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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Because they are responsible for processing a major part of primary consumers of microorganisms and plant materials have strong impacts on ecosystem processes. Nevertheless, concepts and models have already been suggested (Chertov 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, myriopods) 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 ‘alloometric’ 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 microscale, 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 & Titonov, 2016; Bluhm et al., 2019), while soil autotrophic microorganisms are a potentially overlooked one (Schmidt, Dyckmans & Schrader, 2016; Seppe et al., 2017; Potapov, Korotkevich & Titonov, 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.](https://example.com/fig1.png)
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., 2019a, 2021b). 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; Erkten 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

![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).](image-url)
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

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 nitro 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 macro-detritivores as a whole (e.g. protists–oligochaetes dashed arrow). Summarised from Lavelle (1996), Scheu & Setälä (2002), Pokarzhvevskii et al. (2003), Erktan, Or & Scheu (2020) and Potapov et al. (2021b).
(A) Allometric predation

Real prey  Optimum prey  Predator

Overlap

Optimum PPMR

Living body mass, log scale

(B) Allometric predation, effect of a predator trait (pack hunting)

Optimum PPMR

Living body mass, log scale

**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.

(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 ‘epigean’ 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; ‘endogean’ 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 channeling 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
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 fluxweb (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.

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   |                 |                 |            |
| Parasitic – animal parasites are typically much smaller than their hosts | Parasitic nematodes and protists | PPMR ≪ 1 |          |
| Filtering the environment – feeding on the environment to filter the prey | Earthworms | PPMR ≫ 100 | Pokarzhevskii et al. (2003) |
| Mass predation – adaptations, such as the tongue of an ant eater, allowing hunting of many prey targets (usually social insects) simultaneously | Anteaters | PPMR >100 | Redford (1985) |
| Cooperative hunting – joint handling of prey with accomplices, allows handling of larger prey | Ants, some pseudoscorpions | Increases PPMR range | Cerdá & Dejean (2011) |
| Venom – venom paralyses and allows handling of larger prey | Spiders, centipedes, ants | Increases PPMR range | Cerdá & Dejean (2011); Laigle et al. (2018) |
| Hunting devices – adaptations, such as spiders webs, allow to handle larger prey | Spiders | Increases PPMR range | Herberstein (2011) |
| Prey traits |                 |                 |            |
| Protective metabolites – e.g. poison. Requires specific adaptations to overcome and thus reduces predation at community level | Some diploponds, termites, amphibians and others | Reduces interaction strength | Eisenbeis & Wichard (1987) |
| Physical protection – protective cover, e.g. strong cuticle, shell, scales or spines | Oribatid mites, isopods, millipedes, gastropods, testate amoebae | Reduces interaction strength | Bauer & Pfiiffer (1991); Peschel et al. (2006) |
| Agility – 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) |
| Carnivore – carnivore may strike back while being attacked | Predatory groups | Potentially reduces predation pressure |          |
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 among 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., 2019b). 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 biomass of all nodes were equal and ignored metabolic losses across nodes because of the lack of an appropriate empirical dataset. 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 to consumers represents the 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 (Fuji, 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
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.
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 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
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

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**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- (<0.3 μg), meso- (0.3 μg 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.
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 (Krashkevskaya 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; Stefan et al., 2017; Potapov et al., 2019c). 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).

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.
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 et al., 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 et al., 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 (Manning et al., 2018)                                      |
| Herbivory                         | Sum of outgoing energy fluxes from plants                                  | Reflects consumption of living plant material in the food web (Barnes et al., 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 and translocation of recalcitrant detritus, e.g. dead wood (Bradford et al., 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 et al., 2003) and nitrogen mineralisation rate (de Vries et al., 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 et al., 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 et al., 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 slopes, reflects overall structure of the food web (Mulder, 2013; Cezilly & Trebilco, 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 DescTools 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...
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

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 (Krashevska 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.
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 channeling to various consumer-driven ecosystem functions. I connected soil protists, invertebrates and vertebrates into a single inter-connected analytical framework and by linking energy channelling along the size- and spatial food-web dimensions, 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).

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 (Arje 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 approach to validate and re-inquire 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 that 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.

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 biochemical 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 food-web 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.