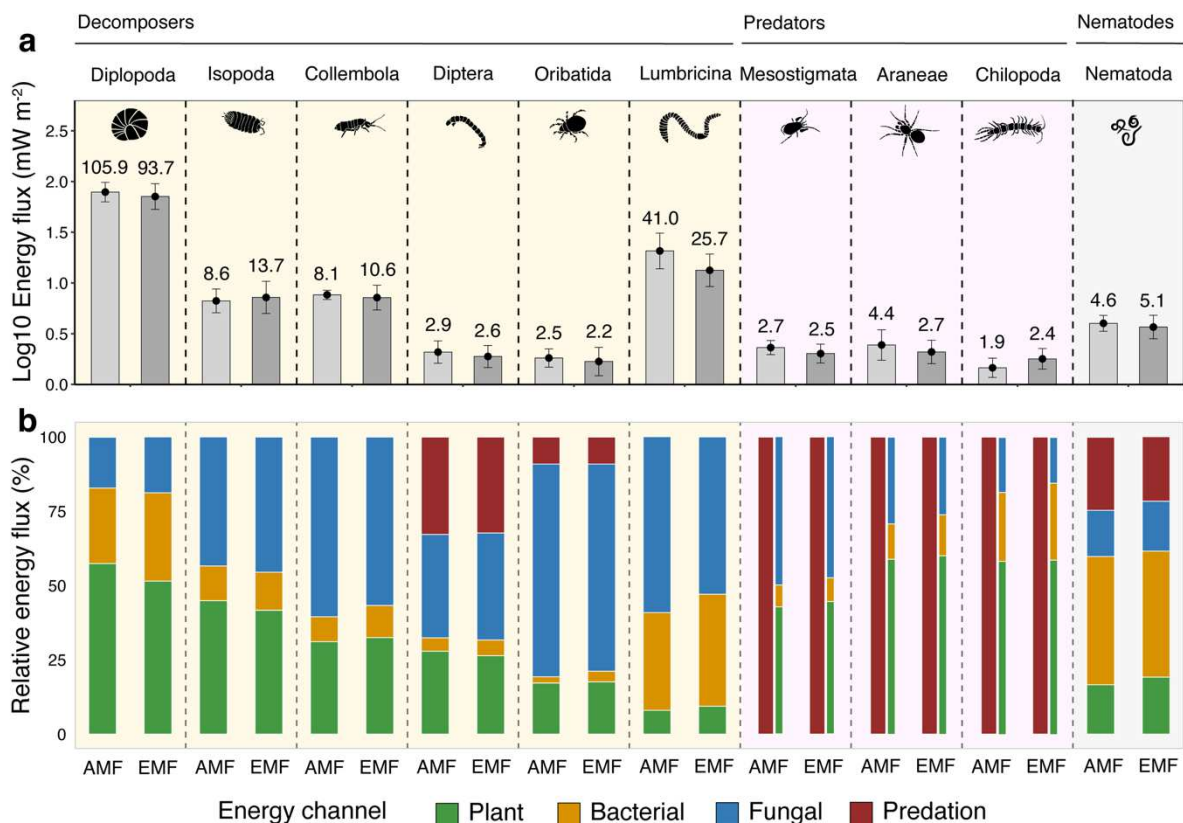


Fig. 3 | Energy flux partitioning and distribution across soil invertebrate taxa in arbuscular mycorrhizal (AMF) and ectomycorrhizal (EMF) dominated deciduous forests. **a**, Mean energy fluxes (mW m^{-2} , mean $\pm$ s.e.) of soil invertebrate taxa are shown for AMF-dominated (light grey) and EMF-dominated (dark grey) forests. Bars show $\log_{10}$ -transformed energy fluxes, with untransformed values given above the error bars. **b**, Relative contributions of energy flux from plant (green), bacterial (yellow) and fungal (blue) resources, as well as predation (red) to per-taxon energy flux. Taxa are arranged within the size-based groups nematodes, microarthropods (Collembola, Oribatida, Mesostigmata), macroarthropods (Diplopoda, Isopoda, Diptera, Araneae, Chilopoda) and earthworms. Within these groups, taxa are separated into decomposers and predators according to trophic position; decomposers are ordered according to their proportional use of plant resources. For predators, CSIA-AA-based resource use (inferred from $\delta^{13}\text{C}$ values of essential amino acids (eAAs) and expressed as the relative contributions of plant-, fungal- and bacterial-derived resources) was not used in food-web reconstruction, but is shown here for comparison (see Supplementary Fig. 4). Nematodes are presented separately because they span multiple trophic levels. Statistical results from linear mixed-effects models are provided in Supplementary Table 5. Soil animal icons were created by S. Meyer.

Energy channelling in the ‘size-trophic spectrum’

Different soil fauna groups occupied distinct domains along a continuous body size spectrum: nematodes dominated the smallest classes (0.000001–0.01 mg), microarthropods the intermediate classes (0.001–1 mg), macroarthropods a broad intermediate-to-large range (0.01–100 mg), and earthworms the largest classes (1 mg to >100 mg) (Fig 4a). Total community energy flux varied nonlinearly with the consumer body size, increasing steeply at small sizes, peaking at microarthropods, and levelling off and slightly declining towards macroarthropods and earthworms across both AMF- and EMF-dominated forests (Fig 4b and Supplementary Table 6; size class effect: $\chi^2 = 362.7$, $P < 0.0001$). When resolved by channel, absolute energy fluxes showed distinct size-dependent patterns. Plant-channel flux increased with body size, peaked in macroarthropods, and declined in earthworms ($\chi^2 = 182.6$, $P < 0.0001$). Bacterial-channel flux was highest in the smallest nematodes, decreased at intermediate sizes, and increased again towards larger macroarthropods and earthworms ($\chi^2 = 177.0$, $P < 0.0001$). Fungal-channel flux increased sharply from nematodes to microarthropods and remained high towards larger size classes ($\chi^2 = 233.3$, $P < 0.0001$). Predation flux peaked in macroarthropods ($\chi^2 = 71.6$, $P < 0.0001$).

To clarify body-size-associated changes in energy channelling independently of the total energy flux, we analysed the relative contribution of each energy channel to the total flux within consumer size classes. The relative importance of the plant energy channel was highest in macroarthropods but lowest in small nematodes, microarthropods, and earthworms ($\chi^2 = 105.5$, $P < 0.0001$). The bacterial energy channel showed higher proportional allocation in the smallest nematodes and the largest earthworms ($\chi^2 = 203.3$, $P < 0.0001$). The fungal energy channel peaked in microarthropods and the largest earthworms but was lowest in macroarthropods ($\chi^2 = 142.4$, $P < 0.0001$). Predation contributed proportionally most in nematodes, declined towards microarthropods, and increased again across macroarthropod-dominated classes, where it remained broadly stable ($\chi^2 = 71.7$, $P < 0.0001$).

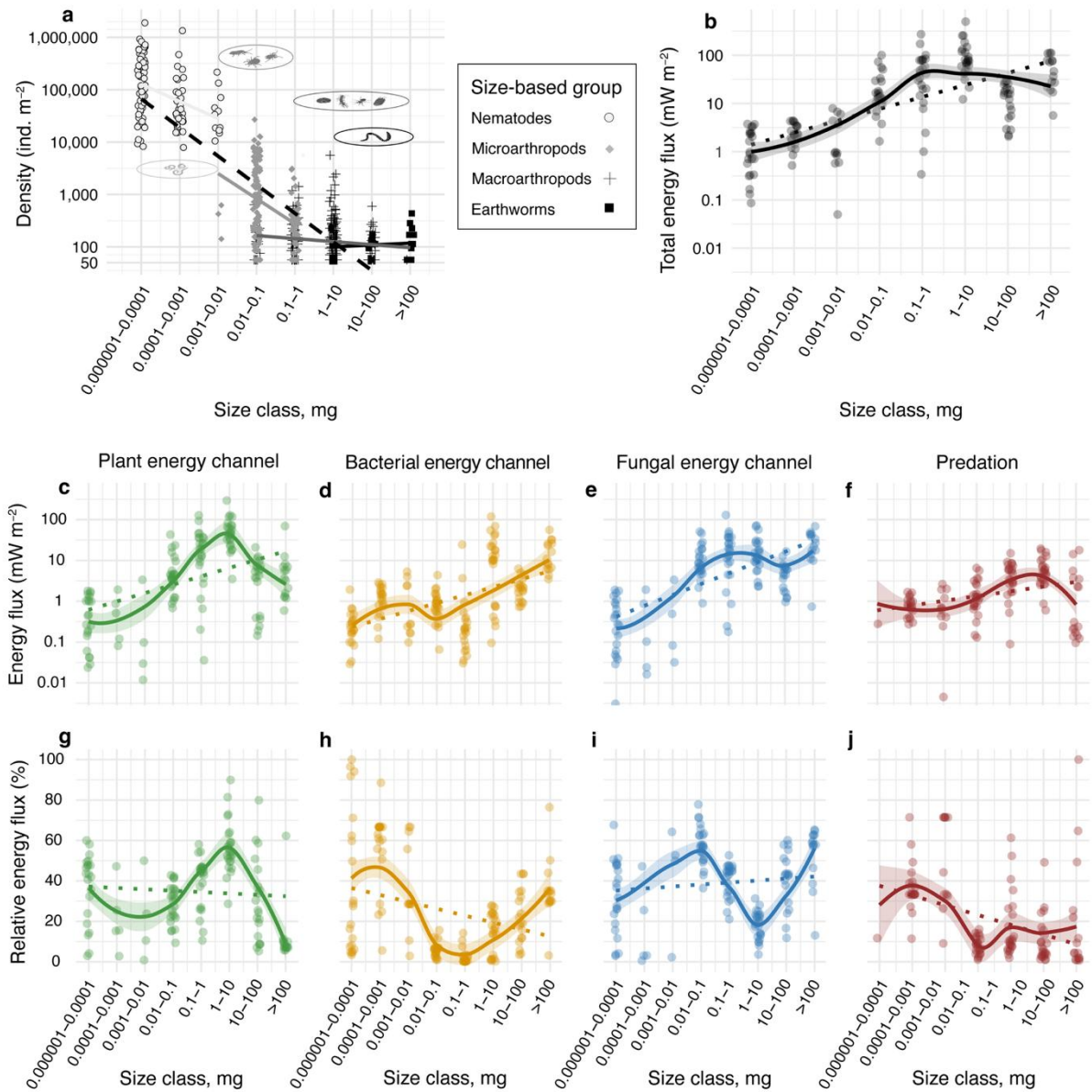


Fig. 4 | Size-trophic spectrum in soil food webs across temperate deciduous forests. Soil fauna were grouped into eight equal $\log_{10}$ -scaled body-mass classes, from 0.000001 to >100 mg. Points represent site-level density or energy flux estimates within a given body-mass class (size-based groups are given separately in panel a). **a**, Density spectrum of soil fauna along the body-mass gradient. Silhouettes and point symbols indicate the characteristic body-mass ranges of four size-based groups: nematodes (light-grey circles), microarthropods (medium-grey diamonds), macroarthropods (dark-grey crosses), and earthworms (black squares). The black dashed line indicates the overall linear fit of site-level soil-fauna density across the body-mass spectrum. **b**, Total energy flux (black line) along the body-mass spectrum. **c–j**, Absolute energy flux (**c–f**) and relative contributions to the total energy flux (**g–j**) within the given size class of the energy fluxes from plants (green), bacteria (yellow) and fungi (blue) and predation (red). Solid and dashed lines indicate nonlinear and linear fits, respectively. Data from AMF and EMF forests are given together. Linear mixed-effects model outputs are provided in Supplementary Table 6. Soil animal icons were created by S. Meyer.

Discussion

By combining the energy flux approach with CSIA-AA, we reconstructed realistic soil food webs and quantified energy channelling across size classes of soil fauna in temperate deciduous forests dominated by AMF or EMF. Contrary to our first hypothesis, the two forest types showed remarkably similar overall patterns of energy channelling. Instead, generally in line with our second hypothesis, energy channelling followed a consistent size–trophic spectrum across forest types, with bacterial channels being highest at the smallest nematodes, fungal channels peaking in microarthropods, plant channels peaking in macroarthropods, fungal and bacterial channels becoming prominent again in earthworms, and predation being highest in nematodes before remaining lower but comparatively stable across macroarthropods.

Despite well-established differences between AMF- and EMF-dominated forests in litter quality, microbial functioning and soil carbon storage^{16,17,39,40}, the major energy channels supporting soil-fauna food webs were strikingly similar across the two systems. This convergence is notable given that mycorrhizal associations are widely expected to shape how carbon enters soils and is transformed during decomposition (slowly decomposing litter and greater soil carbon retention in EMF-dominated forests^{17,40,41}, and faster decomposing litter, microbial turnover and nutrient cycling in AMF-dominated forests^{16,39}). Yet these pronounced differences in basal carbon-processing did not translate into equally strong divergence in consumer-level energy channelling, suggesting that soil animal food webs reorganise contrasting basal inputs into broadly conserved patterns of energy channelling. This observation is consistent with recent CSIA-AA evidence showing that trophic positions and basal resource use of major soil-fauna groups differ little between AMF- and EMF-dominated deciduous forests⁸, as well as with broader evidence that resource use by major decomposer taxa remains remarkably similar across temperate forests²⁷. This convergence does not preclude strong effects of tree community composition on belowground functioning. Recent work across European forests shows that leaf and fine-root economic traits can shape soil food-web functioning and shift energy channelling between fine-root- and litter-derived resources¹⁰. The apparent discrepancy may instead reflect differences in resource resolution: tree traits may alter the use of specific plant-derived inputs by microorganisms, whereas mycorrhizal dominance may have weaker effects on the broader plant, fungal and bacterial channels sustaining soil fauna. A likely explanation is that differences in basal carbon processing do not necessarily alter the subset of microbial and detrital resources actually accessible to soil fauna. For example, differences in fungal guild composition may not translate directly into shifts in the fungal resources actually used by consumers if saprotrophic and other microbially processed resources remain sufficiently available in both systems^{28,42}. Accordingly, mycorrhizal dominance appears to strongly shape basal decomposition and soil carbon dynamics, while remaining only partly coupled to the major energy channels sustaining soil-fauna food webs.

Major soil invertebrate taxa differed consistently in their connection to energy channels. Nematodes received energy predominantly from bacteria (Fig. 2), in line with classical soil food-web concepts that place them in the bacterial energy channel⁴³. Their contribution to community-wide flux nevertheless remained small in our forests (~2%), likely reflecting the very low nematode densities recorded at our sites at the time of sampling, which were more than 30-fold lower than the average reported for temperate forest soils⁴⁴ and suggesting that their contribution might be underestimated. Microarthropods relied mainly on the fungal channel, with a secondary contribution from the plant channel. This pattern was most evident

in Collembola and Oribatida, both of which obtained most of their energy from fungal resources, more strongly so in Oribatida (Fig. 3). Such a pattern is consistent with the close trophic association of soil microarthropods with fungi^{45–48} and with recent evidence from forests across Germany showing broad dominance of fungal energy channelling in these taxa²⁷. By contrast, macroarthropods relied primarily on the plant channel (Fig. 2), with Isopoda contributing most strongly to this pattern, whereas Diplopoda used plant and microbial resources more evenly (Fig. 3). This contrasts with recent findings from German beech and spruce forests, where both taxa relied predominantly on the fungal energy channel²⁷. This discrepancy may be partly explained by differences in sampling season and associated shifts in species composition and resource availability⁴⁹. Some methodological explanation is also possible, because basal resource use was resolved here using four essential amino acids rather than the five used previously²⁷, which may have slightly affected source resolution. Even so, this uncertainty is unlikely to alter the main conclusion that macroarthropods in our systems relied mainly on the plant energy channel, highlighting the need for cross-system studies combining CSIA-AA with quantitative energy-flux approaches to disentangle ecological variation from methodological sensitivity. The largest invertebrates, earthworms, derived the largest share of their energy from the fungal energy channel (Fig. 3), consistent with recent studies from beech and spruce forests²⁷ but contrasting with earlier work in grasslands^{50,51}, likely reflecting higher fungal biomass in forest soils⁵². Together, these comparisons indicate that major soil invertebrate taxa define distinct basal entry points that organise energy channelling within the soil animal food web.

The body-size spectrum of soil fauna has long been recognised as an important descriptor of community structure and its consequences for ecosystem processes^{4,33–35}, but our results show specifically the mechanism behind this link: the relationship between body size and energy flux is not a simple monotonic scaling pattern, but reflects a systematic non-linear replacement of energy channels. Relative energy fluxes from bacterial, fungal and plant resources peaked in different body-size compartments, indicating that body size is a major axis along which basal resources are accessed and processed in soil. A likely explanation is that body size mediates both access to resources and the way in which those resources are exploited. Soil is not a homogeneous feeding environment, but a structurally complex matrix composed of pores, aggregates, and water-filled channels that constrain which resource types different consumers can reach⁵³. At the same time, body-size-related morphological and behavioural traits shape how those resources are processed once encountered^{34,54,55}. Smallest consumers in our study, represented largely by nematodes, had access to more bacterial resources in tiny water-filled micropores and rhizosphere microsites, linking them to rapid microbial turnover and nutrient mineralization^{26,56,57}. Intermediate-sized microarthropods, relied on fungal biomass that penetrates soil matrix in the form of mycelium, is not restricted to micropores, and partly accessible for grazing, whose consumption affects fungal-driven decomposition and litter transformation^{28,58–61}. Macroarthropods relied on plant resources, which are ample in litter, at the litter–soil interface, and in the root-associated pore space; by fragmenting and transforming coarse detritus, these consumers facilitate its entry into downstream animal and microbial processing^{30,62}. However, the shift from microbial towards plant diet along the body size spectrum (nematodes to macroarthropods) was reversed at the largest end, where earthworms relied predominantly on microbial resources, especially fungi. This is connected to the unique ecological strategy of mass-soil consumption by earthworms, linking the largest body-size classes to microbially transformed organic matter, nutrient mineralization and soil bioturbation^{32,63–65}. These patterns indicate that soil invertebrates resolve into a body-size–trophic spectrum, that is, a predictable organisation of energy

channelling across consumer body sizes, which in turn links the size structure of soil fauna to the ecosystem functioning of forest soils.

Predation contributed most to total energy flux in nematodes, declined towards microarthropods, and then remained comparatively stable across macroarthropods. The high predatory share in nematodes reflects long trophic chains and active predation at the smallest end of the soil food web⁴, where confined microsites in rhizosphere and detrital hotspots can intensify predator–prey encounters^{53,66,67}. By contrast, although predatory Mesostigmata contributed substantially within the intermediate microarthropod classes (Fig. 3), their proportional importance was diluted by the dominance of fungal-feeding Collembola and Oribatida. In the larger macroarthropod classes, predation remained relatively constant because Araneae and Chilopoda maintained a persistent predatory compartment alongside the plant-centred detritivore compartment (Fig. 3). CSIA-AA broadly supported reconstructed predator energy channels in Araneae and Chilopoda, but less so in Mesostigmata, where only the plant channel showed a significant correspondence (Supplementary Fig. 4). This points to some limitations of trait-based soil food-web reconstructions in predicting predator feeding relationships, particularly for taxa such as Mesostigmata. However, this does not affect the major conclusions of our study. Predation therefore emerges as another integral, size-structured component of the size–trophic spectrum, showing potential decline in top-down control from small to large body-size compartments while still generally reflecting basal resource channelling at lower trophic levels. In this sense, basal resource contributions measured in predators may also be informative for inferring, at least roughly, the main routes of energy channelling at lower trophic levels.

Conclusions and implications

Our study provides an empirically parameterised view of energy channelling in soil food webs across AMF- and EMF-dominated temperate deciduous forests. We reveal that the partitioning of energy among plant-, fungal- and bacterial-based channels, as well as total energy flux and predation, remains broadly similar between the two forest types. Instead, energy channelling in soil food webs is structured primarily by the taxonomic composition and body-size distribution of consumer communities. These patterns resolved into a consistent size–trophic spectrum, shifting from predominantly bacterial channelling in nematodes to fungal-dominated channelling in microarthropods, to plant-dominated channelling in macroarthropods, before returning to predominantly microbial channels in earthworms. Across AMF- and EMF-dominated forests, this consistent organisation of energy channelling across body-size classes links the size spectrum of soil fauna to key soil processes, including litter breakdown, microbial turnover and nutrient cycling, and thereby to key aspects of temperate forest ecosystem functioning.

These findings point to broader implications of the size spectrum in consumer communities. Since body size consistently predicts resource use across soil consumers, soil size spectrum may provide a tractable framework for diagnosing energy channelling in soil food webs (and potentially in other food-web types⁶⁸). If this coupling between body size and dominant energy channels extends beyond the studied systems, shifts in the size structure of soil-fauna communities could be used to infer corresponding changes in decomposition, microbial turnover and trophic transfer. Such a framework could be especially valuable for forest management, restoration and global-change research, because body-size distributions can often be assessed more consistently across sites and times than complete trophic interactions or taxonomically resolved feeding links^{34,54}. Broadly, this perspective provides an integrative

link between soil biodiversity and ecosystem functioning, connecting variation in faunal composition to ecosystem-level processes^{4,35}. A key next step is therefore to test how general the size–trophic spectrum is across ecosystems that differ strongly in vegetation type, litter quality, management intensity and climate, including grasslands, arable soils, coniferous forests and forests across wider biogeographic gradients. Combining such comparisons with experimental manipulations, CSIA-AA-informed energy-flux reconstructions, and empirical assessment of soil functions will be essential for determining where this spectrum is maintained, where it shifts, and whether body size can serve not only as a descriptive axis of soil biodiversity, but also as a predictive axis for diagnosing changes in belowground functioning under environmental change.

Methods

Field sites and experimental design

The study was carried out in deciduous temperate forests with domination of either EMF- or AMF-associated trees situated across Denmark and Germany (Supplementary Fig. 1). The study design included paired EMF and AMF sites at 12 locations (n = 24 sites in total). In AMF systems, the dominant tree species across sites were maple (*Acer sp.*) and/or ash (*Fraxinus excelsior*), while in EMF systems, the dominant tree species across sites were oak (*Quercus sp.*) and/or beech (*Fagus sylvatica*). Soils were silty loam with pH ranging between 4.3–7.1 (AMF) and 3.7–6.6 (EMF). Details on these sites are available in Supplementary Table 1 and in ref.⁸.

Soil sampling

Soil samples for extracting microarthropods, macroarthropods and earthworms were collected by taking four soil cores (15 cm in diameter) per site (96 soil cores in total), including both litter and the top 10 cm of the underlying soil, in September and October 2023. For nematode extraction, four additional soil cores (5 cm in diameter) were collected per site (96 soil cores in total) from the 0–10 cm soil layer during the same sampling period. Samples were transported to the laboratory within 2 days of sampling and stored in plastic bags at 4 °C until further analysis.

Soil nematodes

Soil nematodes per soil sample were extracted and counted from approximately 25 g of fresh soil using a modified Baermann method and preserved in 4% formaldehyde⁶⁹. From each site, 100 randomly selected nematode individuals were inspected under the inverted microscope and assigned to trophic guilds of bacterial feeders (Ne-B), fungal feeders (Ne-F), root feeders (Ne-R), root- or fungal-feeders (Ne-R/F), predators (Ne-P) and omnivores (Ne-O)²⁴. To approximate mean body mass per sample and trophic group, we measured body length and width from ten randomly chosen individuals. Nematode fresh body mass was then estimated from published body length–body mass regressions based on the mean body length and width of each trophic group at each site⁷⁰. Nematode abundances were first expressed per gram of dry soil and subsequently converted to densities per square meter using soil bulk density (and sampling depth) data.

Soil microarthropods, macroarthropods and earthworms

Soil meso- and macro-fauna (microarthropods, macroarthropods, and earthworms) were extracted from intact soil cores using a dynamic heat gradient (Kempson extraction), with temperature gradually increasing from 25°C to 50°C over seven days⁷¹. Extracted specimens were preserved in 70% ethanol, counted to determine abundance per square meter, and identified under a dissecting microscope to the family or order level, yielding 31 taxonomic groups. To enable subsequent image-based body-size estimation, all individuals from each sample were then arranged in Petri dishes and scanned at high resolution following the Soil BON Foodweb imaging protocol (https://soilbonfoodweb.org/wp-content/uploads/2024/02/SBF-Team-Imaging-samples_v1.3.pdf).

To estimate body mass, all individuals in each scanned sample were digitally annotated in BIIGLE (<https://biigle.de/>, Biodata Mining Group, Bielefeld University), and the two-dimensional projected body area of each specimen was extracted from these annotations. Individual fresh body mass was then estimated for each taxonomic group at each site using taxon-specific allometric regressions relating projected body area to body mass (Details on regressions are available in Supplementary Table 2). Biomass of each taxonomic group and total community biomass per site were subsequently calculated either by multiplying mean individual body mass by population density or, when all individuals in a sample were measured, by summing individual-level mass estimates.

Parameterising feeding preferences using CSIA-AA and literature data

Compound-specific stable isotope analysis of amino acids (CSIA-AA) provides a powerful approach for quantifying both trophic position and the use of bacterial, fungal and plant basal resources in soil food webs, with plant resources comprising litter and living roots and/or shoots³⁷. We used previously published CSIA-AA measurements from the same study sites⁸, but reran the Bayesian mixing model to generate site-specific estimates of basal resource use for the present analysis. This re-analysis followed the same modelling framework as ref.⁸, but generated taxon-by-site resource proportions rather than the AMF-versus EMF-level estimates reported in the original publication. The dataset comprised CSIA-AA measurements for nine major high-rank soil invertebrate taxa occurring across the study sites: microarthropods (Collembola, Mesostigmata and Oribatida), macroarthropods (Araneae, Chilopoda, Diplopoda, Diptera and Isopoda), and earthworms (Lumbricina) (Supplementary Table 3). For the present study, the relative contributions of bacterial, fungal and plant basal resources were re-estimated by fitting Bayesian mixing models in *MixSIAR*⁷² to the $\delta^{13}\text{C}$ values of four essential amino acids (leucine, threonine, phenylalanine and methionine) in consumers. Bacteria, fungi and plants, characterised by distinct $\delta^{13}\text{C}$ signatures of these amino acids, were used as source end-members, and the models returned the proportional contribution of each basal resource type to consumer diets. Trophic position (TP) was estimated from the same CSIA-AA dataset using the Glu–Phe $\delta^{15}\text{N}$ framework, based on triplicate-averaged $\delta^{15}\text{N}$ values of glutamic acid (Glu) and phenylalanine (Phe), applying site-specific β values derived from primary producers and a trophic discrimination factor of 7.6‰^{8,73,74} (The original TP values are available in Supplementary Table 4).

To integrate CSIA-AA-derived resource use into the energy-flux framework, we parameterised feeding preferences for plant-derived (P), bacterial-derived (B), fungal-derived (F) resources and for animal prey (predation). Living plant tissues (e.g., roots and shoots) and dead plant material (litter) were combined into a single plant-derived channel, because their

$\delta^{13}\text{C}$ signatures of essential amino acids are not distinguishable using CSIA-AA and both ultimately derive carbon from photosynthesis. CSIA-AA-based P/B/F proportions were used directly for the main decomposer taxa Collembola, Oribatida, Diplopoda, Diptera, Isopoda and Lumbricina. Mesostigmata, Araneae and Chilopoda were treated as predators a priori, based on literature evidence and their high CSIA-AA-estimated trophic positions. For the remaining taxa lacking CSIA-AA measurements (Astigmata, Coleoptera, Diplura, Formicidae, Gastropoda, Hemiptera, Lepidoptera, Opilionida, Prostigmata, Protura, Pseudoscorpionida, Symphyla, Thysanoptera, and Nematoda), basal-resource preferences were assigned using the trait matrix of ref.²². To align these trait-based feeding assignments with the analytical resolution of CSIA-AA, resource categories in the trait matrix were functionally aligned with the three basal energy channels resolved by CSIA-AA (plant-, fungal-, and bacterial-derived resources). Accordingly, detailed resource categories in the trait matrix (e.g., algae, dead wood, soil organic matter and other detrital pools) were not retained as independent feeding categories but were aggregated based on their ultimate biosynthetic origin. Predation was treated as a distinct feeding preference. For most taxa, predation was assigned directly based on the trait matrix. However, for omnivorous taxa (i.e., Diptera), which exhibit widespread omnivory and frequent predation on other invertebrates in addition to detritivory²², CSIA-AA-derived TPs were used to refine feeding-role classification. Specifically, taxa with $\text{TP} \leq 2$ were classified as herbivores or primary decomposers (using their CSIA-AA P/B/F proportions, predation = 0), those with $2 < \text{TP} \leq 3$ as secondary decomposers or omnivores (using their CSIA-AA P/B/F proportions, $0 < \text{predation} < 1$), and those with $\text{TP} \geq 3$ as predators (using their CSIA-AA P/B/F proportions, predation = 1) (full data with all feeding preferences are available from Figshare; Data availability).

Soil food-web reconstruction

All data manipulations and statistical analyses were done in R version 4.2.2 (R Development Core Team, 2021) with RStudio interface v. 1.4.1106 (RStudio, PBC). We employed a 'multichannel' food-web reconstruction approach²² to construct realistic soil food webs. We compiled all taxonomic groups, including nematodes, microarthropods, macroarthropods, and earthworms, into a single table, which contains the following traits for each group: feeding preferences to plants, fungi, bacteria, and animal food (predation on animals within soil food web), mean body mass, body mass variation (standard deviation), biomass per square metre. The table was supplemented with information on microhabitat preferences (ground, litter, coarse detritus and soil), protection traits and C and N content for each taxonomic group from ref.²² (raw data are available from Figshare; Data availability).

Weighted trophic interactions were reconstructed for each site-specific food web using a rule-based algorithm³, which integrated five core principles: (1) Phylogenetic constraints on diet: Feeding preferences for basal resources and predation capabilities were primarily defined by the known trophic ecology of each taxonomic group²². (2) Predator-prey body-mass relationships: The potential interaction strength between a predator and a prey group was scaled by their body-size compatibility. For each predator, we defined an optimal prey body-size distribution based on a preferred predator-prey mass ratio (PPMR) of 100⁷⁵. This theoretical distribution was then adjusted using predator-specific functional traits (e.g., venom, specialised mouthparts) that modify prey-size selectivity. The final interaction plausibility was quantified as the overlap between the predator's adjusted optimal prey-size distribution and the actual body-size distribution of each potential prey group within the web. (3) Spatial niche overlap: Trophic interactions require co-occurrence. We quantified vertical

stratification overlap by assigning each taxonomic group a presence score (1 = dominant, 0.5 = present, 0 = absent/negligible) across four soil layers: ground surface, litter, coarse detritus, and mineral soil. Pairwise Bray–Curtis dissimilarity between groups was calculated from these scores, with higher dissimilarity (lower overlap) reducing potential interaction strength³. (4) Biomass-driven encounter probability: Predation links were weighted to reflect the principle that predators are more likely to encounter and consume prey that are more abundant (i.e., have higher local biomass)³⁸. (5) Prey defence attenuation: The strength of a predation link was multiplicatively reduced by a prey protection coefficient (1 = none, 0.7 = moderate, 0.4 = strong), assigned based on the group's dominant physical, chemical, or behavioural defences⁷⁶. These five principles were combined algorithmically to generate a weighted trophic interaction matrix for each of the 24 site-based food webs (reconstruction code available on Figshare; see Code Availability). Data from the four samples per site were averaged prior to reconstruction. The soil food web in each site was treated as an independent biological replicate in subsequent analyses (n = 24; Supplementary figs. 2-3).

Energy flux estimation

Energy fluxes among food-web nodes were quantified by combining the reconstructed interaction networks with node biomasses, body-mass–dependent metabolic losses and mean annual temperature using the R package *fluxweb*³⁸.

In brief, the mean metabolic rate (I , W g⁻¹) for each taxon is calculated using the Boltzmann–Arrhenius allometric equation³⁶:

$$\ln(I) = \ln(i_0) + (a-1) \times \ln(M) - E(1/kT),$$

where i_0 is a normalization factor, a is the allometric exponent, M is the individual fresh body mass (g), E is the activation energy, K_B is the Boltzmann constant and T is the site-specific temperature in Kelvin. The mean annual temperature (September and October in 2023) was taken from public sources (full data are available in Supplementary Table 1).

Energy fluxes were quantified assuming an energetic steady state (i.e., for any predator present in the system, there is sufficient prey production to sustain it), following ref.³⁸, in which energetic losses of each node are balanced by assimilated energy from its resources. For each taxon i , the energy balance is described as:

$$X_i + \sum F_{ij} = \sum F_{ji} \times e_{ij},$$

where X_i represents metabolic energy losses, F_{ij} the energy flux from taxon i to its consumer j , F_{ji} the flux received by consumer j from resource i , and e_{ij} the assimilation efficiency. Solving the system of energy-balance equations simultaneously for all nodes yields the quantitative energy fluxes throughout the food web.

The diet-specific assimilation efficiencies (e_a) for animal prey were estimated from nitrogen content using the logistic model proposed by ref.⁷⁷:

$$\text{logit } e_a = 0.471 \times \text{nitrogen (\%)} - 2.097,$$

where nitrogen content (%) for each prey node was obtained from published databases³. Assimilation efficiencies for basal resources followed ref.³ and were specified as 0.21 for plant material, 0.96 for bacteria, and 0.36 for fungi. The *fluxing* function was then applied to the reconstructed interaction networks to obtain pairwise energy fluxes among all nodes, expressed in mW m⁻².

Statistical analyses

To test our hypotheses, at each site we calculated community biomass and total energy flux (mW m^{-2}) of all soil invertebrates, individual size classes and taxa. We further classified energy fluxes according to ‘energy channels’ representing sums of outgoing fluxes from specific resources consumed: plant energy channel (living plants and leaf litter), bacterial energy channel (bacteria), and fungal energy channel (fungi). Due to the steady-state energetic system assumptions, predation automatically contributed to the plant, bacterial and fungal energy channels in the shares according to the feeding preferences of predators (losses due to predation are added to the energy flux to the prey; see ref.⁵ for details). Predation was also used as a separate metric, represented by a sum of outgoing fluxes from all invertebrate nodes.

To test Hypotheses 1 and 2, we fitted linear mixed-effects models (LMMs) to $\log_{10}$ -transformed energy fluxes using the *lme4* package⁷⁸. Analyses were conducted at three levels of biological organisation: total community energy flux, integrating all soil-invertebrate guilds included in this study (30 guilds); size-based groups (nematodes, microarthropods, macroarthropods and earthworms); and major high-rank soil invertebrate taxa within these size-based groups. For total community energy flux, mycorrhizal type (AMF vs. EMF) was fitted as a fixed effect. For analyses of size-based groups and major taxa, fixed effects included mycorrhizal type, group identity, and their interaction. A nested random-intercept structure was included for site within location (1|location/site). Fixed effects were evaluated using Wald χ^2 tests implemented in the *car* package⁷⁹. Major taxonomic groups considered in the taxon-level analysis comprised dominant decomposers (Diplopoda, Isopoda, Collembola, Diptera, Oribatida and Lumbricina), predator groups (Mesostigmata, Araneae and Chilopoda), and nematodes.

To test Hypothesis 2, animals were assigned, independently of taxonomy, to eight body-mass classes on a $\log_{10}$ scale spanning 0.000001 mg to >100 mg: 0.000001–0.0001 mg, 0.0001–0.001 mg, 0.001–0.01 mg, 0.01–0.1 mg, 0.1–1 mg, 1–10 mg, 10–100 mg, and >100 mg. These classes broadly encompassed nematodes at 0.000001–0.01 mg, microarthropods at 0.001–1 mg, macroarthropods at 0.01–100 mg, and earthworms at ≥ 1 mg. For each site and body-mass class, we quantified total energy flux, absolute fluxes in each energy channel, and the proportional contribution of plant-, fungal-, bacterial- and predation channels. These energy-flux metrics were analysed using mixed-effects models with mycorrhizal type, body-mass class, and their interaction as fixed effects, and site nested within location as a random effect. The results were displayed using the *ggplot2* package⁸⁰.

To evaluate whether predator basal-channel use inferred from reconstructed food webs was supported by an independent isotopic estimate, we compared reconstructed predator energy channels with CSIA-AA-derived feeding preferences in the three principal predator groups represented in the food-web reconstruction: Mesostigmata, Araneae and Chilopoda. CSIA-AA-based feeding preferences were inferred from stable isotope ratios of $^{13}\text{C}/^{12}\text{C}$ ($\delta^{13}\text{C}$) in essential amino acids (eAAs) and expressed as the relative contributions of plant-, fungal- and bacterial-derived resources to each predator group. Reconstructed predator energy channels were obtained by tracing all incoming fluxes to each predator group back to their basal origin in the energy-flux matrices, summing fluxes within plant, fungal and bacterial channels, and expressing these channel-specific sums as proportions of total incoming predator flux. For each predator group, separate linear models were then fitted for plant, fungal and bacterial channels, with reconstructed predator channel proportion as the response

681 variable and the corresponding CSIA-AA-derived resource contribution as the predictor.
682 Ordinary least-squares linear regressions were fitted in R using the *lm()* function in the *stats*
683 package.

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698 Conflicts of Interest

699 The authors declare no competing interests.

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