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Original article

Multiple dimensions of soil food-web research: History and prospects

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ABSTRACT

Soil food webs are at the nexus of soil biodiversity, functioning, and stability. With a research history of over 35 years, soil food-web research remains a challenging and relatively specialised field. Initially receiving wide attention after the general model of William H. Hunt and colleagues in 1987, the field diversified over the last two decades across ecosystem and community ecology, empirical and theoretical approaches, network and energy flux analyses. Here we reflect on the history, status, and trends in soil food-web research and identify major perspectives and synthesis directions. After briefly reviewing modelling approaches, structure, and quantification of functioning, we distinguish modern trends in tools that can streamline food-web research, a need for proper empirical validation, collaborative approaches to push the field forward, and conclude with application perspectives. In the light of increasing data availability and public awareness about soil biodiversity, we call for synthesis across multiple dimensions of soil food-web research (e.g. different methodologies and disciplines, various spatiotemporal scales, multiple trophic levels and phyla of life), integrating the soil food-web approach to biodiversity and environmental studies, and making it more accessible to a wider community of scientists.

1. Introduction

Soil is biodiverse and vital for multiple ecosystem processes and aboveground life [1,2]. The link between multiple components of soil biodiversity and ecosystem function has been demonstrated through both experiments [3] and observational studies [4,5]. For example, highly diverse and interconnected communities of soil organisms accumulate carbon under ecosystem restoration [6]. Additionally, recent data syntheses have allowed us to get a first understanding on the global distribution of multiple soil taxa [7–12], carbon pools, and nutrient cycles in soil [13,14], highlighting hotspots for soil biodiversity and functioning. However, many mechanisms that underpin the contribution of soil biodiversity to ecosystem functioning remain poorly understood because of the high diversity of soil organisms [15,16] and opacity and complexity of the soil environment [17,18].

Biological processes in soil are driven mainly by the consumption and transformation of organic matter by microorganisms and detritivorous animals [19]. Further energy transfers through trophic interactions to higher trophic levels (microbivores, predators) have feedback effects on the basal consumers and the ecosystem processes they drive [20,21]. In this context, food-web models represent a powerful tool to embrace the complexity of soil communities [22], analyse their stability [23] (Fig. 1a) and also link organisms on multiple trophic levels to organic matter transformation and other ecosystem processes in soil directly and via 'trophic cascades' [21,24]. However, comprehensive soil food-web data and detailed soil food-web studies remain relatively rare due to the high demand for data and uncertainty of information on species and their interactions, and due to the absence of easy-to-use food-web modelling tools.

Studies exploring specific compartments of soil food webs, or even individual trophic interactions, have become more common over the last two decades. Simultaneously, new molecular and isotopic tools have made it easier to measure species interactions and soil functioning [25,26]. At the same time, the research field has also diversified in terms of questions, approaches, applications, and scales. Therefore, a review of this diversification, as well as developments and changes in the field is

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warranted. Here, we briefly review the history of soil food-web research, and reflect on the current status and trends, with the overall aim to provide a literature summary for early career soil ecologists, and identify promising future directions.

2. History of soil food-web research

The idea of understanding and observing trophic interactions in soil systems has fascinated soil ecologists for decades, being one of the 'enigmas' of soil biodiversity [15]. Soil ecologists pioneered the empirical measurement of nutrient flux and mineralization, recognizing the links between soil organisms and the flows of carbon and nitrogen. However, only recently theoretical approaches to quantifying food web dynamics using energetic models were developed. These approaches are now providing great potential for understanding of the importance of soil systems and their biodiversity for multiple ecosystem functions and services such as climate regulation and crop production.

2.1. An early history of developments

While Elton (1927) [27] established the node (species) and link (feeding) approach of trophic interactions (Figs. 2 and 3), the game changer in food-web ecology came from Lindeman's (1942; published posthumously) [28] conceptualised understanding that trophic interactions represented flows of energy and nutrients, and that this transfer of energy and nutrients from one species to another is an inefficient process. The revelation of trophic transfer efficiency had major implications for understanding predator-prey relationships, but also for the cycling of energy and nutrients in food-web structures [29], linking this cycling to what we now call 'ecosystem functions'.

In soil ecology, our understanding of soil food webs started in much the same way: early depictions of connectedness webs in the 1970s (e.g. Refs. [30,31]) mostly used feeding guilds rather than taxonomic groupings, were descriptive and largely incomplete. In 1984, Parker et al. [32] presented one of the first semi-complete soil food webs with both bacteria and fungi, alongside nematodes and microarthropods, although there was still a high degree of taxonomic and functional aggregation among the nodes, something that we still struggle with today. At the same time, soil ecologists had long recognized the links between soil organisms and soil 'fertility' and had started using a soil food-web approach to quantify the role of soil organisms in nitrogen (N) transformations and availability. For instance, it has been demonstrated that N mineralization and N available to plants depends on trophic interactions, specifically the grazing on bacteria by protists [33].

Much like the biodiversity-ecosystem functioning research of the late 1990s (e.g. Refs. [34,35]), early soil food-web research followed three main approaches: addition experiments, removal experiments and observational field studies. Sterile soil microcosms received additions of different groups of soil organisms (e.g. Ref. [36]), or natural soils received different biocides targeting selected functional groups from soils (e.g. Refs. [37,38]) to quantify the role of different soil organisms on N mineralization, while field studies followed seasonal abundance patterns and correlated patterns of N mineralization [39]. This work provided key links between soil biodiversity and important soil processes, but were difficult to translate to a broader context, as results were often context-dependent and therefore idiosyncratic.

Hunt et al. (1987) [21] were the first to use a theoretical (model) approach to calculate N mineralization across a soil food web based on life history and physiology of soil organisms, while incorporating the theoretical principles of trophic transfers. The idea of energy flux calculations based on weighted trophic interactions in a food web was based on an earlier theoretical study [40]. Hunt et al. used estimates of trophic group population size and turnover rates (natural death rate as inverse of life span), their C:N ratio, and estimates of assimilation and production efficiencies to calculate N transfer rates including N mineralization. The example soil food web they used in this model for a shortgrass prairie system suggested that the web is compartmentalised into bacterial- and fungal-based energy channels that became united at the highest trophic levels (Fig. 3). With time, the soil food-web modelling approach of Hunt et al. kicked-off several novel areas of research, including ecostoichiometric and energetic modelling, and relationships between food-web structure and stability. The research that followed sought to understand the abiotic controls on soil food webs [41], and describe soil food-web structure that further demonstrated high connectivity and heterogeneity of soil food webs [42]. Follow-up studies revealed that high species richness in soil food webs increased the compartmentalisation of sub-webs (i.e., energy channels) [42] that fluctuated in dominance over time depending on the environmental conditions. For instance, reductions in soil moisture alters food web structure by reducing the activity and abundance of bacteria and microfauna, while favouring fungi and fungivorous mesofauna [41]. Studies on the structure and dynamics of soil food webs further inspired research of the network stability. The network topology suggested by Hunt et al. was 'diamond-shaped' – dual energy channels arising from a single resource (i.e. plants/detritus) were united by top predators (Fig. 4a). This structure was proposed as highly stable due to a fluctuating energetic asymmetry between the two energy channels — the 'slow' and the 'fast' — connecting the base and the top [43].

Until relatively recently most applications of soil food-web ecology were focused on understanding and quantifying N mineralization as an important process dictating N availability for both above and belowground productivity. However, the soil food web plays a key role in the transformation of carbon (C) that is the basis of the energetic soil food-web approach [44], where these models used ecostoichiometric modelling to track C and N using C:N ratios of food-web members to estimate flux from one node to the next. While historically these models have mostly focused on N mineralization (vs. C dynamics), energetic soil food-web models are experiencing a resurgence as we seek to quantify C transformation in soils. Soil C is now seen as a limiting factor in many soils with continued soil organic carbon degradation and erosion, but also being a key component in climate feedbacks, as the release of C from soils as CO_2 is largely the product of heterotrophic respiration (C mineralization).

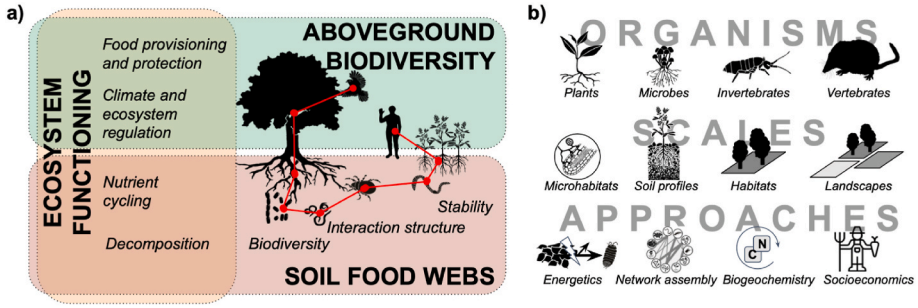

Fig. 1. Soil food webs underpin biodiversity, functioning and stability of terrestrial ecosystems across organisms and scales. Soil food-web research integrates the structure of trophic interactions, biodiversity and community stability in soil systems, linking belowground and aboveground biodiversity to ecosystem functioning (a). There are multiple synthesis dimensions of soil food-web research across organisms (plants, microbes, animals), scales (microhabitats to landscapes), and methodologies and disciplines (e.g. with biogeochemistry and socioeconomics; b). Silhouettes of organisms were drawn by Svenja Meyer or taken from phylopic.org.

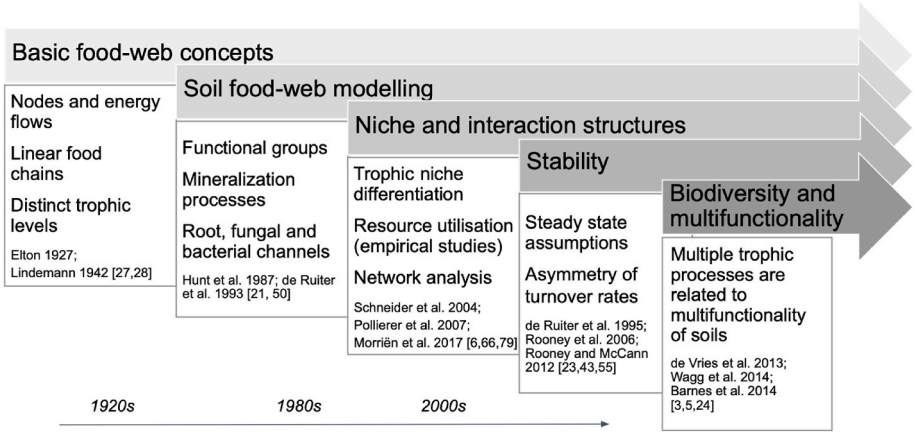

Fig. 2. A simplified history and diversification of soil food-web research. This non-exhaustive scheme highlights major concepts and evolving research directions. Milestone studies that advanced major questions, and were highly cited, are mentioned. Order and shading of the blocks roughly reflect the timeline.

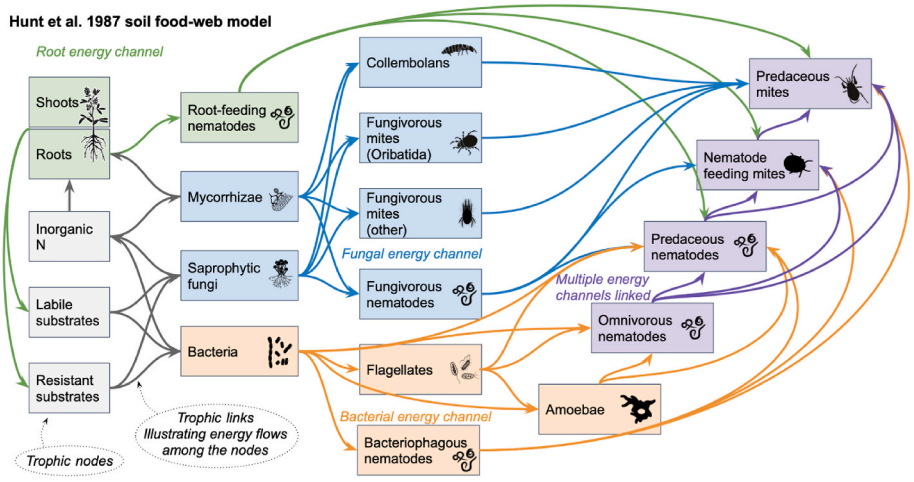

Fig. 3. Reproduction of the classical soil food-web model by William H. Hunt and colleagues. Food web diagram consists of nodes (plants, nutrient pools, microorganisms and invertebrates) connected via trophic links illustrating energy flows among the nodes. The network topology is kept as in the original work. Energy channels based on different resources are highlighted with colours: green – root energy channel, blue – fungal energy channel, orange - bacterial energy channel, purple – mixed energy channels. Energy flows from carbon and nutrient pools are shown in grey.

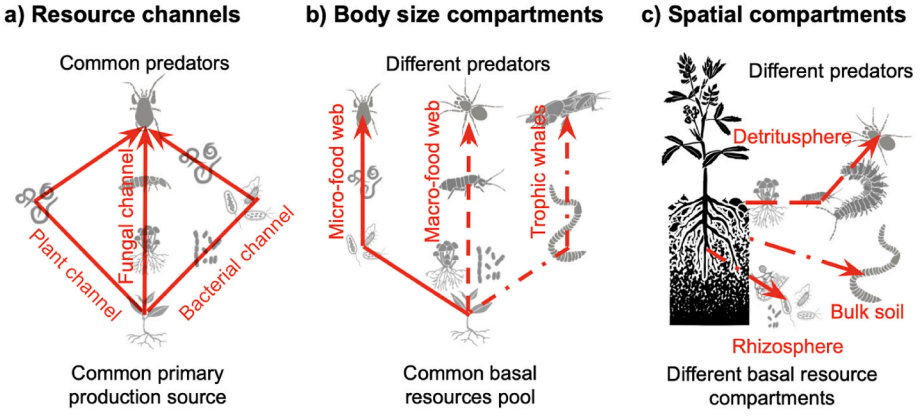

Fig. 4. Different concepts of soil food-web structure. Trophic links and nodes can be clustered to energy channels or food-web compartments according to e.g. resources (a), body size classes (b), and microhabitats (c). Soil food webs probably combine these different types of structures.

2.2. Modelling soil food webs

Quantitative models of energy and elemental flow through soil food webs became possible as qualitative descriptions of soil food-web topology produced enough detail [21], allowing for a rough accounting of microbial and microbivore abundance and consumption [44]. Mathematically, traditional soil food-web models are analysed at equilibrium to calculate consumption rates of each of the 'nodes' ('trophic guilds', 'trophic species') within them [24,44]. This makes them different from the analogous models that are often applied to aboveground systems. Aboveground, input consumption rates are directly measured or estimated from empirical data and these values are used to calculate equilibria (e.g Ref. [45]). By contrast, soil food webs are closer to analyses conducted for aquatic systems, where the flow of resources between

species is estimated at equilibrium using empirical data on biomass and food-web structure (e.g. Ref. [46]).

Most soil food-web models calculate consumption rates using information on trophic structure, physiological efficiency, and population death rate [44]. If all these parameters are known for a single currency like energy, carbon, or nitrogen, then each trophic species has gains and losses that are fully quantified and the model can calculate all of their consumption rates, which is typically achieved by solving the system of equations with rudimentary linear algebra [47,48]. Advanced models accommodate the fact that flows of different chemical elements and energy are interconnected via predictable stoichiometric ratios [49]. Historically, this has been done by using a base currency (e.g. carbon) to calculate the flows of secondary elements like nitrogen assuming fixed stoichiometric ratios [21,50]. More recently, models that calculate consumption rates based on multiple elements simultaneously have been developed [48].

Dynamic modelling of soil food webs that simulate changes over time has also been attempted, but to a lesser degree and with limited success. This is in contrast to simulation models of microbial populations and decomposition (e.g. Refs. [51,52]), which are powerful tools but only focus on a small subset of the soil food web, thus limiting our understanding of cascading changes in other trophic groups. Instead, contributions of other, typically faunal groups to decomposition and nutrient cycling use simulation models that begin with consumption rate parameters calculated using the equilibrium models aforementioned and attempt to predict trends over time or the consequences of removing certain trophic species (i.e., aspects of functional diversity [53–55]). However, these models have struggled to justify the added complexity of higher consumers and in fact concluded that groups at trophic positions beyond 'bacteria' and 'fungi' appear functionally redundant [54]. An alternative perspective is that high-level consumers are more important in defining the response to disturbances and that current models do not have enough data on population regulation to capture these effects (Buchkowski et al., unpublished data).

2.3. Understanding who eats whom in soil food webs

Reconstructing the structure of trophic interactions in soil is an essential step in developing a mechanistic understanding of soil food-web functioning. Most models are based on many assumptions about resource preferences of detritivorous and microbivorous taxa, starting from the seminal work of Hunt et al. [21]. This study used data from observations in other ecosystems and published laboratory experiments to infer feeding habits of various micro- and mesofauna species in a shortgrass prairie. Despite the major impact this study had on development of the research field, we must admit that this approach is very limited for general application across ecosystems because (1) laboratory feeding preferences that are the basis of the suggested reconstruction are hardly transferable to real-world soil communities where resource limitation and distribution might be key drivers [18,56] and (2) trophic niches of species may vary across ecosystems [57,58]. Nevertheless, the food-web structure proposed by Hunt et al. with minor modifications was applied in many following studies across many ecosystems [5,59–61]. Hunt et al. also introduced the concept of bacterial (bacteria-bacterivores), fungal (fungi-fungivores), and root (roots-herbivores) energy channels coupled by generalistic predators as a high-level structure model of soil food webs (Figs. 3 and 4a).

In the meantime, the methodological toolbox in soil ecology has been considerably expanded with various isotopic, biochemical, and molecular tools [25,26,62], allowing for *in situ* trophic-niche quantification. Bulk stable isotope composition of carbon and nitrogen in the consumer's body indicates consumer's trophic position (basal vs high-level consumers) and basal carbon source (freshly-fixed vs microbially processed carbon), thus roughly reflecting trophic niches of different soil animal groups [63,64]. Application of this method revealed unexpected trophic diversity within microarthropods [65,66], allowed for quantification of food-chain lengths in soil [64,67], and revealed the use of additional food resources, such as soil microalgae [68], and subsidies from aquatic ecosystems [69] and canopies [70]. Composition of neutral lipid fatty acids (NLFA) in the consumer body was investigated to detect basal resources using the 'biomarker approach' – some fatty acids can be produced only by specific organism groups, such as e.g. fungi, bacteria and plants [71]. This biomarker approach made it possible to track basal resources through the resource-based energy channels (i.e. across multiple trophic levels [72]) and showed that the strength of these energy channels varies with ecosystem type [73,74]. Combining information on both trophic position and basal resources, amino acid stable isotope analysis [75] showed how the degree of microbial versus detrital feeding changes with the ecological niche of soil oligochaetes [76,77] and confirmed predominant feeding on saprotrophic fungi in temperate forest microarthropods [78]. Special attention has been paid to quantifying the carbon coming from living plant roots ('root' energy channel) with isotopic labelling of plants [79,80]. In such isotopic labelling experiments, labelled carbon (usually $^{13}CO_2$) is introduced in the system and then tracked by sampling different organisms and pools of organic matter in the soil. These experiments clearly showed that the root energy channel spans far beyond herbivorous soil invertebrates and even rhizosphere microorganisms, supplying the majority of soil and litter detritivores and predators via root exudates, mycorrhizal fungi, and food-web interactions [79,81]. Furthermore, the development of gut content DNA-based analyses provided information on fine-resolution predator-prey [82,83] and fungivore-fungi [84] trophic interactions, which in general demonstrates a high degree of generalism in food choice among soil invertebrates. Finally, recently designed transparent microfluidic chips made possible visual observations of trophic interactions in micro-food webs in conditions imitating complex soil environments [85,86]. One of the major outcomes of all these empirical developments was re-visioning of soil food-web structure [87]. In particular, the concept of fungal versus bacterial channels was questioned [88], as well the generalisation of soil food webs having a resource-based organisation [89–91]. It appears that soil food webs are reticulated and have multiple structural dimensions, such as resource, spatial, and size (Fig. 4a–c) [22,92]. In this light, the fast-slow energy channel differentiation and related network stability (see above) received a new twist: small organisms and micro-food webs can be considered as the fast energy channel, while large invertebrates (e.g. earthworms, diplopods) can be considered as the slow energy channel that sequester energy in the biomass of their bodies, being even named 'trophic whales' for this function [92–94].

An alternative approach to understand the soil food-web structure is co-variation of different trophic guilds in space or time. Given sufficient replication, structural-equation modelling can provide information on how hypothetical interactions among nodes are realised in the changes in node abundances or biomasses [95,96]. Conceptually, a similar approach is co-occurrence network analysis. For many years microbes were not well resolved in soil food-web analyses, only treated as very rough units (e.g. as microorganisms, bacteria or fungi) or only cursorily included [21,59]. Arguably the major breakthrough in understanding this microbial diversity was the invention of high-throughput sequencing, showing an immense diversity of millions of bacteria, fungi, protists and other microorganisms [97–99]. The blessing of the millions of data obtained in any single study now is at the same time a curse for food-web studies because functional knowledge on many of these organisms remains unknown and because the immense data needs to be simplified. One proposed solution to reduce this complexity and understand structure and stability of microbial communities is to identify potential food-web links among different taxa, which is routinely done using correlation-based co-occurrence networks [100,101]. Co-occurrence networks are certainly meaningful to identify plant-pollinator links or host-parasite interactions, and are also proposed to be useful to discover predator-prey interactions and, therefore, describe food-web structure. However, trophic interactions in soil are

very complex and co-occurrence networks are poor predictors for these interactions, at least without detailed time series data. Even if a single predator population feeds on a single prey population, predators and prey can both be in a growing phase (positive correlation), or resource depletion phase when predator is on the peak, while prey is decreasing (negative correlation) [102]. In such a situation, a snapshot is often unable to detect causal links and this makes correlation-based inferences in networks hardly useful to infer predator-prey interactions. The situation is even more complex in soil than in other environments as many species are rather generalist in their food-choice [15,91]. Correlations in abundance/occurrence in such a situation may rather show bottom-up or environmental processes that simultaneously affect both predator and prey [102]. Moreover, in addition to predator-prey interactions, correlations between organisms may also reflect competitive, commensal, symbiotic etc. relationships, further complicating the inference of trophic relationships between organisms from this type of analysis. Therefore, robust network analysis of soil food-web structure must be complemented with empirical tests [6] and potential interactions are to be constrained with existing knowledge [103].

2.4. Quantification of soil food-web functions and stability

Converting soil food-web models into estimates of ecosystem functions is achieved by either (1) aggregating all processes/energy transfers to understand net effects or (2) comparing the effects of individual trophic species to the whole to quantify their relative importance. Both these calculations can be applied to energetic fluxes, elemental fluxes, or key ecosystem processes like decomposition rate [24,104,105]. More recent efforts have been focused on understanding the effects of higher trophic species using the second approach, because the aggregated contributions of the entire soil food web is often indistinguishable from those of microbial taxa and perhaps their direct consumers (e.g. Ref. [105]). This has involved calculating the indirect effects of these organisms on energetic or elemental fluxes by considering the overall food-web fluxes after their removal [54,105] (Buchkowski et al., unpublished data).

The indirect effects of higher trophic species, like mites, springtails, or spiders, are sometimes non-trivial (e.g. Ref. [105]), but remain poorly estimated and are likely underestimated for two reasons. First, soil food-web models estimate equilibrium abundances without any potential for multiple stable states. Second, soil food web models represent a very small proportion of the diversity of soils meaning that strong effects are averaged out with weaker ones. For example, the effect of mites on fungal biomass can be small overall even if a particular mite has a strong effect on a functional important fungal group like white-rot fungus. A promising approach is a combination of modelling and experiments to understand the effect of high trophic levels on soil functions. For example, in a year-long mesocosm experiment Staddon et al. [106] observed a trophic cascade associated with the loss of top predators (mesostigmatid mites) which coincided with increased abundance of prey species and overall nitrogen limitation in the system.

Recent static energy-flux based models were focused on quantification of fauna-driven ecosystem functions via summarising energy fluxes to specific feeding guilds. Specifically, the sum of energy fluxes to decomposer animals was used to quantify animal contribution to decomposition processes, herbivores to quantify herbivory, and predators to quantify predation [24,107]. Energy flux to biomass ratio was used to evaluate overall herbivore and predation control in food webs [108]. The same approach can be applied to get a more refined information on the energy channelling and linked ecosystem functions for multiple food resources, in different soil microhabitats, and along food chains of different animal size classes, ultimately indicating 'trophic multifunctionality' of soil food webs [22]. While this approach was not initially applied to quantify engineering effects of detritivores – which results in relocation of organic matter and changes food availability for soil (micro)organisms, having indirect effects on soil biological functions – energy fluxes outcoming from litter and soil as basal resources may roughly inform us about the magnitude of these non-trophic effects. However, many links between energy fluxes in soil food webs and processes of carbon transformation and translocation in soil remain to be tested [109].

Soil food webs have also been evaluated for their stability. Since most existing models have a single stable equilibrium, stability has been evaluated as the ability of the food web to recover from small disturbances [110] and the ease with which individual trophic species go extinct [54]. The high profile work on stability has focused on understanding the properties of soil food webs that make them stable [110, 111] with some examples of how stability and community properties might connect (e.g. Ref. [112]). For example, soil food-web models using lumped taxa are less stable when they contain strong feedback loops caused by omnivory [111], while empirical data from *in situ* microbial communities suggests that instability arises from both abundance fluctuations and species loss depending on the taxa and the disturbance type [112].

3. Future perspectives

Diversification of the research field and recent development of methodologies and international collaborations in soil ecology open new avenues for streamlining of the soil food-web research in the context of transdisciplinary approaches and intradisciplinary syntheses. In this section we provide promising approaches and synthesis directions, concluding with a need for the integration of soil food-web models in practice.

3.1. Digital tools to streamline soil food-web research

New methods continue to improve our ability to study the immense complexity of soil life, including trophic interactions and food-web structure. Molecular sequencing approaches have made it possible to quantify diverse microbial communities and stable isotope techniques have helped measure trophic niches, feeding links and feeding rates. Given that there are relatively few 'comprehensive' soil food-web reconstructions published (and none of them is actually based on a full empirical *in-situ* assessment of trophic interactions), empirical data remains a major limitation and a knowledge gap to be filled.

With the growth in available methods and data, we face the challenge of standardising information collection and streamlining of data analysis. Latest developments in IT tools including machine-learning approaches are anticipated to help us in covering knowledge gaps in soil food-web research. The increasing accuracy of automated image-based soil organism identification tools [113–115] stands to dramatically increase the number of soil food-web models that could be built. Image analysis allows for rapid counting and classifying soil animal taxa, including information on their body sizes that can be used to recalculate biomasses [116]. These tools are likely to be most powerful for soil food-web research, because food webs often use genus or family level groupings that are likely to be easier for automated systems to classify accurately.

Analytical tools for analysing soil food-web dynamics are available in R software including the *fluxweb* package focused on energetic food webs [47] and the *soilfoodwebs* package focused on elemental fluxes and stoichiometry (Buchkowski et al., unpublished data). These packages integrate and streamline the basic linear algebra and differential equations routines that are already available in R and most other statistical or modelling software (e.g., MatLab, Mathematica, etc). The strength of *fluxweb* is the ability to include individual physiological efficiencies for every consumer-resource relationship, while its weakness is the focus on a single currency such as energy or carbon. The strength of *soilfoodwebs* is the integration of multiple chemical elements and the ability to simulate models away from equilibrium, while its weakness is a single physiological efficiency per trophic species and being limited to two

chemical elements.

Finally, tools are being developed to help synthesise the growing number of approaches and general diversification of soil food-web research. There is a diversity of terms and synonyms in trophic classifications for consumers (e.g. detritivores, saprophages, primary decomposers, secondary decomposers, microbivores) and their links to food resources [22]. Aligning these classifications and making them consistent and comparable across studies is a major step towards the knowledge synthesis [117]. A major progress here is achieved with development of the 'Soil Food Web Ontology' (Le Guillarme et al. *in this issue*; https://github.com/nleguillarme/soil_food_web_ontology). This tool promises to aid trophic trait dataset standardisation, semantic data integration, automated food-web reconstruction, and trophic information extraction from the literature.

3.2. Empirical description of the structure and its spatiotemporal variation

Empirical *in-situ* validation of soil food-web structure is virtually absent for complex soil food webs. Even the most complete descriptions either combine assumptions with empirical measurements [90,103], or focus on a single/few energy channels [118], or apply semi-quantitative tools [73], or are way too simplistic [24,93]. Delivering such data to test assumption-based structure would be necessary to build robust and realistic soil food-web models. This can be achieved with a combination of empirical methods such as compound-specific isotope analysis of multiple animal groups [75], a combination of several empirical methods [119], or complex isotopic labelling experiments of several food resources. Such approaches can provide independent data on resource flows that can help constrain the estimates of consumption rate produced by soil food-web models. Importantly, empirical studies need to prioritise data collection on model coefficients that have the strongest impact on the model outputs. Published sensitivity analyses suggest that resource stoichiometry, production and assimilation efficiencies, and feeding preferences (especially the degree of omnivory and predation) can have a major impact on the total energy flux estimations [48] (A.M. Potapov, unpublished data).

Dynamic nature of soil food-webs in time (e.g. seasonal and inter-annual variations) and space (from microhabitats to landscapes; Fig. 1b) requires special attention in understanding how soil networks are structured and how energy flux fluctuates under different conditions. Future soil food-web studies may address this topic by considering spatial compartmentalisation of energy channelling among litter, rhizosphere, and bulk soil (Fig. 4c) [22,60,120]. Understanding of soil food-web structure on larger scales can be achieved by integrating soil food-web modelling with landscape ecology and community ecology, especially species dispersal [121]. Temporal variations of soil food-web structure are particularly challenging to describe since this requires a lot of data with high temporal resolution. Applying novel approaches, such as image analysis can open the possibility to collect such datasets and thus better understand how energy flux fluctuates with time especially under temperature changes, and if equilibrium models based on annual average abundances can accurately represent soil food-web structure and functioning.

3.3. Joint work to quantify soil food-web functions

As a complex approach, soil food-web modelling often requires joint efforts for the application and development. For example, getting sufficient data on multiple soil taxa and food-web modelling requires joint work of different soil animal experts and ecological modellers [5]; linking soil food webs to soil ecosystem processes requires collaborations among soil ecologists, soil scientists, and biogeochemical modellers [109]. Examples of large collaborations are increasingly common, allowing for quantification of e.g. soil invertebrate contribution to decomposition [122–124], or drivers of soil food-web composition across major environmental gradients [125]. Recently established Soil BON Foodweb Team aims at global-scale assessment of animal communities across micro-, meso- and macrofauna, which can form a data basis for future global-scale soil food-web modelling and joint experiments [126]. In the framework of these different activities, we need to acquire food-web parameters to more accurately assess flux of energy and nutrients, including estimates and associated uncertainties of trophic transfers, turnover rates, and fluctuations of population biomasses. We also need robust experimental and observational data connecting soil food-web composition and functions with processes at soil/ecosystem level across global environmental gradients. These steps are essential to address global change challenges and require communication within and beyond the research field.

3.4. Integration in practice and with other disciplines

There is increasing interest in soils as its biodiversity and associated functions form the basis for our life [1]. Soil quality, and broadly 'soil health', is a major concept, as a healthy soil supports higher function levels and delivers ecosystem services that are of ecological and human interest [127,128]. There are few major potential uses of soil food webs in this context, and one of them is bioindication. Especially farmers need to be aware of the state of their soils to determine what crop species to grow and predict their success. Complex soil biodiversity analyses including food web analyses will provide in-depth insides on the state of a soil. To convert this information to decision making, however, 'translation tools' have to be created. Indication is also important to assess the state of natural sites, like in restoration of agricultural or forest sites [6,129], and in speeding up restoration natural or contaminated sites [130], with information on trophic groups being of potential. Currently, soil quality assessments using nematodes are largely based on changes in abundances of nematode trophic groups [131]. There is ample opportunity for improving this information and extending it to other animal groups as different soil food-web compartments respond differently to external changes and therefore can deepen insights on soil health. For example, protist communities, especially microbial predators, have been shown to respond more than communities of bacteria and fungi to changes in carbon input as well as over seasons [132]. Different ecological and trophic groups of soil arthropods also have distinct responses to various environmental factors and ecosystem disturbance, holding a great bioindication potential [133]. An increasing effort in joint assessment of multiple trophic levels of soil biodiversity and soil food-web modelling [5,6,126] can synthesise these different indicators in a single system for complex evaluation of soil health. Effective implementation of such complex evaluation, however, is not possible without rapid assessment approaches (see section 3.1). Here, we are missing (1) automated tools to produce data from samples and summarise soil health indicators, and (2) adjusting such tools to the interests and capabilities of relevant practitioners such as farmers and monitoring agencies. Streamlining, calibrating, and scaling-up image analysis and DNA approaches, and co-constructing and disseminating easy-in-use tools are urgently needed to make progress in this direction.

Another application of soil food-web research is in the area of agroecosystem management and manipulations. As fertiliser application doses are being restricted and many pesticides get entirely banned, there is a need for change to more 'nature-based' solutions [134]. Precision farming is a term often used today as it entails farm- or even sub-farm-specific management practices [135]. Yet, information gained to inform precision farming currently does not include soil biodiversity and soil food webs. Many biological agents are being actively investigated, or already being applied to stimulate plant's nutrient uptake and fight plant pests, including bacteria (e.g. species of *Streptomyces*, *Rhizobia* or *Bacillus*), fungi (*Trichoderma* spp. or Arbuscular Mycorrhizal Fungi (AMF)), entomopathogenic nematodes, predatory mites and many more [136]. Some of these products already are based on food-web interactions such as predatory mites as agents that prey on insect and nematode pests [137] or entomopathogenic nematodes that parasitize

insect larvae [136], but considering little extended food-web interactions in soils. There might be increasing potential for these interactions as studies showed that protist and nematode addition can benefit plant health and yield [138–140]. While food-web interactions cannot directly be applied as potential agricultural bioproducts, the theory behind including interacting agents of different trophic levels should be investigated in more depth considering that biological products often fail to establish, are less specific than chemical products, or in some cases products even do not contain the declared biological agents [141,142]. Therefore, future bioproducts could focus on more complex synthetic communities (SynComs [143]) consisting of multiple interacting trophic level organisms.

Of more fundamental importance is inclusion of soil biodiversity, and in particular soil food webs, in large-scale biogeochemical models [13,144,145]. It has been demonstrated that microbial community composition can be a powerful predictor of decomposition processes at regional [146], and even global scales [147,148]. Accounting for further effects across high trophic levels in soil food webs is the next critical step. There are increasing calls and attempts to include soil food webs in biogeochemical models [109,149], but robust validation of these attempts and their integration in practice is still missing. Here, a synthesis of observational studies with experiments and theoretical modelling across soil ecology and soil science is urgently needed (see section 3.3). Based on such synthesis, we need to create mechanistic soil food-web models that link management decisions and global change drivers with soil food webs and ecosystem functions such as carbon sequestration and nutrient retention. This model and relevant indicators should be integrated in the future soil health evaluation systems, currently based mostly on abiotic parameters, to aid monitoring and management of soils.

Overall, soil food-web research has diversified considerably over the last decades and is in a need for synthesis across its multiple dimensions [150] such as methodologies (traditional approaches and molecular tools, static and dynamic modelling) and disciplines (biodiversity, biochemistry, soil physics, socioeconomics etc.), various spatiotemporal scales (from microns and days to landscapes and centuries), multiple trophic levels and phyla of life (from microbes to large invertebrates and soil-associated vertebrates; Fig. 1b). Here, we aimed at providing an overview of the history and promising directions which, we hope, will inspire soil ecologists to address these synthesis challenges. There is a large potential in the application of soil food webs for bioindication, nature-based solutions, and understanding effects of climate and land use changes, and other global challenges on soils. In this context, a soil food-web approach is a very powerful tool that joins information on biodiversity, functional stability and performance of soils. Making this tool more accessible for the scientific community and practitioners is a big challenge and bottleneck before we can move forward in the understanding of the changing terrestrial biosphere.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Authors of the manuscript are invited editors for the special issue “Synthesizing multiple facets of soil food web research”, including an editor-in-chief of the European Journal of Soil Biology.

Data availability

No data was used for the research described in the article.

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