

Multifunctionality of belowground food webs: resource, size and spatial energy channels

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ABSTRACT

The belowground compartment of terrestrial ecosystems drives nutrient cycling, the decomposition and stabilisation of organic matter, and supports aboveground life. Belowground consumers create complex food webs that regulate functioning, ensure stability and support biodiversity both below and above ground. However, existing soil food-web reconstructions do not match recently accumulated empirical evidence and there is no comprehensive reproducible approach that accounts for the complex resource, size and spatial structure of food webs in soil. Here I build on generic food-web organisation principles and use multifunctional classification of soil protists, invertebrates and vertebrates, to reconstruct a ‘multichannel’ food web across size classes of soil-associated consumers. I infer weighted trophic interactions among trophic guilds using feeding preferences and prey protection traits (evolutionarily inherited traits), size and spatial distributions (niche overlaps), and biomass-dependent feeding. I then use food-web reconstruction, together with assimilation efficiencies, to calculate energy fluxes assuming a steady-state energetic system. Based on energy fluxes, I propose a number of indicators, related to stability, biodiversity and multiple ecosystem-level functions such as herbivory, top-down control, translocation and transformation of organic matter. I illustrate this approach with an empirical example, comparing it with traditional resource-focused soil food-web reconstruction. The multichannel reconstruction can be used to assess ‘trophic multifunctionality’ (analogous to ecosystem multifunctionality), i.e. simultaneous support of multiple trophic functions by the food web, and compare it across communities and ecosystems spanning beyond the soil. With further empirical validation of the proposed functional indicators, this multichannel reconstruction approach could provide an effective tool for understanding animal diversity–ecosystem functioning relationships in soil. This tool hopefully will inspire more researchers to describe soil communities and belowground–aboveground interactions comprehensively. Such studies will provide informative indicators for including consumers as active agents in biogeochemical models, not only locally but also on regional and global scales.

Key words: soil food web, energy flux, network analysis, omnivory, functional traits, predator–prey interactions, feeding preferences, trophic guilds, ecosystem functioning, trophic multifunctionality

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I. INTRODUCTION

(1) Belowground communities and ecosystem functioning

Belowground communities regulate the decomposition and sequestration of organic matter in terrestrial ecosystems. Because they are responsible for processing a major part of primary production (Cebrian, 1999), the detrital system plays a central role in the carbon cycle (Clemmensen *et al.*, 2013; Averill, Turner & Finzi, 2014; Crowther *et al.*, 2019), nitrogen cycle (Li *et al.*, 2019) and other biogeochemical cycles (Xu, Thornton & Post, 2013; Crowther *et al.*, 2019). Microorganisms carry out the basic soil ecosystem processes. Nevertheless, consumers of microorganisms and plant materials have strong indirect effects on these processes *via* microbial grazing, litter shredding, organic matter transformation and translocation (Lavelle *et al.*, 1997; Briones, 2014; Filser *et al.*, 2016; Thakur & Geisen, 2019). However, the direction and magnitude of consumer effects are context dependent and hard to predict and thus common global biogeochemical models often simply ignore them (Deckmyn *et al.*, 2020). In recent years, considerable progress has been made in understanding the global distribution patterns of soil consumers (Crowther *et al.*, 2019; Phillips *et al.*, 2019; van den Hoogen *et al.*, 2019; Guerra *et al.*, 2020; Oliverio *et al.*, 2020; Potapov *et al.*, 2020) and calls to account for soil fauna in global biogeochemical models are becoming increasingly common (Filser *et al.*, 2016; Grandy *et al.*, 2016; Soong & Nielsen, 2016; Deckmyn *et al.*, 2020). Some models have already been suggested (Chertov *et al.*, 2017; Deckmyn *et al.*, 2020). However, the success of any models developed depends largely on whether or not they correctly depict the key functional groups and their interactions in soil.

(2) Holistic approach to describe the consumer community in soil

Soil communities include a huge diversity of consumers that spans phyla, size classes, trophic levels, and vertical layers

(Anderson, 1975; Swift, Heal & Anderson, 1979; Coleman, Callahan & Crossley Jr, 2017; Potapov *et al.*, 2021b). Soil ecosystem functioning is driven by multiple components of the soil biota, including microorganisms, micro- meso- and macrofauna (Bradford *et al.*, 2002; Wagg *et al.*, 2014; Delgado-Baquerizo *et al.*, 2020). This functional complexity calls for a holistic approach to describing soil communities across consumers of different body sizes, similar to the size spectrum approach commonly used in marine ecosystems (Blanchard *et al.*, 2017). There have been several conceptual and empirical attempts to apply the size spectrum approach to terrestrial belowground communities (Mulder, 2006; Petchey & Belgrano, 2010; Turnbull, George & Lindo, 2014), but they provide only simplified information because terrestrial food webs have more complex size structures than marine ones (Potapov *et al.*, 2019a, 2021b). The food-web framework is, however, a promising way of describing the functioning of terrestrial food webs because it unites the functional, biodiversity and stability aspects of biological systems (Hines *et al.*, 2015; Barnes *et al.*, 2018). Indeed, soil food-web properties may explain various soil functions better than environmental variation alone (de Vries *et al.*, 2013).

(3) Belowground food-web reconstructions

Most studies exploring the functioning of soil food webs assume a dominant role of basal resources in structuring food-web topology, stemming from the seminal work of Hunt *et al.* (1987). These ‘traditional’ resource-based reconstructions were used to estimate energy fluxes and quantify nitrogen mineralisation in bacterial, fungal and plant energy channels in grasslands and agroecosystems (Hunt *et al.*, 1987; de Ruiter *et al.*, 1993). The approach also has been used to explore patterns of interaction strengths and was developed into the concept of ‘fast’ (e.g. bacterial) *versus* ‘slow’ (e.g. fungal) energy channels, jointly driving ecosystem stability (de Ruiter, Neutel & Moore, 1995; Rooney *et al.*, 2006). However, these ideas were mostly conceptualised for, and applied to, micro-food webs

(protists, nematodes, microarthropods) in soil (Moore, McCann & de Ruiter, 2005) because it is more difficult to apply such ideas to macro-food webs (insects, spiders, myriapods) where resource-based energy channelling is reticulated (Wolkovich, 2016; Potapov *et al.*, 2021b).

Another set of studies diagnosed soil food-web structure and functioning using the abundance distribution of body size classes of soil biota from bacteria to earthworms (Mulder, 2006; Mulder, den Hollander & Hendriks, 2008; Mulder & Elser, 2009). The core idea of this ‘allometric’ approach is that the abundance–body mass relationship can serve as an indicator of environmental changes and is also linked to ecosystem functions performed by different size classes (Mulder & Elser, 2009; Petchey & Belgrano, 2010; Turnbull *et al.*, 2014). The link between size spectrum and food-web structure is based on the assumption of a linear correlation between body size and trophic level across the food web. However, this correlation is weak and multidirectional in soil (Potapov *et al.*, 2021b). The size spectrum approach is also simplistic because it does not account for traits other than body size, such as food resource preferences and the spatial distribution of soil organisms.

The importance of the spatial distribution of energy fluxes in soil food webs has been emphasised on the micro-scale, e.g. rhizosphere processes, on the macroscale, e.g. below–aboveground energy transfer by mobile fauna (Scheu, 2001; Wardle *et al.*, 2004) and for the horizontal patchiness of soil communities (Ettema & Wardle, 2002). For example, soil food-web structure can vary with soil depth due to differences in the vertical distribution of different functional groups of soil fauna (Berg & Bengtsson, 2007). However, there is no systematic study of the spatial organisation of energy channelling in soil food webs beyond the microscale.

Three, mostly independent, research directions are suggested by the literature overview above. These three correspond to three dimensions of soil food-web structure: (i) resource-based energy channelling, (ii) body size distribution and (iii) spatial organisation of trophic interactions in soil. Jointly, these structural dimensions are able to describe various aspects of functioning of soil food webs and their role in terrestrial ecosystems. Despite recognition that niche separation in soil occurs along more than one axis (e.g. food, habitat, time; Moore, Walter & Hunt, 1988), so far, soil food-web reconstructions and analyses have focused on a single food-web dimension. Moreover, trophic interactions in soil food webs are generally reconstructed based on uncertain knowledge or on traditional assumptions about which interactions occur. How these interactions are identified often lacks transparency and thus cannot be applied across different soil communities. Such reconstructions may, therefore, lack precision and this may affect the ecological conclusions drawn from them. The trophic interactions thus need to be validated against empirical *in situ* evidence, which has rarely been done previously.

(4) Revision of belowground food webs with novel tools

The methodological toolbox in soil trophic ecology is now much more diverse than it was some 20–30 years ago. Novel tools such as stable isotopes, fatty acids, and gut DNA analyses provide more realistic empirical descriptions of trophic links and food-web structure in cryptic belowground communities (Brose & Scheu, 2014; Potapov *et al.*, 2021a). The use of such novel tools has changed our understanding of soil food-web structure and functioning (Bradford, 2016). It has become evident that a major part of the energy fuelling soil food webs is root derived (Ostle *et al.*, 2007; Pollierer *et al.*, 2007) and channelled through both bacterial and fungal pathways (Pollierer *et al.*, 2012; de Vries & Caruso, 2016). It was also emphasised that feeding across multiple energy channels is widespread for most belowground consumers, including many microfaunal groups (Digel *et al.*, 2014; Geisen, 2016; Wolkovich, 2016). At the same time, a range of feeding strategies was revealed in decomposer mesofauna groups, such as Collembola and Oribatida (Maraun *et al.*, 2011; Potapov *et al.*, 2016). The role of ectomycorrhizal mycelia as a major food resource for soil fauna has been challenged (Potapov & Tiunov, 2016; Bluhm *et al.*, 2019), while soil autotrophic microorganisms are a potentially overlooked one (Schmidt, Dyckmans & Schrader, 2016; Seppely *et al.*, 2017; Potapov, Korotkevich & Tiunov, 2018). However, these findings have been largely ignored in existing soil food-web reconstructions. In a recent review, Potapov *et al.* (2022) attempted to synthesise classic knowledge with these recent findings by reviewing literature on the feeding habits of individual animal groups. The conceptual paper presented herein is based on information in that previous review and aims to develop a holistic approach to describe soil food webs across their resource, body size and spatial dimensions and deliver a set of functional indicators that describe the effects of consumers on ecosystem functioning and stability. In the following chapters I first revise generic food-web organisation principles in relation to the soil system, then describe the multichannel food-web reconstruction approach and suggest functional indicators illustrating them with a hypothetical and an empirical example, and finally discuss the limitations of the approach, the main knowledge gaps and a way forward for soil food-web research.

II. ESSENTIAL CONCEPTS IN FUNCTIONAL SOIL FOOD-WEB RESEARCH

(1) Basal resources of soil food webs

Energy in food webs flows through consumer trophic chains, which may be clustered in energy channels based on a certain similarity. Resource-based energy channelling clusters trophic chains on the basis of the basal resources they use. This is probably the most common way to understand the structure and functioning of belowground food webs (Fig. 1A).

However, the classification of basal resources and corresponding energy channels is often unclear. For example, the traditional distinction of root, bacterial and fungal energy channels (Hunt *et al.*, 1987) is hardly applicable to macrofauna detritivores feeding mainly on litter and soil organic matter, and ignores autotrophic microorganisms. The general distinction between green and brown (i.e. grazing and detrital) channels (Moore *et al.*, 2004) introduces ambiguity in the case of food chains based on root exudates and mycorrhizal fungi that are associated with living plant roots (i.e. green energy channel) being intimately interlinked with soil organic matter sequestration and decomposition (i.e. brown energy channel). Revision of these concepts should be the subject of a focused study introducing ontologies to reduce ambiguity and increase the reproducibility of soil food-web research. Herein I consider basal resources as the main organic pools at the base of the soil food web that support soil consumers and that are associated with different ecosystem-level processes (Fig. 2). Different feeding adaptations are needed to consume different basal resources and by feeding on different resources consumers affect different ecosystem processes, including transformation, translocation and decomposition of organic matter, nutrient mineralisation, plant growth, microbial dispersal and others (Briones, 2014).

(2) Resource stoichiometry and assimilation efficiency

Basal food resources of soil food webs vary greatly in their elemental proportions and profitability for consumers.

Assimilation efficiency, i.e. the proportion of ingested food that is assimilated by a consumer, will differ among resources such as living plants, detritus, microorganisms and animal tissues (Jochum *et al.*, 2017; Lang *et al.*, 2017). Detritivores have to eat more food to maintain stoichiometric ratios of C:N:P in their bodies (Pokarzhevskii *et al.*, 2003; Jochum *et al.*, 2017) and thus consume a larger volume of food than, for example, predators do. Detritivores with a low assimilation efficiency exhibit the largest effects on their environment *via* feeding activities, as exemplified by earthworms that consume hundreds of tons of soil per hectare per year (Lavelle & Martin, 1992). Thus, assimilation efficiency is one of the important parameters for quantifying ecosystem-level effects of resource–consumer interactions (see Section (7)). Assimilation efficiency can be predicted well by using, for example, the nitrogen concentration of the food resources (Jochum *et al.*, 2017). Accounting for nitrogen concentrations or C to N ratios in resources and consumers is thus a promising approach for predicting interaction strengths in soil food webs (Buchkowski & Lindo, 2021).

(3) Trophic guilds and taxonomic groups

Food webs are often reconstructed based on ‘trophic species’ that represent groups of biological species that share a similar pool of resources and predators (Yodzis & Winemiller, 1999; Luczkovich *et al.*, 2003). In soil, such groups are traditionally termed trophic guilds and have a more functional focus, being linked to the exploitation of a specific basal resource

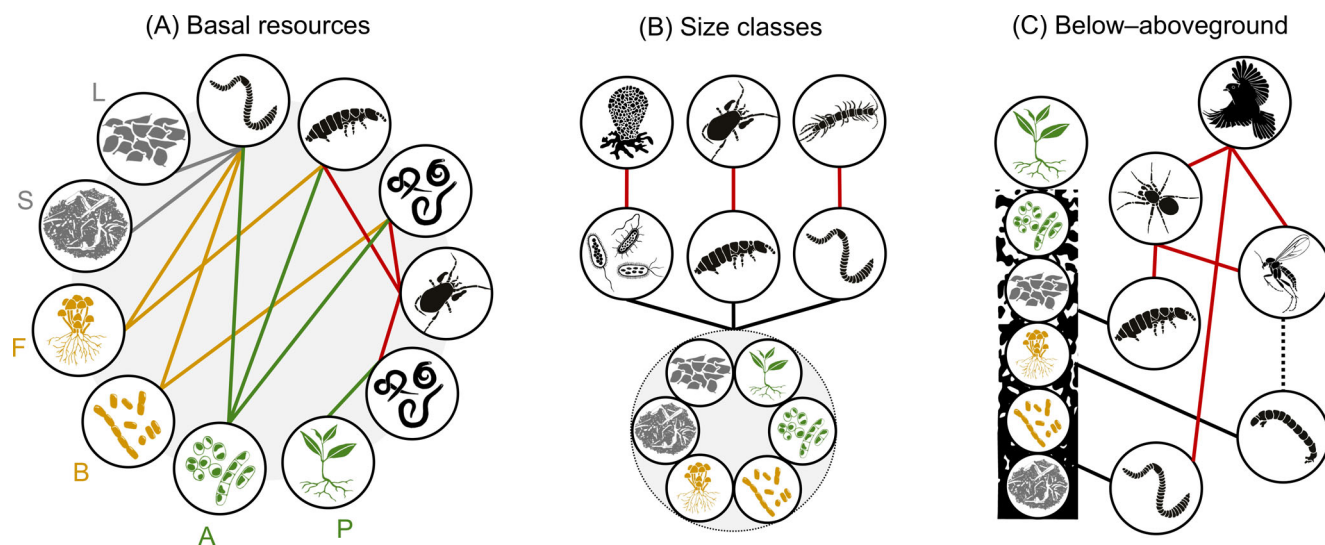


Fig. 1. Structural facets of energy channelling in soil food webs. (A) Energy channels based on different resources have different turnover rates and control different ecosystem-level processes such as herbivory, decomposition and nutrient cycling. The ‘brown channel’ unites detrital (grey lines), and fungal and bacterial channels (dark yellow lines); the ‘green channel’ is based on living autotrophic organisms (green lines); predators couple different resource-based channels (red lines). For resource abbreviations refer to Fig. 2. (B) Different size classes of soil consumers impact different ecosystem functions and are controlled by different environmental factors. Energy from all resources is channelled in parallel *via* several size-based energy channels, each coupled by different predatory groups. (C) Consumers in the soil rely on spatially structured basal resources, and translocate organic matter vertically and horizontally, subsidising aboveground predators with prey biomass *via* vertical movements of soil fauna and winged insects that develop in the soil.

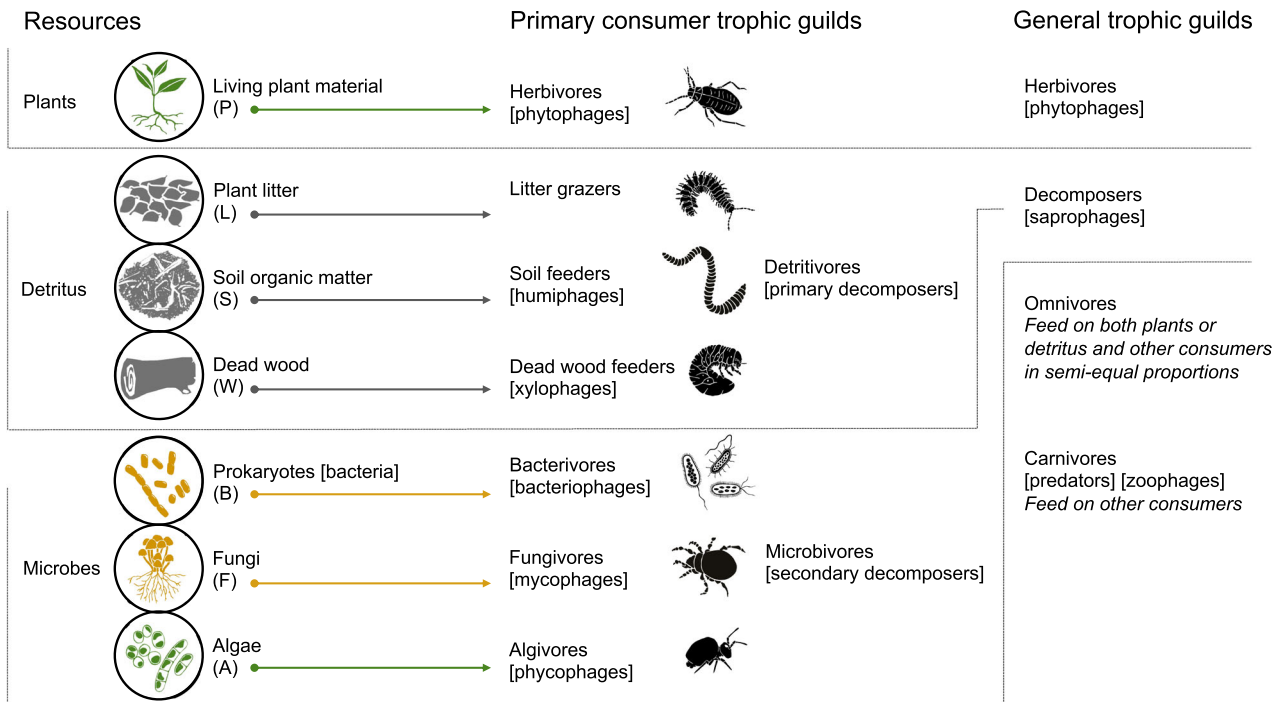


Fig. 2. Basal resources and corresponding consumer trophic guilds in soil food webs. Animals and protists feeding on both detritus and microorganisms form a general guild of ‘decomposers’ that affect decomposition *via* food consumption. Decomposer prokaryotes and fungi, i.e. ‘saprotrophs’, are considered as resources in the present framework. Abbreviations for resources are given in parentheses; synonyms are given in square brackets. Colours highlight the ‘brown’ (grey and dark yellow) and ‘green’ energy channels (green). Dissolved organic matter is assumed to be used primarily by prokaryotes and fungi and thus is not explicitly considered here. Summarised from Swift *et al.* (1979), Striganova (1980), Hunt *et al.* (1987) and Potapov *et al.* (2022).

in a specific way, and even having similar microhabitat preferences (Moore *et al.*, 1988; Faber, 1991; Brussaard, 1998). To obtain correct estimates of food consumption, such groups should also share similar physiology and stoichiometry (Buchkowski & Lindo, 2021). In most reconstructions, pure trophic classifications such as detritivores, bacterivores, fungivores, herbivores, carnivores and omnivores are mixed with high-rank taxonomic classifications (Hunt *et al.*, 1987; de Vries *et al.*, 2013; Gongalsky *et al.*, 2021). This is justified, not only because taxonomic identification is the basis of food-web research, but also because trophic niches in soil fauna can, to a large extent, be predicted using phylogenetic (taxonomic) relationships among groups (Cardoso *et al.*, 2011; Potapov *et al.*, 2016; Potapov, Scheu & Tiunov, 2019c). A hybrid taxonomic and guild approach (Brousseau, Gravel & Handa, 2018; Laigle *et al.*, 2018) also allows consideration of a number of phylogenetically conserved traits such as physiology, stoichiometry, and reproductive and defence strategies. Even though there are several reviews of the commonly used trophic guilds and functional groups (e.g. Moore *et al.*, 1988; Brussaard, 1998; Briones, 2014), no comprehensive trophic guild classification across size classes in soil has previously been compiled, nor has a common vocabulary across taxa been clearly defined. For the present study, commonly used trophic classifications corresponding to the basal

resources are provided in Fig. 2. In the reconstruction below, I rely on the multifunctional classification compiled in the accompanying review (Potapov *et al.*, 2022).

(4) Size classes of soil consumers

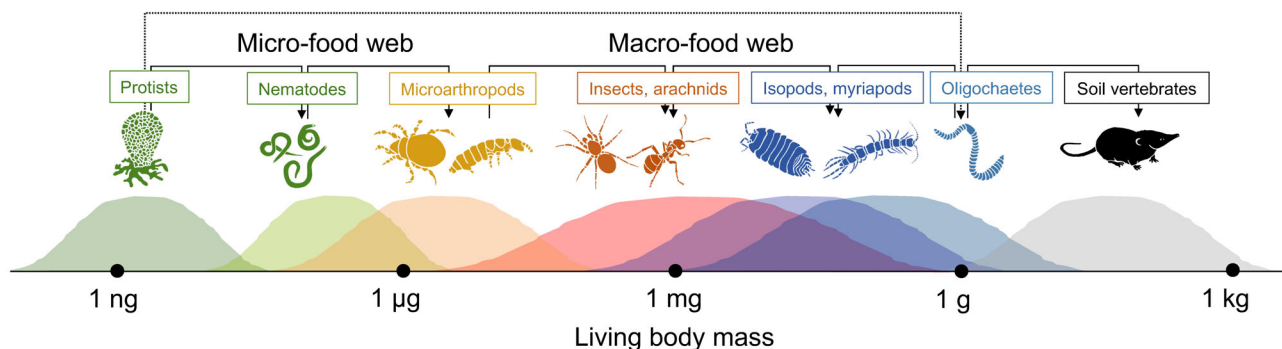
Consumers, from protists to large invertebrates, may span from few micrometres to dozens of centimetres in body length and over 12 orders of magnitude in body mass in a single soil community (Mulder *et al.*, 2008; Potapov *et al.*, 2021b). Body size is a very general trait that affects a number of organism characteristics including metabolism, growth rate and trophic interaction partners among others (Brown *et al.*, 2004; Woodward *et al.*, 2005). Different size classes in soil inhabit different environments (water, air pores and holes, or bulk soil), have different mobility restrictions and vertical stratification, exhibit different degrees of trophic specialisation, and vary in their engineering roles (Fig. 3) (Scheu & Setälä, 2002; Wardle, 2002; Briones, 2014; Erktan *et al.*, 2020). However, body size is poorly related to the trophic level across the entire food web since top predators are present in different size classes (Fig. 1B) (Potapov *et al.*, 2019a, 2021b). The conventional classification into micro-, meso- and macrofauna is based primarily on body width, since it is the main characteristic that restricts the

movement abilities of organisms in the soil (Swift *et al.*, 1979). For food-web analysis, living body mass is very important since it provides information on which prey a predator is able to handle (Cohen *et al.*, 1993). The body mass perspective results in elongated animals such as nematodes, myriapods and oligochaetes being assigned to larger size classes than those based on body width and to smaller size classes than those based on body length (Fig. 3) (Potapov *et al.*, 2021b). Non-linear variations in trophic level with body mass suggest that small-sized soil-dwelling microarthropods are involved in micro-food webs together with microfauna, as depicted also in traditional soil food-web models (Hunt *et al.*, 1987; Potapov *et al.*, 2021b). By contrast, large microarthropods that live mostly in fresh litter and on the ground surface, are involved in macro-food webs (Potapov *et al.*, 2021b). Describing soil communities using the size spectrum approach has the further advantage of correctly evaluating the food-web roles and ecosystem impacts of juvenile organisms (Gongalsky, 2021; Potapov *et al.*, 2021b). Since different size classes of soil consumers impact different ecosystem functions and are controlled by different environmental factors, the size spectrum is an integrative indicator for the soil community (Mulder, 2006).

(5) Predator–prey interactions, mass ratios and traits

Generalist feeding is a common feature in soil food webs and is especially evident in predatory groups (Scheu & Setälä, 2002; Digel *et al.*, 2014). However, generalist feeding greatly hinders the systematic occurrence of species-specific

interactions in soil. Such interactions are rare because communication (whether chemical or in other forms) between animals in the soil is difficult and because community composition is very variable across space. When an empirical assessment of trophic interactions is not feasible, trophic interactions are reconstructed based on expert knowledge and existing evidence in the literature (Hunt *et al.*, 1987; Digel *et al.*, 2014). Generalist feeding makes realistic the assumption that most of the physically possible interactions actually may occur in nature. However, the occurrence and frequency of such interactions should be assessed for specific communities and environmental conditions. Predator–prey mass ratios (PPMRs) can be used to define interactions that are possible physically (and energetically profitable) (Brose *et al.*, 2008) (Fig. 4A). Body masses alone correctly predict more than 50% of trophic interactions across size classes of consumers in marine and aboveground food webs where trophic interactions are typically more specialised (‘allometric’ models; Petchey *et al.*, 2008). The few PPMR estimates that exist for soil predators suggest that the optimum varies around 100, i.e. the predator is approximately 100 times heavier than its optimum prey (Brose *et al.*, 2008). However, purely allometric models have a large uncertainty when being tested against empirical data on soil macropredators (Eitzinger *et al.*, 2018). Indeed, predators may also feed on prey much smaller, or handle prey of comparable size, depending on specific predator and prey traits (Fig. 4B) (Brose *et al.*, 2019). In soil communities, key traits that may modify PPMRs, and the presence and intensity of predator–prey interactions, are often attributed to certain taxonomic groups and include hunting adaptations and



Nutrient mineralisation, trophic specialisation, abundance, turnover rate, dormant stages

Engineering role, mobility, feeding generalism, biomass

Fig. 3. Body mass spectrum of consumers in soil. Well-established soil communities embrace consumers spanning over 12 orders of magnitude in body mass. Small-sized consumers have a high turnover rate and affect nutrient cycling *via* microbial grazing. Large-sized consumers have a high biomass and play important engineering roles in soil *via* transformation and translocation of organic matter. Predator–prey trophic interactions (black arrows) occur predominantly among organisms of similar size, with micro-food webs being partially disconnected and consumed by macrodetritivores as a whole (e.g. protists–oligochaetes dashed arrow). Summarised from Lavelle (1996), Scheu & Setälä (2002), Pokarzhevskii *et al.* (2003), Erktan, Or & Scheu (2020) and Potapov *et al.* (2021b).

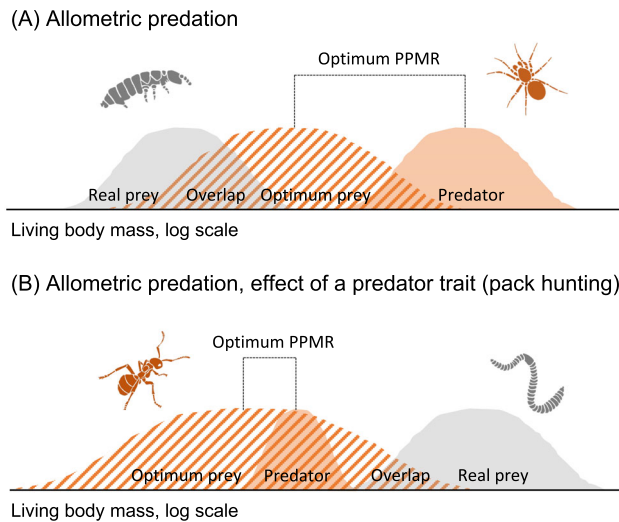


Fig. 4. Feasible predator–prey interactions depend on body mass ratios. Small prey has a low handling time, but also is less energetically profitable than large prey, shaping an ‘optimum’ predator–prey mass ratio (PPMR) distribution (Brose *et al.*, 2008). (A) Optimum PPMR together with population body mass distribution of a predator (orange-filled distribution) and a prey (grey-filled distribution) can be used to predict interaction strength between them (overlap of the lined ‘optimum’ prey body mass distribution with the grey distribution). (B) Specific traits of predator and prey may modify PPMR and interaction strength. Despite ants being smaller than earthworms, pack hunting and venom shifts and widens the PPMR distribution, making the predation feasible.

ingestion mechanisms of predators, as well as protective metabolites, physical structures and behaviour of prey (Table 1) (Brousseau *et al.*, 2018; Laigle *et al.*, 2018). For example, strongly sclerotised groups such as oribatid mites have been shown to be rarely attacked by predators (Peschel *et al.*, 2006). However, the effectiveness of different protection mechanisms against different predators has not been systematically studied in soil. Together with body mass, these traits are expected to provide more realistic reconstructions of trophic interactions in generalist soil food webs.

(6) Vertical stratification of soil food webs

Soil is a stratified environment so that there are divergent evolutionary pressures on fauna living on the surface, and those in the mineral soil (Ghilarov, 1949). These divergent pressures create vertical stratification of forms and functions in soil communities (Ellers *et al.*, 2018). Mobile ‘epigeic’ groups of arthropods inhabit the surfaces of fallen leaves, wood, stones, and bare soil; ‘hemiedaphic’ invertebrates inhabit coarse detritus, such as decomposing litter or wood; ‘endogeic’ invertebrates inhabit lower organic and mineral soil layers, including the rhizosphere. Classifications related to vertical stratification have been developed for different soil taxa including, for example, earthworms (Bouché, 1977),

springtails (Gisin, 1943) and gastropods (Ellers *et al.*, 2018). Vertical stratification of taxonomic groups propagates to the corresponding vertical stratification in the structure and energy fluxes in soil food webs (Berg & Bengtsson, 2007; Okuzaki *et al.*, 2009) and related ecosystem functions (Faber, 1991). Moreover, the spatial distribution of basal resources also structures energy channelling in soil food webs: fresh organic detritus and algae are more abundant in the surface layers, while soil organic matter and roots are more abundant in the mineral soil (Fig. 1C) (Ponge, 2000). Vertical stratification also provides information on the spatial niche differentiation among different functional groups (Faber, 1991) that limits predator–prey interactions among groups that live in different layers. Many large fauna, however, move vertically through the soil profile during their development, or depending on the environmental conditions (Dowdy, 1944). This pattern is especially evident for holometabolous insects (flies, beetles) many of which have larval stages in the soil and flying adults (Ghilarov, 1949). But even true soil-dwelling invertebrates, such as earthworms, channel energy from soil organic matter ‘directly to the sky’ when they are eaten by birds (Fig. 1C). Detrital subsidy is probably indispensable for aboveground predators in virtually all terrestrial ecosystems, but its quantification and origin have seldom been studied (Scheu, 2001; Hyodo, Kohzu & Tayasu, 2010; Hyodo *et al.*, 2015).

(7) Metabolic ecology and energy flux approach

The impacts of soil animals and protists on ecosystem functioning are, in most cases, linked to the consumption of other consumers, microorganisms, litter and soil and to burrowing in search of food. Consumption rate, in turn, is defined primarily by the metabolic demands of an organism – the amount of energy it needs to sustain its life. The metabolic rate scales sublinearly with living body mass, varies with phylogenetic position of the consumer, and increases steadily with environmental temperature (Brown *et al.*, 2004; Ehnes, Rall & Brose, 2011). Metabolic rate accounts for the different metabolic demands of small and large organisms per unit of body mass and is thus a universally comparable measure of organism and population impacts on ecosystem functioning across size classes, superior to biomass or numeric abundance. Resource consumption rate depends primarily on the metabolic demands of an organism and on the efficiency with which it can assimilate its food resources (see Section (2)). In an energetically steady-state system (i.e. losses equal gains for each food-web node), consumption rate also depends on the position of a consumer in the food web because lower trophic levels sustain higher trophic levels with energy. Consumption rate, after accounting for assimilation efficiency and losses of energy to higher trophic levels in the food web, represents the total energy flux out of all resource nodes to a consumer, which can be used as a measure of its ecosystem-level impact (Barnes *et al.*, 2014, 2018). The energy flux approach has been applied in traditional soil food-web models to quantify the contribution of soil consumers to nitrogen mineralisation (Hunt *et al.*, 1987; de

Table 1. Predator and prey traits, modifying interaction strength and predator–prey mass ratios (PPMRs). Numbers that are shown in the ‘expected effects’ column are general theoretical expectations rather than strict rules

Trait description	Exemplar groups	Expected effect	References
Predator traits			
<i>Parasitic</i> – animal parasites are typically much smaller than their hosts	Parasitic nematodes and protists	PPMR \ll 1	
<i>Filtering the environment</i> – feeding on the environment to filter the prey	Earthworms	PPMR \gg 100	Pokarzhevskii <i>et al.</i> (2003)
<i>Mass predation</i> – adaptations, such as the tongue of an anteater, allowing hunting of many prey targets (usually social insects) simultaneously	Anteaters	PPMR > 100	Redford (1985)
<i>Cooperative hunting</i> – joint handling of prey with accomplices, allows handling of larger prey	Ants, some pseudoscorpions	Increases PPMR range	Cerdá & Dejean (2011)
<i>Venom</i> – venom paralyzes and allows handling of larger prey	Spiders, centipedes, ants	Increases PPMR range	Cerdá & Dejean (2011); Laigle <i>et al.</i> (2018)
<i>Hunting devices</i> – adaptations, such as spiders webs, allow to handle larger prey	Spiders	Increases PPMR range	Herberstein (2011)
Prey traits			
<i>Protective metabolites</i> – e.g. poison. Requires specific adaptations to overcome and thus reduces predation at community level	Some diplopods, termites, amphibians and others	Reduces interaction strength	Eisenbeis & Wichard (1987)
<i>Physical protection</i> – protective cover, e.g. strong cuticle, shell, scales or spines	Oribatid mites, isopods, millipedes, gastropods, testate amoebae	Reduces interaction strength	Bauer & Pfeiffer (1991); Peschel <i>et al.</i> (2006)
<i>Agility</i> – morphological adaptations allowing an animal to escape rapidly from a predator (e.g. jumping)	Springtails, orthopterans	Potentially reduces predation pressure	Hopkin (1997); Larabee & Suarez (2015)
<i>Carnivore</i> – carnivore may strike back while being attacked	Predatory groups	Potentially reduces predation pressure	

Ruiter *et al.*, 1993). More recently, the approach was linked to biodiversity and expanded to include more ecosystem functions (Barnes *et al.*, 2014, 2018; Jochum *et al.*, 2021). For instance, Barnes *et al.* (2014) infer ecosystem functions such as herbivory, decomposition and predation from the energy fluxes to corresponding trophic guilds of macroinvertebrates.

Widespread application of this approach to soil food webs, however, is hampered by the generalist feeding of soil animals and their poorly documented feeding preferences. Both these factors often make trophic guild assignment uncertain. We therefore need more realistic reconstructions, incorporating different aspects of detritivory, widespread omnivory and multichannel feeding, and specific body size and spatial structures of soil food webs. Such realistic reconstructions will better describe mechanisms behind animal diversity–ecosystem functioning relationships in soil. Below, I build on the classification of soil consumers given in Potapov *et al.* (2022) to reconstruct soil food webs. I then use the energy flux approach, as implemented in the R package *flux-web* (Gauzens *et al.*, 2019), to propose novel indicators of their functioning. The suggested multichannel reconstruction

unites the resource, size and spatial dimensions of soil food webs and can be applied from a local to a global scale.

III. RECONSTRUCTION OF MULTICHANNEL FOOD WEBS

(1) Food-web reconstruction

I propose a novel ‘multichannel’ approach of soil food-web reconstruction which predicts trophic interaction strengths in a given soil community using prior knowledge of species biology, basic food-web principles and the key traits of consumers. Multichannel reconstruction of soil food webs relies on trophic guilds as the network nodes that are distinguished based on multiple trait similarities. The assignment of traits to groups can be based on published, or directly measured, empirical data. The reconstruction of trophic interactions among groups is based on trait relationships that are extrapolated from existing experiments to generic rules. The approach thus produces a hypothetical food-web structure

that describes reality to the best extent possible given current knowledge. The reconstruction approach is conceptually close to the multidimensional niche model of food-web reconstruction, which assumes that trophic interactions are formed and selected along several trait dimensions (Allesina, Alonso & Pascual, 2008). Here, these dimensions are represented by phylogenetically defined feeding preferences, body sizes, protection mechanisms and vertical stratification as well as other traits that are expected to modify PPMR or consumption rate (see Section II). Each of the trait dimensions is used to produce a plausible interaction matrix, with all matrices finally multiplied together (Fig. 5; see online Supporting Information, Appendix S1 for a detailed description of food-web reconstruction, and Appendix S2 for the associated R code). The full list of trophic guilds and corresponding traits was compiled in an accompanying review (Potapov *et al.*, 2022) and is provided in Tables S1 and S2. The following assumptions were used to calculate plausible interaction matrices and reconstruct trophic links:

- (1) There are phylogenetically inherited differences in feeding preferences for various basal resources and predation capability among soil animal taxa that define their feeding interactions (Laigle *et al.*, 2018; Potapov *et al.*, 2019c). These preferences were assigned according to information in Potapov *et al.* (2022) (see Table S2).
- (2) Predator–prey interactions are primarily defined by the optimum PPMR. Typically, a predator is larger than its prey, but certain predator traits (hunting devices and behaviour, parasitic lifestyle) can considerably modify the optimum PPMR (Fig. 4; Table S3).
- (3) Strength of the trophic interaction between a predator and a prey is defined by the overlap in their spatial niches related to vertical differentiation, with greater overlap leading to stronger interactions.
- (4) Predation is density (biomass) dependent (Gauzens *et al.*, 2019). Due to a higher encounter rate, predators will preferentially feed on prey that is locally abundant.
- (5) Strength of the trophic interaction between a predator and a prey can be considerably reduced by prey protective traits (Peschel *et al.*, 2006; see Table S4).

To illustrate this multichannel reconstruction process, I selected groups from the list of trophic guilds of soil consumers that commonly co-exist in the soil food webs of temperate forests (Table S1). I followed the assumptions described above to produce the most probable weighted trophic interaction matrix. Similar approaches have been applied before to reconstruct invertebrate food webs (Digel *et al.*, 2014; Hines *et al.*, 2019). Here, however, I make the assumptions behind such reconstructions clearer and more reproducible for future studies. The reconstruction included trophic levels from primary consumers to intraguild predators and size classes from protists to vertebrates (Fig. 6). In this reconstruction, I assumed that the biomasses of all nodes were equal and ignored metabolic losses across nodes because of the lack of an appropriate empirical

data set. Thus, the interaction strengths in this hypothetical example are feeding preferences that are assumed to represent energy fluxes, with the goal of illustrating the multichannel food-web reconstruction concept. Calculation of real energy fluxes is possible by combining this reconstruction with empirical biomass data as implemented in the *fluxweb* package (Gauzens *et al.*, 2019; Jochum *et al.*, 2021) (see Appendix S2).

(2) From interactions to functions

Reconstruction of a food web and calculation of the energy fluxes allows quantification of different aspects of how consumers contribute to ecosystem functioning (see Section (7)). In the absence of the appropriate biomass data, below I assume that the calculated interaction strengths are a proxy for energy fluxes. In comparison with existing applications of the energy flux approach, I treated most basal consumers as omnivores, with many basal resource–consumer links and involvement in different resource-based energy channels (Fig. 7A,B). Omnivory of basal consumers represents multichannel feeding that is widespread in soil decomposers (Brose & Scheu, 2014; Wolkovich, 2016) and is prevalent in most food webs (Thompson *et al.*, 2007; Wolkovich *et al.*, 2014). Ecosystem functions can be inferred from such complex food webs by summing individual fluxes, for example summing all outgoing fluxes from plants to other food-web nodes reflects total herbivory (Barnes *et al.*, 2020) (Fig. 7A).

Focusing on resource-based energy fluxes, it is possible to quantify bacterial *versus* fungal energy channelling (Fig. 7B), a measure suggested to indicate food-web stability (Moore *et al.*, 2005) and nitrogen mineralisation (de Vries *et al.*, 2013). Resource-based channels are not linked to trophic functions alone. For example, the energy flux from litter represents consumption of litter by the consumer community, and thus is related to litter decomposition, transformation and translocation (Fig. 7B). The energy flux from soil organic matter similarly represents the consumption of soil and thus soil organic matter transformation and translocation, being linked to biopedturbation and the modification of soil structure (Fig. 7B). Such inferences from energy fluxes about effects that are not purely trophic are justified particularly in soil where habitat and food resources are tightly interlinked (Fujii, Berg & Cornelissen, 2020). Nevertheless, their validation requires direct experimentation.

To illustrate the size aspect of food-web compartmentalisation, I classified all consumers linked to basal resources into three size classes: micro (protists and microfauna less than 0.3 µg living body mass), meso (mesofauna and small macrofauna from 0.3 µg to 10 mg) and macro (macrofauna more than 10 mg). Plotting outgoing fluxes from the basal consumers of different sizes shows remarkable differences between the size-based channels (Fig. 7C). Here this distinction arises from the assumption of allometric trophic interactions, however, it confirms existing empirical data and is therefore likely realistic (Potapov *et al.*, 2019a, 2021b). This reconstruction of size-based channels illustrates that basal resources are exploited by different size classes in different proportions and feeding on multiple resources is more

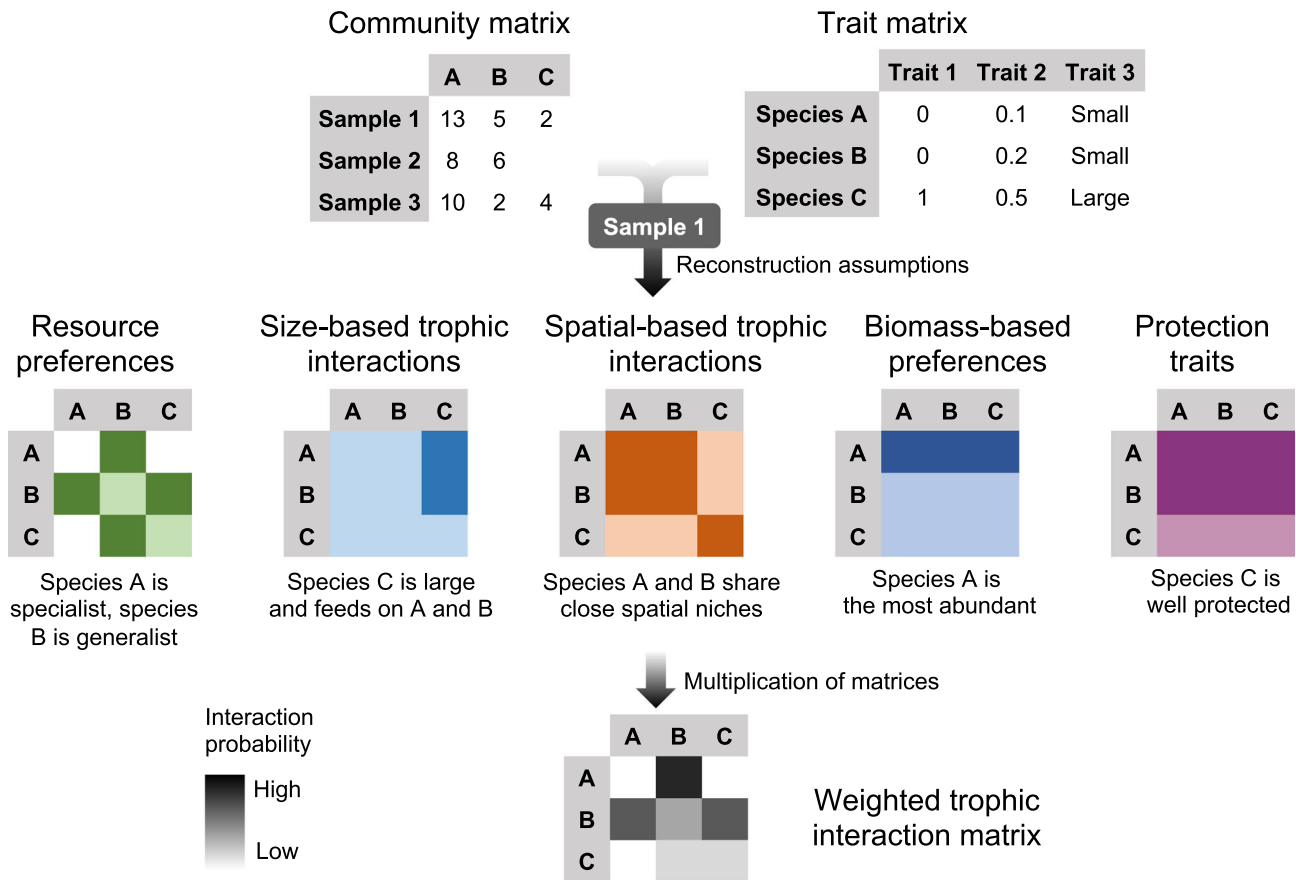


Fig. 5. The algorithm used for multichannel food-web reconstruction. Community and trait matrices are merged and several species–species interaction matrices are calculated based on generic rules (see text). Each interaction matrix represents one trait dimension: feeding preferences, body sizes, spatial preferences, biomasses, and protection. Multiplication of all interaction matrices yields the most probable weighted trophic interaction matrix that then can be used to calculate energy fluxes. Shading intensity shows interaction probability.

pronounced in large primary consumers (Fig. 3). The distribution of energy among different size classes is related to ecosystem functioning and can be used as an integrative functional descriptor of a food web, i.e. an ‘energetic size spectrum’. This descriptor has potential to reflect ecosystem functions of consumers better than size spectrum approaches based on biomass or community metabolism (Mulder *et al.*, 2011; Ehnes *et al.*, 2014) because it reflects multitrophic energy fluxes and thus consumption rates. Size-based energy channelling could be combined with resource-based energy channelling to unravel the contribution to resource-related functions of different food-web size compartments.

To illustrate the spatial aspect of food-web compartmentalisation, I classified all consumers linked to basal resources into endogeic (living in soil or lower litter layer) and epigeic (living in the fresh litter or on its surface) (Fig. 7D). Some predator nodes specialised on one of these channels although many were linked to both endogeic and epigeic channels. Differentiation between endogeic and epigeic channels was partly related to body size classes since many large macrofauna predators are surface-dwelling. It was also partly

related to resource use due to different resource availability in different layers. The energy flux through the endogeic channel is expected to be related to soil structure modification and rhizosphere processes but the energy flux through the epigeic channel is likely to be related to the detrital subsidy available for aboveground consumers (Hyodo *et al.*, 2015). Thus, soil food webs with high energy flux through the epigeic channel are expected to support a higher biomass and diversity of aboveground consumers (Potapov *et al.*, 2021b).

Classifying energy fluxes according to resource, size and spatial perspectives allows us to ask more precise questions related to food-web functioning, for example which size class in which soil layer is most responsible for processing of a certain resource?

(3) Describing the trophic hierarchy of energy channels

Each energy channel in a food web relies on basal resources or consumers and can be tracked to higher trophic levels.

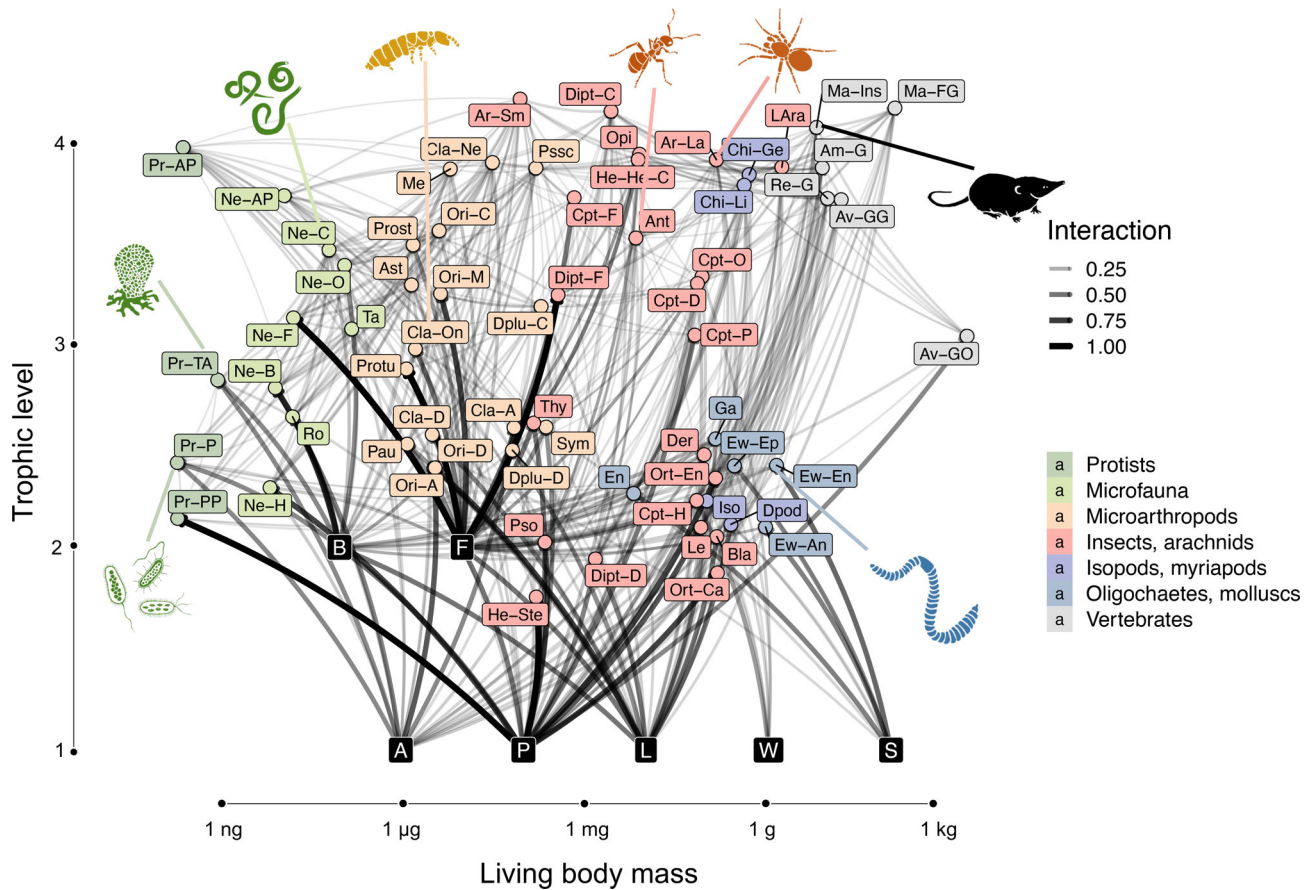


Fig. 6. Reconstructed multichannel meta-food-web of temperate forests, from protists to vertebrates. The 66 consumer nodes are represented by trophic guilds and are arranged based on body mass (*x*-axis) and trophic level (*y*-axis). Node colours indicate broad quasi-taxonomic groups. Resources are shown with black square labels positioned arbitrarily along the body mass axis. The resources prokaryotes (B) and fungi (F) are positioned at trophic level 2 as they receive energy from dead or living primary producers (trophic level 1). The width and darkness of links indicates feeding preferences inferred from the product of the spatial, size, protection and feeding preference adjacency matrices (only interactions comprising >2% of the budget of the consumer node are shown, see key on top left for scale of interaction). Biomass is assumed to be the same across all nodes and so biomass-dependent feeding preferences are not included. For resource abbreviations see Fig. 2; for trophic guild abbreviations see Table S1.

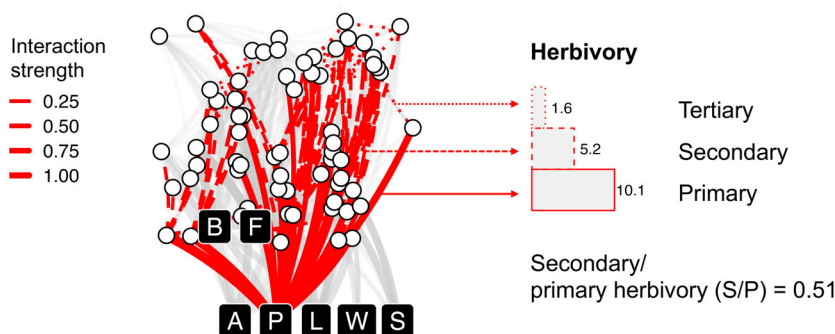
For each predator, the contribution of different basal resources and pathways to these resources can be described and quantified. Thus, for each channel, the amount of energy that reaches higher trophic levels can be estimated. Summing up predator–prey energy fluxes allows the quantification of ‘secondary’ and ‘tertiary’ trophic functions, such as predation, intraguild predation and parasitism (Barnes *et al.*, 2014; Potapov *et al.*, 2019b). These functions can be related to the top-down control of the entire food web, a specific energy channel, or a specific consumer. This can be quantitatively assessed by calculating the ratio of the outgoing energy flux from a food-web node to the biomass of the node (Barnes *et al.*, 2020) or by calculating the ratio of the energy fluxes at the bottom and at the top of the food-web. Such ‘energy flux pyramids’ of primary, secondary and tertiary trophic interactions can vary substantially not only across food webs, but also within a food web across different

energy channels (Fig. 7). Even though my reconstruction did not include biomasses, it recovered several expected patterns in the ratios of secondary to primary energy fluxes (S/P) based solely on feeding interaction strengths. For example, top-down control was higher (larger S/P ratios) in micro- and meso- than in macro-food webs (Potapov *et al.*, 2019b, 2021b) and it was higher for plant-based than for soil-based energy channels (Fig. 7A,B). Specific research questions related to top-down or bottom-up control can be addressed with the energy flux approach, depending on the completeness of the food-web reconstruction (Fig. 8).

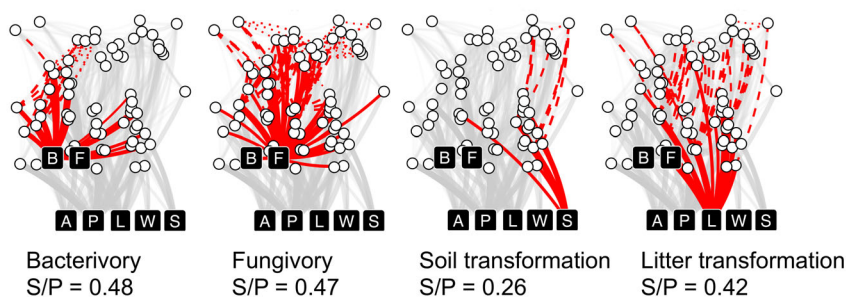
(4) Assessing multifunctionality and energetic inequality

Ecosystem functioning is inherently multidimensional, which has fuelled a spectrum of studies assessing multiple ecosystem

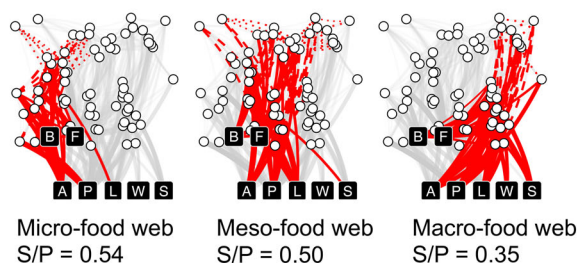
(A) Tracking trophic functions along the trophic chains



(B) Resource-associated trophic functions



(C) Energetic size spectrum



(D) Energetic spatial spectrum

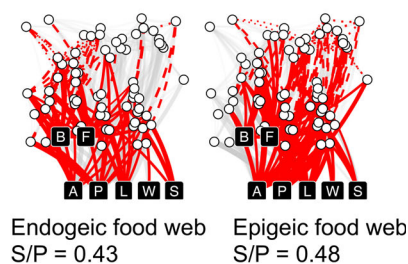


Fig. 7. Inferring ecosystem functioning based on energy fluxes in soil food web. In the absence of biomass data, the calculated feeding interaction strengths (see Fig. 6) are assumed to be a proxy for energy fluxes. The sum of outgoing energy fluxes from a specific food resource represents the total consumption of this resource and is thus related to corresponding ecosystem function(s). Interactions of the first (solid lines), second (dashed) and third (dotted) trophic levels indicate the proportion of energy that is channelled to the next trophic level through a specific channel. The ratio of secondary to primary energy flux (S/P) is related to energy transfer efficiency and top-down control in the corresponding energy channel (A, B), or in the entire food web. For example, the sum of energy fluxes from plants to plant consumers is related to ecosystem-level herbivory (primary herbivory) (A). Channelling of energy through micro- (<math><0.3 \mu\text{g}</math>), meso- ($0.3 \mu\text{g}$ to 10 mg) and macro- (>10 mg) food-web compartments is related to a number of ecosystem-level processes that are driven by different size classes of soil consumers (see Fig. 2) (C). Channelling of energy through endogeic (living in soil or lower litter layers) or epigeic (living in fresh litter or on its surface) food-web compartments is related to detrital subsidy and above–belowground interactions (D). Line thickness is proportional to interaction strength. A full version of this network is provided in Fig. 6. See Fig. 2 for resource abbreviations.

functions simultaneously, i.e. ecosystem ‘multifunctionality’ (Wagg *et al.*, 2014; Manning *et al.*, 2018; Grass *et al.*, 2020). Total energy flux in a food-web has been suggested to be a proxy for ecosystem multifunctionality, since it comprises the sum of individual trophic functions. However, if a single trophic function predominates, total energy flux does not reflect functional diversity. In that case, approaches that

consider all functions to be equally important are preferable (Potapov *et al.*, 2019b). ‘Total flux’, ‘average flux’ and ‘flux threshold’ approaches resemble the ‘summing’, ‘averaging’ and ‘threshold’ approaches commonly used to assess multifunctionality (Manning *et al.*, 2018). By treating individual resource, size and spatial energy channels as functions, it is possible to calculate different multifunctionality indices for

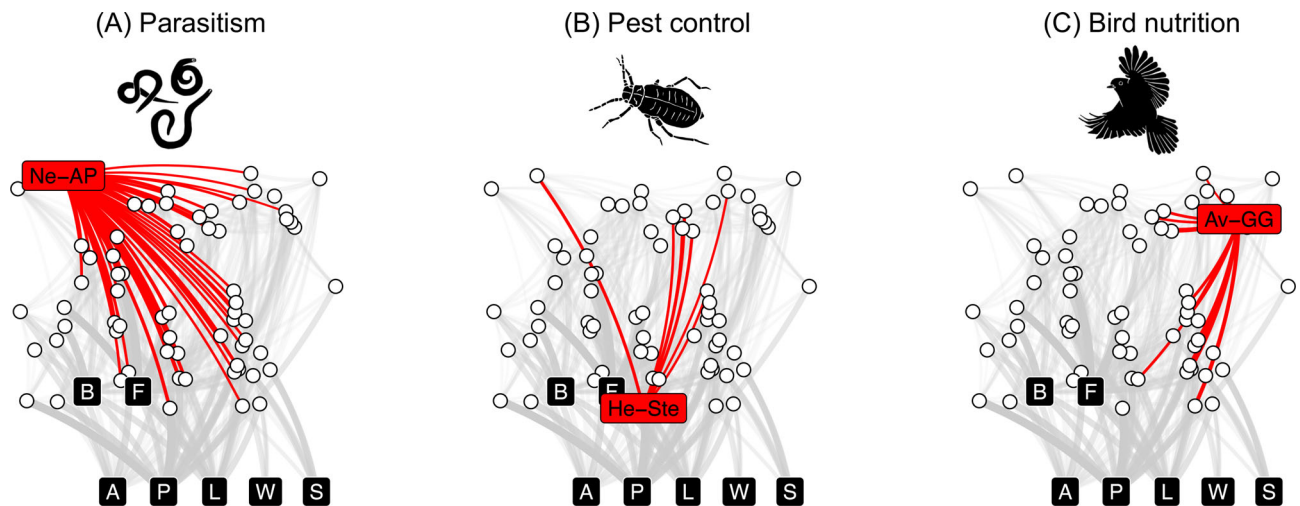


Fig. 8. Assessing specific food-web processes with energy fluxes. In this model, the calculated feeding interaction strengths are assumed to be a proxy for energy fluxes. The sum of energy fluxes from hosts to parasites can be used to assess community-level parasitism (A). The sum of outgoing energy fluxes from a pest can be used to quantify its top-down control (Barnes *et al.*, 2020) and identify potential key biocontrol agents (B). The sum of incoming energy fluxes to a bird can be used to identify potential animal groups and basal resources that play the most important role in its nutrition (C). See Fig. 6 for a full version of the network. Resource abbreviations are defined in Fig. 2.

soil food webs using the multichannel reconstruction (Table 2).

Another key aspect of a food-web is stability. Development of the resource-based energy channelling paradigm in soil food webs allowed the formulation of the concept of ecosystem stability as being driven by the balance between the fast (e.g. bacterial) and the slow (e.g. fungal) energy channels (Moore *et al.*, 2005; Rooney *et al.*, 2006). I suggest that this vision can be extended, for soil organisms, beyond ‘bacterial *versus* fungal’ energy channelling to include other resource- and body size-related energy channels (Potapov *et al.*, 2021b). My hypothesis is that ecosystem stability and multifunctionality are both linked to the balance across different energy channels, decreasing in food webs with large energetic imbalances. Such imbalances can be observed across resources (e.g. bacteria-dominated systems), size spectra (e.g. earthworm-dominated systems), spatial distribution (e.g. ground surface disturbance) and trophic levels (e.g. systems with overdominance of primary consumers). Inequality could be quantified e.g. with Gini coefficients, widely used in social sciences to quantify income inequality (Table 2) (Ceriani & Verme, 2012).

(5) Case study and comparison with traditional reconstructions

To illustrate the multichannel reconstruction with an empirical example, I re-analysed data on nematodes, mesofauna and macrofauna collected from rainforests and oil palm plantations in Sumatra, Indonesia (Krashevskaya *et al.*, 2019; Potapov *et al.*, 2019b). I used empirical data on abundance and body masses together with trophic guilds (Table S2) to reconstruct the soil food webs. This reconstruction included biomasses and thus estimations of ‘real’ energy

fluxes. To demonstrate the value of my approach, I applied in parallel multichannel reconstruction (Fig. 9B) and traditional soil food-web reconstruction that assumes differentiated resource-based channelling in soil food webs (Fig. 9A) (Hunt *et al.*, 1987; de Ruiter *et al.*, 1993; Moore *et al.*, 2005). Energy fluxes were assessed in both reconstructions with the *fluxweb* package (Gauzens *et al.*, 2019) and used to calculate a set of functional indicators. Various technical aspects of the energy flux reconstruction are given in Jochum *et al.* (2021). I also calculated basic descriptors of food-web topology: connectance (proportion of realised links), graph centralisation (concentration of interactions around central nodes of the network; Freeman, 1978) and modularity (presence of interaction clusters; Fig. 9C) (Newman & Girvan, 2004; Laigle *et al.*, 2018).

The absolute values of virtually all calculated network parameters and functional indicators differ between the two reconstructions, highlighting the importance of network topology in food-web analysis (Fig. 9C). The multichannel reconstruction resulted in higher network connectance and a slightly lower network modularity, reflecting reticulated energy channels in the soil food-web (Fig. 9B). The multichannel reconstruction also resulted in a lower total energy flux estimation, higher estimations of herbivory and bacterivory and a much lower estimation of detritivory. These differences reflect the trophic level omnivory of soil consumers – most detritivores feed on microorganisms rather than on the dead plant material itself (Swift *et al.*, 1979; Larsen *et al.*, 2016; Steffan *et al.*, 2017; Potapov *et al.*, 2019e). Microbial feeding increases assimilation efficiency in comparison to detrital feeding and reduces the estimations of total energy flux and detritivory compared with dead plant material feeding (Fig. 2).

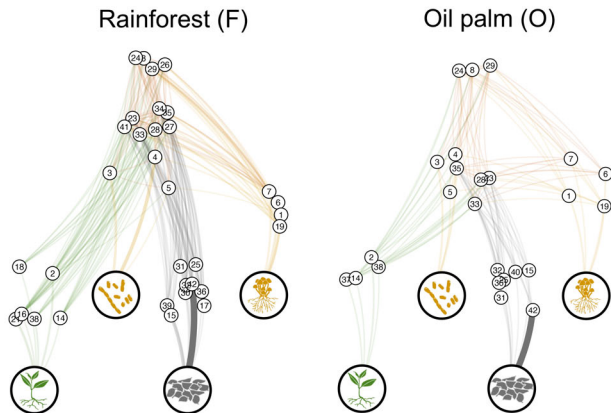
Table 2. Functional indicators based on energy fluxes in the multichannel food-web reconstruction. This non-exhaustive list includes general indicators hypothetically linked to food-web functioning and stability

Indicator	Calculation	Information and hypotheses
Total energy flux	Sum of all energy fluxes in the food web	Reflects ecosystem multifunctionality and is positively correlated with biodiversity (Barnes <i>et al.</i> , 2014, 2018)
Average trophic multifunctionality	Average standardised energy fluxes, representing the set of functions of interest	Reflects ecosystem multifunctionality, assuming all functions to be equally important (Potapov <i>et al.</i> , 2019b)
Threshold trophic multifunctionality	Sum of energy fluxes above a certain threshold, representing the set of functions of interest	Reflects ecosystem multifunctionality, assuming all functions to be equally important (<i>cf.</i> Manning <i>et al.</i> , 2018)
Herbivory	Sum of outgoing energy fluxes from plants	Reflects consumption of living plant material in the food web (Barnes <i>et al.</i> , 2014, 2020)
Litter transformation	Sum of outgoing energy fluxes from leaf litter	Reflects decomposition, transformation and translocation of litter (Lavelle, 1996; Briones, 2014)
Soil transformation	Sum of outgoing energy fluxes from soil organic matter	Reflects aggregation, (de)stabilisation, transformation and translocation of soil organic matter (Jones, Lawton & Shachak, 1994; Lavelle, 1996)
Wood transformation	Sum of outgoing energy fluxes from dead wood	Reflects decomposition, transformation and translocation of recalcitrant detritus, e.g. dead wood (Bradford <i>et al.</i> , 2014)
Fungal to bacterial energy channelling	The ratio of outgoing energy fluxes between fungi and bacteria	Reflects slow-to-fast energy channelling in the food web (Moore <i>et al.</i> , 2005) and nitrogen mineralisation rate (de Vries <i>et al.</i> , 2013)
Predation	Sum of outgoing energy fluxes from consumer (non-resource) nodes	Reflects the biomass of prey being killed per unit of time and area (Barnes <i>et al.</i> , 2014; Nyffeler & Birkhofer, 2017)
Top-down control	Proportion of predation in the total energy flux, or to the prey node biomass/energy flux	Reflects effectiveness of top-down control in the food web, or specific energy channel (Barnes <i>et al.</i> , 2020) (S/P in Fig. 7)
Energetic size spectrum slope	Regression slope in body masses–energy flux space (food-web nodes represent observations)	Similar to size spectrum slope, reflects overall structure of the food web (Mulder <i>et al.</i> , 2008; Trebilco <i>et al.</i> , 2013) and varies predictably with soil pH and stoichiometry (Mulder & Elser, 2009)
Resource inequality	Gini coefficient (Ceriani & Verme, 2012) based on outgoing energy fluxes across basal resources; for calculation see the <i>DescTools</i> package (Signorell, 2021)	Reflects diversity of resources at the base of the food web. High inequality is associated with low biodiversity and stability of the system
Consumer inequality	Gini coefficient based on outgoing energy fluxes to consumers across all nodes	Reflects evenness of energy use by consumer community and energetic overdominance. High inequality is associated with low biodiversity and stability of the system
Energetic size spectrum inequality	Gini coefficient based on outgoing energy fluxes to consumers across nodes belonging to different size classes	Reflects evenness of energy use by different size classes of consumers. High inequality is associated with low biodiversity and stability of the system
Energetic spatial spectrum inequality	Gini coefficient based on outgoing energy fluxes to consumers across nodes inhabiting different microsites	Reflects evenness of energy use by consumer community in space (vertically or horizontally). High inequality reflects high heterogeneity of the given function in space

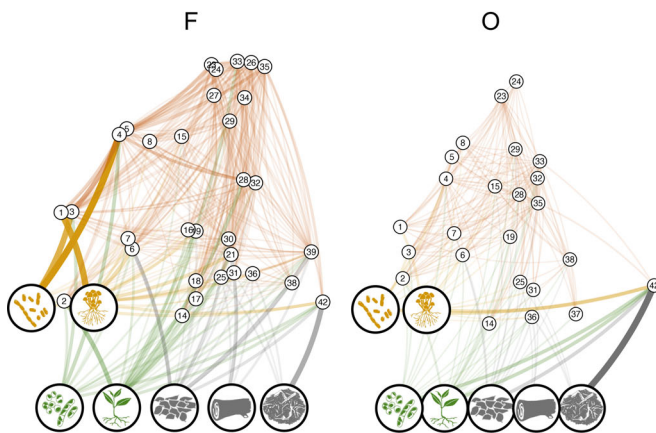
Effects of the land-use change from rainforest to plantations differed in magnitude and sometimes direction for several indicators between the two reconstructions (Fig. 9C). Although the total energy flux decreased in plantations according to the resource-based reconstruction, it has changed little according to the multichannel reconstruction.

Bacterivory, fungivory and total herbivory were reduced by 53–71% in plantations according to the resource-based reconstruction, but the reduction in the first two categories was much smaller (17%) according to the multichannel reconstruction, and there was an increase in total herbivory of 19% (Fig. 9C). This difference reflects the fact that large

(A) Resource-based food-web reconstruction
(based on the concept of Hunt et al. 1987)



(B) Multichannel food-web reconstruction



(C) Comparison of food-web parameters

Parameter	Hunt et al. 1987			Mulichannel		
	F	O	Effect %	F	O	Effect %
Network structure						
Connectance	0.21	0.18	-14	0.29	0.25	-14
Centralization	0.45	0.45	0	0.54	0.37	-31
Modularity	0.47	0.23	-51	0.42	0.21	-50
Energy fluxes, mW m⁻²						
Total flux	81.5	61.3	-25	49.8	54.7	+10
Total detritivory	43.0	52.1	+21	7.8	26.6	+241
Litter transformation				4.0	5.3	+33
Soil transformation				2.5	21.0	+740
Wood transformation				1.3	0.3	-77
Fungivory	6.1	2.3	-62	8.4	7.0	-17
Bacterivory	8.1	3.8	-53	8.3	6.9	-17
Total herbivory	3.1	0.9	-71	9.5	11.3	+19
Vascular herbivory				6.4	6.2	-3
Algivory				3.1	5.1	+65
Predation	21.2	2.2	-90	15.9	3.0	-81
Integrative indices						
Top-down control	0.26	0.04	-85	0.32	0.05	-84
Fungal/bacterial channel ratio	0.43	0.38	-12	0.50	0.50	0
Consumer inequality	0.75	0.93	+24	0.61	0.89	+46
Resource inequality	0.67	0.88	+31	0.36	0.44	+22
Size spectrum inequality				0.29	0.79	+172
Vertical spectrum inequality				0.57	0.91	+60

Fig. 9. Comparing network topologies and energy flux-based indicators in traditional and multichannel soil food-web reconstructions. This comparison is based on empirical data for nematodes, mesofauna and macrofauna collected from rainforests (F) and oil palm plantations (O) in Sumatra, Indonesia (Krashevskaya et al., 2019; Potapov et al., 2019b). (A) Resource-based reconstruction is based on the ideas that primary consumers in belowground food webs diverge in their feeding preferences and cluster in resource-based energy channels, such as fungal, bacterial, root (plant) and detrital, that are coupled by predators (Hunt et al., 1987; Moore et al., 2005). Network nodes are ordered according to resource used (x-axis) and trophic position (y-axis). (B) Multichannel reconstruction captures widespread generalism in resource preferences with resource-based energy channels being to a large extent reticulated (Digel et al., 2014; Wolkovich, 2016) and consumers being clustered also in body size and spatial energy channels (Potapov et al., 2021b). Network nodes are ordered according to body mass (x-axis) and trophic position (y-axis). Colours of the network edges highlight predation (dark orange), ‘brown’ (grey and dark yellow) and ‘green’ energy channels (green). Node numbers denote different trophic guilds, the numbers for the same guilds are the same in A and B. (C) Comparison of network topology, energy fluxes and integrative indicators of the two reconstructions. The difference in indicators between oil palm plantations and rainforests is shown as the percentage change (effect %); red denotes a reduction in plantations, blue denotes an increase in plantations, black denotes little change (effect < 10%). Integrative indices are described in Table 2; some indices cannot be calculated from resource-based reconstruction (missing values in the table). The two reconstructions resulted not only in different absolute estimations of functional indicators but also show different effects of oil palm cultivation.

detritivores (earthworms in plantations in this case) can feed on multiple resources and thus in part trophically compensate for the decline in the abundance of specialised bacterial,

fungal and plant-feeding fauna. The results of the multichannel reconstruction better reflect independent empirical data showing that conversion of rainforest into oil palm

plantations increases the plant energy channel in soil food webs (Klarner *et al.*, 2017; Susanti *et al.*, 2019) and reduces the bacterial, but not the fungal, energy channel (Susanti *et al.*, 2019). In fact, resource-based reconstruction showed that the ratio of fungal to bacterial energy channelling is reduced in oil palm plantations. This contradicts empirical data from several invertebrate taxonomic groups (Susanti *et al.*, 2019).

In both reconstructions, estimates of detritivory were higher in oil palm plantations, despite the lower directly measured litter decomposition in this system compared to that in rainforest (Krashevskaya *et al.*, 2018). However, in contrast to the resource-based reconstruction, it was possible with the multichannel reconstruction to distinguish divergent patterns in litter, soil and wood transformation processes (Fig. 9C). A strong decline in the energy flux related to wood transformation suggests that this index may reflect decomposition of recalcitrant organic matter and may be better related to overall litter decomposition (Table 2). A similar decline in both reconstructions was observed for total predation. However, the traditional approach assumed that all predators couple all energy channels, whereas the multichannel approach made it possible to distinguish between predators, coupling (and controlling) different resource, size and spatial energy channels. Network graphs (Fig. 9B) illustrate a substantial reduction of large-sized predators in the soil food webs of oil palm plantations (*x*-axis reflects body mass), clarifying the mechanisms of predation decline observed in previous reconstructions (Barnes *et al.*, 2014; Potapov *et al.*, 2019b).

Gini inequality indices further reflected unbalanced energy channelling along the size- and spatial food-web dimensions, thus reflecting not only general changes in food-web energetics but also the mechanisms behind these changes (e.g. resource shift or changes in ecosystem structure). In the example given, multichannel reconstruction made it possible to reveal a strong increase in inequality across the size spectrum, vertical spectrum and among consumers [i.e. the dominance of the earthworm node; this group of soil feeders (Fig. 2C) has a large body mass and inhabits soil in plantations]. Increased energetic inequality indicates that food-web multifunctionality and stability may be compromised in plantation systems (Table 2).

IV. EVALUATION AND THE WAY FORWARD

(1) Critical evaluation and knowledge gaps

My main goal was to make soil food-web reconstructions more realistic and more accessible by providing a reproducible analytical framework and by linking energy channelling to various consumer-driven ecosystem functions. I connected soil protists, invertebrates and vertebrates into a single interaction network, allowing the simultaneous quantitative comparison of their ecosystem roles. This reconstruction is scalable across different food-web compartments and different spatial scales. It also can deliver informative ecosystem

indicators, some of which could be used to include consumers in biogeochemical models.

However, food-web reconstruction is only as good as our knowledge of soil animal biology, and this knowledge is still fragmentary (Geisen *et al.*, 2019). The feeding habits of many groups have not been validated with rigorous empirical approaches and much of the available information comes from a few well-studied species or ecosystems (Potapov, Tiunov & Scheu, 2019d; Velazco *et al.*, 2021). Shifts in feeding habits is a known response of some soil consumers to environmental changes (Krause *et al.*, 2019), which is hard to include in the food-web reconstruction without direct assessment of trophic interactions. Food webs in different ecosystems are assembled from different species and trophic guilds but the same trophic guild may also shift its ecosystem role if major changes occur in the environment (Susanti *et al.*, 2019). These systematic between-ecosystem variations that could bias comparisons based on feeding guilds should be explored further. Another critical aspect of the food-web reconstruction is defining preferences for omnivorous species that feed both on basal resources and on other consumers (Jochum *et al.*, 2021). Biomass-defined preferences overestimate the contribution of basal resources to the diet due to their omnipresence. In my reconstruction I manually adjusted feeding on basal/animal resources according to existing knowledge (Potapov *et al.*, 2022). This is more realistic than the common practice of assigning equal preferences to all resources (Barnes *et al.*, 2014; Jochum *et al.*, 2021). Nevertheless, such decisions could propagate into biased energy flux estimations (Jochum *et al.*, 2021) and require further validation of feeding preferences across different trophic guilds. Finally, several other assumptions behind the reconstruction, such as the coefficients used for protective mechanisms and PPMRs, should be tested and the effects of different traits quantitatively assessed (Peschel *et al.*, 2006; Schneider & Maraun, 2009; Eitzinger *et al.*, 2018). Despite all these uncertainties, this multichannel food-web reconstruction produced realistic results based on relatively simple rules. Furthermore, this reconstruction is open to further improvement. Importantly, assumptions about food-web topology in traditional food-web reconstructions (Hunt *et al.*, 1987) have never been critically tested and often are not in agreement with empirical data (Digel *et al.*, 2014; Geisen, 2016; Wolkovich, 2016).

The multichannel reconstruction is scalable and can be applied across or within food-web compartments. However, the approach has less power if only a few species from one compartment or size class are considered because of the potentially large effect of species-specific interactions that might be overlooked. This uncertainty is in part counteracted in reconstructions across food-web compartments by the wide range of trophic guilds and taxa considered. Body mass range is particularly important for the reconstruction because of allometric predator–prey interactions. Unfortunately, many studies target only a small component of a soil food-web. In order to change this fragmentary vision to a more holistic approach, this review provides a tool for describing and quantifying entire soil communities, from

microbes to vertebrates. Despite being labour intensive and requiring a diverse toolbox, complex assessments of animal communities provide unique opportunities for understanding ecosystem functioning and are feasible with a collaborative approach. Such assessments will become more accessible with the development of new techniques such as image-analysis tools that provide taxonomic identification together with body size and biomass estimations (Ärje *et al.*, 2020).

Revealing the mechanisms that control energy channelling in soil food webs and testing how different energetic configurations of soil food webs affect ecosystem processes in controlled experiments can deliver holistic food-web indicators. A solid test of the multichannel reconstruction approach will require (i) empirical data on trophic interactions in soil food webs across size classes [e.g. using gut DNA analysis, isotopic labelling or compound-specific isotopic approaches (Traugott *et al.*, 2013; Pollierer *et al.*, 2019)] in conjunction with (ii) empirical data on ecosystem functioning. Such studies would allow us to validate and refine the multichannel reconstruction, which is a crucial step for upscaling soil food-web effects on ecosystem functioning and including these effects in biogeochemical models. At present there are very few data that relate soil food webs across size classes to multiple soil functions and this needs to be addressed in the future.

(2) Expanding dimensionality

This multichannel reconstruction focuses on the dimensionality of soil food webs across resources, size classes and soil layers. Future developments may introduce additional dimensions, such as the temporal dimension. Although inhabiting the same layer and having similar size, some species or functional guilds may have limited interactions due to differentiation in their daily or seasonal activity patterns. For example, most amphibians are active at night whereas reptiles are often active in the day. Many holometabolous insect groups are active in soils seasonally, before their aboveground imago emerge. Furthermore, in the spatial dimension I focused on the vertical stratification of soil food webs but it would also be possible to consider the horizontal distribution. Soil food webs are clustered around microsites with high activity, i.e. ‘hotspots’, such as the drilosphere and rhizosphere (Thakur *et al.*, 2020) and local food webs are connected through mobile surface- and aboveground-dwelling consumers into meta-webs (Mougi & Kondoh, 2016; Hirt *et al.*, 2018), which also can be quantified using energy fluxes.

Among specific traits, elemental composition can be considered in the food selection (Buchkowski & Lindo, 2021). Node-specific cannibalistic interactions could be quantified and incorporated. Trait-matching algorithms, such as visual hunting *versus* camouflage protection, could be accounted for. Individual trophic flexibility varies among species (Krause *et al.*, 2019) and defines food choice under different settings, for example depending on resource availability. This characteristic can be included in the model to assign node-specific trophic flexibility. In fact, any functional trait can be incorporated into the multichannel reconstruction to improve

predictions of trophic interactions or summarise certain trophic functions. An increase in complexity of the reconstruction due to the incorporation of additional traits will not necessarily lead to a proportional increase in the complexity of the calculations if the trait data and programming code are openly shared (see Table S2 and Appendix S2).

(3) Beyond the soil

This review focused on soil food webs because these food webs are cryptic and less well understood than those in water or above ground and because I was able to validate this approach using my own knowledge. Nevertheless, the energy flux approach can be applied across ecosystem types (Barnes *et al.*, 2018) and the multichannel reconstruction can be expanded to include aboveground, freshwater and marine consumers. By introducing the spatial aspect of habitat preference in the network reconstruction, I enabled quantification of energy exchange between ecosystem compartments based on energy fluxes through the nodes that belong to different ecosystem compartments. Network stability and motifs, total fluxes, channel structures, trophic hierarchies and related ecosystem functions can be statistically compared among food-web compartments, ecosystem types and ecosystems.

V. CONCLUSIONS

- (1) Soil food webs are organised along several dimensions, according to resource use, body size classes and environmental heterogeneity in space. Until now, soil food-web reconstructions did not consider these dimensions together and a reproducible approach to describe widespread omnivory and multichannel feeding of soil-associated consumers has not been available.
- (2) This review describes the multichannel reconstruction of soil food webs based on generic food-web organisation principles and functional classification of consumers, including protists, invertebrates and vertebrates. The reconstruction can be applied using data on trophic guild abundances, even if the trophic links have not been measured directly in the field.
- (3) Using the energy flux approach together with multichannel reconstruction allows existing and proposed novel quantitative indicators of trophic functions and food-web stability to be generated. These indicators can be used to assess trophic multifunctionality (analogous to ecosystem multifunctionality) and a wide spectrum of single trophic and ecosystem functions, including herbivory, detritus transformation and translocation, microbial grazing and dispersal and top-down control.
- (4) The multichannel reconstruction differs from traditional food-web reconstruction in estimated network topology parameters and calculated trophic functions. The multichannel reconstruction was consistent with some independently measured ecosystem functions

and food-web parameters, but this conclusion remains tentative since systematic research is needed for validation. An advantage of multichannel reconstruction is that it can describe multiple aspects of food-web functioning, providing higher resolution and a better mechanistic understanding of observed food-web variations than traditional food-web reconstructions.

- (5) Further development and application of the multichannel reconstruction will allow us to achieve realistic and holistic functional descriptions of soil consumer communities in different ecosystems. Additional characteristics of trophic guilds can be flexibly incorporated into the multichannel approach, bridging food-web ecology with functional trait ecology. After validation with controlled experiments, the suggested functional indicators could be used to depict the contributions of animals and protists to the processes of organic matter transformation and nutrient mineralisation and could allow inclusion in biogeochemical models of features such as the top-down control of ecosystem functioning by consumers in soil on the local, regional and even global scale.

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VIII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Description of food-web reconstruction.

Table S1. List of trophic guilds used in the example reconstruction for temperate forests.

Table S3. Correction coefficients for predator traits used in food-web reconstruction.

Table S4. Correction coefficients for prey traits used in food-web reconstruction.

Appendix S2. R code for multichannel food-web reconstruction.

Table S2. Full list of trophic guilds with trait values used in the model.

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